Received: 21 January 2023 | Revised: 22 August 2023 | Accepted: 28 August 2023
DOI: 10.1111/faf.12791

ORIGINAL ARTICLE

FISH and FISHERIES WILEY

Dynamic human, oceanographic, and ecological factors mediate transboundary fishery overlap across the Pacific high seas

Timothy H. Frawley[1,2] | **Barbara Muhling**[1,3] | **Stephanie Brodie**[1,2] | **Hannah Blondin**[4] | **Heather Welch**[1,2] | **Martin C. Arostegui**[5] | **Steven J. Bograd**[1,2] | **Camrin D. Braun**[5] | **Megan A. Cimino**[1,2] | **Nima Farchadi**[6,7] | **Elliott L. Hazen**[1,2,4] | **Desiree Tommasi**[1,3] | **Michael Jacox**[1,2,8]

[1]Institute of Marine Science, University of California Santa Cruz, Santa Cruz, California, USA
[2]Environmental Research Division, NOAA Southwest Fisheries Science Center, Monterey, California, USA
[3]Fisheries Resources Division, NOAA Southwest Fisheries Science Center, San Diego, California, USA
[4]Hopkins Marine Station, Stanford University, Pacific Grove, California, USA
[5]Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA
[6]San Diego State University, San Diego, California, USA
[7]Graduate Group in Ecology, University of California, Davis, California, USA
[8]Physical Sciences Laboratory, NOAA Earth System Research Laboratories, Boulder, Colorado, USA

Correspondence
Timothy H. Frawley, Environmental Research Division, NOAA Southwest Fisheries Science Center, 99 Pacific Street, Suite 255A, Monterey, CA 93940, USA.
Email: tfrawley@ucsc.edu

Funding information
National Oceanic and Atmospheric Administration, Grant/Award Number: NA17OAR431026, NA20OAR4310507 and NA20OAR4320278; NASA Earth Science Research Program, Grant/Award Number: 80NSSC19K0187

Abstract

The management and conservation of tuna and other transboundary marine species have to date been limited by an incomplete understanding of the oceanographic, ecological and socioeconomic factors mediating fishery overlap and interactions, and how these factors vary across expansive, open ocean habitats. Despite advances in fisheries monitoring and biologging technology, few attempts have been made to conduct integrated ecological analyses at basin scales relevant to pelagic fisheries and the highly migratory species they target. Here, we use vessel tracking data, archival tags, observer records, and machine learning to examine inter- and intra-annual variability in fisheries overlap (2013–2020) of five pelagic longline fishing fleets with North Pacific albacore tuna (*Thunnus alalunga*, Scombridae). Although progressive declines in catch and biomass have been observed over the past several decades, the North Pacific albacore is one of the only Pacific tuna stocks primarily targeted by pelagic longlines not currently listed as overfished or experiencing overfishing. We find that fishery overlap varies significantly across time and space as mediated by (1) differences in habitat preferences between juvenile and adult albacore; (2) variation of oceanographic features known to aggregate pelagic biomass; and (3) the different spatial niches targeted by shallow-set and deep-set longline fishing gear. These findings may have significant implications for stock assessment in this and other transboundary fishery systems, particularly the reliance on fishery-dependent data to index abundance. Indeed, we argue that additional consideration of how overlap, catchability, and size selectivity parameters vary over time and space may be required to ensure the development of robust, equitable, and climate-resilient harvest control rules.

KEYWORDS
albacore tuna, dynamic ocean management, fisheries overlap, North Pacific transition zone, pelagic longlines, stock assessment

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1 | INTRODUCTION

Managing the demands of human activities and biodiversity conservation remains a central challenge for ocean governance, due in part to the dynamic spatial and temporal nature of ocean systems (Halpern et al., 2008; Lewison et al., 2015). Many marine taxa, and large pelagic predators in particular, undertake extensive feeding and reproductive migrations driven by dynamic oceanographic processes, species-specific thermal tolerances and shifts in prey distribution (Block et al., 2011). Marine fisheries are likewise variable across time and space as harvesters respond to seasonal and interannual shifts in ocean conditions (Frawley, Blondin, et al., 2021; Ortuño Crespo et al., 2018; Watson et al., 2018), changes in animal abundance (Pinsky et al., 2021; Rogers et al., 2019), management regulations (Frawley, Muhling, et al., 2021; Gonzalez-Mon et al., 2021), and other socioeconomic factors (Barnes et al., 2016; Kroodsma et al., 2018). Understanding how fisheries interactions with target and non-target species vary over space and time is increasingly recognized as an essential component of sustainable and equitable ecosystem management (Cadrin & Secor, 2009; Hazen et al., 2018). Yet, scientific understanding of the intertwined human and natural processes mediating fisheries interactions across time and space remains limited, particularly when extractive activities are concentrated on the high seas in areas beyond national jurisdiction.

Pacific Ocean tuna and billfish fisheries, including both industrial high-seas fishing operations and small-scale domestic and subsistence sectors, represent ~70% of the global commercial catch of these species (Moore et al., 2020). Operating over large areas that often span multiple jurisdictions and geopolitical boundaries, these fisheries function as an important source of food and trade income for both developed and developing countries (McCluney et al., 2019). As many coastal fish stocks have declined due to overfishing and habitat degradation, pelagic species are an increasingly important source of livelihoods and revenue (Bell et al., 2018), particularly across Pacific Island Countries and Territories where tuna fishing and processing industries may represent a substantial proportion of the total gross domestic product. Despite their economic and cultural importance, considerable uncertainty persists regarding the distribution and biology of many pelagic fish species, including the nature and extent to which they interact with different fishing fleets and gear types (Frawley et al., 2022), and the degree to which such patterns and processes are impacted by environmental variability. Indeed, there is growing concern that climate-driven changes in the distribution and abundance of pelagic organisms may disrupt sustainable resource management and negatively impact developing ocean economies (Bell et al., 2021; Pinsky et al., 2018).

Given the magnitude and extent of such anticipated impacts, an improved understanding of the physical, environmental, and socioeconomic factors that aggregate pelagic marine resources and fishing efforts and mediate their interactions is urgently needed to ensure accurate assessments of stock status and promote the design

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of equitable and effective harvest control strategies (Miller, 2007). Although the use of real-time information to mitigate fisheries by-catch (Howell et al., 2008; O'Keefe & DeCelles, 2013) and other human-wildlife risks (Blondin et al., 2020) continues to gain traction, limited effort has been made to employ "dynamic ocean management" to determine target catch and allocate quota. Among those examples that do exist, most rely upon in-season genetic analysis (Beacham et al., 2004) and biological sampling (Needle & Catarino, 2011) rather than environmental and socioeconomic data (Lewison et al., 2015).

Here, we use the North Pacific albacore (*Thunnus alalunga*, Scombridae), one of the only Pacific tuna stocks primarily targeted by longline fishing gear that is not listed as overfished or experiencing overfishing (ISSF, 2022), as a test case to examine how seasonal and interannual oceanographic variability mediate overlap between different longline fishing fleets, gear types and albacore life history stages. Building on previous work describing the global environmental niche of pelagic longline fishing vessels (Frawley et al., 2022; Ortuño Crespo et al., 2018) and the habitat associations (Lee et al., 2020; Muhling et al., 2019) and migratory strategies (Childers et al., 2011; Muhling et al., 2022) of the North Pacific albacore, we (1) identify and describe the spatial and environmental drivers influencing the distribution of different fishing fleets and albacore life stages; (2) quantify changes in spatial niche overlap between each fishing fleet and albacore life stage within and between years; and (3) explore how spatial overlap and fishery interactions may be mediated by different configurations of longline fishing gear. While previous research has identified static areas of overlap between different species and gear types (Guy et al., 2013; White et al., 2019), our analysis highlights the utility of dynamic models to identify underlying social–ecological processes and obtain mechanistic insight.

2 | STUDY SYSTEM

2.1 | Physical oceanographic context

Several characteristics of North Pacific oceanography are important for contextualizing movements of highly migratory species in the region and the fisheries that target them (Figure 1). Along the western boundary, the Kuroshio current transports warm nutrient-rich water to the north, generating an intense eddy field (Ji et al., 2018; Qiu, 2019) that influences the distribution and concentration of pelagic organisms (Durán Gómez et al., 2020; Morioka et al., 2019; Seki et al., 2002). At the eastern boundary lies the California Current with southward flowing, cooler waters, and seasonal (spring/summer) coastal upwelling that supports a productive marine food web (Checkley Jr & Barth, 2009). The eastward-flowing North Pacific Current forms a boundary between nutrient-rich subpolar waters and nutrient-poor subtropical waters, which coincides with a strong chlorophyll gradient known as the transition zone chlorophyll front (TZCF). The TZCF influences the distribution of pelagic predators and associated forage across the North Pacific high seas (Polovina et al., 2001, 2017), and its position can vary seasonally by over 1000 km (from ~30 to 50° N). Bounded by these major currents, the oligotrophic North Pacific Subtropical Gyre is an energetically quiescent biome in which mesoscale anticyclonic eddies may act as ecological hotspots by maximizing foraging opportunities for pelagic predators (Arostegui et al., 2022).

2.2 | North Pacific albacore biology, ecology, and life history

Albacore tuna is a highly migratory species distributed in temperate and tropical waters across the globe. The spatial distribution and migratory behavior of the species change with ontogeny: juveniles associate with productive, temperate ecosystems, and adults are more common in warmer, subtropical waters (Childers et al., 2011; Farley et al., 2014; Nikolic et al., 2017). In the North Pacific, albacore spawning has been reported in subtropical waters between the Philippines and Hawai'i where sea surface temperatures exceed 22–24°C (Ashida et al., 2020; Reglero et al., 2014). Tagging data show that immature juveniles undertake extensive foraging migrations between the offshore North Pacific and productive areas of the California and Kuroshio Currents, with the ability to traverse the North Pacific basin within a single season (Childers et al., 2011; Muhling et al., 2022). Size and age at maturity are variable, with mature fish reported as small as 74 cm fork length, immature fish as large as 98 cm fork length, and length at 50% maturity 87–88 cm (Ashida et al., 2020). Although vertical habitat use by adults is less well-documented than for juveniles, existing work suggests that adult albacore may forage at depth and are often found deeper in the water column as compared to juveniles (Chen et al., 2010; Domokos et al., 2007; Nikolic et al., 2017).

