LETTER

Sub-mesoscale fronts modify elephant seals foraging behavior

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Scientific Significance Statement

Oceanic fronts with scales from 1 to 50 km, called sub-mesoscale fronts, are ubiquitous in the world oceans and are known to enhance plankton abundance and to aggregate pelagic predators. However, observational evidence of their impact on the upper trophic levels remains sparse. The fundamental obstacle is the difficulty of accessing the fine-scale ocean physics and the animal's behavior at the same time. We tackle this obstacle by analyzing a new generation of high-frequency sensors deployed on Kerguelen's southern elephant seals giving access to the sub-mesoscale structures along animals' tracks and to seal's underwater feeding behavior. We show that sub-mesoscale fronts are favorable regions for elephant seals, increasing their foraging activity and prey accessibility.

Abstract

Sub-mesoscale fronts—with scales from 1 to 50 km are ubiquitous in satellite images of the world oceans. They are known to generate strong vertical velocities with significant impacts on biogeochemical fluxes and pelagic ecosystems. Here, we use a unique data set, combining high-resolution behavioral and physical measurements, to determine the effects of sub-mesoscale structures on the foraging behavior of 12 instrumented female southern elephant seals. These marine mammals make long voyages (several months over more than 2000 km), diving and feeding continuously in the Antarctic Circumpolar Current. Our results show that elephant seals change their foraging behavior when crossing sub-mesoscale fronts: They forage more and at shallower depths inside sub-mesoscale fronts compared to nonfrontal areas, and they also reduce their horizontal velocity likely to concentrate on their vertical diving activity. The results highlight the importance of sub-mesoscale fronts in enhancing prey accessibility for upper trophic levels, and suggest that trophic interactions are stimulated in these structures.

Satellite altimetry and modeling studies of the last two decades revealed that the oceans are crowded with a large number of mesoscale eddies of sizes 50–200 km (Fig. 1). These mesoscale structures account for 80% of the kinetic energy in the global ocean (Ferrari and Wunch 2009) and significantly impact primary production, biogeochemical fluxes (e.g., McGillicuddy, 2016) and top predators (Cotté et al. 2007; Dragon et al. 2010; Tew-Kai and Marsac 2010; Cotté et al. 2015; Gaube et al. 2017). A new vision of ocean dynamics has emerged in the last 10 years showing that finer-scale structures such as elongated density filaments (sub-mesoscale fronts), with widths of 1 to 50 km and time scales of hours to days, play an important role in oceanic transport (Sasaki et al. 2014; McWilliams 2016). Indeed, these elongated filaments found mainly between mesoscale eddies capture most of the vertical motions in the first 400 m below the ocean surface (Klein and Lapeyre, 2009). These vertical motions result from frontogenesis processes along the boundaries of sub-mesoscale density anomalies. Recent high-resolution modeling studies (of order 1 km) demonstrated that the vertical motions stimulate primary production by bringing nutrients into the well-lit surface layer (Perruche et al. 2011; Lévy et al. 2012; Mahadevan 2016). Within the Antarctic Circumpolar Current (ACC), such sub-mesoscale structures are abundant,

involving numerous elongated filaments with complex patterns (Fig. 1). While these sub-mesoscale features are ubiquitous in satellite images of ocean color and sea surface temperature, they are not captured by current altimeters or climate-resolving circulation models.

To date, the impact of sub-mesoscale fronts on upper trophic levels remains largely unknown due to the practical difficulty of simultaneously recording physical and biological data at high resolution. The very few studies addressing this topic with in situ observations revealed that sub-mesoscale fronts are favorable habitats for several organisms such as zooplankton (Powell and Ohman, 2015), juvenile tunas (Snyder et al. 2017), and elephant seals (Siegelman et al. 2019), that exploit sub-mesoscale fronts to enhance their foraging activity. Here we focus on southern elephant seals (SES) living in the ACC; these previous studies suggest that sub-mesoscale fronts may have an impact on these marine mammals' behavior. Among top marine predators, elephant seals are particularly well-suited for such studies, their large size allowing them to carry miniaturized sensors (Rutz & Hays 2009), which are able to measure their location, diving behavior, and environment (temperature, salinity, light, fluorescence). We use such data to test whether the SES foraging behavior is different in sub-
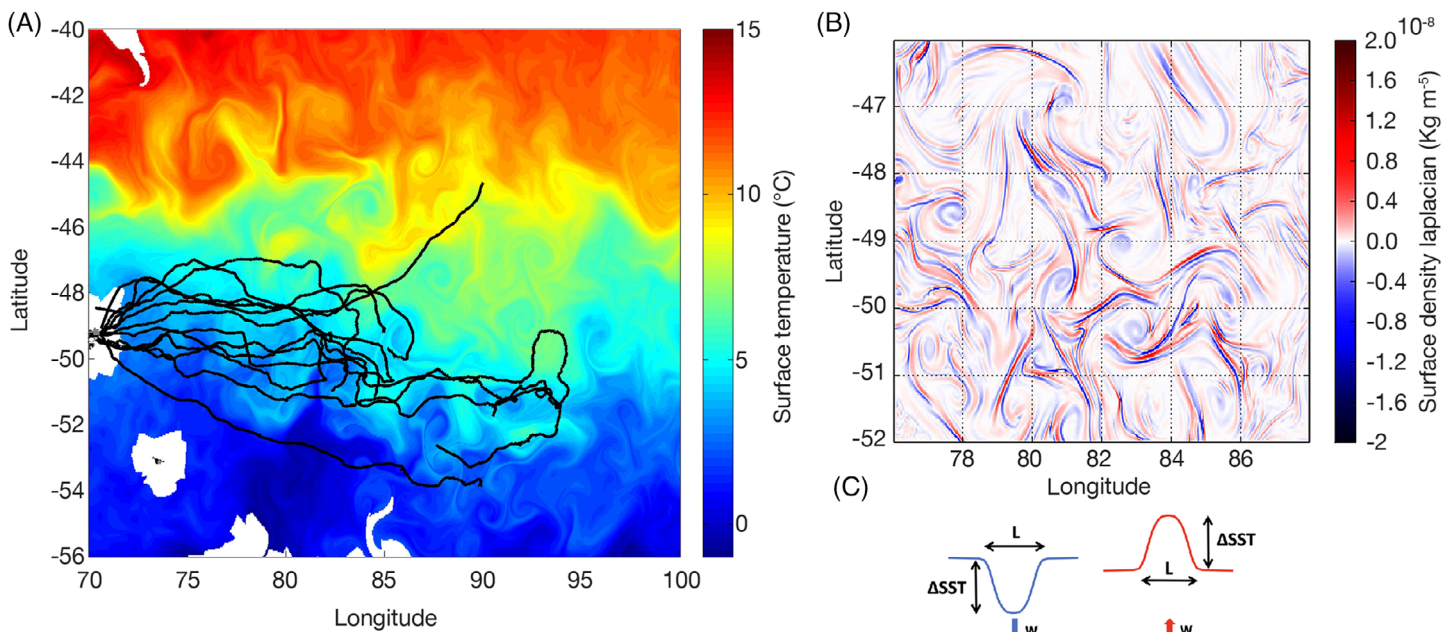

