

Key Points:

- Neon flying squid catches are 1.6-fold greater on the warm side of oceanic fronts, peaking approximately 10 km into warmer waters
- Thermal habitat and prey-related productivity favor squid aggregation near and on the warm side of fronts
- Frontal inclination geometrically amplifies the warm-side displacement recorded relative to the surface front

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Asymmetric Catch Distribution of Neon Flying Squid Across the Oyashio Extension Frontal Zone

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Abstract Mesoscale oceanic fronts are critical hotspots for marine productivity and fisheries, yet the fine-scale mechanisms linking frontal dynamics to the specific distribution of catches remain poorly understood. This study investigates this link by analyzing a high-resolution, decade-long (2009–2021) fishery dataset for neon flying squid (*Ommastrephes bartramii*) in the Northwest Pacific's dynamic Kuroshio-Oyashio Extension region, particularly within the Oyashio frontal zone. Using a frontal coordinate system and a null model based on simulated fishing operations, we identify a systematic asymmetric catch distribution, with catches 1.6-fold higher on the warm side of fronts and an optimal fishing offset of approximately 10 km into warmer waters. We propose that the observed pattern reflects three complementary components: thermal habitat, prey-related productivity, and a geometric amplification associated with frontal inclination. Neon flying squid forage and are captured at night within the upper water column, with approximately 50 m used as a representative nocturnal depth. Because the front is displaced warmward with depth, an aggregation located near or slightly warmward of the 50 m front is represented farther toward the warm side when the catch is recorded at the surface position of the fishing vessel and referenced to the surface SST front. Our findings offer a depth-dependent perspective grounded in the subsurface structure of oceanic fronts, helping to clarify how predator behavior and subsurface oceanography interact to shape surface catch patterns and informing fisheries applications and ecosystem-based management in dynamic frontal systems.

Plain Language Summary Oceanic fronts, where different water masses meet, are like oases in the ocean, teeming with marine life and attracting fishing fleets. Analyzing over a decade of fishery data, we discovered a striking pattern: fishermen consistently catch 1.6 times more neon flying squid on the warm side of these fronts. Our research offers a new explanation by looking beneath the surface. We found that these fronts are not vertical walls, but are tilted, sloping downwards into the warmer water. At night, squid move into the upper ocean to feed and are caught below fishing vessels. The front at this subsurface fishing depth is displaced toward warmer water relative to the front seen at the sea surface. Because catches are recorded at the surface positions of the vessels, squid aggregating near the subsurface front appear farther toward the warm side when their locations are compared with the surface front. This discovery provides a subsurface roadmap to these fishing hotspots. It not only helps fishermen work more efficiently but also helps scientists understand how ocean physics and animal behavior combine to create areas of rich marine life, which is crucial for managing ocean resources sustainably.

1. Introduction

Mesoscale oceanic fronts, the dynamic boundaries between distinct water masses, are fundamental drivers of marine ecosystem structure and productivity (D'Asaro et al., 2011; Franks, 1992; Belkin & Gordon, 1996; Lima et al., 2002; Klein & Lapeyre, 2009; Lutjeharms et al., 1985; Mahadevan, 2016; McWilliams, 2016, 2021). These dynamic oceanic structures modulate multiple ecological processes, including migration, foraging, reproduction, recruitment, and communication (Bakun, 2006; Olson et al., 1994; Polovina et al., 2001; Woodson et al., 2012). These features create biological “hot spots” in the open ocean through two primary mechanisms: enhancing nutrient supply via physical processes like upwelling and mixing (bottom-up enrichment), and aggregating plankton and prey through flow convergence (physical concentration) (D. G. Ainley et al., 2009; Clayton et al., 2014; Murphy, 1995; Hunt et al., 2013). Consequently, fronts are widely recognized as critical habitats that attract and sustain elevated biomass across all trophic levels, from phytoplankton to apex predators, thereby

shaping high-yield fishing grounds globally (Bakun, 2006; Belkin, 2021; Bost et al., 2009; Franks, 1992; Genin et al., 2005; Godø et al., 2012; Haney, 1986; Lévy et al., 2024; Mahadevan, 2016; Olson et al., 1994; Palacios et al., 2006; Scales et al., 2014; Tseng et al., 2014; Woodson & Litvin, 2015; Woodson et al., 2012). While the paradigm of fronts as zones of aggregation is well-established, the fine-scale distribution patterns of mobile predators across these features, and the precise biophysical mechanisms that govern them, remain poorly resolved. Understanding this linkage is critical for advancing ecological theory and improving fisheries management in the dynamic ocean systems.

Among the world's most dynamic marine ecosystems, the Kuroshio-Oyashio Extension (KOE) region in the Northwest Pacific stands out as a natural laboratory for studying frontal dynamics (Deser & Kwon, 2007; Joh et al., 2023; Kida et al., 2015; Na et al., 2018; Qiu, 2001; Wu et al., 2019). As the confluence zone of the warm, saline Kuroshio Current and the cold, nutrient-rich Oyashio Current, the KOE is characterized by intense mesoscale eddy activity, some of the sharpest sea surface temperature (SST) gradients on the planet, and exceptionally high biological productivity (Ito et al., 2013). This region serves as a critical feeding and migration corridor for numerous commercially important pelagic species, including the neon flying squid (*Ommastrephes bartramii*) (Kida et al., 2015). The persistent and powerful frontal systems of the KOE make it an ideal setting to investigate the fine-scale physical-biological interactions that structure marine ecosystems, offering insights that are relevant to Western Boundary Current systems globally. It is important to note that the frontal structures in this region are not limited to the primary Kuroshio front located farther south, but include dynamically evolving secondary and transition-zone fronts, particularly those associated with the Oyashio frontal zone, shaped by downstream adjustment of the Kuroshio, mesoscale eddy activity, and mixing processes within the transition zone. The downstream evolution, shallow vertical structure, and biophysical significance of such transition-zone fronts have been extensively synthesized within broader conceptual frameworks of western boundary current systems (Olson, 2001, 2002). In this study, we focus on objectively detected daily mesoscale frontal features located primarily within the Oyashio frontal zone of the Kuroshio–Oyashio transition region, rather than assuming a fixed or quasi-stationary boundary. This approach acknowledges the dynamic and spatially heterogeneous nature of the transition-zone frontal system.

The ecological significance of fronts is often conceptualized through Bakun's "ocean triad" hypothesis, which posits that successful fish recruitment and foraging depend on the co-location of three critical processes: nutrient enrichment, prey concentration, and larval or predator retention (Agostini & Bakun, 2002; Bakun, 1996; Woodson & Litvin, 2015). While frontal zones inherently provide mechanisms for enrichment (e.g., upwelling) and concentration (e.g., convergence), the processes governing the retention of highly mobile predators within these ephemeral hotspots are less understood. This is particularly true when subsurface structure is considered, as it may interact with predator behavior in ways not apparent from surface observations alone. A critical knowledge gap therefore exists in understanding how the vertical structure of fronts interacts with the behavior of pelagic predators, and how this interaction may contribute to spatially consistent foraging patterns within frontal systems.