2.3 | Fishery interactions

Across the North Pacific, albacore are primarily harvested using troll and pole-and-line fishing gears (which target juveniles in surface waters) and pelagic longlines (which fish at depths of 25–400 m; Figure 1). In addition to differences in size selectivity between fishing gears, ontogenetic differences in movement patterns and vertical behavior result in different age classes being retained by fisheries using the same gear but operating in different seasons and/or areas. Juvenile albacore are predominantly landed by the USA and Canadian surface fisheries operating in the California Current in the summer and fall, in addition to the Japanese pole-and-line fleet, which fishes western Pacific waters from late spring to early fall (Kiyofuji, 2013). In contrast, longline vessels generally operate farther south and catch larger and older fish, though size composition varies substantially across fishing fleets (International Scientific Committee (ISC) for Tuna and Tuna-like Species in the North Pacific Ocean, 2020; Figure 1). The majority

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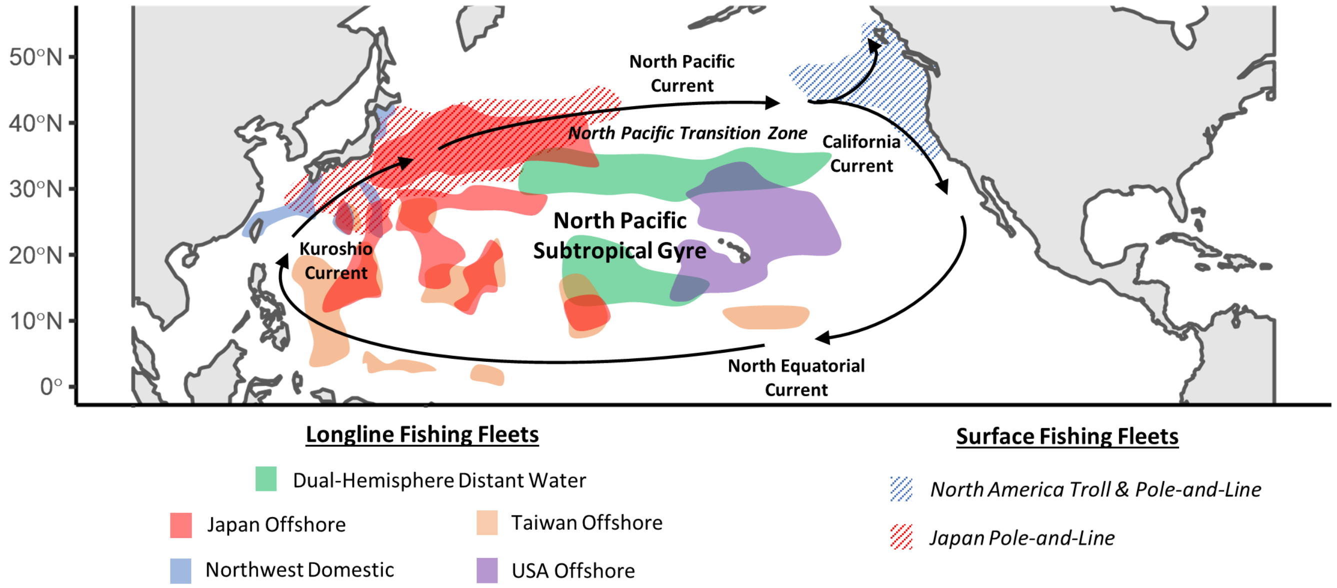

FIGURE 1 Study map indicating the focal fishing grounds of the primary fleets that overlap with known North Pacific albacore distribution. The longline fleets (which are the focus of this analysis) are depicted in solid colors. Their approximate fishing areas were determined by the methodology described by Frawley et al. (2022), which considered AIS observations between 2017–2019. Major surface fishing fleets interacting with North Pacific albacore (not explicitly modeled in this study) are depicted in dashed colors. The area extent of the North America Troll & Pole- and -Line fishery was based on 2010–2016 data described by Frawley, Muhling, et al. (2021), while the area extent of the Japanese Pole-and-Line fishery was based on 2010–2018 data as described by Matsubara et al. (2019).

of longline albacore catch has historically been by Japanese, Taiwanese, and USA fishing fleets, though in recent years landings by Chinese and Vanuatuan vessels have increased (International Scientific Committee (ISC) for Tuna and Tuna-like Species in the North Pacific Ocean, 2020).

Identifying fishing fleets based on flag state and gear type alone may obscure operational distinctions that structure the nature and extent of high-seas pelagic longline fishing activity. Here, we consider five functional fishing fleets as defined by Frawley et al., 2022. Principal North Pacific pelagic longline fleets (as observed using AIS technology) are differentiated into (1) the Dual-Hemisphere Distant Water fishing fleet, which targets albacore and is primarily composed of Taiwanese and Vanuatuan flagged vessels; (2) the Japan Offshore fleet, a diverse and predominantly Japanese flagged offshore fleet that may switch targets seasonally between adult bigeye (*Thunnus obesus*, Scombridae), yellowfin (*Thunnus albacares*, Scombridae), and albacore tunas (using deep-set longline fishing gear) and swordfish (*Xiphias gladius*, Xiphiidae) and blue shark (*Prionace glauca*, Carcharhinidae) (using shallow-set longline fishing gear); (3) the Northwest Domestic coastal longline fleet of primarily Japanese-flagged vessels that seasonally targets juvenile albacore in waters off the southeast and southwest coast of Japan from January to March (Ijima & Satoh, 2014; Satoh et al., 2013); (4) the Taiwan Offshore fleet, that harvests bigeye and yellowfin tuna in tropical waters (Sun & Yeh, 2000; Williams & Ruaia, 2020), and has increasingly begun landing albacore of unknown size-age classes in the past decade as market and fishery dynamics have shifted (Campling et al., 2017; WCPFC, 2019); and (5) the USA Offshore fleet comprised of vessels using both shallow-set (swordfish targeting) and deep-set (bigeye targeting) gear types (Teo, 2017; Woodworth-Jefcoats et al., 2017). The majority of the USA Offshore fleet's operations are confined to the North Pacific where juvenile and adult albacore may be landed as non-target species, though a small number of vessels travel seasonally to the South Pacific, joining a domestic fleet based out of American Samoa, where deep-set gear is used to target adult albacore.

2.4 | Management & stock assessment context

The North Pacific Albacore stock is considered healthy and not subject to overfishing, but progressive declines in catch and stock biomass have been observed over the past several decades (International Scientific Committee (ISC) for Tuna and Tuna-like Species in the North Pacific Ocean, 2020) as fishing fleets have consolidated and modernized. From 1994 to 2018, surface fisheries reported approximately 56% of the total North Pacific albacore catch (International Scientific Committee (ISC) for Tuna and Tuna-like Species in the North Pacific Ocean, 2020). However, as surface fleets target younger fish that have not had the chance to spawn, their impact on the spawning stock biomass is inferred to be twice that of longline fisheries (International Scientific Committee (ISC) for Tuna and Tuna-like Species in the North Pacific Ocean, 2020). While the stock assessment does endeavor to capture heterogeneity in fleet selectivity within and between gear types, flag states, and fishing areas using an "areas-as-fleets" approach, persistent uncertainty remains regarding (1) the accuracy and completeness of underlying catch (Heidrich et al., 2022; Kiyofuji, 2020) and observer data upon

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which such designations are based and (2) how fisheries length (i.e., age-class) selectivity parameters may vary within them over time and space based on fine-scale operational heterogeneity. Although the use of AIS and VMS vessel monitoring technology is increasingly mandated for fishing fleets targeting pelagic resources managed by international agreements (Emery et al., 2018), to-date efforts to incorporate such data into the development of harvest strategies and/or audit the accuracy and completeness of associated catch and effort reports and/or biological sampling records has been limited.

3 | METHODS

3.1 | Summary

To quantify spatiotemporal variation in North Pacific albacore tuna overlap with pelagic longline fisheries, we relied on a holistic approach that integrated AIS vessel tracking data, physical and oceanographic measurements, archival tag data, and fisheries observer reports (Figure 2). Briefly, AIS (2017–2019), archival tag (2001–2015), and shallow- and deep-set fisheries observer data (1994–2019) were first analyzed independently to identify and describe different fishing fleets and albacore size-age classes. Machine learning techniques (Boosted Regression Trees) were then used to quantify the environmental associations of five fishing fleets and two albacore life stages and predict their daily distribution across North Pacific waters between 2013 and 2020. Finally, co-occurrence of juvenile and adult albacore and the five fishing fleets was quantified using a spatial overlap metric (Schoener's Index (*D*)). Additional details and descriptions are provided in each of the subsections below and the Supplemental Methods.

3.2 | Physical and oceanographic data

Environmental variables used to fit vessel and species distribution models were sourced for 1994–2020 from observation- and model-based products (Table S1) served through the Copernicus Marine Environmental Monitoring Service. Environmental variables chosen for inclusion have previously been identified as being important in describing the physiological and ecological requirements of highly mobile marine predators (Brodie et al., 2018; Muhling et al., 2019), and the fishing fleets that target these species (Ortuño Crespo et al., 2018). These included absolute dynamic topography (ADT), primary productivity averaged across the upper 200 m of the water column, dissolved oxygen at 200 m depth, sea surface temperature (SST) and its spatial standard deviation (SST_sd), sea level height anomaly (SLA), eddy kinetic energy (EKE), mixed layer depth (MLD), surface chlorophyll-a concentration, and lunar illumination. Chlorophyll-a and EKE were log10 transformed to account for right-skewed distributions. Daily EKE was calculated from the meridional and zonal components of geostrophic velocity anomalies. Static environmental variables included bathymetric depth and its standard deviation (termed rugosity) and distance to shore. Daily environmental data corresponding to species and vessel locations were extracted, with data averaged over a circle with a 1.25° diameter (i.e., 5 × native 0.25° resolution) to encompass albacore archival tag error (Braun et al., 2018) and to represent the broad spatial extent of individual pelagic longline sets. Vessels in USA pelagic longline fisheries typically set mainlines of 65–75 km length (Bigelow et al., 2006), and the gear can drift substantially between deployment and recovery.

3.3 | Biological data

We used data from archival tags implanted in 25 juvenile albacore to build a Vertical Behavior Model (VBM; see below) and a juvenile Species Distribution Model (SDM; see below). Comprehensive descriptions of archival tagging data collection and processing procedures are provided in the Supplemental Methods in Appendix S1. In brief, 25 archival tags from albacore tagged off the US West Coast and Baja California between October 2001 and September 2015 yielded 10,243 days of data. Fish were between 63.5 and 89.9 cm straight fork length at release and were at large between 62 and 1034 days. Tagged albacore were highly migratory, with movements spanning the international dateline and fish occupying habitats across most of the temperate North Pacific during tag deployment (Muhling et al., 2022). These horizontal movements are consistent with the limited tagging data that exist from albacore tuna sampled in the Western Pacific Ocean (Kiyofuji et al., 2013). The most probable tracks of the albacore fitted with our archival tags were constructed using the HMMoce package (Braun et al., 2018; see Supplemental Methods in Appendix S1).

We used fishery-dependent observer records from the USA pelagic longline fishery to build an adult SDM. Hawai'i-based pelagic longline vessels primarily target swordfish, bigeye tuna, and yellowfin tuna, but may also catch albacore (Cooper et al., 2022). A small number of vessels also travel seasonally to American Samoa to target the South Pacific albacore alongside USA-flagged vessels based out of American Samoa. We obtained observer records for Hawai'i-based vessels for 1994–2019, and American Samoa-based vessels for 2006–2019 from the NOAA Pacific Islands Fisheries Science Center. We used observer records from both the North and South Pacific to train the adult SDM in order to best capture the impact of both environmental and gear configuration variables on albacore presence and ensure sampling over a broad range of environmental conditions (Karp et al., 2023). Vessel distribution analyses of USA-flagged vessels were subsequently constrained to the Hawai'i-based fleet primarily operating in the North Pacific (i.e., the USA offshore fleet), as justified by our focus on the North Pacific albacore resource (i.e., the activities of American Samoa-based fishing vessels were not modeled explicitly).

