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ARTICLE

Evidence of Temperature-Driven Shifts in Market Squid *Doryteuthis opalescens* Densities and Distribution in the California Current Ecosystem

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Abstract
Climate change is impacting the abundance and distribution of marine resources. The consequences of these impacts are likely to alter trophic interactions between species within an ecosystem and affect fisheries opportunities for coastal communities. Market squid *Doryteuthis opalescens* comprise the largest fishery (by volume) in California, USA, and questions persist about whether the changing ocean conditions are leading to an increase in squid abundance in traditional fishing locations as well as marginal habitats in northern areas. To examine this potential phenomenon, we used fisheries-independent survey data collected by the National Marine Fisheries Service between 1998 and 2019 to develop a spatiotemporal model that estimates changes in the squid density from central California to northern Washington. We found a fivefold increase in the squid index of abundance across the entire spatial domain of the surveys during the sampling period, with the largest increases occurring in the Oregon and Washington strata. Although our model demonstrated that encounter rates and squid densities for the surveys increased in warmer and more saline waters, large shifts in squid distribution were only associated with deviations in ocean temperatures that could be characterized as marine heatwaves. This analysis adds to a growing body of work documenting the spatiotemporal response of marine resources to both long-term trends in warming ocean conditions and episodic events, such as marine heatwaves. Furthermore, it demonstrates the need for ecosystem assessment models with the ability to forecast changes in species distribution and abundance at spatiotemporal scales that are relevant for coastal fishing communities.

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A pressing question facing scientists and resource managers alike is how changing ocean conditions will affect the distribution of marine species. Shifts in spatial and temporal distribution can have large ecological and societal impacts. For example, species shifts can alter marine food web dynamics (Wells et al. 2016) and can affect the availability of targeted resources to the fishing industry, thus impacting coastal communities and economies (Pinsky et al. 2018; Rogers et al. 2019). Improving our understanding of how climate perturbations may affect the spatiotemporal distributions of marine organisms is seen as a key component to ecosystem-based fisheries management (Rogers et al. 2019; Thorson 2019a; Holsman et al. 2020).

In the California Current Ecosystem (CCE), located off the U.S. West Coast, the market squid *Doryteuthis opalescens* is an ecologically important species and its sensitivity to fluctuations in ocean conditions is well documented (Reiss et al. 2004; Zeidberg et al. 2006; Van Noord and Dorval 2017; Van Noord 2020). Market squid are pelagic and semelparous, with a life span of up to 1 year (Spratt 1979; Jackson and Domeier 2003). Their range spans from British Columbia, Canada, to Baja California, Mexico, with highest abundances occurring off the central and southern coasts of California (Wing and Mercer 1990; Vojkovich 1998). As one of the top-five most common prey items in predator diets in the CCE, market squid are an important conduit for the transfer of energy from low to high trophic levels (Szoboszlai et al. 2015). They feed primarily on small zooplankton, such as copepods and euphausiids, and provide sustenance for marine fishes, mammals, and seabirds (Chen et al. 1996; Zeidberg 2013; Van Noord and Dorval 2017). Market squid populations also experience large and rapid fluctuations in response to environmental conditions. For example, El Niño–Southern Oscillation cycles have been identified as an important driver of their size, growth, and population dynamics (Jackson and Domeier 2003; Reiss et al. 2004; Perretti and Sedarat 2016), and their abundance and distribution have been shown to expand and contract under warm and cool ocean conditions, respectively (Koslow and Allen 2011; Van Noord and Dorval 2017). Such changes in their abundance and distribution can affect their availability to predators and to fishing communities.