Fig. 1. (A) Trajectories of the 12 female SES tagged during austral spring 2011, 2012, and 2013 east of Kerguelen Islands (69°E, 49°S) are shown in black. For illustration, they are superimposed on a snapshot on 05 November 2013 of SST obtained from satellite observations by a five-day Lagrangian advection of SST field (AMSR-E) by geostrophic velocity from altimetry (AVISO) (see methodology in Dencausse et al. 2014). White areas are regions where no data were available for the advection. (B) Spatial second derivative of surface density (Laplacian) from a realistic high-resolution ocean general circulation model (NEMO, Community Ocean Model, 1/36°) in the ACC east of Kerguelen islands, in the region of the study. This field is known to drive strong vertical velocity (W) field in the upper oceanic layers during frontogenesis, and captures the smallest scales of density (Capet et al. 2007*b* part II, fig. 5). (C) Schematic of the vertical motions associated with filaments temperature anomalies when density is mainly explained by temperature. The density Laplacian is maximum at small scales L of the order of 10 km and its sign is associated with upwelling (W > 0) for a warm filament ($\Delta SST > 0$, in red) and downwelling (W < 0) for a cold filament ($\Delta SST < 0$, in blue) (from Klein and Lapeyre 2009, fig. 9b).

mesoscale fronts compared to nonfrontal regions (especially mesoscale eddies). Our hypothesis is that the elephant seals' foraging is intensified in sub-mesoscale fronts where frontogenesis should drive strong upward motions, enhanced primary production, and aggregation of upper trophic levels.

We test our hypothesis by studying adult female SES from the Kerguelen Islands. These mammals travel long distances (about 2000 km) at sea during their postbreeding and postmolt migrations, diving repeatedly to mesopelagic depths and foraging mainly in oceanic waters of the ACC in the Polar Frontal Zone east of Kerguelen Islands (Bailleul et al. 2010). They tend to follow the diurnal vertical migration of their mesopelagic preys, diving generally deeper during the day (Hindell et al. 1991, McIntyre et al. 2010). While top predator bio-logging programs can now record animal behavior at high resolution, the colocation of such data sets with sub-mesoscale structures remains challenging. Indeed, cloud-piercing space-borne instruments (altimeters and radiometers) do not resolve the sub-mesoscale band, and sub-mesoscale-resolving ones (optical and infrared sensors) are hindered by cloud coverage. To overcome the resolution limitation of altimetry, some Lagrangian approaches have been used, allowing for the estimation of sub-mesoscale frontal regions in the mesoscale field captured by altimetry (e.g., Lyapunov exponent calculation, as in Tew-Kai et al. 2009; Cotté et al. 2011; Lehahn et al. 2018; or advection of low resolution sea surface temperature (SST) fields in De Monte et al. 2012). This growing body of work demonstrates the correspondence between top predators' favored locations and reconstructed (putative) sub-mesoscale features. For instance, Lagrangian approaches revealed that during some parts of their trajectories, elephant seals increase their foraging effort when following reconstructed sub-mesoscale filaments (Della Penna et al. 2015). However, the coarse resolution and the lack of the ageostrophic component in the altimetry-derived velocity field, combined with the exclusion of any other process but horizontal advection, only allows recovering the filamentation process in a qualitative way. To date, the lack of physical information with sub-mesoscale resolution along the animal's track remains a fundamental challenge for studying the interaction between the elephant seals and their environment at high resolution.

This work tackles these limitations by taking advantage of a new generation of high-resolution bio-loggers mounted on 12 SES, tracked by GPS, in the Kerguelen area (Indian sector of the Southern Ocean, Fig. 1A). These bio-loggers include a temperature-depth recorder combined with an accelerometer allowing the detection of the rapid head movements that characterize prey capture attempts. These in situ observations give information about both the sub-mesoscale hydrographic structures along the animals' trajectories and, at the same time, their underwater feeding behavior. Given these fine-scale observations, we attempt to quantify the influence of sub-mesoscale features on the foraging behavior of SESs. We

test the hypothesis of an advantage for SESs foraging on sub-mesoscale fronts by quantifying changes of SES feeding index and/or prey accessibility compared to other regions.