3.4 | Modeling

Below we present information relevant to the construction of Vertical Behavior Models (VBMs), juvenile and adult albacore Species Distribution Models (SDMs), and Vessel Distribution Models

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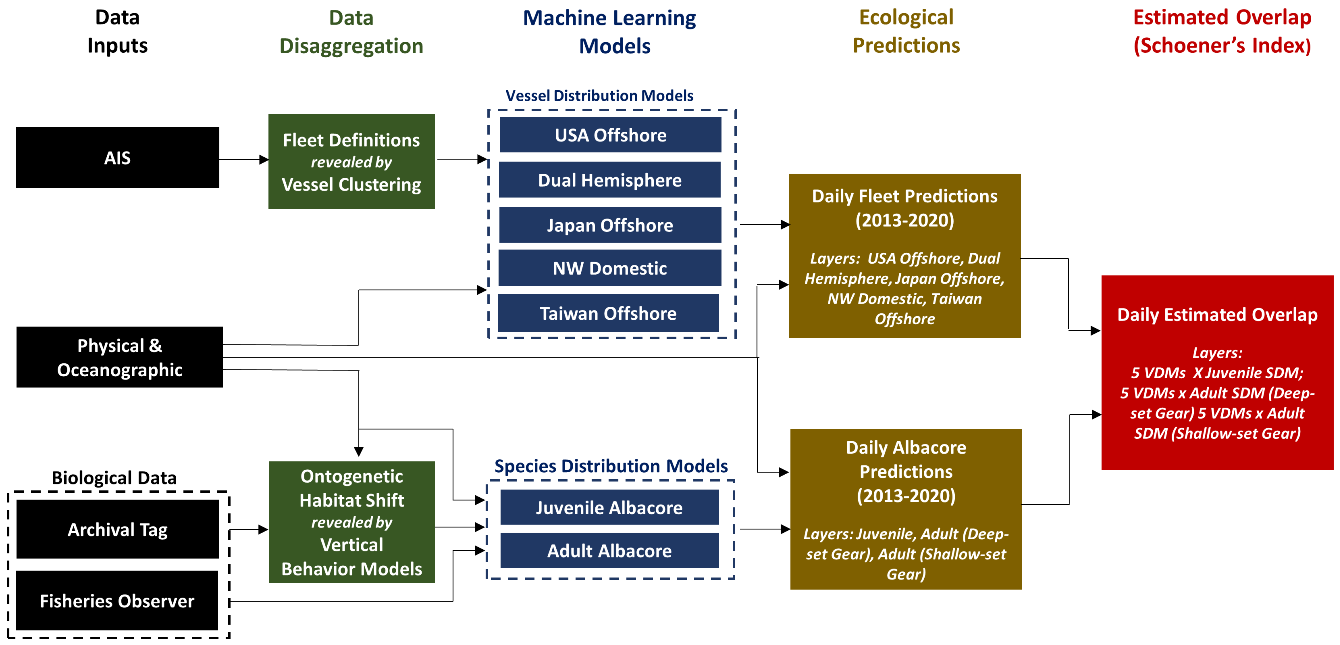

FIGURE 2 Schematic of datasets and workflow used to conduct the analyses presented in this study.

(VDMs). Although such terms are often used interchangeably in the literature, in this analysis, we refer to the predictive outputs of models constructed using pseudo-absences (i.e., VBMs, VDMs and the juvenile SDM) as "habitat suitability" and the predictive output of models constructed incorporating true absences (i.e., the adult albacore SDM) as "probability of occurrence."

3.4.1 | Vertical behavior models

In constructing VBMs designed to empirically quantify the difference in albacore tuna habitat associations by life history stage, we used archival tag data to (1) characterize the effect of environmental, ontogenetic, and diel factors on albacore vertical behavior and (2) assess the length at which tagged albacore changed from displaying surface-oriented juvenile behaviors to deeper, more adult-like behavior. VBMs were built using Bayesian Additive Regression Trees (BARTs) in the *embarcadero* package (Carlson, 2020). The BART formulation is Bayesian and applies priors to shape the posterior probability of models. BARTs are far more computationally intensive than other tree-based models such as Boosted Regression Trees (BRTs) but have the advantage of providing estimates of statistical uncertainty (Carlson, 2020). As previous work has shown a strong effect of time of day on albacore vertical behaviors (Cosgrove et al., 2014; Muhling et al., 2022), we built separate BART models to predict daytime and nighttime mean depths. Day and night at tagged fish locations were delineated using nautical dusk and dawn and calculated using the *suncalc* package (Thieurmel et al., 2019). Environmental predictors were similar to those used for the SDMs (see below), with the addition of lunar illumination, and estimated fish length (Table S2). We estimated the daily fork length of each tagged albacore using recorded lengths at release and recapture and the number of days at large, assuming linear growth rates (based on Xu et al., 2016; see Muhling et al., 2022 for more details). Both the daytime and nighttime models incorporated fish of all sizes available in the tagging dataset (63.5–103 cm FL). Model fit and suitability was assessed using R^2 against withheld testing data.

3.4.2 | Species distribution models

The juvenile albacore SDM was trained using daily locations from archival tag data. Based on the results from the VBMs (Figure S1), we only included dates and locations where fish were estimated to be juveniles (≤92 cm FL; see Supplemental Methods in Appendix S1). We generated background pseudo-absences to allow the use of a binomial SDM. These pseudo-absences were randomly located within a convex hull encompassing all juvenile tag locations and generated using the *grDevices* and *sp* packages in R (Pebesma & Bivand, 2005; R Core Team, 2021). We extracted relevant environmental predictors (as described in Table 1; Table S1) and removed variables that had high multicollinearity (see Supplemental Methods in Appendix S1). SDMs predicting the probability of albacore presence were built using BRTs with a Bernoulli family (Brodie et al., 2018). A randomly selected 50% of the available data was used for model training, and model fit was assessed using the withheld 50% (test) dataset. The skill of the juvenile SDM was quantified via the Area Under the Receiver Operating Characteristic (ROC) curve (AUC) and assessed favorably against withheld test data (AUC = 0.91). Predictions from the juvenile SDM were additionally validated by comparison with publicly available albacore catch and effort data from the Japanese pole-and-line fishing fleet operating in the Western Pacific (Figure S2) as well as

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TABLE 1 Physical and environmental predictors for species distribution models and vessel distribution models.

Variable	Juvenile SDM	Adult SDM	D.H. D.W. (Fleet1001) VDM	Japan offshore (Fleet1003) VDM	N.W. domestic (Fleet1004) VDM	Taiwan offshore (Fleet1008) VDM	USA offshore (Fleet1010) VDM
Absolute dynamic topography (ADT)	**10.11**	**8.72**	1.92	9.66	3.82	10.53	**14.25**
Sea surface temperature (SST)	**35.78**	**46.74**	**58.25**	**18.30**	1.33	**23.27**	11.84
Bottom depth	**20.56**	2.13	3.05	5.3	**13.33**	4.38	4.86
Sea level height anomaly (SLA)	4.50	4.55	0.39	8.33	0.17	2.49	0.08
Mixed layer depth	5.06	1.97	**20.31**	1.00	0.46	0.09	0.27
Eddy kinetic energy	4.27	0.94	0.31	5.53	0.57	1.52	0.14
Log (surface chlorophyll)	5.22	2.52	2.28	6.28	0.45	4.74	0.59
Rugosity	4.26	2.5	0.67	0.55	3.20	0.38	0.25
Dissolved oxygen at 200 m	NA	**19.35**	2.11	**15.61**	**20.17**	**17.43**	2.57
Primary productivity (Upper 200 m)	6.09	1.47	3.81	8.83	1.04	5.25	**35.78**
Standard deviation of SST	4.17	1.18	0.13	1.34	0.12	0.16	0.21
Hooks between floats	NA	2.64	NA	NA	NA	NA	NA
Floatline length	NA	3.22	NA	NA	NA	NA	NA
Total hooks per set	NA	2.07	NA	NA	NA	NA	NA
Distance to shore	NA	NA	**6.79**	**19.27**	**55.31**	**29.76**	**29.15**

Note: Relative predictor importance (% importance to the model) is shown, with three most influential variables for each model bolded.

previously published information regarding the spatial distribution and movement patterns of juvenile albacore tuna across the North Pacific (Kiyofuji et al., 2013; Ochi et al., 2016; Snyder, 2016).

The adult albacore SDM was trained on the fishery-dependent data (Braun et al., 2023; Karp et al., 2023; Pennino et al., 2016), with comprehensive details provided in the Supplemental Methods in Appendix S1. Briefly, presence was defined as sets in the Pelagic Observer Program database where at least one albacore >92 cm fork length was measured and recorded. Absence was defined as sets where no albacores were recorded. Of the 82,405 sets total, 15,211 sets (18.4%) contained at least one adult albacore. We used similar environmental predictors for the adult SDM as for the juvenile SDM, with some modifications (Table 1; Table S1). Dissolved oxygen at 200 m was included as a predictor in the adult SDM, as it was not strongly collinear with any other variables across the spatial extent of the training data. To capture heterogeneity in fishing operations related to variable species targeting and to help reduce the influence of these biases in the analysis (see Supplemental Methods in Appendix S1), we also included three predictors describing gear configurations (as documented in observer records): the number of hooks between floats, the number of total hooks per set, and the length of the floatline on each set (Table 1). As with the juvenile SDM, the adult SDM showed good skill against withheld test data (AUC = 0.89). Predictions from the adult SDM were additionally validated using publicly available catch and effort data from the Japanese longline fishing fleet operating in the Western Pacific (Figure S3), as well as previously published information concerning the known distribution of albacore larvae (a proxy for the presence of mature adults) in the North Pacific (Reglero et al., 2014), and fisheries committee reports documenting the latitudinal barriers demarcating the division between adult and juvenile albacore habitat (Chen et al., 2010; Ochi et al., 2016).

Environmental data where juvenile and adult albacore presences were sampled was subsequently compared with values obtained from across the entire North Pacific to confirm that environmental extrapolation was limited for important model covariates (Figure S4). Following model validation, both BRT SDMs were used to produce daily estimates of the probability of juvenile and adult albacore occurrence across the North Pacific. Although we explored the use of the BART framework and associated confidence intervals (Section 3.4) in the construction and projection of juvenile and adult albacore SDMs and the VDMs, ultimately BARTs proved challenging to operationalize due to code dependencies and computational expense.

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3.4.3 | Vessel distribution models

Five VDMs were constructed for functional longline fishing fleets operating in the North Pacific. Although the North Pacific albacore is also targeted by fishing fleets using troll and pole-and-line fishing gear (Figure 1), we were not able to model these fleets due to the limited usage of AIS technology among these small-boat (i.e., <24 m) operators (Taconet et al., 2019). Functional longline fleets were defined by Frawley et al. (2022) on the basis of the seasonal center of gravities, vessel characteristics (i.e., length and tonnage), inertia (i.e., range), exclusive economic zone (EEZ) behavior (i.e., the proportion of fishing time spent fishing in sovereign or territorial waters vs. foreign waters vs. the high seas), and estimated species overlap (i.e., co-occurrence in time in space with gridded catch totals reported by RFMOs). Additional details are provided in the Supplemental Methods in Appendix S1. Daily vessel location data used to build VDMs were obtained from a public database maintained by Global Fishing Watch (Kroodsma et al., 2018). VDMs were fitted using BRTs with a Bernoulli family using data from 2017 to 2019, which are the same years used for fleet identification in Frawley et al. (2022). Pseudo-absences were generated using random background selection (Hazen et al., 2021) at a 1:1 ratio of presence to pseudo-absence (Barbet-Massin et al., 2012) within the fleet-specific convex hull polygons based on vessel location datasets. VDMs were cross-validated and assessed using AUC and True Skill Statistic (TSS). VDMs were well fit (range of explained deviance: 35%–72%) and showed very good predictive performance (range of AUC: 0.87–0.98; range of TSS: 0.56–0.86; Table S3). Fishing ground suitability was then predicted for every day from 2013 to 2020. Predictions of fleet presence in out-of-sample years (2013–2016 and 2020) looked similar to fitted years (2017–2019), with the highest error seen in the Japan Offshore and Taiwan Offshore fleets (Supplemental Methods in Appendix S1; Figure S5).