Market squid are a valuable resource for commercial fisheries and coastal economies on the U.S. West Coast. As a target species, the market squid has directly contributed (on average) to 22% (69,853 metric tons) of total annual landings volume and 12% of total annual ex-vessel revenue (US$47 million) over the last 20 years, making it a top-ranked species in U.S. West Coast fisheries (Heine 2017; Rogers-Bennett and Juhasz 2014; PacFIN, no date). Market squid are landed primarily in California, where they comprise the largest fishery by landings in the state; however, market squid catches are also incredibly volatile (Heine 2017). For example, statewide California catches increased from 2,800 metric tons in 1998 to 118,000 metric tons in 2000. Outside of California, landings have occurred in Oregon over the past 5 years (PacFIN, no date), with the initial increase in landings coinciding with anomalously warm ocean conditions associated with the 2014–2016 marine heatwave (MHW) in the northeast Pacific Ocean (Bond et al. 2015). Oregon squid landings still pale in comparison to those in California, yet the recent trend raises questions about how expected increases in ocean temperatures combined with MHWs (Di Lorenzo and Mantua 2016; Oliver et al. 2019; Laufkötter et al. 2020) may affect the abundance and distribution of market squid and their proximity to fishing areas and ports.

There is a growing number of examples of temperature-induced species distribution shifts in coastal marine ecosystems as spatial models and metrics are increasingly applied to monitoring data (e.g., Pinsky et al. 2013; Thorson et al. 2016a). These shifts are often manifested as a poleward expansion in a species' range or as a latitudinal change in a population's mean location (e.g., center of gravity [COG]). Both have important implications for marine fisheries. Range expansions can create opportunities for new fisheries at the leading edge of a species' range with poleward shifts in the COG, or they could close down existing infrastructure if the targeted resource becomes less available and less economically viable for fishing communities at the trailing edge of the species' range. Multiple studies have documented or projected changes in the distribution of squid populations with warming ocean temperatures in various marine ecosystems (e.g., Alabia et al. 2016; van der Kooij et al. 2016; Yu and Chen 2018). For example, recent research has shown increased market squid densities in Alaska during El Niño years; however, their persistence in these northern waters remains to be seen (Cavole et al. 2016).

Here, we use 22 years of fisheries-independent survey data to improve our understanding of the spatiotemporal dynamics of market squid in the northern region of the CCE. While this region represents only about 5% of the commercial market squid catch along the U.S. West Coast (Heine 2017), the surveys use the same gear type and represent a large geographic area across which the distribution of squid appears to be expanding. The main objectives of this study were to (1) develop a geostatistical model that generates inferences about the abundance and distribution of market squid in coastal waters from northern California to northern Washington, (2) estimate the range expansion and/or contraction based on the derived quantities for effective area occupied (EAO) and index of abundance, and (3) relate the variability in squid abundance and distribution to broad-scale ocean conditions over the past two decades.

METHODS

Data.— We obtained oceanographic and squid catch data from the Juvenile Salmon and Ocean Ecosystem Survey (JSOES) conducted by the National Oceanic and Atmospheric Administration (NOAA) Northwest Fisheries Science Center from 1998 to 2019 and the NOAA Southwest Fisheries Science Center (SWFSC) salmon survey (henceforth referred to as the "SWFSC survey") from 2010 to 2016 (Table 1; Figure 1). The sampling area was between the northern tip of Washington (48°13.7′N) and Newport, Oregon (44°40.0′N), for the JSOES and between Heceta Head, Oregon (44°00′N), and Pigeon Point, California (37°10′N), for the SWFSC survey. The sampling grid consisted of east–west transect lines with up to seven fixed stations (Figure 1). Both surveys sampled from 1.9 to 55.6 km (from 1 to 30 nautical miles) offshore in late June (JSOES) or from late June to early July (SWFSC). The surveys were designed such that the JSOES would end at Newport, Oregon, and then be continued by the SWFSC in the southern part of the grid.

