Title
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Journal
Fish and Fisheries, 25(4)

ISSN
1467-2960

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Publication Date
2024-07-01

DOI
10.1111/faf.12828

Peer reviewed

Received: 15 August 2023 | Revised: 18 March 2024 | Accepted: 19 March 2024

DOI: 10.1111/faf.12828

ORIGINAL ARTICLE

FISH and FISHERIES WILEY

Marine heatwaves redistribute pelagic fishing fleets

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Funding information
National Aeronautics and Space Administration, Grant/Award Number: 80NSSC19K0187; National Oceanic and Atmospheric Administration, Grant/Award Number: NA21OAR4170247

Abstract

Marine heatwaves (MHWs) have measurable impacts on marine ecosystems and reliant fisheries and associated communities. However, how MHWs translate to changes in fishing opportunities and the displacement of fishing fleets remains poorly understood. Using fishing vessel tracking data from the automatic identification system (AIS), we developed vessel distribution models for two pelagic fisheries targeting highly migratory species, the U.S. Atlantic longline and Pacific troll fleets, to understand how MHW properties (intensity, size, and duration) influence core fishing grounds and fleet displacement. For both fleets, MHW size had the largest influence on fishing ground area with northern fishing grounds gaining and southern fishing grounds decreasing in area. However, fleet displacement in response to MHWs varied between coasts, as the Atlantic longline fleet displaced farther in southern regions whereas the most northern and southern regions of the Pacific troll fleet shifted farther. Characterizing fishing fleet responses to these anomalous conditions can help identify regional vulnerabilities under future extreme events and aid in supporting climate-readiness and resilience in pelagic fisheries.

KEYWORDS

automatic information system, boosted regression trees, dynamic ocean management, marine heatwaves, pelagic fisheries, vessel distribution models

1 | INTRODUCTION

Ocean and atmospheric temperatures are rising (Alexander et al., 2020; Pozo Buil et al., 2021), with wide-reaching impacts on productive marine ecosystems that support global fishery landings (Pauly & Zeller, 2016; Payne et al., 2021). While some climate-driven changes, such as shifts in the timing and intensity of upwelling, are not predicted to occur until the mid-to-late century (~2050–2080; Brady et al., 2017), oceans are already experiencing episodic warm water anomalies, termed marine heatwaves (MHWs; Oliver et al., 2021). MHWs are distributed globally, with hotspots of MHWs occurring in productive ocean regions, including western (e.g. Northeast U.S. continental shelf; Pershing et al., 2015) and eastern (e.g. California Current Ecosystem; Di Lorenzo & Mantua, 2016) boundary currents. MHWs can alter essential habitat for targeted species, which can displace fishing effort (Fisher et al., 2020), reduce fisheries yields (Smith, Burrows, et al., 2021) and compromise food security (Smale et al., 2019). These rapid and pervasive responses to MHWs pose new challenges to marine resource management and the social–ecological systems that rely on ocean resources.

Marine heatwaves may lead to both ecological disruptions, for example, spatiotemporal predator–prey mismatches, and economic disruptions, if targeted populations decline or move out of the range of the fishers who catch them (Rogers et al., 2019; Smith et al., 2023; Smith, Burrows, et al., 2021; Smith, Tommasi, et al., 2021), escalation of bycatch in fisheries (Samhouri et al., 2021; Santora et al., 2020) or provoking the outbreak of harmful algae blooms that can present public health risks (Fisher et al., 2020). Retrospective studies have shown that these responses strain productive U.S. fisheries. For example, the 2014–2016 MHW in the Gulf of Alaska caused several commercially important species, including Pacific cod, to shift to deeper waters and reduce recruitment and spawning biomass (Barbeaux et al., 2020; Li et al., 2019; Yang et al., 2019). Consequently, fishing quotas for Pacific cod declined and the fishery was closed in 2020 (Smith, Burrows, et al., 2021; Smith, Tommasi, et al., 2021). In the California Current, the same 2014–2016 MHW led to a harmful algal bloom, contaminating shellfish with biotoxins and forcing the closure of the lucrative Dungeness crab fishery for months (Fisher et al., 2020), costing fishers >$43 million (Holland & Leonard, 2020). Despite these losses, MHWs may also create new fishing opportunities. For example, longfin squid expansion into the Gulf of Maine during a MHW event in 2012 enabled the development of a profitable new squid market in the region (Mills et al., 2013).

Despite substantial evidence that MHWs impact U.S. fisheries, there is still considerable uncertainty in how the physical properties of MHWs translate to changes in fishing opportunities and the displacement of fishing fleets. This uncertainty likely stems from the substantial variability in intensity, size and duration of MHWs (Oliver et al., 2021; Oliver, Lago, et al., 2018). The generation and modulation of MHWs has been attributed to the interaction of both local (e.g. air-sea fluxes, vertical mixing) and broad (e.g. El Niño-Southern Oscillation; ENSO) processes acting across a range of spatial and temporal scales (Holbrook et al., 2019). This oceanographic complexity means a single heatwave event can yield different perturbations of physical processes and ecologically significant features (e.g. fronts) over relatively fine spatial scales (Holbrook et al., 2019; Welch et al., 2023). Consequently, extreme events, such as MHWs, may present new challenges to current fisheries management strategies (Cavole et al., 2016; Free et al., 2023; Mills et al., 2013), most of which were designed in response to historical variability and with limited consideration of the influence of secular warming (i.e. climate change).

To characterize how MHWs have impacted U.S. pelagic fisheries, we combined high-resolution environmental data with publicly available fishing vessel data to model the distribution shifts of fishing fleets in response to MHWs. Here, we consider how MHWs impact the distributions of two U.S. pelagic fisheries: the pelagic longline fleet in the Northwest Atlantic and the troll fleet in the Northeast Pacific. We tracked two metrics of fleet responses to MHW intensity, size and duration within designated management areas for each fishery: change in the area of core fishing grounds and fleet displacement. Understanding how fishing fleets respond to extreme and episodic warming events is central to developing climate resilient fisheries management that can accommodate future MHWs and ongoing climate change.

2 | METHODS

2.1 | Study system and AIS data

The U.S. Atlantic pelagic longline fishery targets swordfish (*Xiphias gladius*) and tunas (*Thunnus* sp.) from the Grand Banks to the equator (Larkin et al., 2000). The U.S. Pacific troll fishery harvests North Pacific albacore tuna (*Thunnus alalunga*) during the summer and fall (Frawley et al., 2020). To evaluate changes in core fishing ground area and fleet displacement, we acquired automatic identification system (AIS) vessel data collected by global fishing watch (GFW) for both fleets (Figure 1). GFW analyses detections of AIS vessel transmissions from satellite and terrestrial receivers using machine learning techniques to track fishing effort, and provides a publicly available global dataset of >70,000 fishing vessels (Kroodsma et al., 2018). This dataset provides daily fishing effort and vessel presence, measured in units of hours, binned at 1 km resolution by flag state and gear type from 2012 to 2020 (Kroodsma et al., 2018). However, due to the absence of GFW-classified U.S. Atlantic longline vessels for 2012, the temporal extent of AIS data for this fleet spanned between 2013 and 2020. AIS data were filtered to U.S. vessels with apparent fishing effort >1 h per grid cell in relevant