3.5 | Spatial niche similarity analysis

Daily juvenile habitat suitability, adult albacore probability of occurrence, and fishing ground suitability for the five pelagic longline fishing fleets were predicted for every day from 2013 to 2020. These years represent the maximum period of overlap between datasets. To examine how gear usage might impact niche similarity, we considered two sets of adult albacore predictions: one generated using gear values typical of a deep-set targeting bigeye tuna (2100 hooks per set, 25 hooks between floats, floatline length of 22 m), and one generated using gear values typical of a shallow set targeting swordfish (1000 hooks per set, 5 hooks between floats, floatline length of 8 m). This approach was inspired by previously published research (Ward & Myers, 2005), which pooled data from across the Pacific to characterize bigeye and swordfish targeting operations as representative archetypes while comparing catchability and species interactions between daytime deep-set longline fishing activity (targeting bigeye) and nighttime shallow-set longline fishing activity (targeting swordfish).

To focus on core distribution areas for both albacore and fishing fleets, model predictions were subset using model-specific thresholds (Liu et al., 2013; van Beest et al., 2021), determined as the value where the sum specificity and sensitivity for each model were maximized (i.e., the Max *SSS* statistic, see Liu et al., 2013). Albacore predictions were additionally cropped to only retain data in the North Pacific Ocean (>0° N). We then quantified the spatial association between VDMs and SDMs for each day using Schoener's D Overlap Index. This index measures equivalency between the spatial niches occupied by two populations (Schoener, 1970) using the following equation:

$$D = 1 - 0.5 * \sum_{i}^{n} \mid p(\text{fleet})_i - p(\text{albacore})_i \mid$$

where $p(\text{fleet})_i$ and $p(\text{albacore})_i$ are the probabilities of occurrence of a fleet and albacore in grid cell i on a given day, divided by the sum of probabilities across all grid cells on that day. This metric was chosen due to its appropriateness for assessing the overlap between the modeled probability of occurrences and/or habitat suitability (Carroll et al., 2019) and utility in quantifying climate-driven changes (Thorson et al., 2021; van Beest et al., 2021). To assess changes in SDM/VDM overlap over time, monthly anomalies were calculated by subtracting the monthly climatology of overlap (monthly mean from 2013 to 2020) from the mean overlap observed in a given month each year. To assess changes in relative overlap by age-class, we subtracted the overlap value associated with the juvenile albacore habitat model from the overlap value associated with the deep-set configuration of the adult habitat model, and then calculated difference anomalies following the procedure described above. Summary overlap statistics were calculated using the average of all mean monthly overlaps (i.e., mean overlap), the standard deviation of all monthly climatological values (i.e., seasonal variation), and the standard deviation of all monthly overlap anomalies (i.e., interannual variation).

4 | RESULTS

4.1 | Ontogenetic habitat shift revealed by fisheries dependent and archival tag data

US fisheries observer data revealed that variation in habitat use, and fisheries interactions are mediated by gear type and fish size-age class (Figure 3a). Large albacore tuna were most commonly caught in the deep-set longline fishery, where hook depths are typically between 35 and 400 m, fishing waters to the south and west of Hawai'i. Albacore of intermediate size was more commonly observed interacting with shallow-set gear, fishing at depths between 30 and 90 m, in waters further north and east. The smallest juvenile albacore interacting with US fisheries are those targeted by surface troll and pole-and-line fisheries operating out of ports on the US West Coast. VBMs, constructed using data from 25 archival tag

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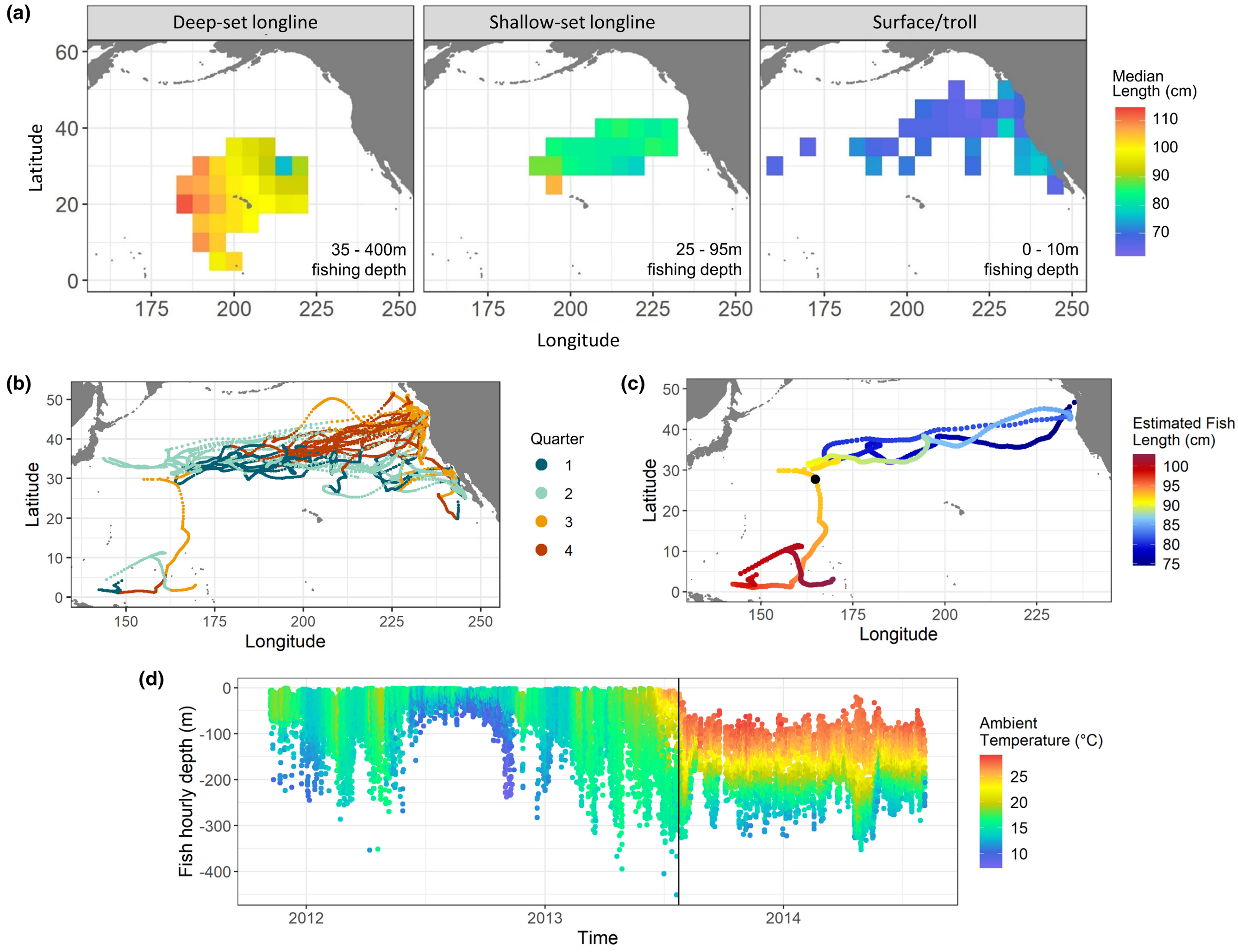

FIGURE 3 (a) Spatial distribution of median length of albacore landed with deep-set longline, shallow-set longline, and troll (i.e., surface) fishing gear. Lengths of fish caught by surface gear are sampled at US and Canadian ports when fish are landed (Childers, 2001), whereas lengths from longline catches are recorded by fisheries observers. Longline gear depths are from Bigelow et al. (2006) and Woodworth-Jefcoats et al. (2018). (b) Daily locations (color-coded by season) of 25 albacore tagged with archival tags. (c) Daily locations for a tagged albacore released as a 74.5 cm juvenile on October 8th, 2011 and recaptured as a 103 cm adult on August 7th, 2014. (d) Hourly fish depth and ambient temperature for the same fish, showing estimated length. The approximate date of transition from surface-based juvenile behavior to subsurface adult behavior is indicated by the black dot in (c) and the black vertical line in (d).

tracks that spanned the international dateline (Figure 3b), suggest that during the daytime, the vertical distribution of albacore was best predicted by fish size and absolute dynamic topography (ADT; Table S2). Overall, larger fish spent more time deeper in the water column than smaller juveniles and all size classes of albacore occupied much deeper depths in the water column during the day than during the night. The transition from shallow juvenile to deep adult behavior was predicted to occur at ~90–95 cm FL (Figure S1). An example track from a tagged albacore at large for nearly 3 years shows this ontogenetic transition clearly, with a distinct change in behavior and habitat occupied around July 2013, when the fish was likely 92–93 cm in length (Figure 3c,d). Albacore tuna were also located deeper in the water column in regions of high ADT, where waters are warm to greater depths, such as in the western subtropical Pacific. During the night, the moon phase was also an important predictor of fish depth, with both adults and juveniles moving deeper during the full moon. Vertical behavior models for both daytime and nighttime showed good skill against withheld test data ($R^2 = .76$ and .73, respectively).

4.2 | Differences in predicted habitat use by life history stage

Stage-specific SDMs showed that juvenile albacores were more strongly associated with temperate latitudes, while adults were more common in subtropical environments in the western North Pacific, with each life stage showing distinct seasonal movements (Figure 4). Juvenile habitat was concentrated in the California Current System during the summer and fall before shifting offshore

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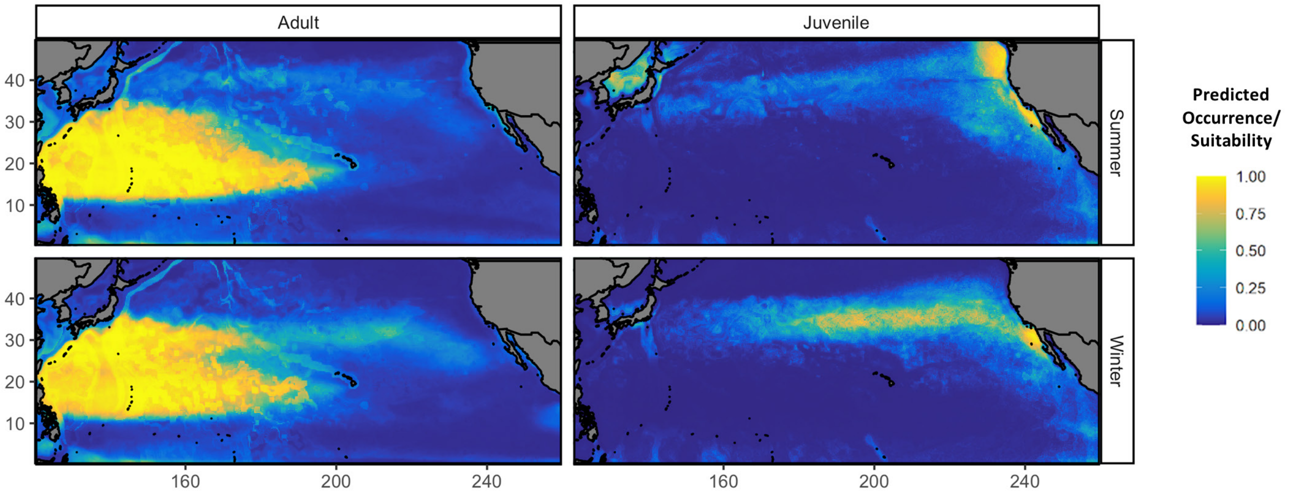

FIGURE 4 Seasonal predictions of adult albacore probability of occurrence and juvenile albacore habitat suitability in the North Pacific during the summer (Jun–Aug) and winter (Dec–Feb) months. The adult albacore predictions are for a deep-set longline gear configuration. Predictions for spring and fall are in Figure S6.

and entering the Kuroshio Current (on the western boundary) in the spring. Adult habitat was most concentrated in tropical and subtropical latitudes in the Western Pacific year-round, with a band of elevated probability expanding north to ~40° N during the summer and fall months, before receding to ~30° N in the winter and spring. The limited area of favorable habitat predicted by the juvenile model as compared to the adult model can be attributed to the strength of juveniles' association with a narrower range of temperate foraging grounds. ADT and SST were important to both SDMs (Table 1), but the partial responses differed (Figure S7A). Juvenile habitat suitability was strongly influenced by SST, peaking between 16 and 18°C. In contrast, the adult probability of occurrence was moderate between 16 and 24°C, with a second larger peak at temperatures >28°C (Figure S7A). Adult albacore were most prevalent where ADT was highest (i.e., in the subtropical western North Pacific), while juvenile albacores were recorded in waters with moderate to high ADT values (>0.5 m) in more temperate regions south of cooler sub-arctic waters where ADT is the lowest.