We conducted survey trawls during the day using a 264 Nordic rope trawl (NET Systems, Bainbridge Island, Washington) with 3-m^2, foam-filled pelagic doors, each fitted with additional 90.7-kg-weight (200-lb) shoes (see NMFS 2008 and Krutzikowsky and Emmett 2005 for a complete description). Net dimensions while fishing were approximately 20 m wide × 18 m high at the mouth, 28 m wide at the tips of the wings (Brodeur et al. 2005; Emmett et al. 2006; Harding et al. 2011), and 200-m total length, with a 16-mm stretched-mesh knotless liner in the cod end. Trawl effort was defined by 30-min tows; however, for our purposes we used area swept as calculated either by the latitude and longitude between start and end points (JSOES) or by using a calibrated mechanical flowmeter (SWFSC survey; General Oceanics, Miami) and the effective width of the trawl opening. To calculate area swept, we chose the width at the mouth rather than at the wings. If squid catches were low, the individual squid were counted; however, if the squid catch was determined to be uncountable in the time between trawls, the total number of squid was estimated by multiplying the number of squid in a subsample that was either weighed or volumetrically measured by the number of subsamples in the total squid catch. The mantle lengths of up to 50 individuals

TABLE 1. Sample sizes for the total number of trawls conducted and the total number and percentage of trawls with positive catches (i.e., number of market squid captured was greater than zero) between 1998 and 2019, presented for each survey individually (Juvenile Salmon and Ocean Ecosystem Survey [JSOES] and Southwest Fisheries Science Center [SWFSC] survey) and in aggregate. The SWFSC survey was conducted from 2010 to 2016; therefore, no data are reported for the nonsurvey years.

	JSOES			SWFSC survey			Aggregate		
Year	Total	Positive	% Positive	Total	Positive	% Positive	Total	Positive	% Positive
1998	37	10	27				37	10	27
1999	49	13	27				49	13	27
2000	27	2	7				27	2	7
2001	47	7	15				47	7	15
2002	53	18	34				53	18	34
2003	64	22	34				64	22	34
2004	56	17	30				56	17	30
2005	43	5	12				43	5	12
2006	68	12	18				68	12	18
2007	52	2	4				52	2	4
2008	52	0	0				52	0	0
2009	50	1	2				50	1	2
2010	55	6	11	61	30	49	116	36	31
2011	54	10	19	68	23	34	122	33	27
2012	69	10	14	52	29	56	121	39	32
2013	50	6	12	54	41	76	104	47	45
2014	48	19	40	67	52	78	115	71	62
2015	45	32	71	66	51	77	111	83	75
2016	45	22	49	33	14	42	78	36	46
2017	52	16	31				52	16	31
2018	64	37	58				64	37	58
2019	50	39	78				50	39	78

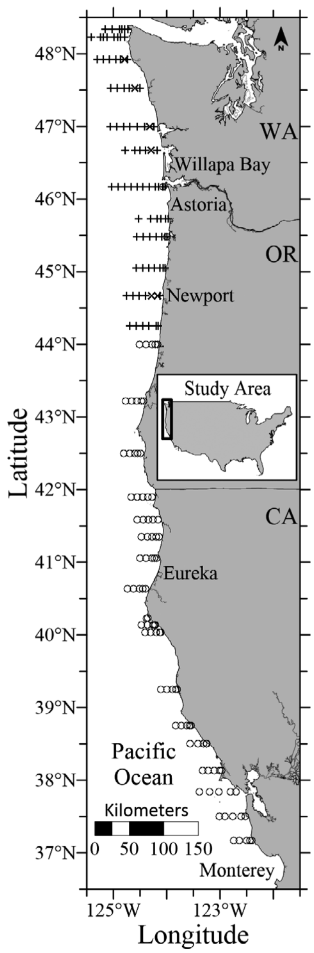

FIGURE 1. Market squid sample locations from the Juvenile Salmon and Ocean Ecosystem Survey ("+" symbols) and the Southwest Fisheries Science Center survey (open circles), or both ("x" symbols) 1998–2019.

were recorded for each trawl. Based on an initial analysis of the size distribution data (Figure S1 available in the Supplement separately online), we found little consistency in distinct length modes that would support separate analyses for squid cohorts. Market squid grow quickly, spawn continuously, and only live a maximum of 1 year (Spratt 1979), making it unlikely that an annual survey would detect cohort differences.

