LETTER

Crossing the line: Tunas actively exploit submesoscale fronts to enhance foraging success

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Abstract

Fronts—i.e., the boundaries between water masses—are ubiquitous in the world oceans and have been shown to significantly influence pelagic ecosystems with enhanced local productivity and increased abundances of forage fish and top predators. Here we use data from archival tags to document how four juvenile albacore tunas foraged at and exploited a thermal front. Of the 3098 observed trips, the albacore mainly swam across the front between the warm side above the thermocline and the cold side below the thermocline with an average of 78 ± 20.4 cross-frontal trips per fish per day. The warm frontal surface waters provided a thermal resource, allowing the tuna to maintain higher body temperatures and thus forage more efficiently in the food-rich waters of the cold side of the front. Foraging success of the tunas decreased as the cross-front thermal gradient weakened. This first look into small-scale use of fronts by a top predator demonstrates that ephemeral, submesoscale oceanic features can play a significant role in pelagic ecology.

Scientific Significance Statement

The boundaries between water masses, known as “fronts,” are oceanic hotspots—known to harbor increased abundances of bacteria, plankton, forage fish, and pelagic predators. Fronts are complex structures that vary in both time and space. The influence of these dynamics on open ocean ecosystems is still an active area of research, and it is not clear how large predators, such as tunas, exploit these features. We used a novel approach to show that albacore tuna use fronts as both a temperature and a food resource, but that their foraging success deteriorates as the horizontal scale of the front increases in size.
strong along-front jets, and occur in most of the world’s large marine ecosystems (Belkin et al. 2009). Often associated with these large fronts are ephemeral (lasting on the order of days), smaller (spanning 1–10 km) fronts, termed submesoscale fronts (Lévy et al. 2012). Submesoscale fronts produce locally enhanced vertical and horizontal currents and high levels of shear that result in the influx of nutrients to surface waters, which in turn lead to higher concentrations and patchiness of nutrients, phytoplankton, and small, nonmotile organisms such as zooplankton (Genin et al. 2005; Lévy et al. 2012; Mahadevan 2016).

We are at the frontier of understanding the dynamics of how fronts alter pelagic ecosystems, and why organisms accumulate (in the case of drifters) or aggregate (in the case of swimmers) at fronts. Fronts provide important habitat for bacteria (Floodgate et al. 1981), planktonic organisms (Landry et al. 2012; Powell and Ohman 2015), the migrating organisms of the deep scattering layer (Landry et al. 2012), forage fish (Tseng et al. 2014), and predators such as tunas (Sund et al. 1981; Fiedler and Bernard 1987), sharks (Sims and Quayle 1998; Queiroz et al. 2012), turtles (Polovina et al. 2000), marine mammals (Bost et al. 2009), and birds (Nel et al. 2001; Bost et al. 2009).

Extensive tagging efforts in the North Pacific have shown that the California Current System (CCS) is a hotspot for migratory predators (Block et al. 2011). The CCS is an eastern boundary upwelling system, that flows from ~50°N equatorward along the west coast of North America. Strong mesoscale fronts form in the CCS through wind-driven upwelling, with cold, saltier water on the coastal side, and warm, fresher water on the offshore side (Checkley and Barth 2009). Shear associated with the formation of these mesoscale fronts results in a substantial number of submesoscale features consisting of filaments of cold, upwelled water intertwining with warm, offshore waters (Capet et al. 2008). The wind-driven upwelling brings nutrients into the surface waters enhancing primary production, while the velocity shear associated with the front formation creates concentrated patches of plankton in the cold waters of the fronts. These dynamics within the CCS result in a productive ecosystem that supports both demersal and pelagic fisheries (Checkley and Barth 2009).

Our knowledge of predator behavior at fronts and the benefit of fronts is limited and speculative. Focus has traditionally been on the presence and absence of predators at mesoscale fronts through analyses of catch data and sightings, as well as movement into and out of frontal areas (Scales et al. 2014b). These types of analyses have provided valuable information on when and where predators encounter fronts (Sund et al. 1981; Fiedler and Bernard 1987; Sims and Quayle 1998; Polovina et al. 2000; Nel et al. 2001; Bost et al. 2009; Queiroz et al. 2012; Scheffer et al. 2012; Scales et al. 2014b), but have yet to address how the predators exploit the front.