Materials and methods

Kerguelen southern elephant seals dataset

To understand the influence of sub-mesoscale fronts on SES behavior, we use a unique high-resolution physical and ecological data set collected by 12 female SESs from the Kerguelen Islands colony during their journeys in the ACC (Rivière et al. 2019). The female SES leave the Kerguelen Islands for 2- to 3-month, 3000 km, post-breeding voyages during the southern spring–early summer (October to January) (Fig. 1A). This period corresponds to the phase when SES females need to regain energy by feeding in the open ocean. Their diet is mostly composed of mesopelagic fish, dominated by Myctophids, found at 300–700 m depth (Cherel et al. 2008). The SESs were equipped with miniaturized temperature and pressure sensors (*Wildlife Computers MK10 Fast-loc time-depth recorders*) with a two-second sampling interval (precision of $+/-0.05°$C for temperature, and resolution of 0.5 m with an accuracy of $+/-1\%$ of reading for depth), combined with head-mounted 3D accelerometers with a sampling frequency of 16 Hz (resolution of 0.05 ms^{-2}). These loggers do not interfere with the behavior or the demographic performances of the animals (McMahon et al. 2008, Walker et al. 2012, Gallon et al. 2013).

These SESs perform about 60 dives per day, down to depths of 500–1000 m. Over the 12 individuals, we found an average dive duration of 21 ± 4 mn. Between each dive, SESs return to the surface where they breathe for 1 to 2 min (Fig. 2) and where they are located through Argos transmitters and GPS. GPS localization, with a spatial resolution of 50 m, insures an accuracy less than 100 m. GPS fixes were obtained for almost every surfacing interval. When GPS tags did not record true locations, we estimated likely latitudes and longitudes of dives in between true locations using a linear interpolation between the closest locations before and after these dives. The mean distance covered during dives (Supporting Information Fig. S1) is about 1 ± 0.4 km. The cumulative distance of the 12 horizontal trajectories was more than 20,000 km, totaling 25,378 dives. We estimate the seal horizontal tracking velocity based on the time and distance differences between GPS positions (with relative error less than 0.2%). Tracking data were filtered by removing the locations that would have implied seals velocities greater than 2.8 ms^{-1} according to the algorithm described in Viviant et al. (2010) and Guinet et al. (2014). Velocities larger than this threshold are unrealistic and likely to be due to GPS positioning errors.

Identification of sub-mesoscale fronts using SST from SES high-resolution data set

Sub-mesoscale elongated filaments (density fronts) emerge during frontogenesis processes that can produce an intense vertical velocity field. These strong vertical velocities counterbalance
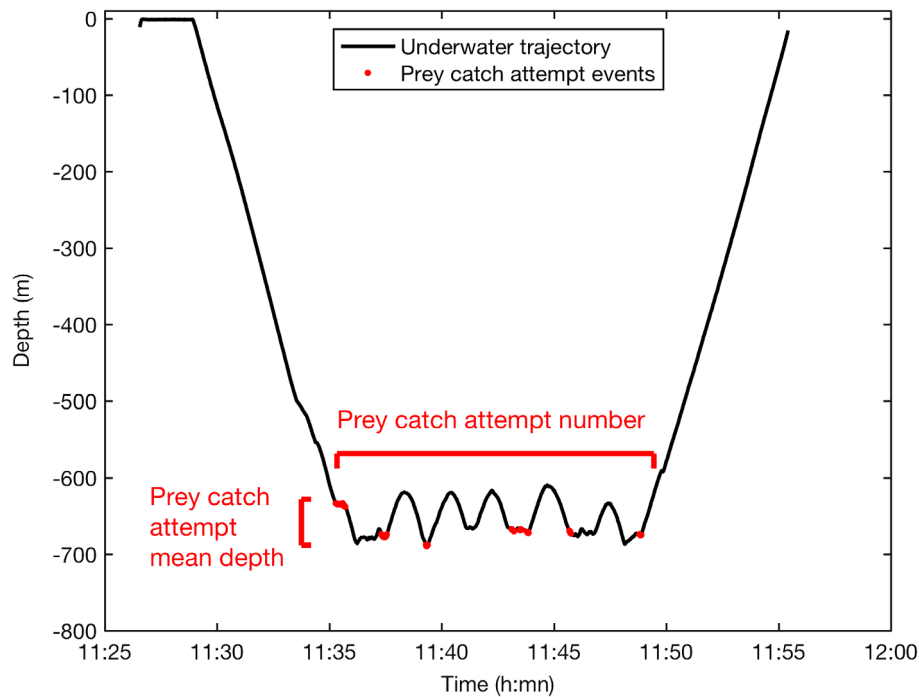
Fig. 2. Prey catch attempt events (red dots) are superimposed on a particular dive of a female SES (black line) observed on 2 November 2011. The *x*-axis is time, *y*-axis is the depth measured by the CTD. The two foraging behavior indices used in this study are illustrated in red: Prey catch attempt number index is calculated as the number of prey catch attempts during the dive; prey catch attempt mean depth is the average depth at which prey catch attempt events are detected.

the sharp density horizontal gradients formed by the mesoscale strain field. Theoretical studies showed that the spatial distribution and amplitude of these vertical motions are related to the ratio between the density anomaly and the squared width of these filaments, L^2 (equivalent to the second-order spatial derivative of density) (Garret and Loder 1981; Klein and Lapeyre 2009, fig. 9b). This ratio is maximum when L is of the order of 10 km (see in Capet et al. 2007*b* Part II, fig. 5). This is illustrated in Fig. 1B in the ACC with a high-resolution numerical simulation showing the alternating signs of this ratio in thin filaments. If the surface density is mainly explained by SST, then a positive value of this ratio corresponds to a positive SST anomaly and upward motions (red warm filament in Fig. 1C) and a negative value corresponds to a negative SST anomaly and downward motions (blue cold filament on Fig. 1C).

Consequently, in this study we chose to define a sub-mesoscale front as a surface density anomaly with horizontal scale of the order of 10 km. However, the data set we use contains temperature but not salinity and hence not density. Nevertheless, by analyzing another high-resolution data set with similar horizontal resolution for temperature and salinity (Siegelman et al. 2019), but without the associated foraging information, we have shown that over 90% of sub-mesoscale surface density fronts correspond to SST fronts when detected with the same methodology as developed below (see Supporting Information for details). Therefore, SST alone can be used for

detecting the vast majority of sub-mesoscale fronts. Using this approach, we define the SST as the temperature measured by the seals' logger between 0 and 15 m depth during their ascending phase, to minimize the influence of air temperature. We assume that the drift of the animal during its stay at the surface (about 120 s) is small, as elephant seals are known to remain vertical and motionless with their heads outside the water to breathe during those surface intervals. Moreover, as the smallest horizontal scales (in 2D) of the SST cannot be estimated from the SES data set (limitations are detailed in the discussion), we used the simplest definition of sub-mesoscale fronts based on the strongest along-trajectory SST gradients at the smallest scales.