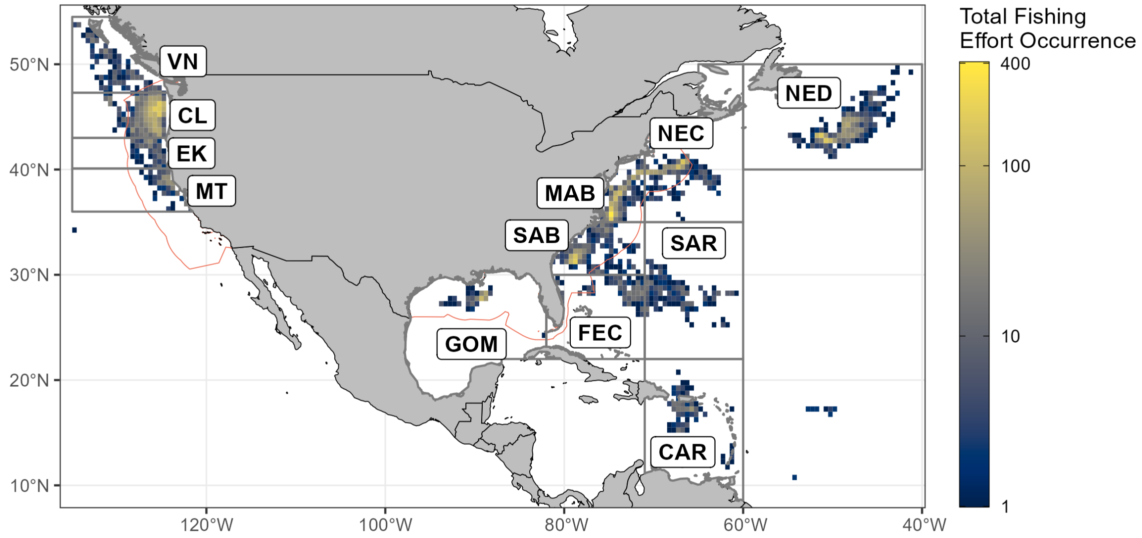

FIGURE 1 Fishing effort and management areas for both U.S. pelagic fleets. Total fishing effort occurrence (daily presence locations of fishing) from the Automatic Identification System (AIS) of the U.S. Atlantic pelagic longline fleet (2013–2020) and the U.S. Pacific pelagic troll fleet (2012–2020). Grey boundaries in the Atlantic are the designated management areas for the northwest Atlantic pelagic longline fleet and in the northeast Pacific are management areas defined by the International North Pacific Fisheries Commission (INPFC). Northwest Atlantic management areas: Northeast Distant (NED), Northeast Coastal (NEC), Mid-Atlantic Bight (MAB), South Atlantic Bight (SAB), Sargasso Sea (SAR), Florida East Coast (FEC), Gulf of Mexico (GOM), and Caribbean (CAR). Northeast Pacific management areas: Vancouver (VN), Columbia (CL), Eureka (EK), and Monterey (MT). Red coloured boundaries represent the U.S. Exclusive Economic Zones.

spatial and temporal bounds of interest (Supplemental Methods) and were aggregated to 0.08° resolution to align with the resolution of the environmental data (Methods S1 and Table S1). Fishing fleet responses to MHWs (see Section 2.5) were evaluated within 8 of 11 northwest Atlantic management areas and 4 of northeast Pacific management areas (Methods S1 and Figure S1). Additional descriptions of the two fisheries and details on filtering the AIS data are given in the Supplementary Information.

2.2 | Characterizing MHWs properties: Intensity, size and duration

MHWs were identified as discrete periods of SST anomalies (SSTa) exceeding a 90th percentile for a duration of 1 month or longer using methodologies adapted from Hobday et al. (2016) and employed by Jacox et al. (2020). Daily SST data from NOAA's 0.25° Optimum Interpolation SST version 2.1 (OISST; Reynolds et al., 2007), from 1982 to 2020, were averaged per month for each management area. OISST is assimilated from multiple observational sources (satellites, buoys, ships, and Argo floats; Reynolds et al., 2007), and has been commonly used for MHW detection (Jacox et al., 2020; Oliver et al., 2021; Perez et al., 2021). The use of monthly SST in our analysis limits identified MHWs to 'main events' (i.e. heatwaves lasting at least a month) while also having consistent trends compared to MHW analysis using daily data (Jacox et al., 2020). In this study, MHWs and their properties were identified and calculated using two methodologies: grid cell (intensity & size) and area-average (duration) analysis (Figure S2).

For the grid-cell analysis, we calculated a time series of monthly SSTa relative to 30-year monthly climatological baseline from 1982 to 2011 per grid cell. For each grid cell, MHWs were then identified as periods when monthly SSTa exceeded a 3-month seasonally varying 90th percentile threshold. This threshold was calculated for each month using the pooled monthly SST across all years from the 30-year climatology within a 3-month window centred on the month. MHW properties such as intensity (mean SSTa of all classified MHW grid cells) and size (proportion of MHW-classified grid cells) were calculated for each month within a management area.

For the area-average analysis, monthly SST averaged across each management area was used to identify whether a management area was in a MHW state, and to calculate the monthly duration of MHW events. Following the same methodology as the grid-cell analysis, time series of monthly SSTa relative to a 30-year monthly climatological baseline from 1982 to 2011 was calculated for each management area. MHW duration was calculated as the consecutive months the SSTa in a given management area exceeded a 3-month seasonally varying 90th percentile threshold (i.e. consecutive months a management area was in a MHW state).

2.3 | Environmental variables

A suite of static and dynamic environmental variables was used to build fishery-specific models of fleet distributions (Table S1). Environmental variables included in the models have previously been identified as being important in describing the distributions of large pelagic fishes (Brodie et al., 2018; Muhling et al., 2019), and the fishing fleets that target these species (Crespo et al., 2018; Frawley et al., 2023). Five dynamic environmental variables (four surface variables and one subsurface variable) were sourced or derived at a daily temporal resolution from the high-resolution (0.08°) data-assimilating HYbrid Coordinated Ocean Model (HYCOM; Chassignet et al., 2007). HYCOM combines numerical modelling techniques with data assimilation methods by merging observational data with model simulations to accurately simulate and predict ocean dynamics (Chassignet et al., 2007), which has been widely used to relate environmental variables to top marine predator distributions and movements in both regions of our study (Arostegui et al., 2023; Braun et al., 2019; Crear et al., 2021; McHenry et al., 2019). HYCOM variables included: sea surface temperature (SST; °C), SST standard deviation (calculated over a 0.24° spatial resolution), sea surface height (SSH; in meters), SSH standard deviation (calculated over a 0.24° spatial resolution) and bulk buoyancy frequency (s^{-1}). The five static environmental variables included in the models consisted of two static seafloor relief variables, two variables describing the distance from the nearest feature (i.e. fishery-specific ports and seamounts), as well as lunar illumination. Static seafloor relief variables included bathymetry and its standard deviation (rugosity; calculated over a 0.24° spatial resolution). Additionally, fishery-specific ports and locations of seamounts were used to calculate static grids representing distance to these features (distance to nearest port & distance to nearest seamount; Methods S1). Lunar illumination, which represents the fraction of the moon's visible disk that is illuminated, was included as it is known to affect the vertical distribution of swordfish and thus its catchability (Lerner et al., 2013; Scales et al., 2017; Sepulveda et al., 2010).

2.4 | Vessel distribution models

We applied an established and robust species distribution modelling method to build vessel distribution model (VDMs) to understand oceanographic drivers of fishing fleet distributions' response to MHW conditions (Crespo et al., 2018). We built VDMs for each fishery to model the probability of fishing effort occurrence as a function of environmental variables using boosted regression trees (BRT), which are a powerful machine learning method with flexible parameter estimation and have demonstrated strong predictive performance for modelling the distributions of highly migratory species (HMS) and pelagic fisheries (Abrahms et al., 2019; Becker et al., 2020; Braun, Arostegui, et al., 2023; Brodie et al., 2020; Elith et al., 2008; Hazen et al., 2018; Welch et al., 2022, 2023), even under novel environmental conditions (Muhling et al., 2020; Welch et al., 2023). The predictive strength of BRTs can be attributed through the use of boosting to optimize partitioning of variance, ability to fit complex nonlinear relationships and its hierarchical structure so that interactions between environmental variables are automatically modelled (Elith et al., 2008). Additionally, unlike more commonly used semi- and parametric techniques, BRTs are robust to outliers, missing data, collinearity among environmental variables as well as the inclusion of irrelevant variables (Elith et al., 2008).

We describe model outputs from VDMs as *suitable fishing grounds*, which follows the established terminology from species distribution models that have analogous model structures. Previous studies have modelled fishing ground suitability (Crespo et al., 2018) and while several studies have explicitly modelled the behaviour of vessels (e.g. Burgess et al., 2020; Smith, Burrows, et al., 2021; Smith, Tommasi, et al., 2021) our VDMs measure the *fishing grounds* on which vessels can act on rather than modelling specific agents (sensu Smith et al., 2019). The VDMs for both fisheries were built with the response variable of presence: pseudo-absence using a Bernoulli family distribution in the *dismo* R package (Hijmans et al., 2021). We generated pseudo-absences by randomly selecting unfished grid cells from within a convex hull of the total AIS locations for each fishery. Furthermore, we applied a 1:1 presences: pseudo-absences ratio, which has been recommended for BRT modelling approaches (Barbet-Massin et al., 2012; Hazen et al., 2021). To evaluate multiple candidate VDMs with different hyperparameter configurations, we used various model performance indices such as area under the receiver operating characteristic curve (AUC), true skill statistic (TSS) and explained deviance on two training and testing dataset combinations: (1) 10-fold cross-validation (90% training/10% testing for each fold) and (2) 'Leave One Out' (LOO) cross-validation in which a year of data was iteratively left out from training and used for testing. VDMs were tuned by testing the optimal hyperparameter values for tree complexity, learning rate and number of trees using the *caret* (Kuhn, 2008) and *dismo* R packages (Hijmans et al., 2021; Supplemental Methods). Daily fishing ground suitability for both fishing fleets was predicted from 2012 to 2020 within each fisheries' study domain and averaged by month to match the temporal scale of the MHW time series calculated from the OISST data. Although the U.S. Atlantic longline fleet VDM was fitted from 2013 to 2020, MHWs conditions in 2012 were consistent with the fitted years across management areas (Figure S3).