In addition to higher concentrations of prey, it is hypothesized that thermal fronts also provide mobile predators with physiological advantages over their prey. Warmer body temperatures translate into faster swimming speeds, better visual acuity, and increased digestion rates (Altringham and Block 1997; Dickson and Graham 2014). The advantages of warmer body temperature are so great that tunas and some other pelagic fishes have evolved regional endothermy, i.e., the ability to maintain parts of their bodies above ambient temperature (Dickson and Graham 2014). At thermal fronts, regional endotherms and ectothermic predators alike can take advantage of the warmer water to attain warm body temperatures relative to ectothermic prey located in the cold waters across the front, thus maximizing the difference in both swimming speed and sensing capabilities between predator and prey. This hypothesis was tested using a mathematical model, and it was found that juvenile tuna—whose capacity to retain heat was less than those of larger, adult tunas—could theoretically exploit the warm waters of the front to assist in thermoregulation and thus improve foraging performance in the food rich, cold waters of the front (Kirby et al. 2000). However, there has yet to be any empirical data to support this theory.

Here we examine the behavior and foraging success of four juvenile albacore tuna, Thunnus alalunga, tagged within the CCS at a thermal front. Enhanced fishery catches of albacore tuna are associated with oceanic fronts (Xu et al. 2017) and coastal frontal systems (Nieto et al. 2017) within the CCS on both seasonal and interannual scales. This study provides the first empirical measures of foraging behavior and success by pelagic predators at a front. Our characterization of how albacore utilize and benefit from the CCS frontal features provides insights into the general allure of fronts to pelagic predators.

Materials and Methods

The albacore tagging data were collected by the Albacore Archival Tagging Program, an ongoing collaborative effort between the Southwest Fisheries Science Center and the American Fishermen’s Research Foundation (details on the tags and tagging procedures can be found in Childers et al. 2011). The tags consisted of a cylindrical housing implanted in the fish, that holds an internal temperature sensor (measuring body temperature), a pressure sensor (measuring depth) and a clock, and a stalk that protruded outside the fish, housing an external temperature sensor (measuring water temperature), and a light sensor. Fish locations were estimated using light-based geolocations and the unscented Kalman filter (Lam et al. 2008).

To find times when tagged albacore were exploiting fronts, we flagged 24 h periods during which an individual’s water temperature measurements within 5 m of the surface varied by more than 1°C. We chose this value as a first-pass filter because (1) it is a typical magnitude of temperature gradients of fronts in the CCS (Powell and Ohman 2015) and
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(2) it was small enough to capture most surface temperature fronts, but large enough to exclude variations in temperature due to vertical mixing. Among the possible fronts evident in the tagging dataset, we limited the study to one particular front where multiple individuals were exploiting the same temperature front in the same geographic area (i.e., within an approximated location measurement error, 300 km) for an extended period of 2 weeks. The four fish exploiting this front were tagged off Baja California, Mexico in July and November of 2003 and averaged 87.0 ± 2.45 cm in fork length at the time of deployment and 94.0 ± 2.45 cm at recovery (Supporting Information Table 1). By focusing on these fish at this particular front, we could compare movement and foraging across multiple fish in the same prey field and oceanographic conditions. Furthermore, the combination of the long residence time and the number of fish exploiting the same front ensured that the front was highly sampled both horizontally and vertically.

To estimate the physical features of the front, the thermal properties of the front were assumed to be stable while the fish were in proximity to the front. We used vertical measurements of depth and water temperature collected by the fish every minute during this time to define temperature-depth profiles for the warm and cold sides of the front. To determine the temperature at depth for the cold and warm sides of the front, we fit a double Gaussian curve to frequency distributions of water temperature measurements in 2 m depth bins:

\[ G = a_1 e^{-\frac{\left( \frac{T - T_{cold}}{c_1} \right)^2}{2}} + a_2 e^{-\frac{\left( \frac{T - T_{warm}}{c_2} \right)^2}{2}} \]  