Environmental covariates (e.g., temperature and salinity) have been shown to affect the encounter rate and CPUE of squid in the North Pacific (e.g., market squid in the northeast Pacific: Koslow and Allen 2011; neon flying squid *Ommastrephes bartramii* in the northwest Pacific: Yu et al. 2016, 2020). At each station in our study, temperature and salinity were measured with a conductivity–temperature–depth profiling instrument (Sea-Bird Electronics, Inc., Bellevue, Washington) to within 5 m of the bottom or a maximum depth of 200 m, from which we extracted the average temperature and salinity for the top 20 m, corresponding to the 18-m height of the trawl. The absolute correlation between temperature and salinity averaged over the top 20 m was 0.6, which is less than the standard of 0.7 that suggests collinearity between two predictor variables.

We note that a marine mammal excluder device (MMED) was added to the SWFSC surveys from 2012 to 2016 and to the JSOES from 2014 to 2019 to prevent the capture of nontarget species. During different years, the MMED was placed in either an upward or downward position to test the effects. In paired trawls with and without the MMED in different positions, squid catches declined by 12% when the MMED was in an upward position and by 52% when the MMED was in a downward position (Wainwright et al. 2019). Therefore, we adjusted the total squid catches a priori for years with the MMED by using the catch ratios for the upward and downward positions (12% and 52%, respectively) as reported by Wainwright et al. (2019).

Spatiotemporal model.— To examine the distribution of market squid, we used the Vector-Autoregressive Spatio-Temporal (VAST) package in R (Thorson 2019b). The VAST model uses a geostatistical smoother to estimate the changes in squid densities and presence over space and time. For our analysis, we used VAST's geostatistical delta-generalized mixed model, which consists of two parts: the probability of encountering squid during a survey (i.e., encounter rate),

$$\Pr(c_i > 0) = \text{Bernoulli}(p_i; c_i > 0), \tag{1}$$

and the probability of positive densities if squid were encountered,

$$\Pr(C = c_i | C > 0) = \text{Gamma}\left(\sigma^{-2},\ r_i a_i \sigma^2; c_i\right). \tag{2}$$

For the ith sample, c_i is the observed number of squid captured, p_i is the predicted probability of positive catches, r_i is the expected density (number/km^2) of squid captured given positive catches with an offset a_i for the effort in square kilometers (i.e., the distance fished times the average width of the net [0.020 km]), and σ^2 is the observed error not explained by biological or environmental covariates (random variation in the spatiotemporal distribution of the catches). We chose the gamma distribution for its flexibility and regular use in describing the distribution of spatiotemporal population data (Thorson et al. 2015; Anderson et al. 2017).

The model assumes a logit link for the encounter rate,

$$\text{logit}(p_i) = \overbrace{\beta_p(t_i)}^{\text{intercept}} + \overbrace{\omega_p(s_i)}^{\text{spatial}} + \overbrace{\epsilon_p(s_i,\ t_i)}^{\text{spatiotemporal}} + \overbrace{\lambda_p(k) Q(i,\ k)}^{\text{catchability covariates}}, \tag{3}$$

and a log-link for the positive catch,

$$\log(r_i) = \overbrace{\beta_r(t_i)}^{\text{intercept}} + \overbrace{\omega_r(s_i)}^{\text{spatial}} + \overbrace{\epsilon_r(s_i,\ t_i)}^{\text{spatiotemporal}} + \overbrace{\lambda_r(k)Q(i,\ k)}^{\text{catchability covariates}}, \quad (4)$$

where β_p and β_r represent annual deviations in the encounter rate and positive catches, ω_p (s_i) and ω_r (s_i) are the expected spatial effects across all years, and ε_p (s_i, t_i) and ε_r (s_i, t_i) are the spatial deviations between years. The kth environmental or survey covariate for the ith observation is represented by $Q(i,\ k)$, and the $\lambda_p(k)$ and $\lambda_r(k)$ are the predicted effects of the covariates for the encounter rate and density, respectively (Table 2).