2.5 | Fleet responses to MHWs

We measured two metrics of fleet distribution responses to MHWs: change in core fishing ground area and fleet displacement. These two metrics capture how productive a management area was likely to be for each fishery and how vessels displaced during MHW conditions, respectively. To evaluate differences within and among fishing areas, we calculated these metrics within each designated management area for each fishery at the monthly scale. Both metrics involved converting monthly spatial predictions of fishing ground suitability into binary suitability maps by applying fleet-specific thresholds that classify core fishing ground and remove noncore areas. Identified core fishing grounds were a subset of suitable habitat and this classification was used to ensure that regions with a low probability of fishing effort occurrence did not bias results and that we are only capturing fishing grounds vessels will likely act on (Hazen et al., 2013; White et al., 2019). We explored the sensitivity of multiple threshold values on our fleet response metrics (Table S2, Figures S4 and S5), which resulted in defining core fishing grounds as the average top 75th percentile of suitability values across mapped spatial predictions for each fleet (Hazen et al., 2013, 2018; Lezama-Ochoa et al., 2023; White et al., 2019). Our selection of threshold stemmed from habitat selection literature to discern home range from core areas (i.e. selection of habitat within home ranges), which traditionally have used a 50th percentile threshold (Silva-Opps & Opps, 2011). While there are multiple widely accepted approaches for selecting a threshold to convert suitability maps into binary maps, the 75th percentile was selected as more conservative thresholds would sometimes result in a complete loss of core fishing grounds during MHWs for certain regions, whereas lower threshold values would include too much area. Similar to previous studies that have explored different threshold values for fishing ground suitability (Crespo et al., 2018), the fishing ground suitability landscape may vary among thresholds but the overall patterns were largely insensitive to threshold (Figures S4 and S5).

2.5.1 | Change in core fishing ground area

We examined the relationship between percent change in core fishing ground area to MHW intensity, size and duration to consider which MHW properties exert the largest influence on fleet dynamics. To account for the seasonality in fishing effort across management areas, gains and losses in core fishing grounds were expressed as month-year deviations relative to climatological monthly baseline conditions. A time series in percent change in core fishing grounds was calculated per management area using:

$$\text{Percent change in core fishing grounds} = \frac{(M - B)}{B}$$

where M represents the sum of cells classified as core fishing grounds in a single month-year and B represents the average of summed core fishing grounds in a single month over the entire time period (i.e. monthly baseline conditions). To examine whether percent change in monthly core fishing grounds is driven by monthly MHW intensity, size, duration ($n = 108$ months for each management area) and regional variation, we fitted a linear mixed-effects model. For this model, management area ($n = 12$) was included as a random intercept term to account for the within and among regional MHW variability. Additionally, the slopes for MHW intensity, size and duration were set to vary for each management area. To easily interpret and compare coefficients from the models, predictor variables were standardized and scaled by subtracting the mean and dividing by the standard deviation. Interpretation of coefficients from the model will represent the average percentile change in core fishing ground area in each management area per one unit increase in a MHW property when the other properties are at their mean. Residual plots were assessed visually to confirm that both fleets' linear mixed-effects models satisfied the assumptions of normality and homogeneity of variance.

2.5.2 | Fleet displacement

To investigate how predicted fleet distributions changed in response to MHWs relative to non-MHW conditions, we calculated the displacement of monthly centre of gravities from core fishing grounds (COG; mean latitude/longitude coordinate pairs) between the two conditions. As a baseline value for these comparisons, we used the monthly average COG of non-MHW months (i.e. months a management area was not classified as being in a MHW state) for each management area. This allowed us to create a robust comparison of how shifts in fleet distributions differed during non-MHWs months (i.e. natural variability), which we refer to $COG_{baseline}$, relative to COGs during MHWs for the same month. Specifically, displacement distances were quantified as the Euclidean distance (km) between the monthly COGs and the $COG_{baseline}$ per management area (Figure S6). Distances were calculated using the 'st_distance' function from the *sf* R package (Pebesma, 2018). To account for the different sizes of management areas, the calculated distances were weighted by the total area (km^2) of that management area (hereafter termed 'relative distance'). To test if the distribution of relative distances were the same or farther (i.e. left skewed) during MHW months compared to non-MHW months for each management area, we performed a right-tailed Kolmogorov–Smirnov (KS) goodness of fit test (Massey, 1951). Using the KS test ensured that significant differences in the results were not influenced by the means of the compared distributions.

3 | RESULTS

3.1 | Spatial variation among MHW properties

Our characterization of MHWs between the two coasts revealed an average of 30 and 16 MHW events across the northwest Atlantic and northeast Pacific management areas, respectively, during 2012–2020. Temporal patterns of MHW events varied significantly among northwest Atlantic management areas (Figure 2 and Figure S7), suggesting differential impacts of MHWs on a sub-regional scale (Figure 2 and Figure S7; ANOVA, $F_7 = 335.1$, $p < .001$). In contrast, management areas in the northeast Pacific experience broadly similar impacts of MHW events across this region (Figure 2; ANOVA, $p > .05$). Across the northwest Atlantic, this spatial heterogeneity of MHW intensity was particularly evident between the northern (north of Cape Hatteras; NED to MAB; 35.2° N) and southern (south of Cape Hatteras; FEC to CAR) management areas, as northern regions typically experienced sea surface temperature anomaly (SSTa) an order of magnitude warmer than southern regions (Figure S8). This latitudinal trend between the northern and southern management areas was also observed for MHW size in the northwest Atlantic (Figure S8). MHW size for the northeast Pacific differed among management areas as well;