where \( a_1, a_2, c_1, c_2, \) and \( H \) are constants describing the amplitudes \( (a_1, a_2) \) and widths \( (c_1, c_2, H) \) of the two Gaussian curves while \( T_{cold} \) and \( T_{warm} \) are the mean temperatures representative of the front’s warm and cold sides, respectively, for each depth bin. The data were then smoothed over 5 m vertically and interpolated linearly such that a temperature was assigned to each 0.1 m. The depth of the top of the thermocline was estimated as the depth at which the temperature fell below 1°C the maximum temperature on each side of the front. Because of the error in the tuna geolocations relative to satellite remote sensing, the sea surface temperature (SST) corresponding with the cold and warm sides of the front were defined as the maximum \( T_{cold} \) and \( T_{warm} \), respectively. These fish-derived SSTs were later matched with the corresponding SSTs in the satellite imagery.

To examine the albacore’s exploitation of the front, we quantified both distribution and movement patterns while at the front. We defined four distinct areas of the front: the surface and deep waters of the warm side of the front (WS and WD, respectively), and the cold side of the front (CS and CD). It is important to note that the accuracy of the position of the fish within the frontal regions rests on the ability of the temperature sensors to equilibrate with the surrounding temperature sensors. Given coefficients of conductance of similar tags, we estimate that the sensors can capture temperature changes of 18°C min⁻¹ within 0.5°C over a period of 2 min and temperature changes of 2°C min⁻¹ over a period of 1 min (for more details, see Snyder and Franks 2016). We address this technical limitation by creating a buffer zone of 0.5°C between the warm and cold sides of the front. Fish were flagged in a region if their temperature at a given depth was above or below 0.25°C of the middle temperature between the cold and warm profiles. Fish whose temperature depth measurements fell within the 0.5°C buffer zone were deemed to be “in transit.” The “surface” was defined as waters shallower than 5 m above the top of the thermocline, and the “deep” as deeper than 5 m below the top of the thermocline. We calculated the percent time spent in each of these regions as a function of time of day, and we counted the movements among the different regions, noting the time of day, the origin, and destination of those movements. All values reported are the grand mean (i.e., the mean of the mean values per fish) ± standard deviation from the grand mean.

To quantify the horizontal spatial scale of the fronts, we coupled the archival tag data with satellite imagery within the geographical region bounded by 25°N to the south, 27°N to the north, 113.4°W to the east and 115.4°W to the west. We chose the Jet Propulsion Laboratory’s Multi-Scale Ultra-High Resolution SST product (MUR, http://mur.jpl.nasa.gov/), which had the highest spatial resolutions (~ 1 km) available for this study period. The horizontal location of the front was dynamic while the fish were exploiting the front. Thus, horizontal distance between the warm and the cold surface waters was estimated as the daily nearest-neighbor distance between satellite SST measurements corresponding to the tag-derived SSTs defining the warm and cold sides of the front. We then defined the cross-front distance as the fifth percentile of the nearest-neighbor distances.

To test whether the front served to elevate body temperature and/or foraging success, we examined aspects of each albacore’s thermoregulation and foraging during their 2 weeks at the front. We compared their median body temperature and thermal excess (i.e., difference between body and water temperature measured by the internal and external temperature sensors, respectively) during the residence time in the CD region after coming from either the WS or CS waters of the front.

We used a qualitative measure of foraging success by comparing the increases in body temperature after sunset, often termed the “heat increment of feeding” (HIF) associated with specific dynamic action, with the cross-front distance (Whitlock et al. 2013). We calculated the HIF, which is estimated as the summation of the difference between an elevated body temperature \( (T_b) \) and the albacore’s nighttime steady-state body temperature \( (T_{ss}) \), using Whitlock et al.’s (2013) model:
where \( t_{\text{start}} \) and \( t_{\text{end}} \) are the start and end times of the HIF. To calculate \( T_{ss} \), we took the mode of the nighttime body temperatures that fell below the average nighttime body temperature, rounded to 0.1°C. Because the methods of Whitlock et al. dealt with a different species of tuna under controlled laboratory conditions, we modified some of their criteria to suit our in situ data. As albacore tuna stay in warm waters near the surface at night, we used only nighttime data to avoid body-temperature changes during the day that could have been caused by diving or increased activity. To remove any effect of perturbations in the sea-surface temperature or short excursions to other temperatures, data were smoothed over 2 h. The start and end of the HIF event were defined as the first time the albacore’s temperature rose above the steady-state temperature and had a positive derivative with time and as the last time the albacore’s temperature was above the steady-state temperature and had a negative derivative with time, respectively. Because the HIF durations of the wild albacore in our study were shorter than those observed in captive bluefin, we excluded start and end times that gave HIF periods less than 2 h (compared to the 4-h cut-off used by Whitlock et al.). We performed type 2 linear regression analyses between the time series of HIF and the cross-front distance to assess whether HIF correlated with cross-frontal width (a measure of frontal strength). As the magnitudes of HIF values can vary based on forage items, sea-surface temperature, and differences among individuals, we only compared values within an individual during their time at the front (Whitlock et al. 2013). In doing so, we assume that the tunas are foraging on similar prey throughout their time at the front.