The procedure for the sub-mesoscale front detection is as follows: strong small-scale SST gradients are identified as surface temperature variation between two consecutive surface locations greater than a given threshold (here 0.19°C km^{-1}, that is, twice the standard deviation of the SST gradient time series, see Supporting Information for more details and a sensitivity study). A sub-mesoscale front is then identified as the contiguous region containing all dives within 5 km of a strong small-scale SST gradient; two such regions that intersect are counted as the same sub-mesoscale front. We thus define a sub-mesoscale front as a region of 10 km or more, along the seal trajectory, that contains one or more strong small-scale SST gradients. This procedure allows us to separate dives located inside sub-mesoscale fronts

from those located outside (nonfrontal regions which may still contain mesoscale eddies).

Characterization of the SES foraging behavior

We quantify SES foraging behavior through the analysis of mouth-opening events detected by the head-mounted three axis accelerometers. Data from the accelerometers were processed according to Viviant et al. (2010) and Gallon et al. (2013) (see also Guinet et al. 2014 for details). Processing consisted of a high-pass filter to remove the noise corresponding to swimming movements. Then, a fixed window of 1 s was used to calculate the standard deviation every second along each acceleration axis. Signals were then processed using a moving standard deviation with a window size of 5 s. Last, a two-mean clustering was performed on the final three signals to distinguish a "high state" from a "low state." A prey catch attempt event is assumed to be occurring when the three axes were simultaneously in a "high state," with a continuous succession of "high states" being considered as a single event. Because linking mouth openings to true prey ingestion was not possible, we considered mouth-opening events to reflect prey capture attempts. Although neither the exact quantity of prey ingested, nor their quality can be assessed, the accelerometer provides an estimate of how many prey catch attempts likely took place within a dive and at what depths. For each dive, we define two indices: the prey catch attempt number and the prey catch attempt depth which is the mean depth at which prey catch attempts events were detected within a dive (Fig. 2). We use these indices to quantify changes in SES females foraging behavior when crossing sub-mesoscale fronts by a threshold method.

SES diving behavior is characterized by a daily cycle correlated with the diurnal vertical migration of their prey (mostly composed of Myctophids: Cherel et al. 2008). At night, when Myctophids are closer to the surface, SES catch more prey per unit of time than during the day when Myctophids are found at greater depths (Guinet et al. 2014). Because our goal is to identify whether SES foraging behavior in sub-mesoscale fronts is significantly different from an average behavior, we calculate a prey catch attempt number anomaly and a prey catch attempt depth anomaly as the differences between the prey catch attempt signals and their mean daily cycle value (see supplemental materials for details). A negative depth anomaly indicates that prey catch attempts were observed closer to the surface than the mean daily cycle depths. As expected, the mean daily cycle (Supporting Information Fig. S3) exhibits higher (lower) prey catch attempt numbers and shallower (deeper) prey catch attempt depths at night (day). On average, SES perform 9.3 prey catch attempts per dive at an average depth of 438 m.

Last, given that our methodology is focused on the detection of persistent changes in seal's foraging behavior in relation to sub-mesoscale structures, a five-dive moving averaging window was applied (corresponding to a distance of approximately 5 km

and time of 1.7 h). This filters out isolated dives, associated with extreme foraging activity but which are unlikely to be related to a change of behavior in a sub-mesoscale front. Then we tested that the main conclusions of this study are not sensitive to this filter.

We identify changes of behavior compared to an average behavior by using a threshold equal to 4.8 for the prey catch attempt number anomaly and 125 m for the prey catch attempt depth anomaly for a given dive. These values correspond to one standard deviation of the signals over the 12 individuals (see Supporting Information for details). For instance, a dive with a prey catch attempt number anomaly larger than 4.8 is considered as an "*extreme high foraging behavior*" compared to the average daily cycle, whereas a dive with a prey catch attempt number anomaly lower than −4.8 is considered as an "*extreme low foraging behavior.*" Note that the choice of thresholds for the detection of "*extreme foraging behaviors*" (and also sub-mesoscale regions) does not impact the main conclusions of this study (see the sensitivity tests in the Supporting Information). Moreover, the main tendencies are reinforced when more conservative thresholds are used, which corroborates the appropriateness of the methodology.

Results

An example of extreme foraging behavior shift during the crossing of a sub-mesoscale front