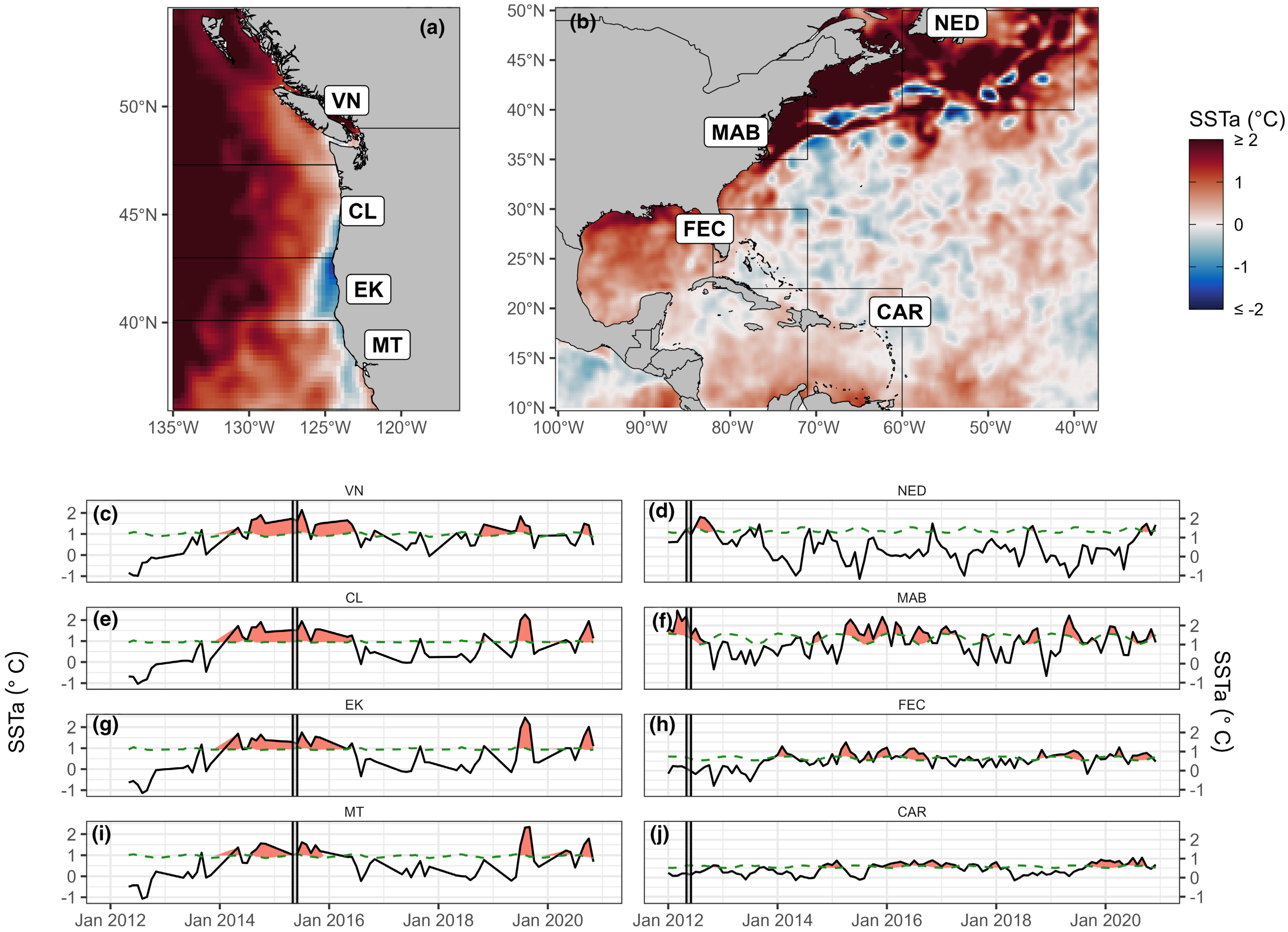

FIGURE 2 Spatiotemporal SSTa and MHW trends in North America. SSTa and MHW in the northeast Pacific during May 2015 (a) and in the northwest Atlantic in May 2012 (b). Area-averaged SSTa time series (c-j; black lines) are shown for each of the management areas (black boundaries) indicated in the SSTa maps. MHWs identified in monthly SST data are shown as red shading. The seasonally varying 90th percentile threshold to define MHWs in each management area are shown as green dashed lines. Grey bars in the time series plots indicate the respective month shown in the corresponding regional maps above. Management areas shown include: Northeast Distant (NED), Mid-Atlantic Bight (MAB), Florida East Coast (FEC), Caribbean (CAR), Vancouver (VN), Columbia (CL), Eureka (EK), and Monterey (MT). SSTa time series is shown for four representative management zones in the northwest Atlantic but see Supplementary Information for all management areas (Figure S7).

however, sizes between central (i.e. middle two management areas) or peripheral (i.e. most northern and southern) management areas were shown to be more similar. MHW duration was highly variable among management areas and did not demonstrate regional patterns like the other MHW properties (Figure S8).

3.2 | Fleet environmental drivers and spatiotemporal distributions

Vessel distribution models (VDMs) for both fleets exhibited high explained deviance and performed well during cross-validation analyses (Table S3). The relative importance of each environmental variable was similar between fleets, with static environmental variables (bathymetry, distance from nearest port and distance from nearest seamount) ranked in the top four variables that contributed most to both models (Figure 3a). Bathymetry and distance from nearest port were the most influential variables driving spatiotemporal distributions in both fleets. These were ranked as the top two variables in both models and cumulatively contributed >50% of relative importance (Figure 3a). Partial response curves showed that both fisheries exhibited a similar response to bathymetry and distance to nearest port with fishing ground suitability increasing closer to port (<250 km) but in deep waters (~1000 to 3000 m; Figure 3b). The most influential dynamic environmental variables differed between the two fleets. These dynamic variables were SST and bulk buoyancy frequency for the U.S. Atlantic longline and Pacific troll, respectively, which are consistent with previous SDMs built for the target species in these fisheries (Brodie et al., 2018; Muhling et al., 2019). The U.S. Atlantic longline fleet revealed a unimodal response to SST with preferences for moderately warm water fishing grounds (~13°C ≥ SST ≤ ~23°C) while the U.S. Pacific troll fleets

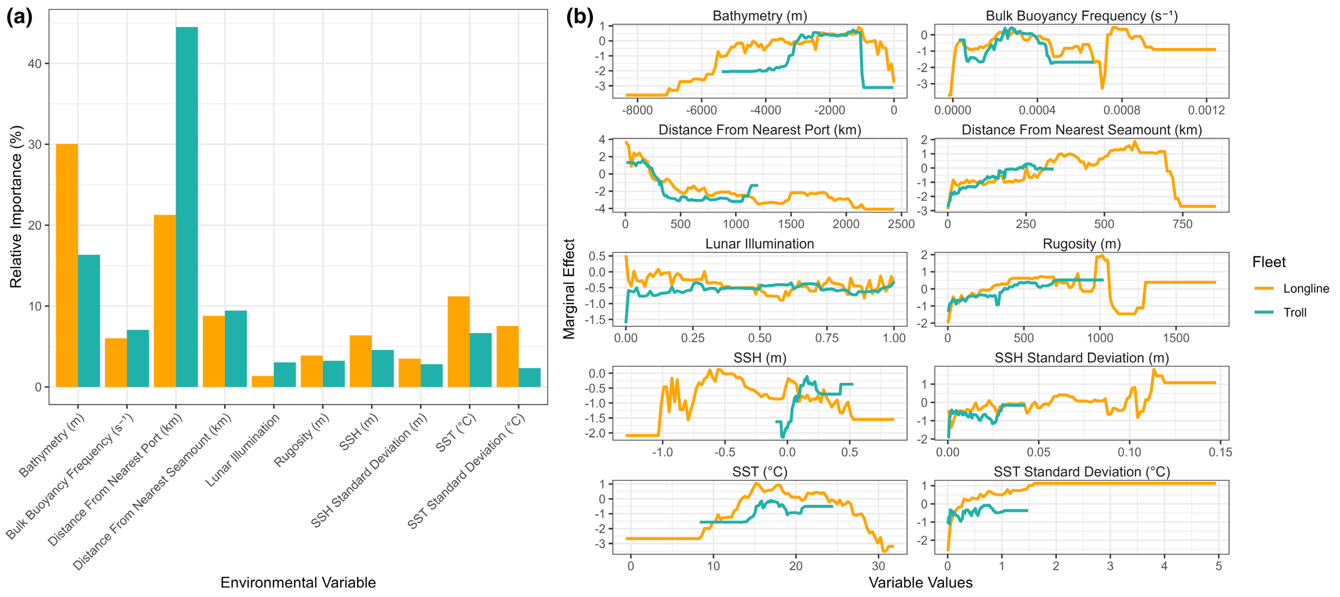

FIGURE 3 (a) Relative importance (%) and (b) the response curves for the environmental variables used in each fleet's vessel distribution model (VDM).

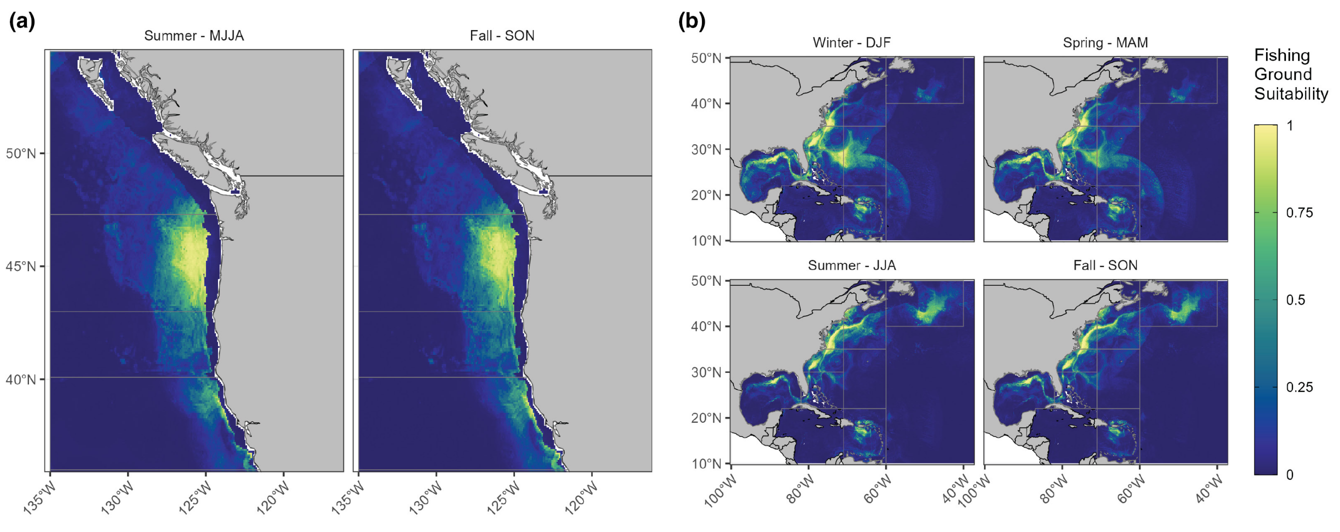

FIGURE 4 Seasonally averaged spatial predictions of suitable fishing grounds for both fishing fleets (2012–2020). Fishing season for U.S Pacific troll fishery (a) ranges from May–November while the U.S. Atlantic longline fishery is year-round (b). Winter = December, January, February (DJF), Spring = March, April, Mary (MAM), Summer = June, July, August (JJA), Fall = September, October, November (SON). Summer seasonal average for troll fishery includes May.

fishing grounds were more suitable in waters with intermediate bulk buoyancy frequency values (i.e. moderately stratified water column).