The neon flying squid, a commercially vital and highly mobile predator in the KOE, serves as an ideal model organism to investigate these fine-scale biophysical interactions (Anderson & Rodhouse, 2001; Arkhipkin et al., 2015; Bower, 1997; Pierce et al., 2008; Rosa et al., 2011; Yatsu et al., 1998; Yu, 2016). As a highly migratory species capable of substantial horizontal movement, its spatial distribution reflects both behavioral and environmental controls (Bower & Ichii, 2005; Snyder et al., 2017). Its pronounced diel vertical migration (DVM)—inhabiting deeper waters by day and ascending to forage within the upper epipelagic layer (~50 m) at night (Bower & Ichii, 2005; Igarashi et al., 2018; Murata, 1993; Murata & Nakamura, 1998; Yatsu et al., 1998; Yu et al., 2015), where the squid are targeted by fishery—provides a useful framework for examining how biological distributions within the upper water column are represented relative to a surface-defined frontal boundary (Labe, 2000; Zhang et al., 2022). While it is known that squid aggregate near fronts, the precise mechanisms governing their distribution across the frontal boundary, particularly the consistent asymmetry observed by fishers, remain unresolved (Chen et al., 2014; Mugo et al., 2014; Prants, 2022).

Here, we examine how thermal habitat, prey-related productivity, and the depth-dependent position of the frontal boundary jointly contribute to the observed surface-referenced catch asymmetry. In particular, we test whether the warmward displacement of the front between the sea surface and the representative nocturnal fishing depth can geometrically amplify a warm-side aggregation formed within the upper water column. By integrating over a decade of high-resolution fishery data with ocean reanalysis products, we identify a systematic warm-side

displacement, with catches 1.6-fold higher approximately 10 km into the warm flank. Our findings offer a depth-dependent perspective grounded in the subsurface structure of oceanic fronts, helping to interpret fine-scale predator distribution patterns.

2. Materials and Methods

2.1. Data Sets

This study integrates high-resolution fishery logbook data with multiple satellite-derived and ocean reanalysis products.

Fishery data: High-resolution squid fishery data from 2009 to 2021 were obtained from the National Data Centre for Distant-water Fisheries of China. The logbook dataset includes daily records of vessel location ($1/60^\circ$ resolution) and total catch (kg), providing the basis for analyzing the distribution of fishing effort and catch. The fishery is conducted primarily using light-lure squid jigging vessels operating at night, and fishing effort is defined as vessel-days (one vessel operating for one day).

Satellite-derived environmental data: To characterize the surface ocean environment, we utilized two daily products from the Copernicus Marine Service (CMEMS). First, SST data from the Operational Sea Surface Temperature and Ice Analysis (OSTIA) system (0.05° resolution) were used for thermal front detection. Second, multi-sensor satellite-derived chlorophyll-a concentrations (4 km resolution) were used as a proxy for prey availability.

Ocean reanalysis data: To investigate the subsurface ocean structure, we used the CMEMS GLORYS12V1 global ocean reanalysis product. This eddy-resolving dataset provides daily three-dimensional ocean state variables, including temperature, at a $1/12^\circ$ horizontal resolution on 50 vertical levels, enabling the reconstruction of the vertical architecture of frontal systems.

2.2. Front Detection and Analysis

2.2.1. Front Identification Algorithm

Mesoscale oceanic fronts were identified from daily satellite SST imagery using the sliding-window-threshold algorithm (SWTA) (Xing et al., 2023). We selected this method due to its enhanced capability in detecting multiscale frontal features compared to traditional gradient-based algorithms. The SWTA employs sliding-window thresholds and a series of morphological operations to identify frontal pixels, allowing it to separate multiscale frontal information. Unlike methods reliant on a single, fixed gradient threshold, the SWTA is robust to gradient variations and can detect a more comprehensive set of frontal features, including weaker or more complex structures that are often missed by other algorithms but remain ecologically significant. This capability is particularly advantageous for the highly dynamic KOE region.

2.2.2. Frontal Coordinate System and Probability Maps

To analyze the distribution of fisheries and environmental variables relative to fronts, we established a frontal coordinate system. Similar frontal coordinate frameworks have been used in previous studies of western boundary current systems (Olson, 2001, 2002). For any given data point (e.g., a fishing location), we calculated its perpendicular distance to the nearest identified frontal line. The point was then classified as being on the “warm side” or “cold side” by comparing its local SST to the SST at the corresponding point on the front. Here the terms “warm” and “cold” flanks refer to relative positions across the front rather than absolute thermal suitability. To ensure each data point was uniquely associated with a single frontal feature, it was referenced only to the closest frontal boundary.

Using this framework, we calculated two spatial probability variables. The frontal probability (R_f), representing the likelihood of frontal occurrence, was calculated for each grid cell as the number of days a front was detected divided by the total number of days in the fishing season. Similarly, the optimal SST probability (R_s) was calculated as the number of days a grid cell's temperature fell within the optimal SST range for squid divided by the total number of days in the fishing season. The depth-dependent optimal temperature ranges were derived from the temperature distributions associated with fishing activity, as described in Section 2.3.

2.3. Null Model for Bias Correction

To distinguish true habitat selection from biases inherent in the spatial and temporal distribution of fishing effort, we developed a null model using simulated fishing points. Fishery-dependent data are intrinsically biased, as fishing effort is not distributed randomly. To account for this, we first defined a sampling domain based on the primary aggregation zones of the actual squid fishery. Then, for each day of the 13-year period, we randomly selected a number of simulated fishing points within this domain equal to the number of actual fishing operations on that day.

This process generated a dataset of simulated fishing locations that preserved the broad spatial and temporal sampling structure of the fishery while removing fine-scale habitat selection signals. By comparing the environmental conditions at actual fishing points with those at simulated locations, we could robustly identify the environmental factors associated with targeted fishing activity.

Using this framework, the optimal temperature ranges at each depth were defined as the temperature intervals where the observed fishing locations showed stronger aggregation relative to the simulated temperature distributions. In other words, the optimal ranges correspond to temperature intervals where the frequency of observed temperatures exceeded the expected background distribution derived from the null model. This data-driven approach avoids prescribing arbitrary temperature thresholds and instead identifies preferred thermal habitats directly from the fishery–environment relationship.

2.4. Reconstruction of the Vertical Frontal Structure

To investigate the vertical architecture of the fronts, we applied the SWTA front detection algorithm to the temperature field at each of the 50 depth levels of the GLORYS12V1 ocean reanalysis data. The depth-resolved frontal structure was then reconstructed by associating frontal positions at each depth level with their corresponding surface expression based on minimum horizontal distance. A subsequent filtering process, guided by principles of physical oceanography, was applied to remove physically inconsistent associations (e.g., abrupt horizontal shifts between adjacent depth levels) that could arise from weak or shallow frontal features. This quality control step enables a consistent estimation of the mean vertical tilt of the frontal systems across the study region.