We first present an example of an extreme foraging behavior (as defined in the methods) along a 50 km-long portion of a seal trajectory corresponding to about 24 h (Fig. 3). As the seal traveled from a warm region to a cool region we detected a 14-km wide sub-mesoscale front by using the SST sampled by the seal (in red in Fig. 3B). The filtered SST (in heavy black) shows the presence of a warm filament characterized by an SST anomaly of 0.75°C, over a distance of 10 km, which is well captured with our methodology. Interestingly, the fine scale SST signal reveals the presence of smaller scale fronts inside this filament that do not appear to be measurement artifacts but the signature of a striation of the temperature field. The seal crosses the sub-mesoscale front during daytime (nighttime is indicated by a gray line on the *x* axis) and abruptly increases its foraging activity inside the front, up to a prey catch attempt number anomaly of 16 events per dive. This increase represents about 1.7 times the daily mean prey catch attempt number per dive (9.3). At the same time, inside the front, the SES was diving at a much shallower depth (by about 150 m) than observed before crossing the front (with a diving depth anomaly lower than −350 m). Then, when the seal left the front, diving depth increased by almost 550 m, which corresponded to 1.25 times the daily mean prey catch attempt depth (438 m). Other examples were also observed at nighttime; the detailed effects of day-/night-time will be detailed in the discussion section.
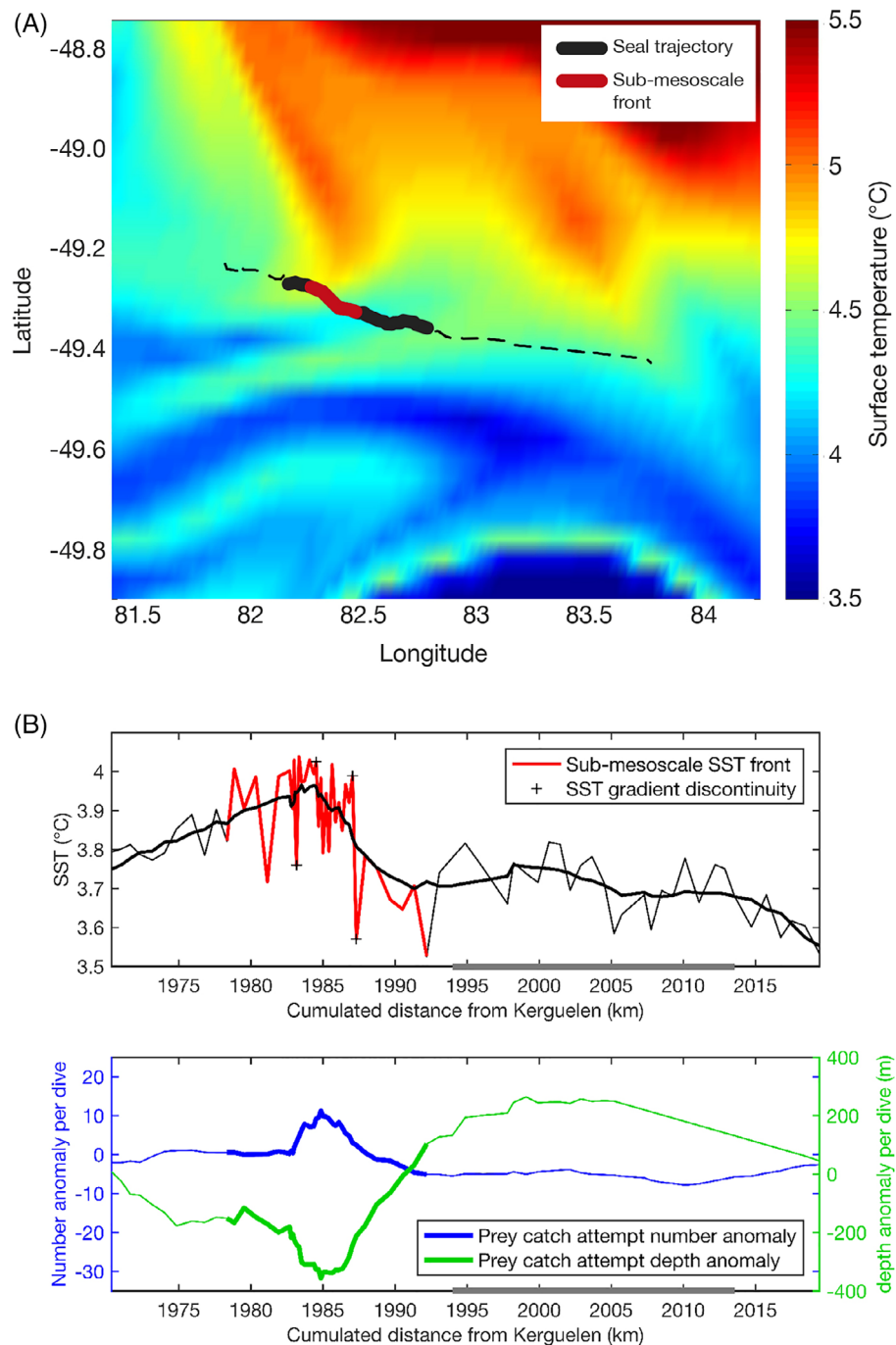
Fig. 3. Simultaneous remotely sensed and in situ measurements along the path of an elephant seal's trajectory. (A) Map of SST obtained by a five-day Lagrangian advection of SST field (AMSR-E) by geostrophic velocity from altimetry (AVISO) (same methodology as Dencausse et al. 2014) on 14 November 2012. Heavy continuous line shows the seal trajectory corresponding to the lower panel (red corresponds to a sub-mesoscale front). Dashed black line is part of the trajectory not presented on the lower panel. (B) Corresponding in situ temperature and behavioral variables measured at the same date: Upper subpanel shows along-trajectory in situ SST from the seal. In red: The sub-mesoscale front detected using the strong gradient discontinuities (black crosses) according to our methodology. Heavy black line corresponds to the SST signal filtered with a 10-dive moving window (approximately 10 km); lower subpanel shows the along-trajectory variation of the two feeding indices (prey catch attempt number anomaly in blue and prey catch attempt mean depth anomaly in green). Nighttime is indicated on the *x*-axis by a gray heavy line.