**Results**

**Frontal dynamics**

Four albacore were observed exploiting the same frontal system from 25 February 2004 to 09 March 2004. Archival tagging data revealed thermal front structure, with a difference of greater than 1°C at depths down to 250 m (Fig. 1). Sea-surface temperature (SST) data of the region revealed a dynamic, spatially complex thermal front system (Fig. 2a). This front formed off Baja California, Mexico near the southern end of
the CCS, presumably through wind-driven upwelling. The cold, nutrient-rich water upwelled near the coast likely drove enhanced primary production at the front, which showed strong mesoscale/submesoscale meandering (Fig. 2a). We found that daily cross-front distances (defined as the fifth percentile of daily nearest-neighbor distances between the CS and WS waters at 16.9°C and 17.4°C) were near the limit of the satellite resolution (~1 km) and increased during the albacores’ residence at the front (Fig. 2b, median 4.2 km; IQR: 3.8–6.5 km; Methods). The small, increasing cross-front spatial scales indicate strong, submesoscale gradients that weakened while the albacore exploited the front.

**Behavior at front**

The juvenile albacore were actively utilizing waters on both the warm and cold sides of the front. They exhibited a characteristic diurnal pattern in behavior, with more diving during the daytime (daily daytime vertical distance: 1215 ± 20.6 m) than at night (daily nighttime vertical distance: 452 ± 44.7 m). At night, the albacore spent the majority (78.9% ± 10.3%) of their time within the WS waters (Fig. 3a), while during the day the albacore split their time mainly between the WS waters (41.3% ± 14.0%) and the CD waters (24.6% ± 8.2%, Fig. 3b). Of their time spent at depth, albacore were mostly on the cold side of the front (69% ± 20%). We observed 4734 movements among the four frontal regions—WS, WD, CS, and CD. A majority of these movements occurred during the day (4191 movements, 89%) rather than at night (524 movements, 11%), with the remainder occurring at either sunrise or sunset (19 movements, <1%). Of the transits among frontal regions, 65% were between the cold and warm sides of the front—of these the majority of movements were between the WS waters and the CD waters (1791 of the 3098 across front movements, Fig. 4).

**Thermal physiology**

In the CD waters, median body temperatures of albacore were about 1.5°C warmer when diving from the WS (19.3 ± 0.5°C) than from the CS (17.8 ± 0.4°C). Thus, residence in the WS waters prior to diving to the CD waters resulted in a ~20% larger temperature difference between their body and water temperature (6.7 ± 0.6°C) than when arriving to the CD from the CS (5.4 ± 0.5°C). At dusk, the albacores’ body temperatures were observed to undergo a period of elevated body temperature followed by a slow drop to a steady-state temperature, characteristic of the HIF associated with specific dynamic action (Fig. 5). We found that for three of the four fish, the relative foraging success (i.e., the magnitude of HIF) was highest when the distance between the WS and CS waters of the front was smallest (Fig. 6). As the cross-front distance increased from submesoscale to mesoscale, foraging success decreased and the albacore left the area.

**Discussion**

Here we have presented the first empirical evidence of tuna exploiting a thermal front to enhance foraging success. Our results support the hypothesis that juvenile tuna utilize thermal fronts as a temperature resource to enhance foraging
performance and suggest that this benefit is dependent on the horizontal scale of the front.