Model estimation, validation, and selection.— We followed Thorson's (2019b) 15-step decision tree when implementing the spatiotemporal model in the VAST package to explore various model structures (Table S1 available in the Supplement separately online). After a preliminary analysis to check that the fixed effects were identifiable and the parameters of the model were estimable for different model combinations, we chose a set of models that were focused on the effects of the environmental covariates, the surveys (with the two surveys treated as an aggregate survey or as separate surveys), and the treatment of the annual differences in squid presence and density (either constant across years, fixed for each year, random independent and identically distributed, or a random walk; Table 3). To compare the fit of the model combinations to the data, we used Akaike's information criterion modified for small sample sizes (AIC_c; Akaike 1974); we then validated the predictability of the top-two models. In total, we evaluated the fit of 16 different models using AIC_c and then compared the predictability using k-fold validation for the top-two models chosen by AIC_c. Additionally, we used goodness-of-fit tests in the DHARMa package to assess model misspecification (Hartig 2017).

Derived variables.— To estimate the changes in squid density and distribution, we derived variables for the COG, EAO (km^2), and total index of abundance (I_t) in year t over the survey domain. The I_t is the product of the estimated encounter rate for location s in year t ($p_{s,t}$), the density for location s in year t ($r_{s,t}$), and the area offset (a_s) for location s $\left(I_t = \sum_s a_s r_{s,t} p_{s,t}\right)$. Similarly, the COG and EAO are derived by dropping terms related to catchability (Thorson 2019b): the COG is based on the estimated densities but accounts for changes in sampling effort that may bias estimates in species shifts (Thorson et al. 2016a), while the EAO describes the area (km^2) necessary to contain a population based on the average density (biomass or number per km^2; Thorson et al. 2016b).

RESULTS

Accounting for the unbalanced temporal and spatial design of the SWFSC survey and JSOES, model 7 (Table 3) provided the most parsimonious fit to the data. This model suggested a large amount of geospatial variability for the encounter rate and squid density, no effect of survey (JSOES versus the SWFSC survey), and a positive relationship between the temperature and salinity covariates for the encounter rate and density of squid. Additionally, model 7 included a random walk for describing the annual differences for the encounter rates and density (Table 3).

With an AIC_c difference (ΔAIC_c) of 2.36, model 15 (Table 3) had the second-best fit to the data and provided a plausible explanation relative to model 7 (Burnham and Anderson 2004). This model was identical to model 7 but included an effect for survey. Model 15 estimated a 7% increase in squid encounters and a 170% increase in squid densities at a given location for the SWFSC survey. For 42 of the 50 k-fold cross validations, we found model 7 to

TABLE 2. Description of the model data, parameters, variables, and subscripts. The fixed-effect parameters governing the spatial and spatiotemporal random processes or the computed quantities used to estimate the anisotropy matrix (see the Supplement available separately online) are not listed here. See Thorson (2019b) for the complete description of the Vector-Autoregressive Spatio-Temporal (VAST) equations.

Model category	Symbol	Description
Indexes	t	Year
	s	Station where catches occurred
	k	Environmental covariate (e.g., salinity, temperature, survey)
Fixed effects	$\beta_p(t)$ and $\beta_r(t)$	Intercepts for the encounter rate (p) and positive catches (r) for year t
	$\lambda_p(k)$ and $\lambda_r(k)$	Coefficient relating the kth covariate to the encounter rate (p) and density (r) of squid catches
Random effects	$\omega_p(s)$ and $\omega_r(s)$	Spatial variability for the presence (p) and density (r) of squid catches
	$\varepsilon_p(s,\ t)$ and $\varepsilon_r(s,\ t)$	Spatiotemporal variability for the presence (p) and density (r) of squid catches
Covariates	$Q(i,\ k)$	The kth environmental covariate and/or survey effects observed during the ith survey tow

TABLE 3. Akaike's information criterion corrected for small sample sizes (AIC_c) and the AIC_c difference (ΔAIC_c) for the 16 models that did or did not include the effect of "survey" (Juvenile Salmon and Ocean Ecosystem Survey and Southwest Fisheries Science Center survey) and the environmental covariates (temperature and salinity) and the characterization of temporal variation for the intercepts (fixed annual, random independent and identically distributed [IID], random walk, or a fixed constant across all years) that were used to estimate the indices of abundance and distribution of market squid from fisheries-independent surveys conducted between San Francisco Bay, California, and Cape Flattery, Washington, from 1998 to 2019.