Seals' behavioral changes at sub-mesoscale fronts

In this section, we analyze the entire data set with a focus on the extreme foraging behavior to reveal how and when the

12 elephant seals changed their foraging behavior when crossing sub-mesoscale fronts (Fig. 4). We separate our dive data set into two categories: inside sub-mesoscale SST fronts and
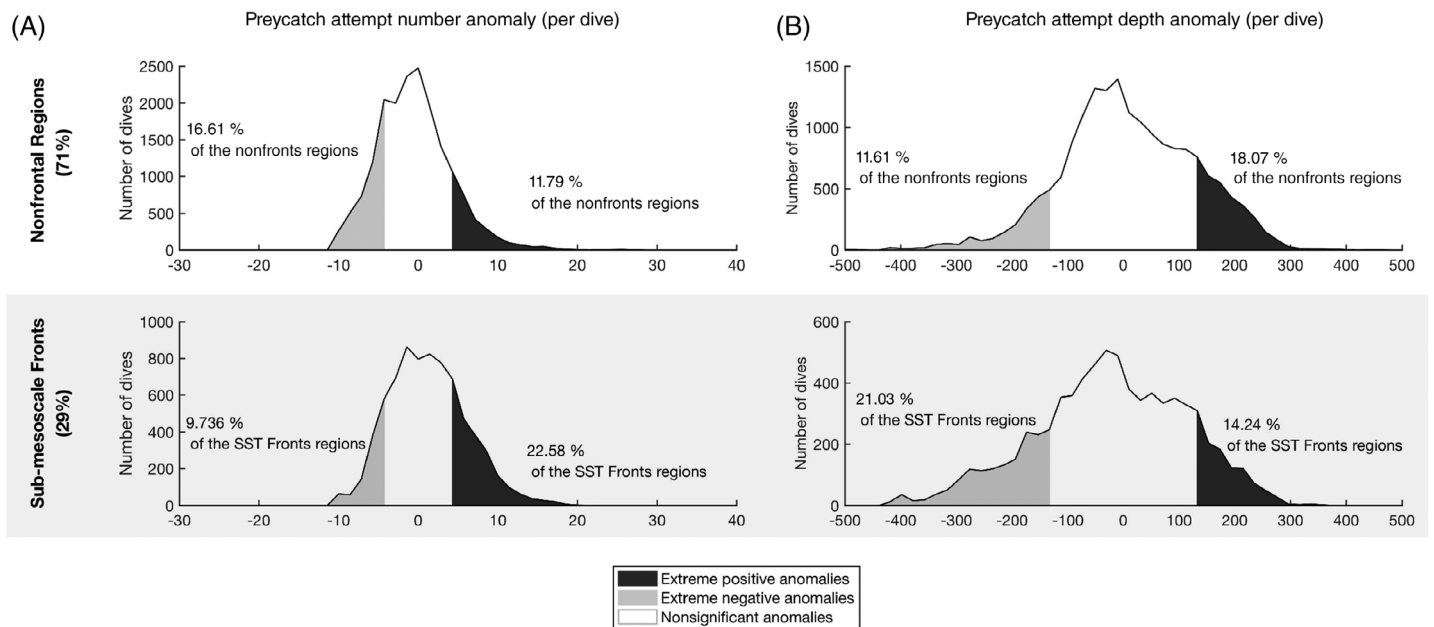
Fig. 4. (A) Frequency histograms of prey catch attempt number anomalies for the nonfrontal regions (top) and sub-mesoscale SST fronts (bottom). Colors distinguish significant anomalies according to their signs. Black ones are higher than $+\sigma$ and gray ones lower than $-\sigma$ (where σ = 4.8 prey catch attempts/dive is the standard deviation of the entire time series including all 12 individuals). Percentage of dive in each zone (black or gray) is indicated. (B) Frequency histograms of prey catch attempt mean depths anomalies for the nonfrontal regions (top) and sub-mesoscale fronts (bottom) (same colors as in A, defined with σ = 125 m).

outside (nonfrontal regions) that correspond respectively to 29% (inside) and 71% (outside) of the dives. We find the same proportion of dives (30%) with extreme foraging behavior (high or low) within or outside sub-mesoscale SST fronts. However, within sub-mesoscale fronts 22.6% of dives display high prey catch attempt activity (black area in Fig. 4A) while only 9.7% (i.e., a ratio of 2.3) display low foraging activity (gray area in Fig. 4A). Comparatively, in nonfrontal regions only 11.8% of dives display high prey catch attempt activity and 16.6% display low activity (ratio 0.7). Moreover, nearly twice as many dives displaying high prey catch attempt activity took place in sub-mesoscale regions when compared to nonfrontal regions, while the proportion of dives displaying low prey catch attempt activity is reduced by half. Extreme prey catch attempt depth anomalies are mostly negative (shallow dives) within sub-mesoscale fronts (Fig. 4B). Within sub-mesoscale fronts SESs performed 1.5 times more extreme shallow dives than extreme deep dives but 1.7 times more extreme deep dives than extreme shallow dives in nonfrontal regions. Finally, the proportion of extreme shallow dives was nearly double (1.8) in sub-mesoscale fronts compared to nonfrontal regions, whereas the proportion of extreme deep dives was slightly reduced (0.8), highlighting the shoaling SES diving behavior within sub-mesoscale fronts. These results are confirmed by a χ^2 statistical test that shows a significant difference between the distributions of prey catch attempt number anomalies in sub-mesoscale fronts and nonfrontal regions (χ^2 = 915.8, df = 22, p-value <2.2e-16) as for the distributions

of prey catch attempt depth anomalies (χ^2 = 647.83, df = 38, p-value <2.2e-16). More precisely standardized residuals confirm the preponderance of extreme positive prey catch attempt number anomalies in sub-mesoscale fronts compared to nonfrontal regions, and the preponderance of extreme negative prey catch attempt depth anomalies in sub-mesoscale fronts compared to nonfrontal regions.