4.3 | Spatiotemporal variability in pelagic longline fishing grounds

VDMs for five North Pacific longline fishing fleets revealed distinct environmental preferences that influenced fishing ground suitability. Six covariates were among the top 3 most influential variables across the five fleets (Table 1): distance to shore (influential in all 5 fleet models), SST (3 out of 5 models), oxygen concentration (3 out of 5 models), primary productivity (1 out of 5 models), ADT (1 out of 5 models), and bottom depth (1 out of 5 models). Spatial and temporal dynamics of fishing ground suitability showed distinct patterns among fleets (Figure 5). The Dual-Hemisphere fleet moves between hemispheres each year to target winter conditions in each hemisphere. The Japan Offshore and Taiwan Offshore fleets shift farther north in summer, coinciding with the seasonal progression of the NPTZ and Kuroshio Current. The Northwest Domestic fleet remains relatively stable between seasons and targets Japan's domestic waters. Finally, the USA Offshore fleet extends north-east during summer but remains relatively stable year-round.

SST, ADT, and oxygen concentration were three important environmental variables driving the predicted distributions of both albacore and functional longline fishing fleets (Table 1). SST had the strongest associations with the fishing grounds of the Dual-Hemisphere Distant Water fishing fleet, which fished within a narrower temperature range that partially overlapped with both juvenile and adult albacore (Figure S7B). The Japan Offshore fleet and the USA Offshore fleet favored comparatively broader temperature extents (i.e., a 15–30°C range and a bimodal 15–17°C, 20–28°C range, respectively) overlapping with both size/age classes, while the Taiwan Offshore fleet fished within a narrow temperature range on the upper end of the sampling distribution that coincided with high predicted probabilities of adult albacore occurrence. The Taiwan Offshore fleet and Japan Offshore fleet fished preferentially in locations with higher ADT, due to a concentration of effort in the western subtropical Pacific while the Dual-Hemisphere Distant Water fleet was associated with lower values of ADT across the temperate NPTZ (Figure S7B).

4.4 | Seasonal variation in spatial niche overlap

Overall, the spatial niches of North Pacific pelagic longline fishing fleets were more similar to adult albacore than juvenile albacore (Figure 6). This result is likely impacted by (1) a greater tendency to actively target or interact with adult albacore as compared to juveniles across high seas fishing grounds and (2) a more expansive

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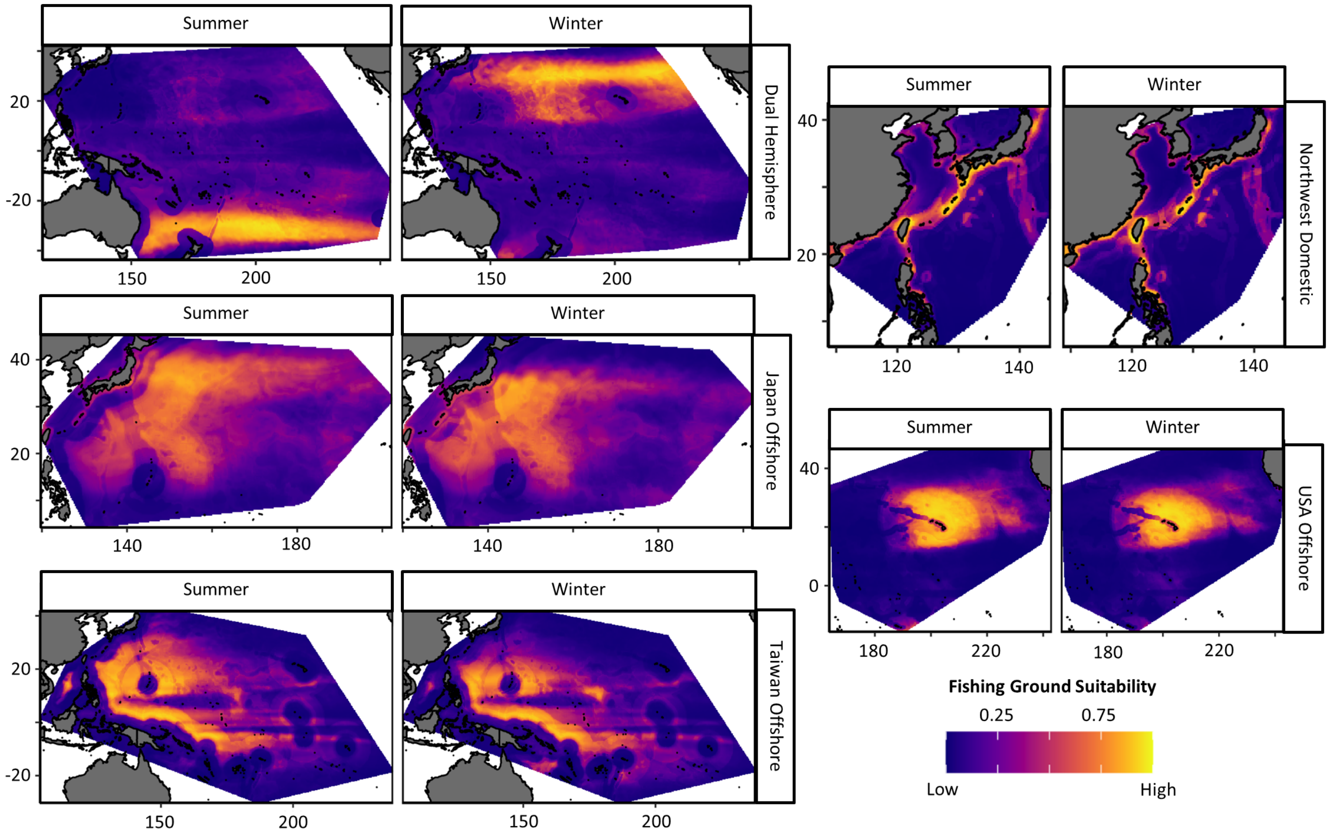

FIGURE 5 Seasonal predictions (summer: Jun-Aug and winter: Dec–Feb) of fishing ground suitability for the USA Offshore fleet, the Japanese Offshore fleet, the Northwest Domestic fleet, the Taiwan Offshore fleet, and the Dual-Hemisphere Distant Water fleet. Predictions were made across the convex hull polygons encompassing observations of member vessels. Some fleets show pronounced seasonal changes in distribution (i.e., the Dual-Hemisphere Distant Water fleet), others have core ranges with seasonal expansions (i.e. USA, Japan, and Taiwan Offshore fleets), while the Northwest Domestic fleet composed of small-vessels with limited ranges is more geographically fixed.

geographic range of adult habitat as compared to juveniles. The spatial niche of juvenile albacore had the highest overlap with the fishing grounds favored by the Dual-Hemisphere Distant Water fishing fleet with overlap peaking in Q1 (Figure 6a). Other notable overlaps with predicted juvenile presence were observed during Q1 and Q2 (peak) for the Japan Offshore fleet and Q1 (peak) and Q2 of the USA offshore fleet (Figure 6a). Minimal overlap with predicted juvenile habitat was observed for the Taiwan Offshore fleet, which favored subtropical fishing grounds, and the Northwest Domestic fleet, which was associated with near-coastal fishing grounds where the predictions of favorable juvenile habitat were limited to a narrow stretch of water East of the Kii Peninsula and south of Hamamatsu between ~33 and 35° N and ~ 136 and 138° E. Overlap with adult albacore probability of occurrence (Figure 6b) was greatest for the Japanese Offshore fleet, with other substantial overlaps observed for the Dual-Hemisphere Distant Water fishing fleet (Q1 peak) and the Taiwan Offshore fleet (Q3 peak). Overall, seasonal variation in niche overlaps with both adult and juvenile albacore was highest for the Dual-Hemisphere Distant Water fishing fleet, followed by the Japan and USA Offshore fleets (for juveniles) and the Taiwan and Japan Offshore fleets (for adults; Figure 6).

4.5 | Spatial niche overlap as mediated by gear configuration

The quantity, timing, and location of spatial niche overlap between North Pacific pelagic longline fishing fleets, and areas of high probability of adult albacore occurrence appear strongly influenced by gear configuration (Figure 7). Sets targeting bigeye tuna (typically deployed during the day) have much deeper median hook depths (~250 m), and a larger number of hooks per set, hooks per float, and distance between floats as compared to swordfish sets (typically deployed during the night) with a shallower median hook depth (<60 m, see Bigelow et al., 2006; Supplemental Methods in Appendix S1). Areas with a high probability of catching adult albacore on shallow-set gear (i.e., targeting swordfish) were of substantially narrower geographic extent (Figure S8) when compared to areas with a high probability of catching adult albacore on deep-set (i.e., targeting bigeye tuna) fishing gear. Variation in adult niche overlap assessed using shallow-set gear predictions as compared to deep-set predictions, both between fleets and across seasons, appears to reflect the degree to which the reduced habitat area associated with shallow-set predictions (Figure S8) coincided with regions of high predicted fishing ground suitability. In the case of