3. Results

3.1. A Systematic Asymmetric Distribution of Catches Across Fronts

Our analysis of over a decade of high-resolution fishery data in the KOE region, particularly within the Oyashio frontal zone, reveals a systematic and pronounced asymmetric distribution of neon flying squid catches relative to mesoscale oceanic fronts (Figure 1). Monthly distributions consistently show that both fishing effort and catches are preferentially located on the warm side of the frontal boundary throughout the main fishing season from July to November (Figures 2a and 2b).

This spatial displacement is quantified in the cumulative 13-year dataset (Figures 2c and 2d). Approximately 60% of the total catch and fishing effort occurred on the warm side of the fronts. This corresponds to more than 50,000 tons of additional catch obtained from the warm compared to the cold side over the study period. The parity position—the point where cumulative catch on both sides are equal—is displaced approximately 10 km from the frontal boundary into the warmer water.

Furthermore, this asymmetry is not a static phenomenon but is strongly modulated by the intensity of the front itself (Figure 3). As the SST gradient across the front increases, the displacement of the catch parity position toward the warm side becomes more pronounced (Figure 3a). Correspondingly, the ratio of warm-side to cold-side catches consistently exceeds 1 and increases with frontal strength (Figure 3b). This relationship suggests that the observed asymmetry is closely associated with variations in frontal intensity.

The vertical structure of the front provides a geometric context for interpreting the relationship between surface intensity and catch asymmetry. Our analysis shows that stronger surface SST gradients are associated with fronts that penetrate deeper into the water column (Figure 3c). While weaker fronts may be confined to the surface layers, stronger fronts are significantly more likely to extend their influence down to the depth range occupied by

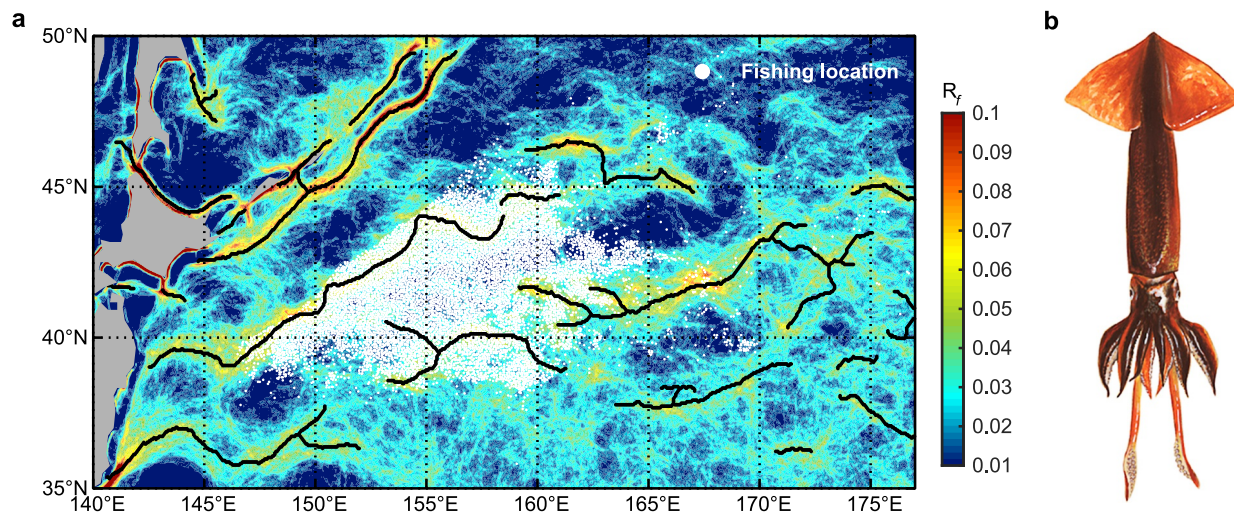


Figure 1. Study area and context for the neon flying squid fishery in the Northwest Pacific. (a) Spatial distribution of fishing locations (white dots) for the Chinese squid-jigging fishery from 2009 to 2021, overlaid on a map of frontal probability (R_f , background color). R_f is calculated from daily satellite-derived SST front detections and represents the probability of frontal occurrence during the main fishing season. Higher R_f values indicate more frequent frontal presence. The solid black lines denote the most persistent frontal positions, corresponding to the zones of maximum frontal probability (i.e., the mean frontal axis inferred from the time-aggregated SST front detections). (b) The neon flying squid (*Ommastrephes bartramii*), the target species of this study.

squid during diel vertical migration (approximately 50–300 m, Figure 3d). Thus, increasing SST-gradient strength is accompanied by both stronger warm-flank catch displacement and greater vertical frontal extent.

3.2. Contributions of Thermal Habitat and Productivity Patterns

Previous studies indicate that the distribution of neon flying squid in frontal zones is influenced by both thermal preferences and prey availability (Alemany et al., 2014; Matsui et al., 2024; Niu et al., 2024). To better understand how these factors relate to the observed cross-frontal asymmetry, we evaluated their spatial patterns using simulated fishing points as a null model to correct for sampling bias.

The neon flying squid is known to exhibit a general preference for warmer waters (Chen et al., 2010; Hatfield, 2000; Li et al., 2023; Wang et al., 2023). Our analysis confirms that SST exerts strong control over squid aggregation, with catches overwhelmingly concentrated in a narrow optimal thermal range of 14–19°C (Figure 4a). The probability of encountering this optimal SST is highest at the frontal boundary itself (Figures 4b and 4c). However, the distribution of this optimal temperature range is symmetrical across the front (Figure 4b) with temperatures on both sides remaining within the species' tolerable range. This indicates that while thermal preference effectively explains why squid aggregate at frontal zones, it cannot account for the strong asymmetric distribution across them.

Prey-related productivity patterns are also associated with squid aggregation. Compared with simulated locations, actual fishing operations occurred in waters with elevated surface chlorophyll-a concentrations (Figure 5a), indicating that fishing activity was concentrated in relatively productive environments. Upwelling on the warm side of the front induced by frontogenesis can stimulate primary productivity (Aoki & Inagaki, 1992; Hoskins, 1982; McWilliams, 2016; Nagai et al., 2008; Pollard & Regier, 1992; Xue et al., 2021; Zhang et al., 2019; Zhu et al., 2024). Consistent with this expectation, the simulated background environment shows that chlorophyll-a concentrations are approximately 15% higher on the warm side of the front compared to the cold side (Figure 5b, blue line). At actual fishing locations, chlorophyll-a concentrations are comparably elevated on both flanks (Figure 5b, gray line), indicating that productive patches occur across the frontal boundary. These results identify a modest warm-flank enhancement in background surface chlorophyll-a; however, surface chlorophyll-a alone does not directly quantify zooplankton biomass or prey availability at higher trophic levels.