Spatial predictions of fishing ground suitability from VDMs demonstrated contrasting patterns between fleets. The U.S. Atlantic pelagic longline fleet exhibited dynamic spatial patterns as their fishing grounds shifted seasonally between the northern and southern waters within the northwest Atlantic (Figure 4). Winter and spring fishing grounds were predicted to be more suitable within the management areas south of Cape Hatteras. Fishing ground suitability declined in southern management areas and during summer and fall with a concomitant increase in the northern management areas, reflecting northward progression of target species, including swordfish (Braun et al., 2019; Neilson et al., 2014) and bigeye tuna (Lam et al., 2014). The U.S. Pacific troll fleet demonstrated relatively static seasonal distributions throughout its May to November fishing season (Figure 4) in which suitable fishing grounds were concentrated off the coasts of Washington and Oregon, particularly offshore of the 1000 m isobath (Figure 4). No suitability predictions were made during winter and spring as these periods are outside the season for this fishery. Contrasts between continuous seasonal spatial predictions of fishing ground suitability and converted seasonal binary maps of core fishing grounds are shown in Figure S9.

3.3 | Effect of MHW properties

Models suggested that changes in core fishing ground area (as defined by the top 75th percentile of suitability values, see Section 2) were primarily driven by MHW size rather than intensity or duration (Figure 5 and Table S4). The strength and direction of this relationship between MHW size and change in core fishing ground area demonstrated a strong latitudinal gradient, with northern management areas expanding as MHW increased in size, while some southern management areas experienced decreases in core fishing area (Figure 5). This latitudinal gradient was observed for both fishing fleets. The U.S. Pacific troll fleet exhibited a stronger and fully positive gradient between its most northern and southern management areas (i.e., increased MHW size resulted in larger magnitude increases in core fishing ground area in northern versus southern management areas). In contrast, the U.S. Atlantic longline fleet showed a more gradual gradient as MHW size coefficients demonstrated positive associations north of Cape Hatteras (i.e. gains in fishing grounds), while steadily declining and turning negative (i.e. loss in core fishing grounds) south of the Cape (Figure 5). The varying influence of MHW intensity, size, and duration has had on changing core fishing grounds in the NED and Gulf of Mexico (GOM) management areas of the U.S. Atlantic longline fleet are shown in Figures 6 and 7.

3.4 | Fleet displacement

Overall, both fleets exhibited significant spatial redistribution during MHWs compared to non-MHW conditions (Figure 8). Similar to the MHW-driven change in core fishing ground area, U.S. Atlantic longline management areas demonstrated a latitudinal pattern where core fishing grounds in northern management areas shifted between MHW and non-MHW conditions (Figure 8b and Table S5). Yet, in management areas south of Cape Hatteras, MHW-induced displacement was significantly larger than natural variability (Kolmogorov–Smirnov tests; $p < .05$; Table S5). In contrast, the U.S. Pacific troll fleet did not demonstrate a latitudinal trend in fleet displacement. Instead, the peripheral management areas (VN & MT) exhibited significant displacement under MHWs compared to non-MHW conditions, while the two central management areas experienced no significant change (CL & EK; Figure 8a and Table S5). Across all management areas, the largest shift in core fishing grounds occurred in the VN management area in the Pacific (235 km).

4 | DISCUSSION

MHWs are known to have significant ecological and economic impacts globally (Smith et al., 2023; Smith, Burrows, et al., 2021; Smith, Tommasi, et al., 2021). In the U.S., intense and persistent heatwaves, like the 2014–2016 MHW in the northeast Pacific, have been linked to unprecedented impacts across multiple trophic levels and economically important fisheries (Free et al., 2023; Santora et al., 2020).

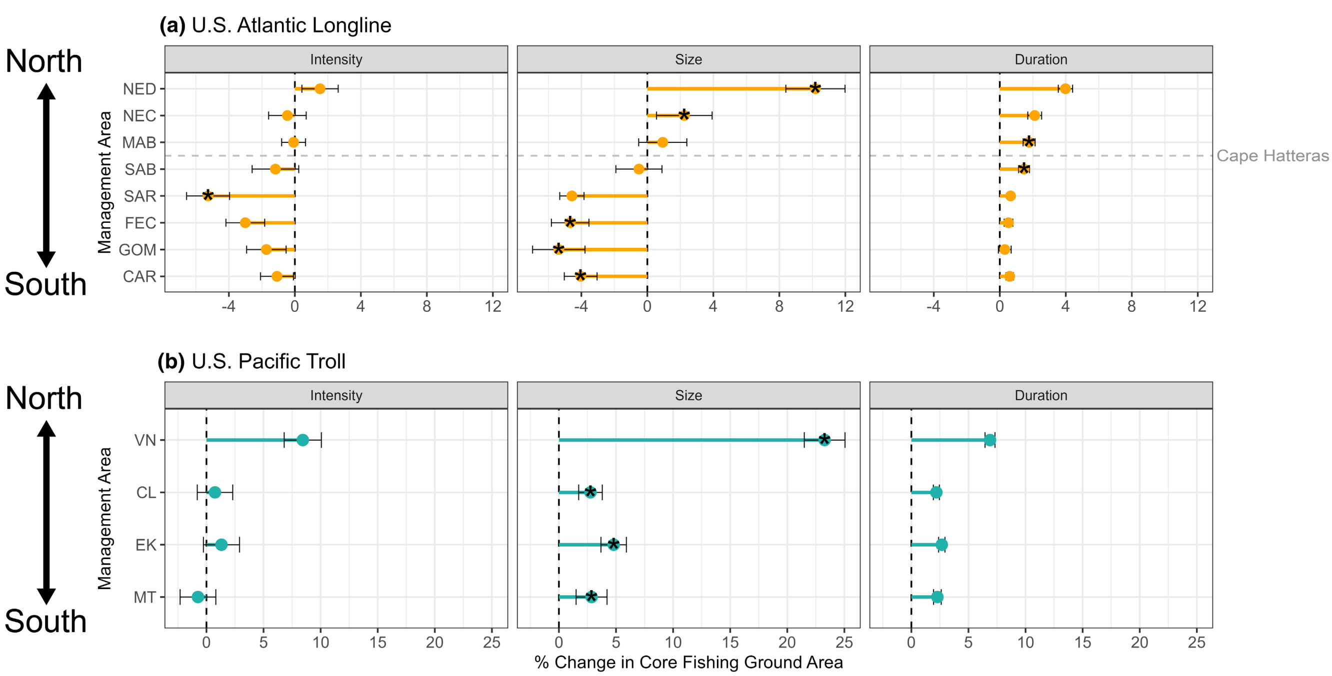

FIGURE 5 Latitudinal relationship between percent change in core fishing ground area and MHW properties (intensity, size, and duration). Coefficient values from the linear mixed-effects model describe the percent change in core fishing ground area in each management area where positive (negative) coefficient values indicate gains (loss) in core fishing ground area. Asterisks (*) denote the MHW property that influences the greatest percent change in core fishing ground area for each management area. Error bars represent the standard error of the model's coefficients.