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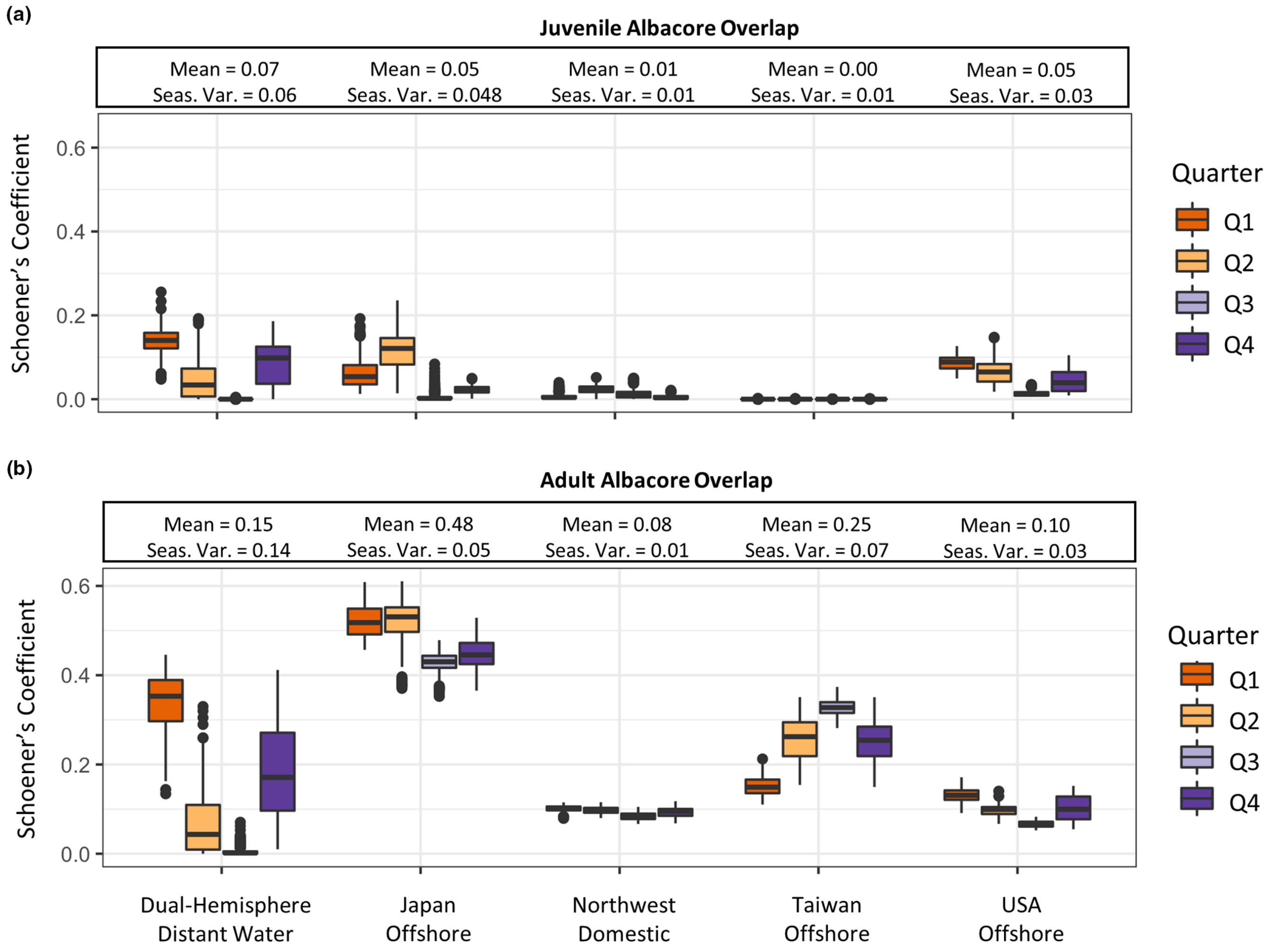

FIGURE 6 Spatial niche overlap (as measured by Schoener's D Overlap Index) between fishing grounds favored by five North Pacific pelagic longline fishing fleets and juvenile (a) and adult (b) albacore tuna (as predicted by deep-set fishing gear) during the four quarters of the year (Q1 = January–March; Q2 = April–June; Q3 = July–September; Q4 = October–December). Larger Schoener's values indicate higher estimated overlap.

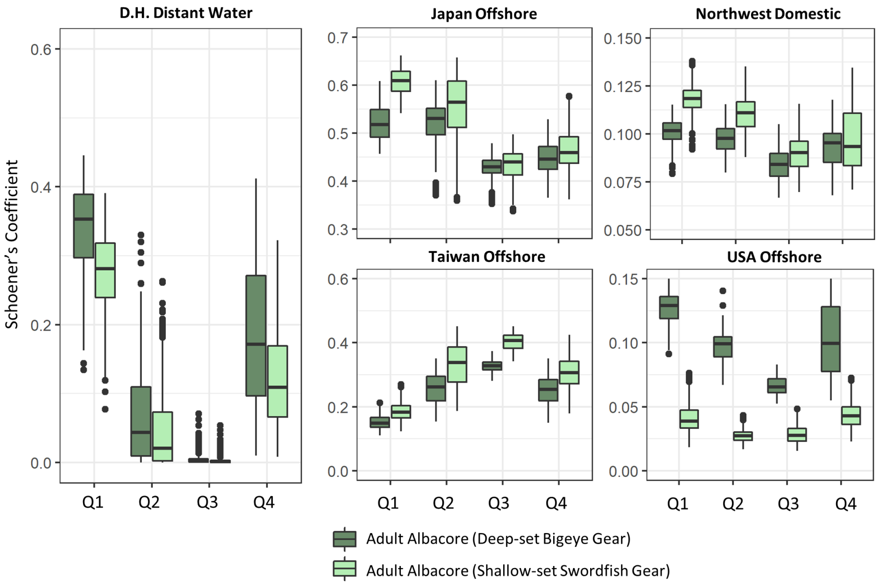

FIGURE 7 Overlap (i.e., spatial niche similarity) of each fleet with adult albacore associated with deep-set gear (i.e., targeting bigeye tuna; dark green) and shallow-set gear (i.e., targeting swordfish; light green).

the USA Offshore and Dual-Hemisphere Distant Water fishing fleets, which are most active in the central Pacific, niche overlap assessed using shallow-set predictions was less than for deep-set predictions, with the magnitude of difference most pronounced during Q1 (the quarter with the highest overlap). In contrast, niche overlap assessed using shallow-set fishing gear was comparatively larger in the western and subtropical North Pacific. For the Taiwan Offshore fleet, this difference was most pronounced in Q3, while increases were largest for the Northwest Domestic fleet and the Japan Offshore fleet in Q1 and Q2 before approaching equivalency in Q3 and Q4.

4.6 | Interannual variation in spatial niche overlap

Interannual variation in the overlap between fishing fleets and juvenile albacore tuna was largest for those fishing fleets targeting waters across the North Pacific Transition Zone (i.e., the Dual-Hemisphere Distant Water, Japan Offshore, and USA Offshore fleets). In contrast, interannual variation in overlap with adult albacore was most pronounced for fleets targeting high seas subtropical waters in the western Pacific (i.e., the Dual-Hemisphere Distant Water, Japan Offshore, and Taiwan Offshore fleets; Figure S9). Pearson's correlations between juvenile and adult overlap anomaly time series for each fishing fleet reveal an inverse relationship for those fleets operating in the Northwest Pacific (Japan Offshore, $r = -.374$, $p < .001$; Northwest Domestic, $r = -.163$; $p = .114$) that may be linked with high interannual variation in fisheries selectivity across that region (Figure S9). In comparison, assessed correlations for the USA Offshore ($r = .296$, $p < .01$), and Dual-Hemisphere Distant Water ($r = .372$, $p < .001$) fleets were positive. In aggregate, overlap with juvenile albacore habitat appeared greatest across North Pacific pelagic longline fishing fleets between 2013 and 2014 and smallest between 2017 and 2018, though there was substantial variation across individual fishing fleets. Basin-scale patterns appeared to be predominantly driven by anomalies observed for the Dual-Hemisphere Distant Water and Japanese Offshore fleets, with comparatively weaker positive (2015, 2016, and 2020) and negative (2017, 2018) anomalies observed for the USA offshore fleet. Analysis of the spatial distribution of niche overlap anomalies alongside changes in the location of the NPTZ (as indicated by the 18°C SST contour) between 2014 and 2017 (Figure 8) suggests that during these years such patterns may have been driven by a northward shift of favorable juvenile habitat in Northeastern Pacific waters (i.e., 165° W-135° W) in Q1 and Q2 and a southward shift in favorable juvenile habitat with Western Pacific waters (i.e., 135° E-165° W) in Q1.

Efforts to untangle patterns and drivers associated with adult overlap anomalies are confounded by a less consistent signal overall (Figure S10A) and the high importance of multiple and/or bi-modal environmental predictors (i.e., dissolved oxygen at 200 m in addition to SST). Broadly speaking, interannual variation appeared driven by differences in adult habitat suitability between 10° N and 25° N and 125° E and 160° E (Figure S10B), as associated with anomalously positive niche overlaps with the Japan Offshore and Taiwan Offshore fleets in Q4 of 2017 and Q1 of 2018 and anomalously negative overlaps in Q3 and Q4 of 2014. Overall, relative differences (i.e., adult niche overlap - juvenile niche overlap) by age -class were most pronounced in 2014 (more juvenile overlap) and 2017 (more adult overlap) for the Japan Offshore fleet (as driven by opposing trends in anomaly time series, Figure S9) and Q1–Q2 of 2016 (more adults) and Q1–Q2 of 2020 (more juveniles) for the Dual-Hemisphere Distant Water fleet (as driven by adult anomalies outpacing juvenile anomalies with the same corresponding sign, Figure S9).

5 | DISCUSSION

Across the Pacific Basin, pelagic longline fisheries represent a substantial proportion of total catch value (Williams & Ruaia, 2020) while exerting significant top-down pressure on open ocean ecosystems (Ortuño Crespo & Dunn, 2017). Yet, the sector is often considered among the least transparent seafood production systems worldwide (Carmine et al., 2020). Despite declining catch rates and deteriorating economic conditions across many Pacific pelagic longline fisheries (Williams & Ruaia, 2020), regulations designed to manage or reduce fishing efforts have been undermined by persistent uncertainty regarding who is catching what fish, where and when (Heidrich et al., 2022). Here we advance an ecological modeling framework to improve understanding of the factors mediating co-occurrence between fishing fleets and their target species. Our analysis highlights heterogeneity in fishing strategies and operations across the North Pacific basin while revealing fisheries niche overlap as a complex process mediated by gear usage, ontogenetic habitat requirements, and dynamic oceanographic conditions.