Together, these results indicate that thermal and trophic conditions contribute to squid aggregation at frontal zones and may also contribute to the cross-frontal catch asymmetry. Because SST and surface chlorophyll-a do

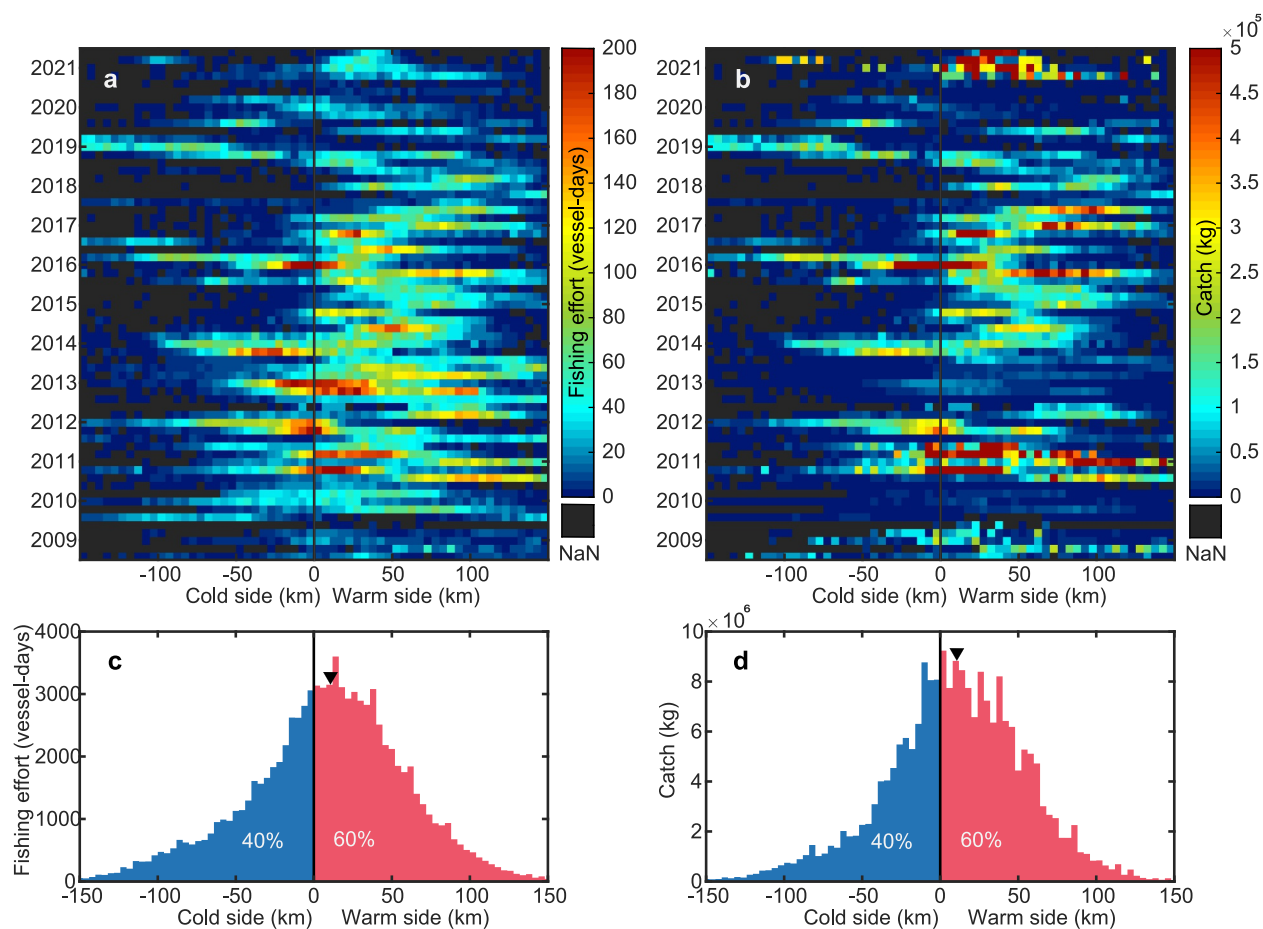


Figure 2. Asymmetric distribution of neon flying squid fishing effort and catches relative to oceanic fronts. (a, b) Monthly distribution of (a) fishing effort (vessel-days) and (b) catches (kg) in the frontal coordinate system during the main fishing season (July–November). Distances are referenced to the daily detected frontal position, with positive values indicating the warm flank and negative values indicating the cold flank. (c, d) Cumulative distributions of (c) fishing effort and (d) catches aggregated over 2009–2021. Approximately 60% of total effort and catch occurred on the warm side of the front. The triangle marker indicates the parity position, defined as the cross-frontal distance at which cumulative effort/catch is equal on both flanks. This position is displaced approximately 10 km toward the warm side, indicating a systematic warm-flank asymmetry.

not resolve the full prey field or the subsequent transfer of biomass across trophic levels, the relative contributions of these processes cannot be quantified from the available surface variables alone.

3.3. Depth-Dependent Frontal Geometry and Surface-Referenced Catch Displacement

Because surface environmental factors alone do not fully explain the observed cross-frontal asymmetry (Section 3.2), we further examined whether interactions between squid vertical behavior and the subsurface frontal structure contribute to the observed patterns. Neon flying squid exhibit pronounced diel vertical migration, occupying deeper waters during the day and ascending into the upper epipelagic layer at night, where they are targeted by the fishery. Based on previous observations, approximately 50 m is used here as a representative nocturnal foraging and capture depth, whereas 300 m is included only as an illustrative daytime reference level (Murata, 1993). These representative DVM depths are not assumed to be fixed biological boundaries or identical across the two frontal flanks. This vertical displacement provides a useful framework for evaluating how a vertically tilted front may translate into different surface-relative positions across depth.

When catch distributions are referenced to frontal positions identified at different depths, a consistent depth-dependent pattern emerges (Figure 6). Relative to the surface front, catches are displaced toward the warm flank (Figures 6a and 6b). When referenced to the 50 m frontal position—representative of the squid's nocturnal habitat—the asymmetry is reduced (Figure 6c). At approximately 100 m depth, the distribution approaches near