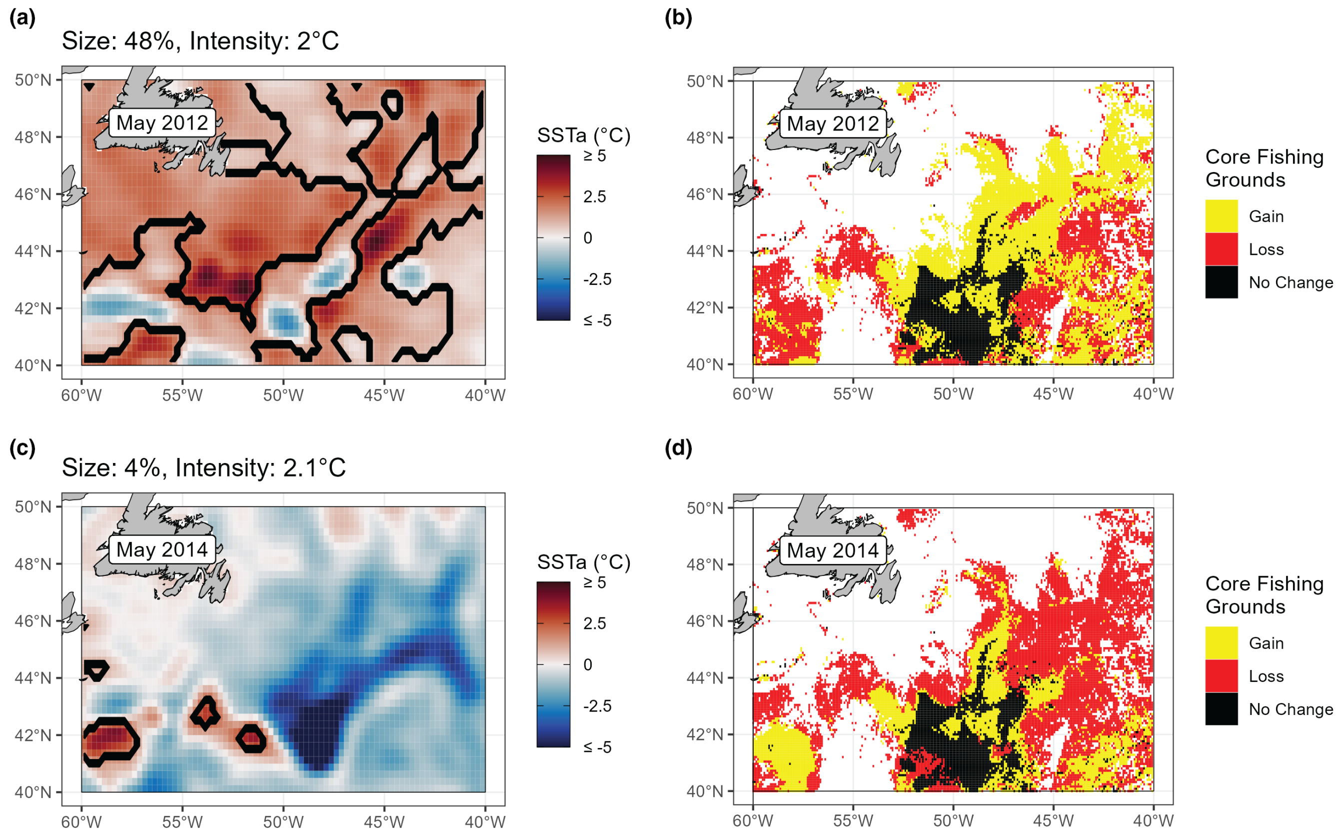

FIGURE 6 Examples of the predicted change in the U.S. Atlantic longline core fishing grounds during a month that experienced a large MHW (a) and a small MHW (c) with similar intensities of temperature and fishing effort in the Northeast Distant (NED) management area during May 2012 and 2014, respectively. Comparison between the two MHWs exemplifies the influence MHW size has on changing core fishing ground area for pelagic fishing fleets (b & d). Size and intensity are indicated for each month-year. Contours on SSTa maps represent the grid cells classified as MHWs.

Although several studies have shown how MHWs have impacted fishery yields (Smith, Burrows, et al., 2021; Smith, Tommasi, et al., 2021), there is a paucity of information on how MHWs elicit impacts on fishing opportunity. In this study, we found that MHWs impacted the size and location of fishing grounds in two U.S. pelagic fisheries. Using AIS fishing vessel data with predictive habitat models for fleets in the Atlantic and Pacific, we demonstrated that the change in core fishing ground size was primarily influenced by MHW size (e.g. spatial extent) rather than intensity or duration on both coasts. Across both coasts, we found a strong latitudinal gradient where greater MHW size resulted in increases in core fishing ground area in the northern management areas and decreases in southern management areas. However, fleet displacement in response to MHWs differed between the two coasts, with southern and peripheral management areas in the Atlantic and Pacific, respectively, demonstrating significantly larger displacements during MHWs than their natural variability.

Our results demonstrate that MHW size had the greatest impact on both the amount and distribution of suitable fishing ground area (Figures 5–7). Although previous work has explored the impact of MHW intensity and duration (Jacox et al., 2020; Oliver et al., 2021; Oliver, Donat, et al., 2018; Oliver, Lago, et al., 2018), the size of MHWs has received less attention (but see Hannah et al., 2021; Piatt et al., 2020; Ross et al., 2021). One cause of size-related effects could be the impact on frontal activity in fishing grounds, as the standard deviation in SST was an influential factor in our models. Frontal features have been shown to be productive foraging habitats for many highly migratory species (e.g. billfish and tunas; Scales et al., 2014; Snyder et al., 2017), and fisheries targeting these species have been found to be associated especially with the thermal signatures of fronts (Scales et al., 2018; Watson et al., 2018). Changes in frontal features, such as dampening of frontal activity during MHWs (Kahru et al., 2018), could reduce potential foraging habitat or decrease predator densities around fronts (Snyder et al., 2017), impacting the probability of catching them (Watson et al., 2018) and causing vessels to redistribute. Regions with low frontal activity (e.g. southern Atlantic management areas) may thus be particularly sensitive to loss of fishing grounds during MHWs. SST gradients are used by marine animals and fishers to track fronts and have been used as a metric to track MHW-induced displacement of a particular thermal regime, with weaker gradients corresponding to greater displacement (Jacox et al., 2020). Similar large-scale displacement has been predicted for a number of highly migratory species in the northwest Atlantic, including several target species of the northwest

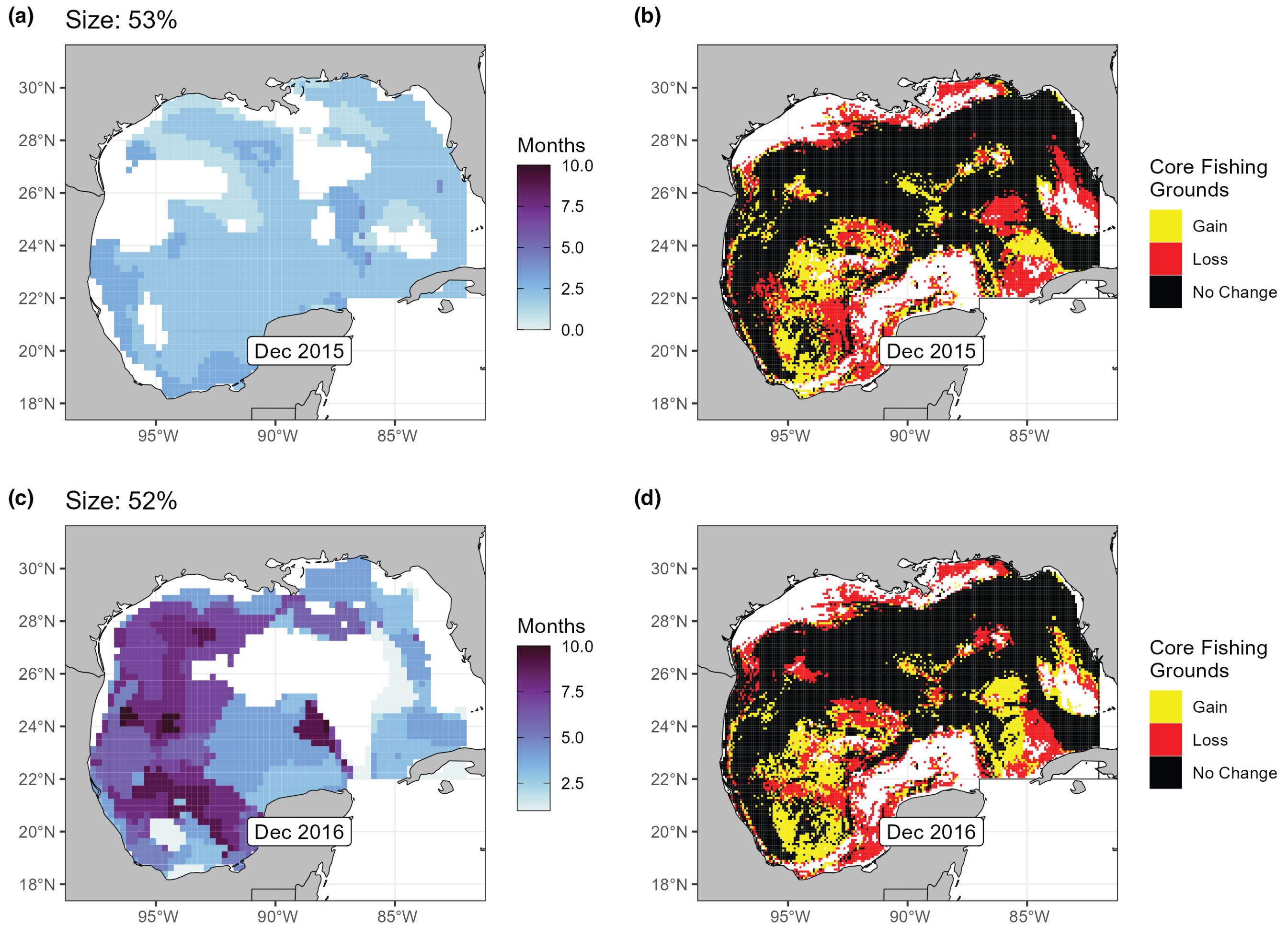

FIGURE 7 Examples of the predicted change in the U.S. Atlantic longline core fishing grounds during a month that experience a short MHW (a) and a long MHW (c) of similar sizes and fishing effort in the Gulf of Mexico (GOM) management area of December 2015 and 2016, respectively. Comparison between the two MHWs exemplifies the lack of influence MHW duration has on changing core fishing ground area for pelagic fishing fleets (b & d). Colour scheme on duration maps indicate the number of consecutive months preceding December 2015 and 2016 (a & c, respectively) that pixels were classified as MHWs. Size percentages indicate the percent of the management area covered by MHW pixels.