Model	Survey	Environmental covariates ($\lambda_p[k]$ and $\lambda_r[k]$)	Intercepts ($\beta_p[t_i]$ and $\beta_r[t_i]$)	AIC_c	ΔAIC_c
1	Not included	Not included	Annual	8,440.7	25.6
2	Not included	Not included	IID	8,439.2	24.1
3	Not included	Not included	Random walk	8,425.0	9.9
4	Not included	Not included	Constant	8,437.9	22.8
5	Not included	Included	Annual	8,427.8	12.7
6	Not included	Included	IID	8,428.9	13.8
7	Not included	Included	Random walk	8,415.1	0.0
8	Not included	Included	Constant	8,427.2	12.1
9	Included	Not included	Annual	8,441.5	26.4
10	Included	Not included	IID	8,441.8	26.7
11	Included	Not included	Random walk	8,427.7	12.6
12	Included	Not included	Constant	8,440.7	25.6
13	Included	Included	Annual	8,428.0	12.9
14	Included	Included	IID	8,431.0	15.9
15	Included	Included	Random walk	8,417.4	2.4
16	Included	Included	Constant	8,429.6	14.5

have a higher predictive ability (lower negative log-likelihood) relative to model 15 for the "out-of-bag" samples. In consideration of the cross validation and better fit to the data, we chose model 7 as the most parsimonious explanation of the observed squid survey data. An analysis of model fit based on the Kolmogorov–Smirnov, dispersion, and outlier tests in the DHARMa package (Hartig 2017) showed no evidence of model misspecification despite a small possibility that the model did not adequately capture some of the largest outliers (Figure S2).

The amount of geospatial variability in the distribution of market squid is evident in the variability in the encounter rates (Figures 2, S3) and squid density (Figures 3, S4) among years and the gradient of higher encounter rates and densities in the southern regions of the study domain (i.e., central California). The 4 years of predictions depicted in Figures 2 and 3 represent every 7 years in the time series data starting in 1998 through 2019 and years with differences in sea surface temperatures (Figure S5). Encounter rates and densities increased over the entire spatial domain from 1998 to 2019; however, we found larger increases in the squid densities for the northern strata of Oregon and Washington (25-fold and 39-fold, respectively) versus the California stratum (fourfold; Figure 4A), while the coastwide aggregate densities increased fivefold.

The addition of the temperature and salinity covariates in model 7 reduced the AIC_c by 9.94 relative to an identical model with no covariates (Table 3, model 3). The median values (and 95% confidence interval) for the observed temperature and salinity during the surveys were 11.3°C (8.3–14.6°C) and 32.1 psu (29.7–34.5 psu), respectively. Model 7 results showed that increases in temperature and salinity concentrations were positively correlated with the encounter rate ($\lambda_{p,temp} = 0.35$; $\lambda_{p,salinity} = 0.53$) and densities ($\lambda_{r,temp} = 0.52$; $\lambda_{r,salinity} = 0.46$). Specifically, a marginal 1°C increase in temperature resulted in a 16% increase in encounter rate and 34% increase in squid density, while a marginal 1 psu increase in salinity resulted in a 31% increase in encounter rate and a 45% increase in squid density.