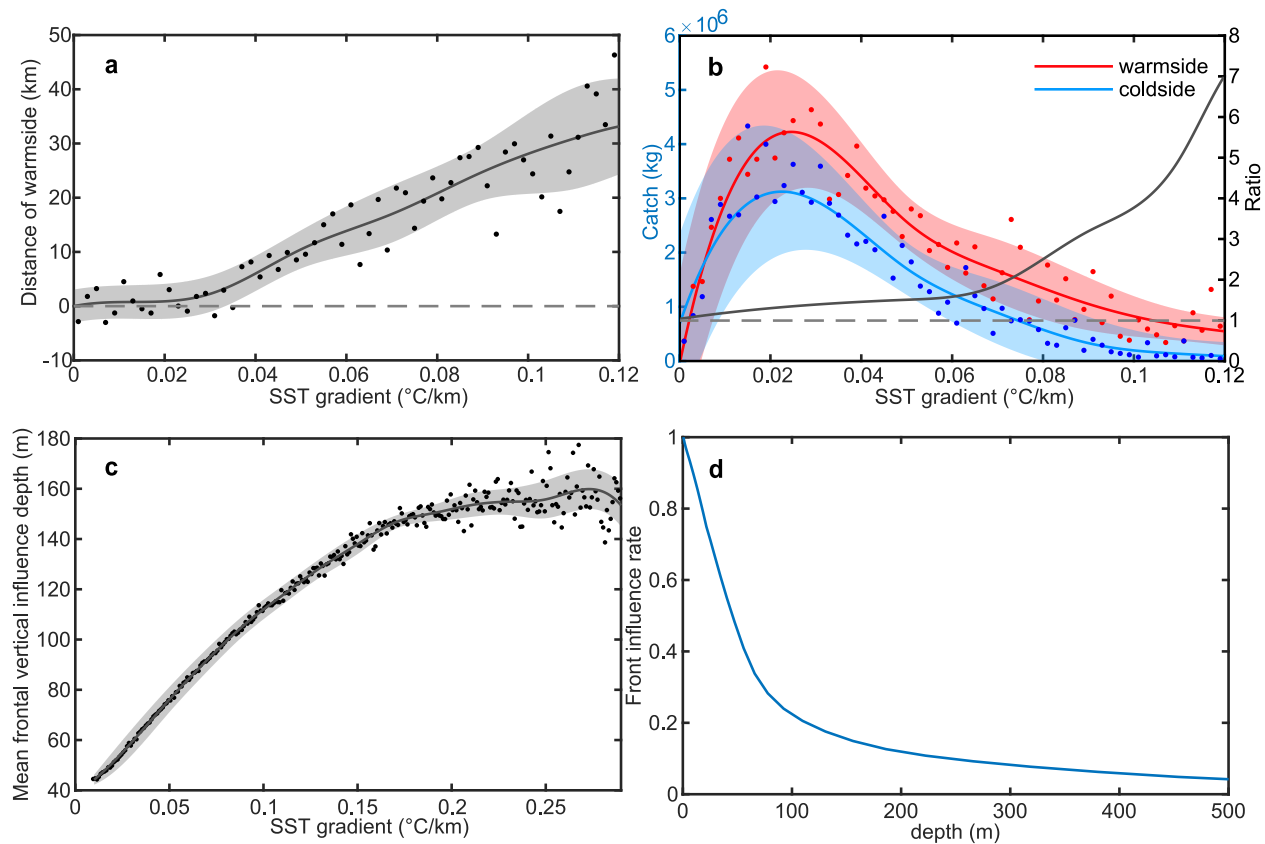


Figure 3. Modulation of catch asymmetry by frontal intensity and vertical structure. (a) Displacement of the catch parity position toward the warm side increases as a function of SST gradient strength. Positive values indicate displacement toward the warm flank. (b) Cumulative catches on the warm side (red line) and cold side (blue line), and their ratio (black line), shown as a function of SST gradient strength. The warm-side displacement increases as fronts become stronger. (c) Mean frontal vertical influence depth as a function of SST gradient strength. The vertical influence depth is defined as the maximum depth at which the frontal thermal gradient remains continuously detectable in the three-dimensional temperature field (see Section 3.3). (d) The proportion of detected fronts remaining continuously identifiable to specified depths, including representative squid DVM depths of approximately 50–300 m. In panels (a–c), dots represent bin-averaged values grouped by SST gradient intervals, and shaded areas indicate ± 1 standard deviation within each bin.

symmetry (Figure 6d). At 300 m depth, the distribution shifts toward the cold flank (Figure 6e). This progressive transition from warm-side displacement near the surface to cold-side displacement at depth suggests that the observed asymmetry varies systematically with the vertical position of the frontal boundary.

To better interpret the depth-referenced patterns, we examined the mean vertical structure of the detected fronts. The mean vertical structure of the detected fronts reveals a consistent warm-ward tilt with depth (Figure 6f). Based on more than 17,000 frontal instances reconstructed from reanalysis data, the frontal boundary does not form a vertical wall but instead slopes downward from the surface toward the warm flank. On average, the frontal position at intermediate depth (approximately 100 m) is horizontally displaced by about 10 km relative to its surface expression. This horizontal displacement is on the order of tens of kilometers. This intermediate depth represents the transition depth at which the apparent catch displacement relative to the depth-specific frontal position approaches zero and changes flank assignment.

The depth-referenced distributions distinguish the squid position relative to the depth-specific front from the position of that front relative to its surface expression. At the representative nocturnal depth of approximately 50 m, 56% of the catch remains on the warm side of the depth-specific front, indicating that a warm-side displacement persists at the fishing depth. When the same catch positions are referenced to the surface SST front, the warm-side proportion increases to approximately 60%. This directional change is consistent with an additional warmward geometric displacement because the 50 m front is located on the warm side of its surface expression. The 100 and 300 m results illustrate how flank classification changes with reference depth, but they are not interpreted as direct observations of an individual migration trajectory or as evidence of a behavioral response to