Atlantic longline fishery (Braun, Lezama-Ochoa, et al., 2023). Our results corroborate this relationship as regions experiencing weaker SST gradients displaced further during MHWs (Figure S10).

While MHW research is almost exclusively focused on their surface signature, MHW impacts may also extend below the surface (Amaya et al., 2023; Großelindemann et al., 2022; Ryan et al., 2021). Previous studies investigating the depth structures of MHWs along the continental shelves of North America found that MHWs can also occur entirely at depth or extend over the full water column on the continental shelf (Amaya et al., 2023; Ryan et al., 2021). Subsurface MHWs corresponded to higher stratification (Großelindemann et al., 2022; Ryan et al., 2021) and had greater intensities (up to 5–7°C), longer durations and spatial extents, which in many cases were as large or exceeded the physical impacts of MHWs trapped at the surface (Amaya et al., 2023; Großelindemann et al., 2022). Similarly to surface MHWs, subsurface MHWs' properties are highly variable regionally, which can be driven by bathymetric features, local oceanographic processes, or linked to large-scale climate forcing (e.g. ENSO; Amaya et al., 2023). Bulk buoyancy frequency, a metric of stratification in the mixed layer, was a consistently important variable in our models and may also be an important driver of suitable fishing ground redistribution under MHW conditions. Taken together, these studies allude to the potential importance of subsurface impacts of MHWs and highlight the need for additional research to understand how MHWs may impact water column thermal structure and associated biology in pelagic ecosystems.

Our results highlight how MHWs drive different responses and potential vulnerabilities among fishing regions. The metrics reported here can be used to identify regions of resilience or vulnerability to MHWs. Southern management areas of the U.S. Atlantic longline fleet were among the most vulnerable to MHWs, as this region experienced declines in core fishing ground area and higher displacement. Although traveling farther to more distant and unfamiliar fishing grounds might produce higher yields and greater profit, expenses are typically higher and more variable (Cabrera &

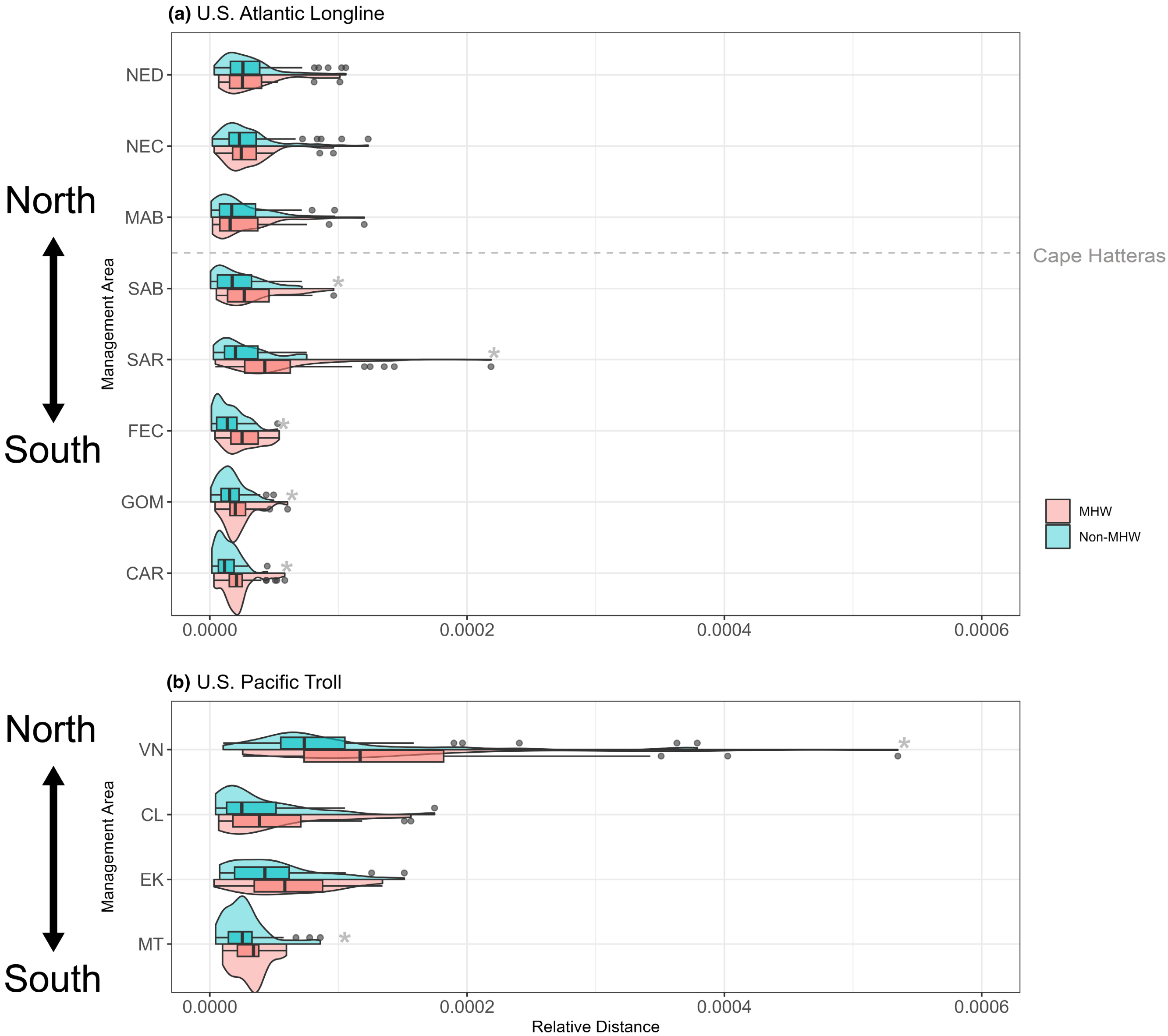

FIGURE 8 Fleet displacement under MHW and non-MHW conditions. Distributions of relative distance (displacement distance scaled by the total area [km^2] of the corresponding management area) that fleets were displaced during marine heatwaves (MHWs) and non-marine heatwaves (non-MHWs) for the management areas of the U.S. Pacific troll fleet (a) and U.S. Atlantic longline fleet (b), ordered latitudinally. Displacement during non-MHWs reflects the natural variability of each fleet's spatial dynamics. Red and blue distributions are the relative distances during MHW and non-MHW identified months, respectively. Grey asterisks (*) next to management areas indicate statistically significant ($a < .05$) differences between MHW and non-MHW distributions from Kolmogorov–Smirnov tests.

Defeo, 2001; Frawley et al., 2021; Young et al., 2019). This 'high risk, high reward' fishing strategy (Allen & McGlade, 1986) therefore may not be ideal under uncertain environmental and economic conditions (Frawley et al., 2021), as is common during a MHW event (Fisher et al., 2020). Previous research has shown some fisheries can be adaptive during MHWs. Analysis on the California Dungeness crab fishery during the 2014–2016 MHW demonstrated vessels responded to MHW-induced closures by either shifting the spatial distribution and intensity of their efforts to areas outside the closures, spilling over into alternative fisheries or stopping fishing entirely (Fisher et al., 2020). While fishery dynamics may return to their pre-MHW state (Fisher et al., 2020; Free et al., 2023), there is uncertainty regarding how MHWs in a warmer climate may erode the effectiveness of such adaptive strategies and resilience of fisheries in the future (Pinsky, 2021). Although our models do not predict vessel-level dynamics, an extension of this work may include leveraging VDM outputs in agent-based modelling approaches (Burgess et al., 2020), using fishing ground suitability to spatially inform the degree of fishing opportunity a fisher can act on. Such an approach could help capture where sources of risk from MHWs stem from (e.g. low portfolio diversification or low fleet mobility) and highlight where development in other dimensions of adaptive capacity may be needed to enhance resilience for pelagic fisheries to future extreme events (Samhouri et al., 2023).