Sea surface temperature anomalies over the 22-year period were variable from year to year, with an extreme cold event in 2008 and extreme heat events during 2014 and 2015, but the temperature deviations within a year were fairly consistent over the spatial domain (Figure S4). This may explain the synchronous increases in estimated squid indices across the California, Oregon, and Washington strata (Figure 4B) and the minimal change in the COG of surveyed squid densities in 18 of the 22 years (Figure 5A). However, between 2014 and 2016 and again in 2019, the COG shifted about 200 km north and about 50 km west (Figure 5A). When we compared the COG to estimates of the area and proximity to shore for MHWs, we found that the largest shifts occurred during years

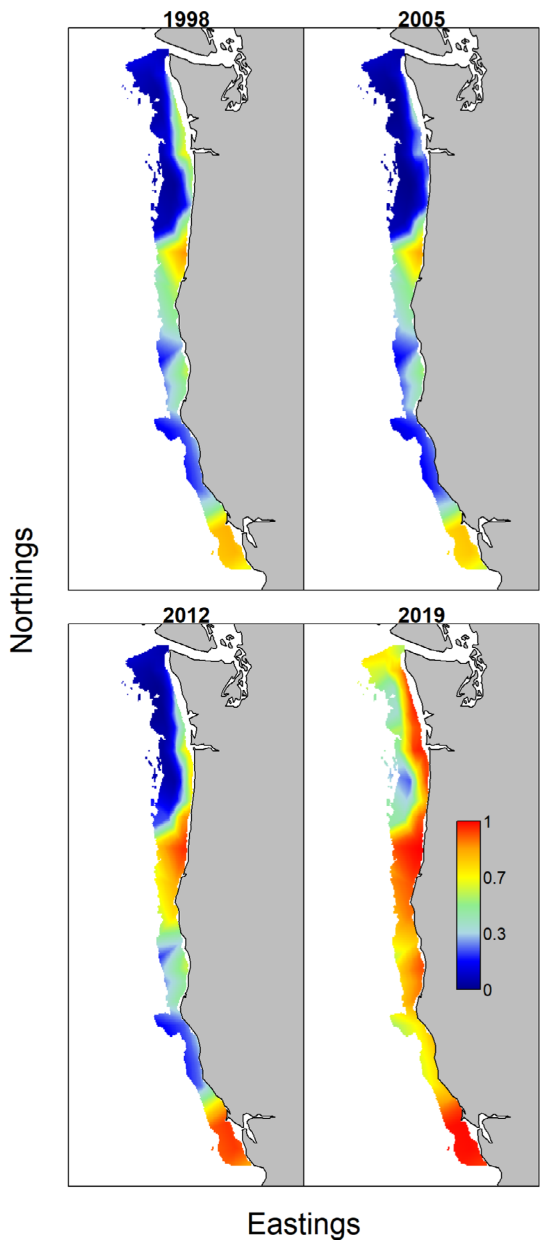

FIGURE 2. Estimated encounter rates for market squid based on fisheries-independent surveys conducted during 1998, 2005, 2012, and 2019. For the complete time series of predicted encounter rates, see Figure S2.