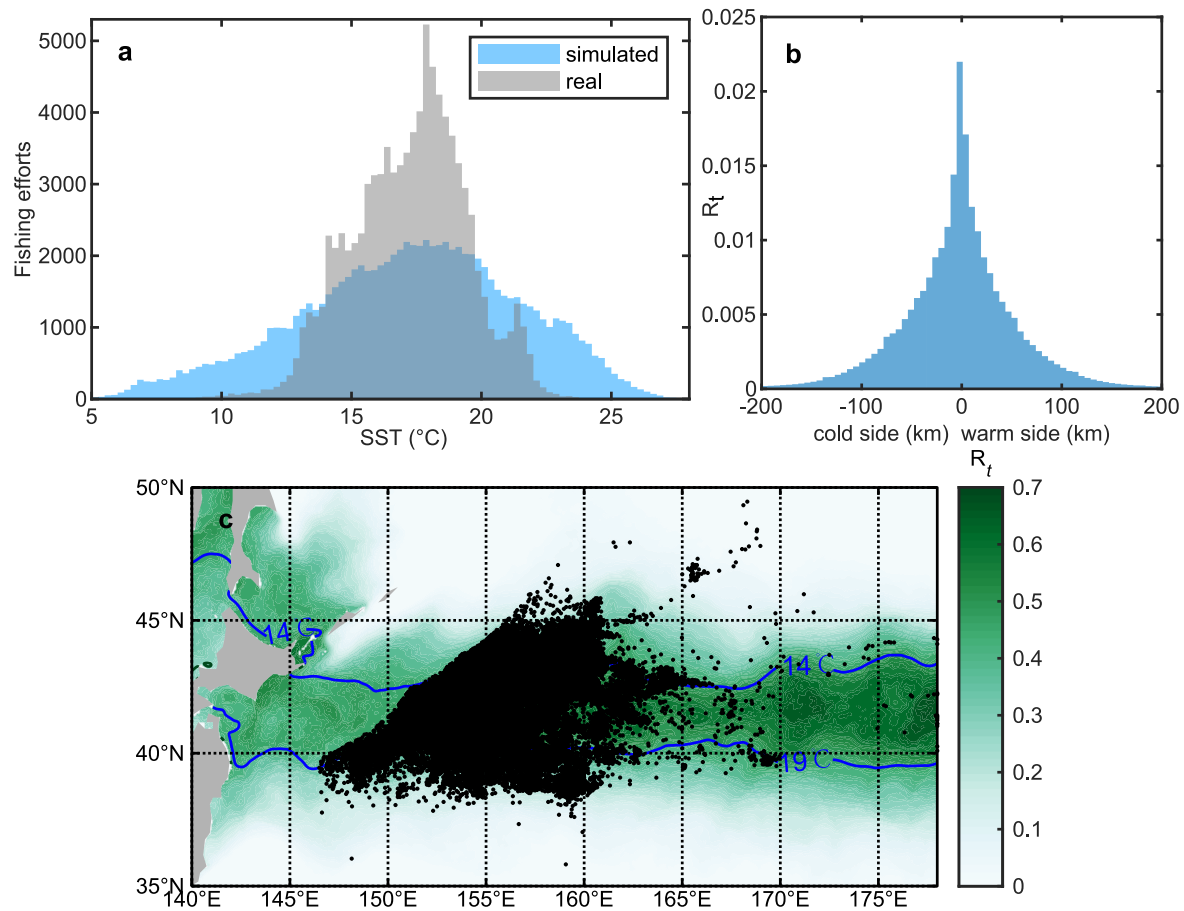


Figure 4. Thermal preference as a driver for squid aggregation at frontal zones. (a) Comparison of sea surface temperature (SST) distributions at actual fishing locations (gray) versus simulated fishing points (blue), which represent the available thermal environment. Catches are concentrated in a narrow optimal range of 14–19°C. (b) The distribution of this optimal SST is symmetrical across the frontal boundary, peaking at the front itself. (c) The spatial probability distribution of the optimal SST range (R_t , background color) aligns well with observed fishing locations (black dots). Blue contour lines indicate the 14°C and 19°C surface isotherms corresponding to the optimal SST window. The optimal thermal habitat aligns closely with frontal zones and fishing activity.

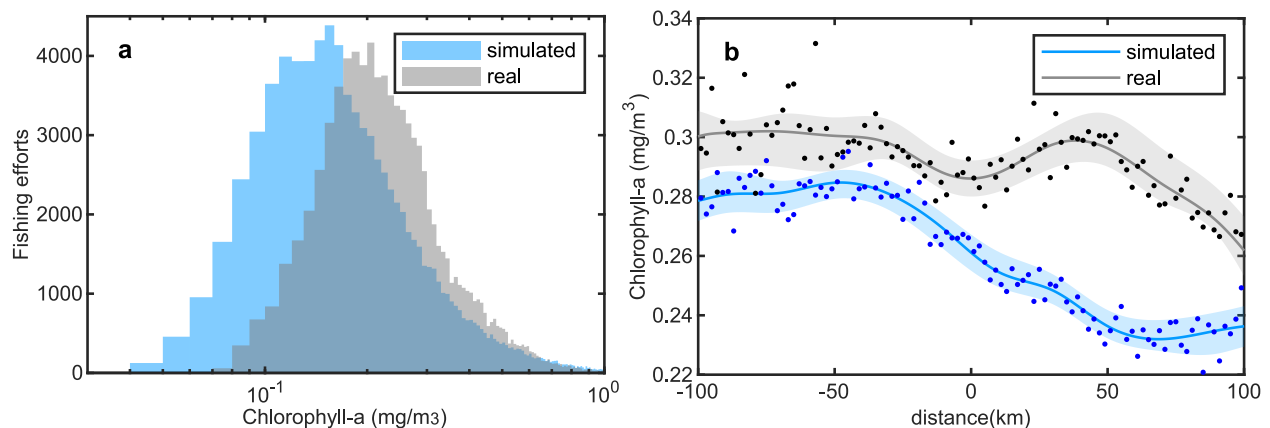


Figure 5. Prey-related productivity patterns across frontal zones. (a) Distribution of sea surface chlorophyll-a concentrations at actual fishing points (gray) compared to randomly simulated locations (blue), illustrating habitat selection toward relatively higher-productivity waters. (b) Mean chlorophyll-a concentration across the frontal coordinate system. Gray line represents actual fishing locations; blue line represents simulated background distribution. Values are averaged within cross-frontal distance bins. Shaded areas indicate ±1 standard deviation within each bin.