**Fronts provide a physiological advantage to predators**

Qualitatively, an increase in body temperature results in increased swimming ability and increased visual acuity (Brill 1996; Altringham and Block 1997; Dickson and Graham 2014). At a front, ectotherms and regional endotherms alike could use the thermal gradient to gain an advantage over prey, by warming their bodies in the warmest waters of the front and foraging in the cold waters of the front (Kirby et al. 2000). Our results indicate that juvenile albacore tuna spend most of their time swimming diagonally across the front between the WS and CD waters. This resulted in warmer body temperatures relative to their ectothermic prey compared to times when they swam vertically from the CS waters to the CD. This implies that the benefits of thermal fronts may decrease as a function of thermoregulatory ability, i.e., fronts may be most advantageous to ectothermic predators and less advantageous to endothermic predators.

Mobile predators may favor the CD waters to take advantage of enhanced local prey concentrations that typically occur there due to enhanced nutrient concentrations (Landry et al. 2012; Powell and Ohman 2015). Unfortunately, we did not have data on the distribution or type of prey at this front nor did we have measures of rates of prey consumption in the various regions of the front. Also, we could not confirm that warmer body temperatures resulted in increased swimming speeds due to the low horizontal resolution of movement; thus, the movement could benefit the tunas by increasing digestion rates rather than swimming speed. Last, potential lags in temperature measurement may have resulted in an underestimation of movement between the WS and CD waters. Even with these shortcomings, the preference for making the longer transit from the CD to the WS (rather than CS) waters and associated warmer body temperatures suggests that the WS must provide an advantage to the albacore. In the future, technological

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**Fig. 4.** Albacore movement between frontal regions. Percent of movements between regions of the front along the available paths. The numbers represent the grand mean percent of movements across fish ± standard deviation.

**Fig. 5.** Estimation of foraging success using HIF. Representative 3-d time series of body temperature from an albacore in the study (Tag number: A1246). Red line denotes body temperature with nighttime represented by black bars. Estimation of HIF was calculated as the area under the curve of archival body temperature data during the nighttime digestion period.

**Fig. 6.** Foraging success at the front. HIF, an indicator of foraging success, as a function of cross-front distance. Solid lines denote slopes significantly ($p < 0.01$) different from zero. Dashed lines denote slopes not significantly ($p > 0.01$) different from zero.
advancements in tag development, such as accelerometers, coupled with the methods presented here or perhaps an extension of Kirby et al.’s (2000) theoretical model would provide even more insight into the physiological benefits of thermal fronts.

**Foraging success may depend on spatial scale of fronts**

In general, we found that foraging success decreased as function of cross-front width suggesting that narrow submesoscale features are particularly advantageous for albacore. This is important as the presence of fronts has been proposed as a criterion for defining marine protected areas (Scales et al. 2014b). Our results support the hypothesis that areas with high occurrences of dynamic, submesoscale fronts (such as the CCS: Kahru et al. 2012) provide productive foraging grounds for juvenile albacore. However, the present study was characterized by some important limitations. First, the measurement error associated with light-based locations limited us to approximating the distance across the front using the satellite images rather than the fish’s locations. Second, our measurements of foraging success were limited to an approximate measure based on HIF rather than a direct measure of stomach contents, and were based on the assumption that prey items did not change during the albacore’s time at the front. An individual fish could have experienced different cross-front distances or switched prey items. Either of these limitations may account for one of the fish not experiencing a decrease in foraging success as the front dissipated. Despite these issues, the results of this study support the hypothesis that the scale of the front may be important to foraging success. To further investigate this relationship, future work could examine stomach contents of predators within the context of the sea-surface temperature gradients of the waters in which they were caught.

Detailed observations of predator use of fronts, such as those presented here, influence how we think about open-ocean habitat use for apex predators—key players in ecosystem function. Our study provides both insights into predator behavior at thermal fronts as well as innovative methods to extract predator behavior at thermal fronts on fine temporal (minute-by-minute) and spatial (meters to kilometers) scales from biologging datasets. This methodology, along with the increased availability of extensive tagging datasets and high-resolution satellite imagery, provide critical tools for understanding how dynamic oceanographic conditions influence open-ocean ecosystems.

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