Although our analysis suggests that northern and central fishery areas of the U.S. Atlantic longline and Pacific troll fleet, respectively, are less impacted by heatwave events, MHWs in these regions could create other conflicts. Vessels may reallocate fishing effort into alternative management areas, and the higher concentrations of vessels may increase fishing pressure on targeted species and potentially generate greater competition among fishers (Ojea et al., 2020). Extreme events and climate-driven ecosystem change (Braun, Lezama-Ochoa, et al., 2023; Lezama-Ochoa et al., 2023) in both of these regions have also exacerbated human–wildlife conflicts, such as greater interaction risks with protected or vulnerable species (Davies & Brillant, 2019; Samhouri et al., 2021). For example, the delayed opening of the Dungeness Crab fishery in California coincided with the onshore compression of productive whale foraging habitat, intensifying the spatial overlap of whales and crab fishing gear, and resulted in an alarming rise in blue and humpback whale entanglements (Santora et al., 2020). Similarly, in the Northwest Atlantic, climate-driven changes to traditional foraging grounds of North Atlantic right whales have spiked entanglements and mortality of these critically endangered species, reversing previously successful recovery rates (Davies & Brillant, 2019). Furthermore, political conflict may arise if suitable fishing grounds in the northern management areas span international borders. This was particularly evident for the U.S. Pacific troll fleet as the VN management area, which was largely within Canadian waters, experienced the greatest gains in core fishing grounds area during MHW conditions. These MHW-induced changes in troll fishing grounds raise important policy and management issues, and negotiations are necessary to sustainably manage such transboundary fisheries (Bograd et al., 2019).

While our analysis broadens our understanding of the impacts MHWs have on pelagic fishing fleet spatial distributions, our approach is not without limitations. First, our study is limited to fishing vessels equipped with AIS which have been recognized to vary by region, regional fisheries management organizations (RFMOs), flag state and vessel size. Recent studies have revealed that public-monitoring systems may not capture the full extent of industrial fishing activities, particularly in Asian and African coastal waters (Paolo et al., 2024). However, AIS is commonly used on large vessels (>24 m), in upper- and middle-income countries, and in distant water fleets (Sala et al., 2018; Taconet et al., 2019). Our analysis likely includes the majority of the U.S. Atlantic longline fleet (U.S. vessels over 19 m typically use AIS in the northwest Atlantic; Larkin et al., 2000; Scott et al., 2007; Taconet et al., 2019), and a substantial proportion of the U.S. Pacific Troll fishing fleet, as larger vessels have yielded a significant percentage of albacore capture (~35% to >50%) since the 1990s (Frawley et al., 2020). However, GFW does not classify any fishing for the U.S. Atlantic longline fleet in 2012 because AIS usage was not widely adopted until 2013 (Taconet et al., 2019). Although AIS data were not available for 2012, we tested the applicability of the existing data to missing years and found that the predicted VDMs were well suited as MHWs were relatively consistent over the study period, even with an atypical MHW in 2012 (Figure S3, Table S3). Another reason AIS is essential for these and other similar analyses is the lack of comparable data sources. Although other vessel tracking data, such as vessel monitoring system (VMS), have more precise spatial resolution, AIS are the only publicly available vessel data.

We also tested the sensitivity of our results to suitable fishing ground threshold as there are several widely accepted procedures to reclassify model suitability into presence/absence. We explored the effect of five different thresholds on our results, and although minor variability was apparent, broad-scale patterns were consistent regardless of threshold (Figures S4 and S5). This finding aligns with previous studies that have explored the influence of different habitat suitability thresholds on SDM outputs and identified broad alignment across thresholds (Crespo et al., 2018; van Beest et al., 2021).

5 | CONCLUSIONS: IMPLICATIONS FOR CLIMATE-RESILIENT FISHERIES

Our findings suggest that if MHW sizes increase in the future, impacts in core fishing grounds and fleet displacement could be substantial, particularly in regions where effort is highly concentrated into a single lucrative fishery (i.e. a 'gilded trap'; Fisher et al., 2020). The northeast Pacific, for example, has experienced the largest MHWs on record in the last decade (Hannah et al., 2021; Ross et al., 2021; Welch et al., 2023). However, whether this trend will continue with long-term warming is still uncertain. While the long-term warming trend should not be conflated with regional climate variability (Jacox, 2019; Xu et al., 2022), MHWs superimposed onto the long-term trend may create larger impacts for fisheries in the future (Pinsky, 2021). Top marine predators, such as sharks, tunas and billfish, are predicted to experience widespread habitat loss and redistribution in both the northwest Atlantic and northeast Pacific in response to climate change (Braun, Lezama-Ochoa, et al., 2023; Hazen et al., 2013). The combination of reduced encounters due to range shifts with temperature variability may lead to greater loss of fishing grounds or altered proximity to fishing ports during future MHW events, intensifying socio-economic stress on fishing communities (Pinsky et al., 2021; Rogers et al., 2019).

As the spatial footprint of fisheries is expected to be impacted in the future, anticipating the effects of extreme ocean events on fisheries and developing adaptive measures will be paramount to supporting climate resiliency in fisheries management (Holbrook et al., 2020). The diversity in MHWs and wide range of top predator responses across MHW events (Welch et al., 2023) poses a considerable challenge for fisheries management to design strategies that incorporate the dynamic spatial and temporal nature of ocean systems and the many anthropogenic ocean activities (Holsman et al., 2019; Lewison et al., 2015). This management challenge may be most acute in pelagic fisheries that use static approaches (e.g. time-area closures), which may be particularly ill-suited to extreme events that occur at finer temporal scales where mobile top predators can respond rapidly to anomalous ocean conditions (Holsman et al., 2019; Lewison et al., 2015). The disconnect between dynamic oceans and static fisheries management approaches will likely become more costly with more frequent, intense and larger MHWs (Oliver, Donat, et al., 2018; Oliver, Lago, et al., 2018). To effectively respond to future MHWs, there may be greater need to implement flexible management approaches that can adapt to changing and extreme conditions as they arise and align at scales relevant to environmental variability and human uses (Lewison et al., 2015).

Emerging dynamic ocean management approaches that can translate shifting environmental and ecological information into near real-time management recommendations has shown promise for mitigating risk during MHWs events (Hazen et al., 2018; Samhouri et al., 2021; Welch et al., 2019, 2023). The methods presented here could be used alongside operationalized tools that produce daily predictions of targeted or protected species to address MHW-driven impacts in real time, such as anticipating unwanted fishery interactions (i.e. bycatch) during MHWs (Crear et al., 2021; Welch et al., 2023). Furthermore, skilful forecasts of MHWs, with lead up times of 12 months, have recently become operational (Jacox et al., 2022) and can be integrated into our model framework to forecast future changes in fishing grounds. Such approaches can offer early warning to managers and fishing fleets at relevant time scales for decision-making (Brodie et al., 2023). Although existing adaptive strategies (e.g. 'adapt on-the-move', 'adapt in-place') used by fleets have shown promise for coping with and reacting to the impacts of MHWs (Fisher et al., 2020; Samhouri et al., 2023), forecasts for fleet distributions will allow for a proactive framework that can help keep pace with MHWs and aid in the development of climate-resilient fisheries.

ACKNOWLEDGEMENTS

We thank Global Fishing Watch for providing the fishing effort data used in this study and T. White for their technical support and assistance. We would also like to thank B. Muhling for their valuable comments and knowledge about the west coast albacore fishery, and Michael G. Jacox and the Conservation Ecology Lab at SDSU for discussion and comments on earlier versions of the manuscript. All authors were supported by NASA Ecological Forecasting Program (80NSSC19K0187) and N.F. was also support, in part, by the NOAA-Sea Grant Population and Ecosystem Dynamics Fellowship (G00013792).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

All fishing effort and environmental data used in this study are publicly available: Global Fishing Watch (https://globalfishingwatch.org/datasets-and-code/), HYbrid Coordinate Ocean Model (https://www.hycom.org/), and Optimum Interpolation SST (https://www.ncei.noaa.gov/products/optimum-interpolation-sst). Results from this study can be viewed and interacted with on the Fisheries and Climate Toolkit (FaCeT) dashboard (https://facet.research.gmri.io/heatwaves). Aggregated data to evaluate fleet responses and code from which acquiring data, analyses and Figures are presented in this paper are publicly available on: https://github.com/nfarchadi/heatwave_impacts_on_fisheries.

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How to cite this article: Farchadi, N., Welch, H., Braun, C. D., Allyn, A. J., Bograd, S. J., Brodie, S., Hazen, E. L., Kerney, A., Lezama-Ochoa, N., Mills, K. E., Pugh, D., Young-Morse, R., & Lewison, R. L. (2024). Marine heatwaves redistribute pelagic fishing fleets. *Fish and Fisheries*, *00*, 1–17. https://doi.org/10.1111/faf.12828