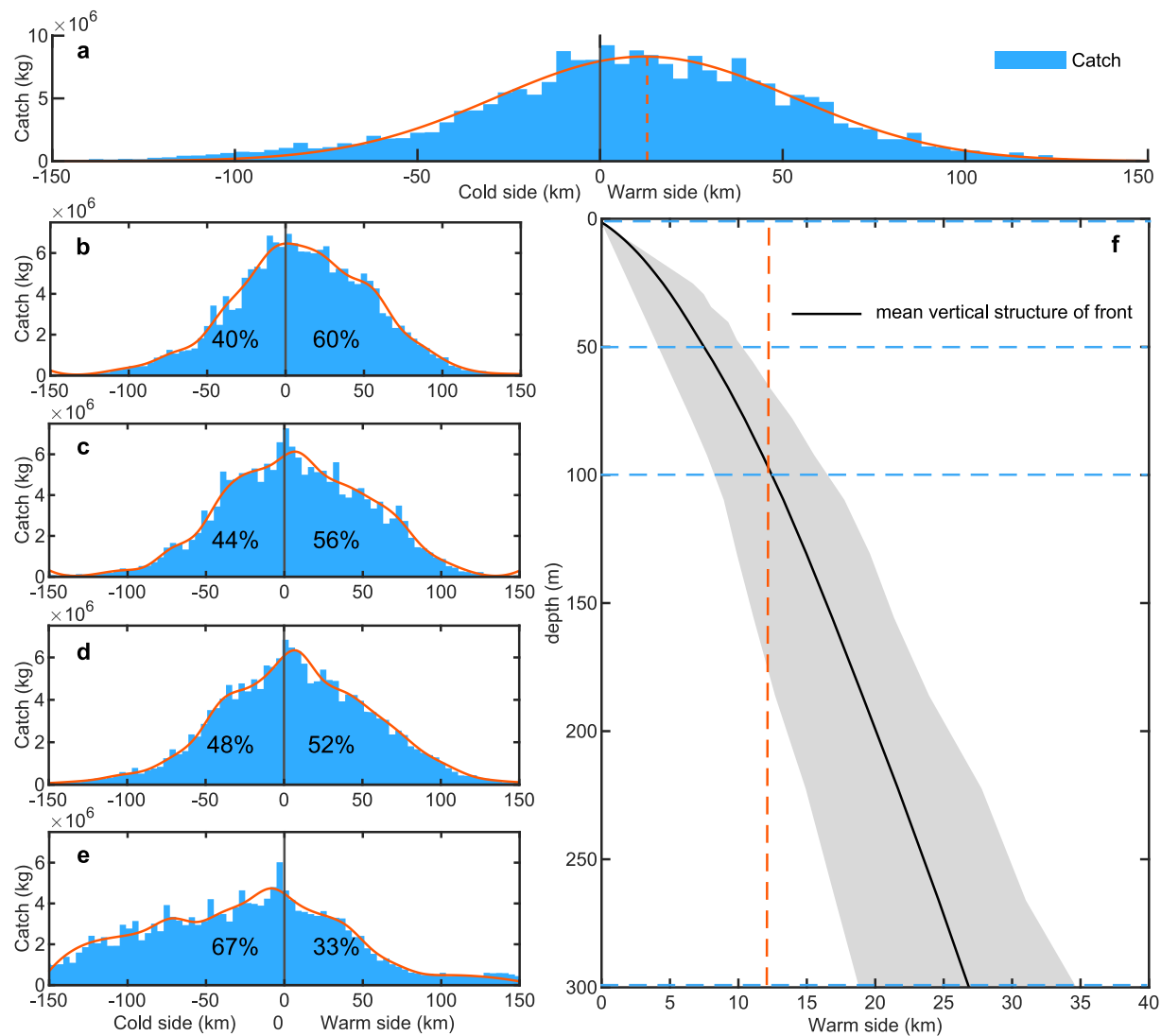


Figure 6. Depth-resolved frontal structure and its relationship to surface-referenced catch asymmetry. (a) Cumulative catch distribution relative to the surface front derived from satellite SST, showing a strong warm-side displacement. (b–e) Cumulative catch distributions referenced to frontal positions identified at depths of (b) 0 m, (c) 50 m, (d) 100 m, and (e) 300 m from reanalysis temperature fields. Percentages on either side indicate the proportion of total catch within each flank. Positive distances denote the warm flank relative to the depth-specific frontal position. (f) Mean vertical structure of the frontal boundary relative to the surface front, illustrating a warm-ward tilt with depth. Shaded areas indicate the interquartile range (25%–75%) across detected fronts. The 50 m level represents the approximate nocturnal fishing depth, whereas 100 and 300 m are included as reference depths for assessing the depth dependence of flank classification.

the deep front. Thus, thermal and trophic conditions may influence the squid distribution relative to the front at the nocturnal habitat depth, whereas frontal inclination affects how that subsurface distribution is represented in the surface frontal coordinate system.

Figure 7 schematically illustrates this geometric relationship between frontal tilt and diel vertical migration. The model highlights how subsurface frontal structure, thermal habitat, and productivity gradients jointly contribute to the spatial organization of squid distribution and fishing activities across the frontal system.

4. Discussion

This study reveals a persistent warm-flank asymmetry in neon flying squid catches across mesoscale fronts in the KOE region. Approximately 60% of the fishing effort and catch occurred on the warm side of the surface SST fronts, with the catch distribution displaced by approximately 10 km into warmer waters. The displacement also increased with frontal intensity. These patterns suggest that the observed asymmetry reflects three complementary

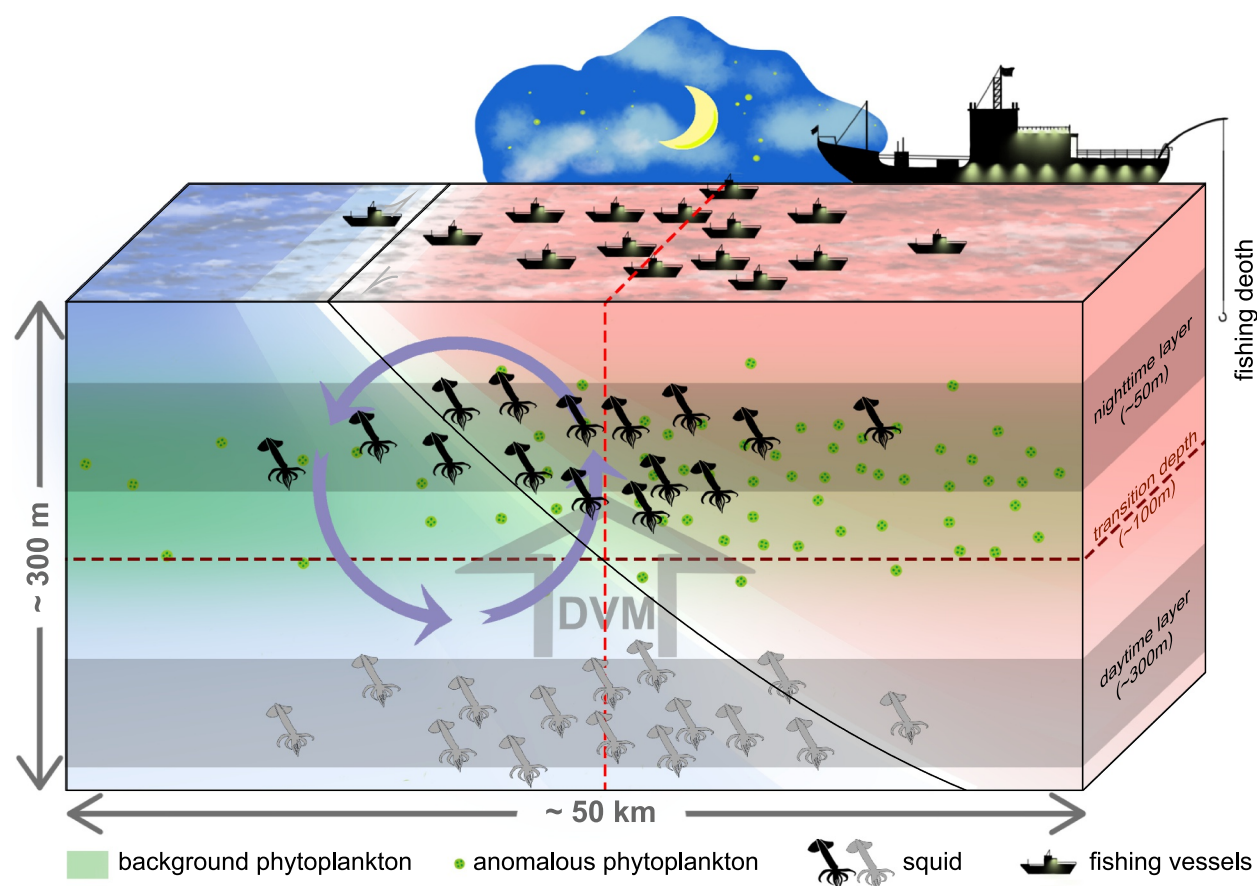


Figure 7. Conceptual schematic illustrating the relationship between frontal vertical structure, squid diel vertical migration, and cross-frontal catch patterns. During daytime, squid generally occupy deeper waters (~300 m is shown as a representative depth). At night, squid ascend to the upper epipelagic layer (~50 m), where the frontal boundary is displaced warmward relative to the surface front. Because catches are assigned to the surface positions of fishing vessels, aggregation near the subsurface front is recorded farther toward the warm side in the surface frontal coordinate system. This depth-dependent alignment, together with thermal habitat and productivity gradients, contributes to the observed warm-side displacement in squid catches. Purple arrows indicate the idealized ageostrophic secondary circulation associated with frontogenesis. Approximate horizontal and vertical scales are indicated for reference. Actual DVM depths and trajectories may vary across frontal conditions.

components: thermal habitat, prey-related productivity, and geometric amplification associated with frontal inclination.