5.1 | Seasonal niche similarity assessments reflect catch logs & field reports

Previous accounts of seasonal and interannual variation in albacore fishery interactions across the North Pacific are challenging to synthesize given the diversity of data sources, methods, and study objectives. Yet our results are broadly consistent with existing reports while providing additional depth and detail. In high latitudes in the central North Pacific, in waters most intensively targeted by the Dual-Hemisphere Distant Water fleet, fishing operations are reported to seasonally interact with juvenile albacore in November-March between 25° and 40° N and 150° E and 140° W (Chen & Cheng, 2019; Lee et al., 2020). These accounts are consistent with our analysis showing elevated niche overlap with this size class during the same time of year, prior to the fleet moving south to target other size classes, species, and/or stocks (Frawley et al., 2022). Similarly, our analysis corroborates reports of the seasonal peak of adult abundance (Q1) inferred from US fleet logbook records across the same region (Teo, 2017), while reporting

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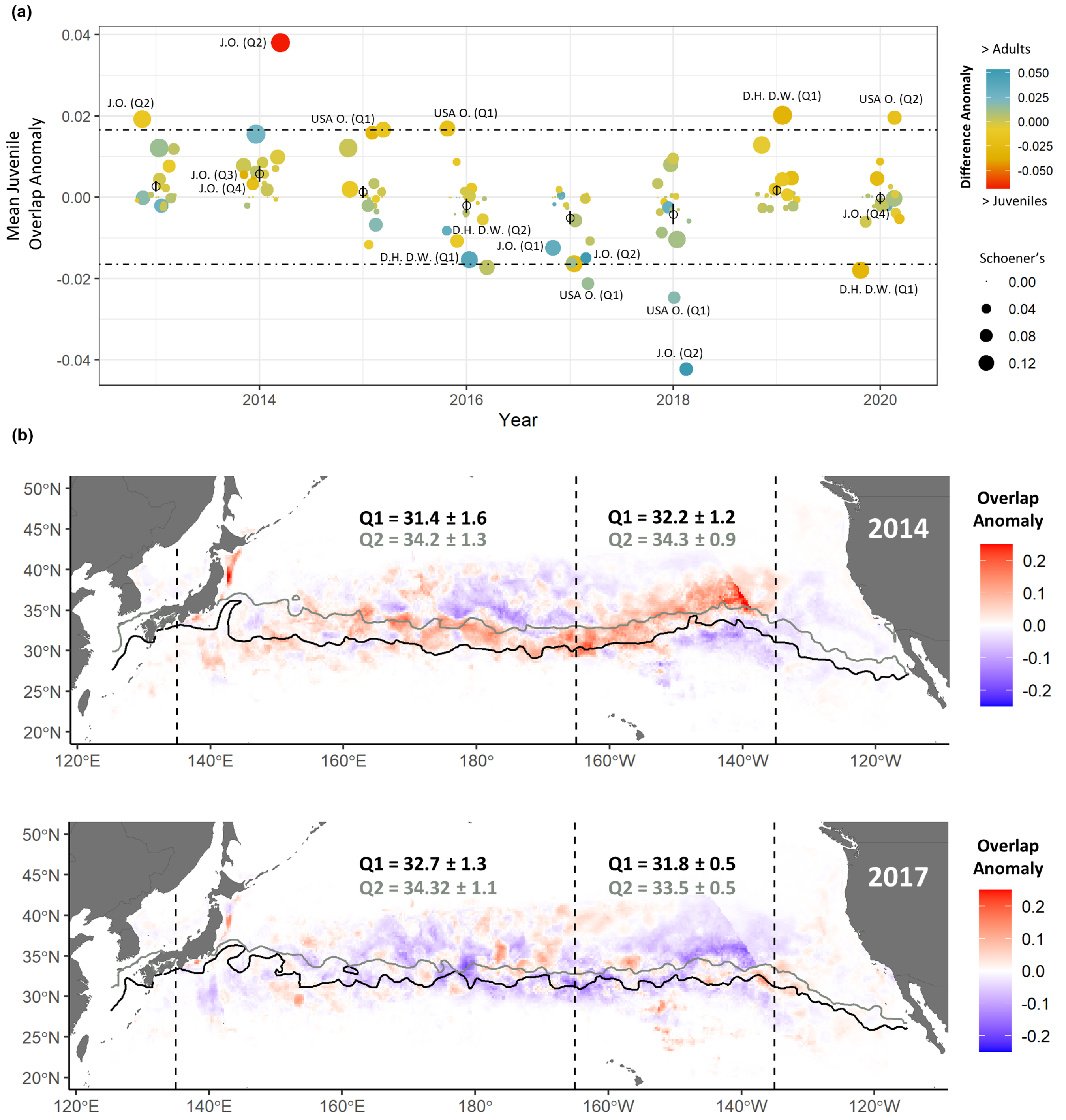

FIGURE 8 Interannual anomalies in niche overlap between predicted albacore habitat and predicted fishing grounds of North Pacific pelagic longline fishing fleets from 2013 to 2020. (a) Annual overlap anomalies across all pelagic longline fishing fleets. Data points represent quarterly means for each fishing fleet ($n = 20$ points per year), sized according to the sum of all monthly overlap values observed during each quarter, and colored according to the difference anomaly between adult overlap and juvenile overlap observed during the same time period (as compared to the climatological average, red values indicate comparatively more juvenile overlap while blue values indicate comparatively more adult overlap). Notable anomalies ($n = 17$) two standard deviations above the mean (either in absolute juvenile overlap or the difference between adult overlap and juvenile overlap) are labeled with the associated fleet and quarter. (b) Spatial anomalies of predicted juvenile albacore habitat overlap with the five fleets, depicting areas with relative increases (red) and decreases (blue) of cumulative overlap, as observed during the years of the study period when cumulative juvenile niche overlap was the largest (2014) and the smallest (2017). Spatial values were assessed by finding the daily products of predicted fishing fleet occurrence and juvenile albacore occurrence for each fishing fleet (i.e., $VDM_i \times SDM_{juvenile}$), summing across all 5 fishing fleets and averaging cumulative daily surfaces by month, subtracting monthly climatological values from observed monthly means, and then averaging monthly anomaly surfaces across specified years of interest. The black (Q1) and grey (Q2) lines indicate the average position of the 18°C SST contour (used as a proxy for the NPTZ), while the corresponding values indicate the seasonal mean contour latitude (±SD) between 135° E and 165° W & 165 °W and 135° W longitude bounds.

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additional information concerning the timing of peak juvenile overlap (Q1) and the variation of both size classes throughout the year. In the Northwestern Pacific however, our ability to compare such results with existing information (i.e, Fujioka et al., 2019) is limited due to challenges in resolving fishing fleets (see Kinney et al., 2022) due to the sparse public availability of gridded, regional catch data (Frawley et al., 2022).

Among those nations and fleets targeting North Pacific albacore, interactions across the Taiwanese small-scale and/or offshore vessels are perhaps the least well documented despite the species comprising an increasingly large proportion of the total catch. According to annual yearbook catch totals provided by the Western and Central Pacific Fisheries Commission, in 2015 albacore comprised just 11% of the catch (384 mt) of these Taiwan-flagged longline vessels (which belong to both Taiwan and Japan Offshore fleets) but by 2019 and 2020 it comprised 61% (3705 mt) and 44% (2226 mt) and is now the predominant species landed by weight. Additional research is required to refine size distribution estimates of this emerging fishery and to determine the degree to which catches originate from vessels targeting waters <30° N (e.g., Taiwan Offshore fleet, which our analysis indicates primarily overlap with adult albacore) or those embedded within multinational fleets operating further north in the Kuroshio Current system (e.g., the Japan Offshore fleet).

5.2 | Interannual changes in spatial overlap and fisheries interaction

Although historical changes in North Pacific albacore distribution and fisheries landings are well-documented (Frawley, Muhling, et al., 2021; Zhang et al., 2014), the mechanism driving these changes and its relationship with basin-scale oceanographic variability and extreme environmental events remains unclear. Across the North Pacific, periodic oscillations in albacore fishery landings (~10 years.) have been observed in conjunction with progressive, long-term declines over the past several decades (International Scientific Committee (ISC) for Tuna and Tuna-like Species in the North Pacific Ocean, 2020). Most recently, following a peak in 2012, landings have fallen to historic lows as abundance reported by both Japan (Fujioka et al., 2019) and the USA (Teo, 2017) have declined alongside total estimated biomass (International Scientific Committee (ISC) for Tuna and Tuna-like Species in the North Pacific Ocean, 2020). Our analysis of interannual variation in niche overlap is broadly consistent with observed landings and estimated abundance trends. In particular, during the 2012–2015 period which predated the most recent decline in fishery landings, elevated juvenile longline catch (Lee et al., 2020) and abundance (Fujioka et al., 2019) coincided with elevated niche overlap with functional longline fishing fleets (Figure 8). In addition, anomalous oceanographic and atmospheric conditions were reported across the region (Bond et al., 2015) in tandem with environmentally driven changes in North Pacific albacore tuna recruitment (International Scientific Committee (ISC) for Tuna and Tuna-like Species in the North Pacific Ocean, 2020).

At the northern edge of the albacore distribution, CPUE is strongly associated with the latitudinal position of the TZCF (Polovina et al., 2001; Zainuddin et al., 2008). The TZCF's position varies seasonally, interannually, and decadally (Bograd et al., 2004) in relation to large-scale climatic indices (e.g., ENSO, PDO, & NPGO) that influence proximate physical forcing (Polovina et al., 2017). With global warming, the latitude of the North Pacific Transition Zone and the TZCF is predicted to shift poleward and increase in variability (Navarra & Di Lorenzo, 2021) as the oligotrophic North Pacific Subtropical Gyre expands (Sarmiento et al., 2004). Concurrently, regional carrying capacity and fishery yield of pelagic tunas are expected to decrease (Woodworth-Jefcoats et al., 2017). Yet, at a more granular level, changes in the fleet-specific overlaps and interactions are likely to be mediated by regional patterns and processes. For example, the Northeastern Pacific marine heatwave in 2013-2015 coincided with anomalously cooler SSTs in waters further south and west (Peterson et al., 2015), shifting the NPTZ and juvenile albacore habitat in opposite directions (Figure 8). Moreover, while fleets interacting with juveniles in the Northeastern Pacific (i.e., the Dual-Hemisphere Distant Water Fleet and the USA Offshore fleet) are acutely impacted by ENSO events, variation in juvenile overlap and interactions in the Northwestern Pacific may additionally be driven by independent and incompletely understood mechanisms mediating interannual variability in the position and strength of Kuroshio and Oyashio Currents and associated meanders (Kimura & Sugimoto, 1997; Navarra & Di Lorenzo, 2021). Likewise, a comprehensive mechanistic understanding of the factors mediating fisheries interactions with adult albacore tuna in the Southwestern subtropics, in addition to overall stock productivity, remains unknown (Zhang et al., 2014).

5.3 | Implications for stock assessment design

In recent years, progressive attrition of troll and pole-and-line fishing efforts has accelerated on both sides of the Pacific (i.e., the Japanese and North American surface fishing fleets) alongside declines in North Pacific albacore CPUE and an observed northward contraction in favored fishing grounds (Frawley, Muhling, et al., 2021; Matsubara et al., 2019). Yet, as of the 2020 Stock Assessment (International Scientific Committee (ISC) for Tuna and Tuna-like Species in the North Pacific Ocean, 2020), the estimated impact of surface fisheries on total stock biomass remains nearly twice that of longline fisheries. Our analysis demonstrates that there may be substantial overlap between some longline fishing fleets and predicted juvenile habitat, and that this overlap may vary substantially within and between years. Since changes in the size distribution of catch and associated estimation of selectivity parameters can affect calculations of fishery impact (Cronin-Fine & Punt, 2021), continued assessment of changes in fleet size

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composition data over time and use of more temporally heterogeneous selectivity curves could be a valuable addition to future stock assessments.

To account for seasonal and regional changes in the availability of different albacore size classes, the stock assessment currently uses an "fleets-as-areas" approach where selectivity parameters vary according to flag, season, area, and/or gear configuration across 5 fixed, rectangular boxes (International Scientific Committee (ISC) for Tuna and Tuna-like Species in the North Pacific Ocean, 2020). Yet relying on such fixed and unevenly applied geographic determinations obscures much of the underlying dynamism and interannual variability that characterize the operational realities of "functional fishing fleets" (Frawley et al., 2022). Likewise, while annual variation in selectivity is applied to the Japanese pole-and-line fleet, all longline fishing fleets are assigned a single, static selectivity curve meant to characterize the size distribution of fish caught by a particular fleet over several decades of fishing activity, with the exception of large-scale changes due to fisheries management measures (e.g., regulatory changes to US longline fleet to mitigate turtle bycatch after 2004). In instances where a significant and negative correlation exists between juvenile and adult overlap anomalies (as is the case for the Japanese Offshore fleet) the use of time-varying selectivity parameters appears warranted. Even in instances where overlap anomalies by life history stage are positively correlated (i.e., the Dual-Hemisphere Distant Water fleet), significant interannual variability in niche overlap associated with relative changes in the magnitude of increase and/or decrease of overlap by life history stage may be best accommodated by dynamic approaches. Currently, a single-size selectivity curve is applied to all Taiwanese fishing vessels (the primary flag state contributing vessels to the Dual-Hemisphere Distant water fleet) operating above 30° N despite reports documenting considerable variability in the size distribution of landed fish (Chen & Cheng, 2019) as well as previous research showing mixed fleet associations and mixed target species (Frawley et al., 2022).