Characterization of the seal foraging behavior at sub-mesoscale fronts

We now explore the relationship between the prey catch attempt number anomaly and the corresponding diving depth anomaly. Scatter plots (Fig. 5) reveal that, whatever the region type, a decrease in diving depth anomaly is associated with an increase in prey capture attempts. However, this increase is larger in sub-mesoscale fronts than in nonfrontal regions. More precisely, even though the scatter plots show a large dispersion, when binned with 100 intervals on prey catch attempt depth anomaly (red crosses in Fig. 5A,B), the prey catch attempt number anomaly is negatively related to the prey catch attempt depth anomaly with a slope of −0.018 prey catch attempt per meter within sub-mesoscale fronts and −0.014 outside. An ANCOVA analysis shows that the difference between these slopes is significant (ANCOVA, F = 69.0, $p < 2 \times 10^{-16}$). This confirms that the seals are feeding more actively and closer to the surface when diving within sub-mesoscale fronts.
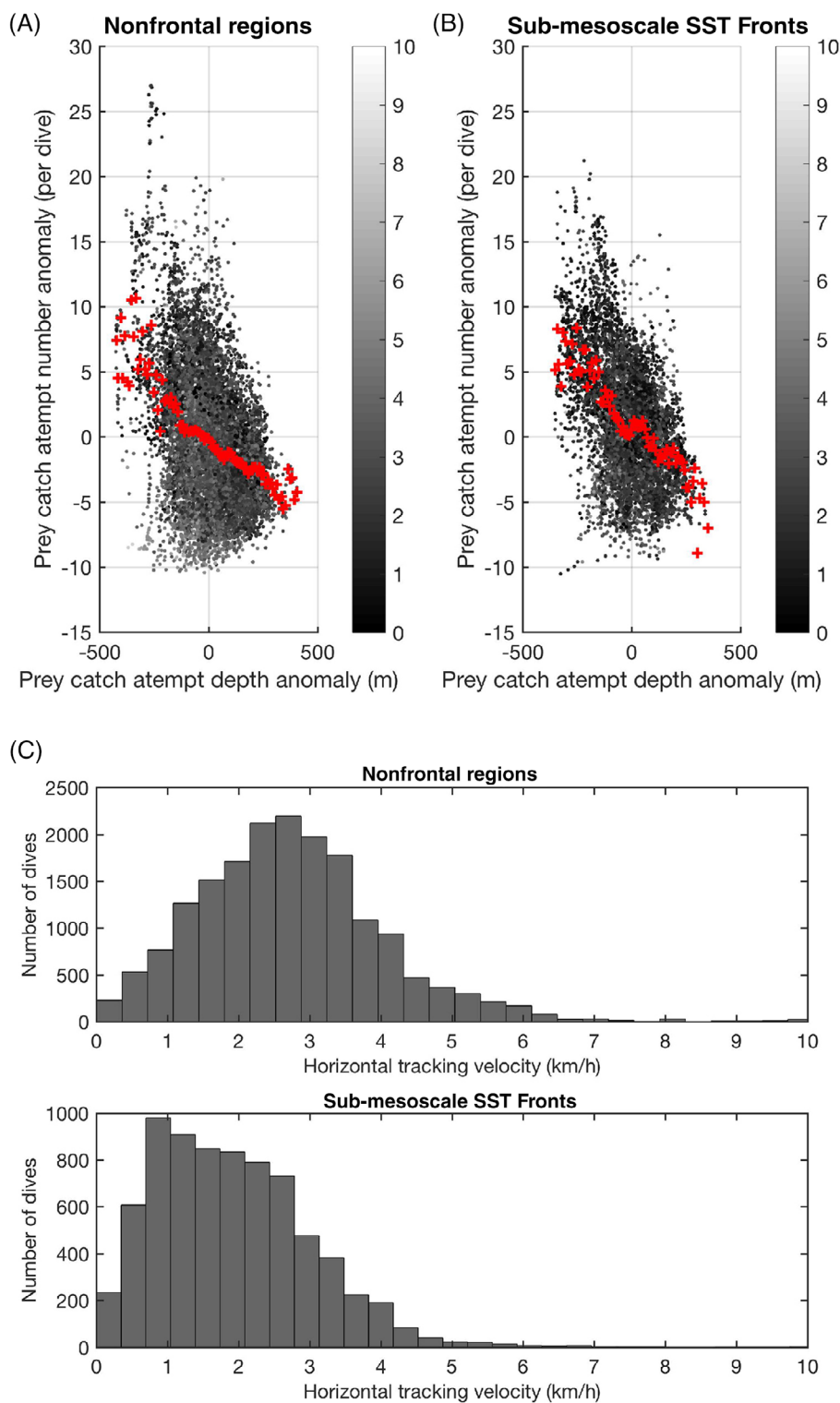
Fig. 5. Scatter plot of the prey catch attempts number anomalies as a function of the prey catch attempt depth anomalies for (A) nonfrontal regions and (B) sub-mesoscale SST fronts. Each gray cross represents one dive and each red one represents an average estimated by gathering abscissa values into 100 classes. Tracking velocity values are indicated in gray scale (km h^{-1}). (C) Frequency histograms of the tracking velocity distribution inside non-frontal regions (upper panel) and inside sub-mesoscale fronts (lower panel).

We quantified changes in SES behavior by examining the distance traveled during dives and the duration of dives, the ratio of which indicates the seal's horizontal tracking velocity (Fig. 5). SES horizontal velocities tend to decrease with increasing prey catch attempt number, with significantly lower values in sub-mesoscale regions ($\sim$1 km h^{-1}) compared to other regions ($\sim$2.5 km h^{-1}) (*t*-test: $t = 29.923$, $df = 13{,}877$, *p*-value $< 2.2 \times 10^{-16}$). Histograms of dive durations and distance between consecutive dives (not shown) reveal that dive durations have similar distributions inside and outside sub-mesoscale fronts (20 ± 4 min), whereas the distance traveled during dives is significantly smaller in sub-mesoscale fronts (0.6 ± 0.4 km) than in nonfrontal regions (1.2 ± 0.4 km) (*t*-test: $t = 30.507$, $df = 14{,}659$, *p*-value $< 2.2 \times 10^{-16}$). This reveals that SESs reduce their horizontal displacements when diving at sub-mesoscale fronts, while displaying more, shallower catch attempt events.

Discussion

In this study we have examined, for the first time with in situ measurements, the relationship between sub-mesoscale fronts and foraging activity of 12 female elephant seals within the Polar Frontal Zone in the ACC. This study reveals that SESs attempt to catch more preys, at shallower depths, at sub-mesoscale fronts compared to nonfrontal regions that include mesoscale eddies. This supports the hypothesis that sub-mesoscale fronts represent favorable foraging habitats for SESs presumably through an increase of their feeding activity driven by increased prey accessibility.