Thermal conditions provide an important basis for squid aggregation within frontal zones. Catches were concentrated within a relatively narrow optimal SST range, and the probability of encountering this thermal habitat was highest near the frontal boundary. However, the optimal SST probability was relatively symmetrical across the front, with both flanks generally remaining within the tolerable thermal range. Thermal habitat therefore helps explain aggregation near fronts but cannot, by itself, fully account for the systematic warm-flank displacement.

Prey-related productivity may further contribute to the asymmetry. Fishing operations occurred in waters with higher surface chlorophyll-*a* concentrations than the simulated background locations, while background chlorophyll-*a* was approximately 15% higher on the warm flank than on the cold flank. This pattern is consistent with upwelling on the warm side of the front induced by frontogenesis, which can enhance nutrient supply and primary production (Hoskins, 1982; McWilliams, 2016; Nagai et al., 2008; Zhu et al., 2024). However, surface chlorophyll-*a* alone does not resolve production rates, zooplankton biomass, or prey availability for squid. The observed chlorophyll-*a* contrast therefore cannot be interpreted as a quantitative measure of the full trophic difference between the two frontal flanks, and its contribution cannot be separated from the other mechanisms using the available data.

Frontal inclination provides a complementary geometric mechanism. During nighttime fishing, neon flying squid ascend into the upper epipelagic layer, with approximately 50 m used here as a representative foraging and capture depth (Bower & Ichii, 2005; Murata, 1993). Thermal and trophic conditions may influence the catch distribution relative to the front within this layer: 56% of the catch remained on the warm side when referenced to the 50 m front. Because the frontal boundary is displaced warmward with depth, an aggregation near or slightly warmward of the 50 m front is represented farther toward the warm side when catches are assigned to vessel positions at the sea surface and analyzed relative to the surface SST front. The increase in the warm-side proportion from approximately 56% relative to the 50 m front to approximately 60% relative to the surface front is consistent with such geometric amplification. This difference does not quantitatively partition the mechanisms, but its direction supports an additional warmward contribution associated with frontal inclination.

The 100 and 300 m reference levels further demonstrate that flank classification depends on the depth at which the frontal boundary is defined. They are not interpreted as direct observations of a fixed migration trajectory or as evidence that squid respond behaviorally to a deep front. Instead, they show that a surface-defined frontal coordinate is not spatially invariant throughout the water column. The mechanism most directly relevant to nighttime fishing concerns the displacement between the surface SST front and the upper-ocean frontal position near the representative capture depth.

The relationship between frontal intensity and catch asymmetry likely reflects several concurrent processes. Intensified frontogenesis may steepen near-surface isotherms, reducing the horizontal displacement over a given vertical interval. At the same time, stronger SST fronts in our analysis had greater mean vertical influence depths, and a subset extended through representative squid DVM depths and to approximately 300 m or deeper. Greater vertical penetration may increase the range over which frontal structure and frontogenesis-related trophic processes overlap with squid habitat. The increasing warm-side displacement with SST-gradient strength may therefore reflect the combined effects of frontal steepness, vertical extent, and biological enhancement rather than frontal inclination alone. Because frontal slope and frontogenetic strain were not quantified separately within each SST-gradient class, this remains a physically consistent interpretation rather than a quantitative attribution.

These findings emphasize the importance of considering subsurface structure when interpreting fishery distributions relative to surface fronts. Surface fronts identify favorable thermal and productive environments, but their positions may differ from the frontal boundaries encountered by vertically migrating predators within the water column. Frontal geometry can therefore influence the apparent position of a subsurface biological aggregation in a surface-based coordinate system. Accounting for this depth dependence may improve interpretation of fishing-ground locations and fishery-dependent distributions in dynamic western boundary current systems.

Several limitations remain. The analyzed records represent fishing effort and catches rather than direct measurements of squid abundance, and catchability may vary with vessel behavior, fishing technology, environmental conditions, and squid behavior. The null model reduces biases associated with the broad spatial and temporal distribution of fishing effort but cannot eliminate all fishery-dependent sampling effects. The results should therefore be interpreted as distributions of habitat-associated fishing success.

The representative DVM depths are also not assumed to be fixed or identical across the two frontal flanks. Actual daytime and nighttime habitat depths may vary with light, oxygen, temperature, prey distribution, and other water-mass properties. The present data do not resolve individual horizontal movements during DVM. In our first-order interpretation, these movements are assumed to be small relative to the mean frontal displacement and variable in direction among individuals and frontal events, rather than producing a consistent warmward displacement in the long-term composite. Such movements may nevertheless alter individual trajectories and the quantitative magnitude of the geometric displacement. Finally, the association of squid with thermal and prey conditions at the depth-specific front remains inferential, whereas the depth-dependent frontal displacement is independently diagnosed from the three-dimensional temperature field. Direct tagging, acoustic surveys, and co-located biological and hydrographic observations are required to quantify actual migration pathways and separate the relative contributions of thermal habitat, trophic processes, and frontal geometry.

5. Conclusion

This study reveals a persistent warm-flank asymmetry in neon flying squid catches across mesoscale oceanic fronts in the KOE region. By combining long-term fishery observations with subsurface oceanographic data, we

show that this cross-frontal asymmetry reflects not only habitat conditions but also the depth-dependent structure of the frontal system.

The results indicate that thermal habitat, prey-related productivity, and frontal-inclination-induced geometric displacement jointly contribute to the warm-side catch asymmetry. At the representative nocturnal fishing depth, squid catches remain preferentially distributed on the warm side of the depth-specific front. Because this subsurface front is displaced warmward relative to its surface expression, the aggregation is represented farther toward the warm side when catches are recorded at sea-surface vessel positions and analyzed relative to the surface SST front. This geometric amplification provides a physical explanation for part of the surface-referenced displacement and operates together with, rather than instead of, thermal and trophic habitat processes. More broadly, these findings highlight the importance of considering subsurface ocean structure when interpreting spatial patterns of mobile predators and fishery-dependent observations in dynamic boundary current systems.

Inclusion in Global Research Statement

The fishery data used in this study were obtained from the fishing logbook records collected by the National Data Centre for Distant-water Fisheries of China at Shanghai Ocean University, under a formal data-sharing agreement. This research adheres to data collaboration protocols to ensure transparency and proper use of the data.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Availability Statement

Daily sea surface temperature (SST) data can be downloaded from the Operational Sea Surface Temperature and Ice Analysis (Donlon et al., 2012; Good et al., 2020; Stark et al., 2007). Chlorophyll-a concentrations data and GLORYS12V1 reanalysis product can be downloaded from the Copernicus Marine Service (Colella et al., 2024; Drévuillon et al., 2024). Squid catch data are available from the National Data Centre for Distant-water Fisheries of China at Shanghai Ocean University. Source data for figures and codes for the main methods are provided on Zenodo via Niu, Z. (2025).

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