While there is a limit to the amount of complexity that can be accommodated within existing assessment models and data aggregation procedures, we suggest that recent observed and future predicted oceanographic changes across the NPTZ (and their capacity to impact albacore habitat and fishery interactions; see Erauskin-Extramiana et al., 2019) make consideration and incorporation of dynamic biological and oceanographic parameters a critical priority. In the short-term, the revision of international data-sharing agreements to increase the public availability of spatially explicit, high-resolution catch, effort and size data may help efforts to move toward dynamic ocean management by democratizing and decentralizing the required supporting analysis. Likewise, efforts to broaden expertise within international working groups dedicated to the development of stock assessment models and management strategy evaluations in order to incorporate the insight of oceanographers, ecological modelers, and coupled-systems scientists may be a necessary first step in moving toward adaptive, ecosystem-based fisheries management.

5.4 | Data limitations in assessing model predictions & realized fisheries interactions

While our analysis advances understanding of the factors mediating North Pacific pelagic longline fisheries co-occurrence with albacore, our approach is not without its limitations. Firstly, the ability to detect vessels and species responses to oceanographic variability can be influenced by the scale at which an analysis is conducted. Habitat preferences can be complex and occur over many nested spatial and temporal scales (Scales et al., 2017). Our models at 1.25 × 1.25 degrees (designed to encompass the resolution of the tag data and the footprint of longline fishing gear) may not capture finer-scale biologically relevant features (e.g., mesoscale and submesoscale eddies) that fish or fishing vessels may target (Arostegui et al., 2022; Watson et al., 2018). Indeed, the level of analysis at which our analysis was conducted may obscure the critical role of seasonal eddies in aggregating pelagic biomass across the Kuroshio Current system (Durán Gómez et al., 2020), resulting in lower-than-expected predicted occurrences in the Northwest Pacific.

Likewise, as theory and methods progress, it is becoming increasingly clear that there are limits to the inferences that can be drawn about fisheries interactions from an analysis of two-dimensional spatial overlap between predators and prey (Goodman et al., 2022; Suraci et al., 2022). While we have characterized spatial overlap across space and time according to gear usage and life-history-specific habitat preferences, additional advances are needed to move toward empirical estimations of fisheries interactions. In addition to the "availability" inferred by two-dimensional horizontal overlap, fisheries interactions are likely to vary alongside "encounterability" (i.e., the propensity for a species to interact with fishing gear within its depth range) and "selectivity" (i.e., the propensity of an organism to be captured once it encounters fishing gear; Murua et al., 2021). Our analysis of gear effects (e.g., deep-set and shallow-set gear) represents an initial effort to explicitly consider albacore foraging behavior and incorporate previous insight obtained by in situ longline gear monitoring studies (Bigelow et al., 2006; Bigelow & Maunder, 2007; Ward & Myers, 2005). While the evidence we provide concerning the impact of gear-type on species interactions may be qualified as suggestive, other recent AIS-based research (Kroodsma et al., 2023) has similarly advanced investigations designed to explore the relationships and interactions between set time, gear configuration, fishing latitude, and species interactions as a promising future line of research. Moving forward, considering additional nuance in gear configuration and deployment strategies (i.e., moving beyond the shallow vs. deep archetypes presented in our analysis) may improve risk and mortality parameters. For example, survival and selectivity within and across pelagic longline fisheries have been shown to vary by leader construction (Ward et al., 2008), hook-type (Curran & Bigelow, 2011), and bait choice (Gilman et al., 2020).

Caution is recommended when extrapolating model predictions in space and time as spatiotemporal extrapolation assumes stationary species–environmental relationships (Rousseau & Betts,

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2022). Despite recognized biases, recent research asserts fishery-dependent data can be used to build robust SDMs, as long as (1) they sample a sufficient environmental range and data are available from both suitable and unsuitable habitats; and (2) they can be effectively validated against external data sources, and/or using expert knowledge to assess model output for ecological and physiological realism (Braun et al., 2023; Karp et al., 2023; Pennino et al., 2016). With respect to the former, we choose to use observations from the North and South Pacific in the construction of the adult albacore SDM to sample over as broad a range of predictors as possible (Karp et al., 2023). Although it is possible some behavioral differences exist between North and South Pacific albacores, previous studies based in the South Pacific show similar environmental and latitudinal associations of juveniles and adults to those in the northern hemisphere (e.g., Williams et al., 2015). With respect to the latter, we found strong agreement between the adult SDM and Japanese longline fishery data (Figure S3), as was the case for the juvenile SDM and Japanese pole-and-line data from the WPO (Figure S2). Additionally, we see minimal environmental extrapolation for two of the most important covariates (SST and ADT) in the albacore models (Figure S4). We conclude that while there is more uncertainty in model predictions in the WPO compared to the EPO, our models reproduce patterns and processes documented in existing scientific and grey literature.

Although we have highlighted the environmental factors driving interannual variation in predicted fisheries overlap, additional data sources and analyses are likely required to quantify observed outcomes for this and other fishery systems. Although AIS represents a valuable and increasingly comprehensive (Taconet et al., 2019) public source of vessel movement data, usage and coverage are inconsistent across fishing fleets, areas, and operations (Frawley et al., 2022; Taconet et al., 2019; Welch et al., 2022). In addition to leveraging private data from vessel tracking systems whose continuous use is obligatory (i.e., Vessel Monitoring Systems data) and/or international observer and logbook programs, studies seeking to identify and describe interannual variation in realized fisheries interactions would be well-served to consider socioeconomic drivers of behavior (i.e., variation in market access and value, fuel costs, etc.) in addition to oceanographic factors. Indeed, though fishers are keen observers of the marine environments and known to actively target certain types of oceanographic features associated with fishing success and the aggregation of target species (Watson et al., 2018), vessel distribution is also known to be impacted by the proximity of other vessels, jurisdictional boundaries, and other physical and socioeconomic factors (Salas & Gaertner, 2004; Welch et al., 2022).

6 | CONCLUSION

With tunas and billfishes increasingly relied upon to support fisheries-dependent livelihoods and food security across the Pacific Basin (Bell et al., 2018), there is a critical need to develop and adopt adaptive management approaches capable of accommodating environmental change and variability. Although effective fisheries management is credited for the recovery of many tuna and billfish stocks worldwide (Juan-Jordá et al., 2022), the intensifying threats associated with climate change are likely to necessitate additional intervention (Bell et al., 2021; Lehodey et al., 2015). This is particularly true for high-latitude temperate stocks like albacore tuna, for whom available habitat is expected to contract and shift poleward (Erauskin-Extramiana et al., 2019). In the absence of approaches designed to accommodate within and between year variability of fisheries catchability and selectivity parameters, the spatiotemporal mismatches between harvest control rules and the species they are designed to manage are likely to grow more pronounced with each passing year.

Dynamic ocean management is an emergent management tool that explicitly accommodates variability by responding to near-real-time information on where animals and humans are located (Dunn et al., 2016; Lewison et al., 2015). Initial applications of this approach have focused on minimizing interactions with vulnerable and/or protected species (Hazen et al., 2018; Howell et al., 2008). Yet recent reviews (Holsman et al., 2017; Pinsky & Mantua, 2014) have highlighted how pelagic fisheries may benefit from similarly dynamic spatiotemporal management approaches designed to adapt to (1) shifting target species life history strategies; (2) changes in how fishery effort is allocated across time and space; and (3) the rapid redistribution of favorable habitat across jurisdictional boundaries. With respect to our test case, the North Pacific albacore, in the coming years, we suggest that real-time monitoring of fleet dynamics in conjunction with disaggregated species (by life history stage) and vessel (by fishing fleet) distribution model outputs could inform the development of dynamic harvest control rules. Although additional research is required to ensure rigor in design and implementation, managers may be well-served in exploring how catch and effort restrictions could vary by season, area, and year alongside variation in habitat quality and abundance to maximize sustainable fishing opportunities and ensure equitable distribution of associated costs and benefits.

ACKNOWLEDGMENTS

This work was supported by a grant from the National Oceanic and Atmospheric Administration Fisheries Office of Law Enforcement (NOAA OLE; NA20OAR4320278). Collectively, we would like to thank NOAA OLE staff, members of the United States Coast Guard, the Pacific Fishery Management Council's Highly Migratory Species Advisory Subpanel, and GFW for helping to direct the research with their ideas, opinions, and experiences. In addition, we would like to thank James Smith and Steve Teo for valuable discussions and feedback provided during early project development; Dawn Golden, Lesley Hawn, Eric Forney, and Brent Miyamoto for assistance in accessing US longline observer data; Rob Ahrens and Kisei Tanaka for internal reviews; and Stephanie Snyder for helping to collect and process archival tag data. T.H.F., B.M., and D.T. were supported in part by NOAA Climate Program Office grants supporting the Future

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Seas research initiative (NA17OAR431026, NA20OAR4310507). C.D.B, S.B., H.W., and N.F. were supported, in part, by the NASA Earth Science Research Program (80NSSC19K0187). M.C.A. was supported by the Postdoctoral Scholar Program at Woods Hole Oceanographic Institution with funding provided by the Dr. George D. Grice Postdoctoral Scholarship Fund.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to report.

DATA AVAILABILITY STATEMENT

Observer data for US pelagic longline fishing fleets, used for the adult albacore SDM and collected by NOAA's Pacific Islands Fisheries Science Center and the National Marine Fisheries Service, are confidential U.S. government data. The raw data cannot be made public, under the Magnuson–Stevens Fishery Conservation and Management Reauthorization Act of 2006, section 402 (b), 16 U.S.C. 1881a. Information on requesting access to these data (including details on whom to contact) can be found at https://www.fisheries.noaa.gov/inport/item/9027. Requests for albacore archival tag datasets, used for the juvenile albacore SDM and VBMs, should be directed to Barbara Muhling (barbara.muhling@noaa.gov), as described in Muhling et al., 2022, though some data are held confidential at the request of the American Fishermen's Research Foundation responsible for initial tag deployment. AIS data used for VDMs is public and can be accessed online at www.globalfishingwatch.org, with related data processing codes and classification lists previously published in Frawley et al., 2022. Physical and Oceanographic data used for ecological modeling was accessed either through the Copernicus Marine Service (https://marine.copernicus.eu/) or the NOAA CoastWatch Program (https://coastwatch.noaa.gov) as described in Table S1.

ORCID

Timothy H. Frawley https://orcid.org/0000-0003-4477-6567
Martin C. Arostegui https://orcid.org/0000-0002-9313-9487
Nima Farchadi https://orcid.org/0000-0003-4718-6984

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How to cite this article: Frawley, T. H., Muhling, B., Brodie, S., Blondin, H., Welch, H., Arostegui, M. C., Bograd, S. J., Braun, C. D., Cimino, M. A., Farchadi, N., Hazen, E. L., Tommasi, D., & Jacox, M. (2024). Dynamic human, oceanographic, and ecological factors mediate transboundary fishery overlap across the Pacific high seas. *Fish and Fisheries*, *25*, 60–81. https://doi.org/10.1111/faf.12791

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