Sub-mesoscale fronts enhance prey accessibility

Sub-mesoscale fronts are the sites of most of the strong vertical velocities in the ocean (McWilliams 2016; Klein and Lapeyre 2009). These vertical velocities can advect nutrients upward, stimulating primary production and biogeochemical fluxes (Lévy et al. 2012). Sub-mesoscale structures are thought to favor aggregation of some components of ecosystems and structure the prey field into narrow bands near the surface (Nordstrom et al. 2013). These structures can enhance prey accessibility in the vertical or horizontal dimension (Hunt et al. 1999, Bost et al. 2009, Tew-Kai et al. 2009, Bertrand et al. 2014). Our results show that these sub-mesoscale fronts are regions where SES prey tend to be closer to the surface and therefore more accessible. Our estimates of prey catch attempt events detected by the accelerometers are not exact. However, several recent studies using seal daily mass ingested estimations, or correlation with body-buoyancy changes or micro-sonar data (Guinet et al. 2014; Richard et al. 2016; Goulet et al. 2019), showed that head-mounted accelerometer data provide a robust proxy for actual prey encounters. Here we hypothesize that changes detected by our threshold method are related to changes in foraging behavior (assuming that missed attempts occur in a constant proportion relative to successful attempts—see Guinet et al. 2014 for a more

complete discussion, see also Richard et al. 2016 or Goulet et al. 2019). Even if no direct measure of energy gain/loss ratio is available during this process, the results we obtained support the hypothesis that inside sub-mesoscale fronts, SES tend to use less energy by (1) diving to shallower depths and (2) gaining more energy by ingesting a greater number of prey per unit time spent diving. The two mechanisms very likely to result in a positive physiological effect for the animal. Furthermore, the SES horizontal tracking velocity is smaller in sub-mesoscale structures, where SESs are likely to favor their vertical diving activity over horizontal movement. Performing three-dimension dive reconstruction, Le Bars et al. (2017) showed that, during the bottom phase of the dive, track sinuosity increases with increasing prey catch attempts. This behavior contributes to a decrease in horizontal velocity. However, knowing whether SES slowdown in sub-mesoscale regions arises because of reduced seal swimming velocity resulting from abundance of preys (as proposed by Della Pena et al. 2015), or reduced oceanic current velocities inside the front (as pointed out in dynamical studies, see Capet et al., 2007*a*; Klein et al., 2008), or a combination of both, remains unanswered.

The enhanced feeding behavior at sub-mesoscale fronts can be quantified by integrating the histograms of prey catch attempt anomalies of Fig. 4. Over the 7426 dives observed in sub-mesoscale fronts, the sum of prey catch attempt anomalies is about 9400, which means an increase of seals feeding activity of 1.26 prey catch attempts per dive above the average value (9.3 per dive). The same calculation outside fronts over 17,952 dives gives a decrease of 0.5 per dive. This difference between fronts and nonfrontal regions (1.76 prey catch attempts per dive) is important for these sea mammals that travel for very long periods in the ACC (2–3 months), diving and feeding continuously to build up energy stores prior their molt.

Daytime vs. nighttime influence

To identify changes in SES foraging behavior, our analysis was performed with behavior index anomalies calculated relative to a daily average cycle. But what is the sensitivity of these results to the day-night cycle in diving activity of elephant seals? The 12 SESs were at sea during late spring and early summer; 61% of dives took place during daytime, and 39% during nighttime, regardless of whether the seals were within or outside fronts. We found that the proportion of dives corresponding to extreme positive/negative feeding behavior anomalies was unaffected by day/night cycles, with the exception of diving depth anomaly at night inside sub-mesoscale fronts (see Supporting Information Fig. S4). While this confirms the robustness of our conclusions using behavior anomalies, it also reveals the effect of sub-mesoscale fronts at night, which confines the diving behavior of elephant seals to a reduced vertical range in shallow waters. Indeed, the proportion of negative depth anomalies at night in sub-mesoscale fronts is reduced to 15.24% (very close to the proportion of

positive anomalies 14.87%) that reflects a more concentrated feeding behavior in the vertical. This may be interpreted as a consequence (1) of the vertical motions inside sub-mesoscale fronts that are able to push up biomass of nonmotile organisms and, at night, aggregate some mesopelagic fishes closer to the surface in narrow layers, or (2) of some layering mechanisms at fronts that concentrate plankton and consequently mesopelagic fishes into thin subsurface layers (Lévy et al. 2018). This effect is not observed during the day because mesopelagic fishes swim deeper in relation to light intensity (Duhamel et al. 2000, Guinet et al. 2014).

Perspectives

All these results highlight the importance of sub-mesoscale fronts for apex predators. However, to further understand SES behavior in a dynamical field of sub-mesoscale structures, more precise information is needed regarding the location of the SES with respect to these features. Indeed, in addition to the absence of salinity measurements making it difficult to quantify the underwater structures of fronts, the angle between the SES trajectory and the sub-mesoscale structure it encounters is unknown and depends on SES's behavior, making it hard to identify the physical structure sampled by the seal. Because of these limitations, SST (or density) gradients cannot be exactly derived from the data set and are generally underestimated as, having encountered a sub-mesoscale front, the seals may travel along it, rather than across it. To date, altimeter data do not allow mapping of sub-mesoscales with enough resolution. The combination of high-resolution observations of future spatial missions (such as SWOT, with an expected resolution 10 times higher than presently available) with new SES in situ data that include density, will allow retrieving a more complete 3D view of the sub-mesoscale structures surrounding the animal. This emphasizes the need for more high-resolution biological data, and in particular, a better characterization of the underwater 3D trajectories of seals during their dives (Le Bras et al. 2017), and the vertical distribution and abundance of their preys. Indeed, both the vertical accessibility, and the prey distributions within well-defined and narrow layers might be critical in explaining the variation in foraging success during seal dives.

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