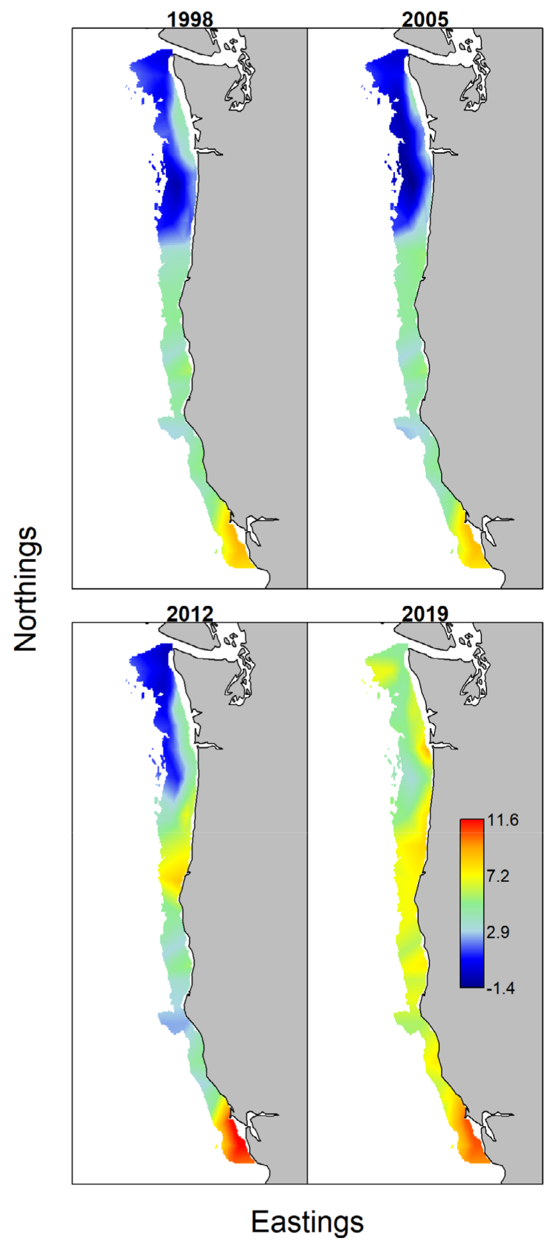

FIGURE 3. Estimated log-transformed densities (number/km^2) of market squid based on fisheries-independent surveys conducted during 1998, 2005, 2012, and 2019. For the complete time series of predicted market squid densities, see Figure S3.

when the heatwaves were very large in area and close to shore (Figure 5B).

To test whether these shifts may have resulted from a density-dependent process, we estimated the slope of the relationship between the natural logarithm of the estimated EAO and the natural logarithm of the estimated index of abundance for the aggregated West Coast densities assuming the same errors-in-variables approach of Thorson et al. (2016b): a slope equal to 1.0 supports a density-dependent response wherein squid are radiating outward from a core habitat, while a slope equal to zero supports a uniform increase associated with increased habitat (Thorson et al. 2016b). Based on the estimated EAO (Figure 6A) and index of abundance (Figure 6B), our model suggested that the increase in squid density across the survey domain was proportional (i.e., slope = −0.03; Figure 6C) and that the shifts were not a density-dependent process and perhaps represented an exogenous

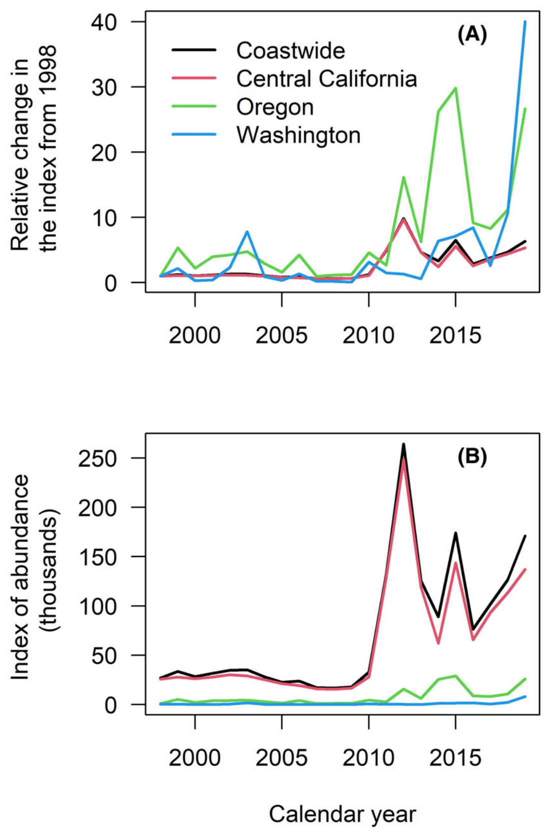

FIGURE 4. **(A)** Relative change in the estimated index of abundance and **(B)** the index of abundance for market squid in the aggregated coastwide domain and in central California, Oregon, and Washington strata.

forcing function associated with habitat changes (e.g., temperature and salinity).

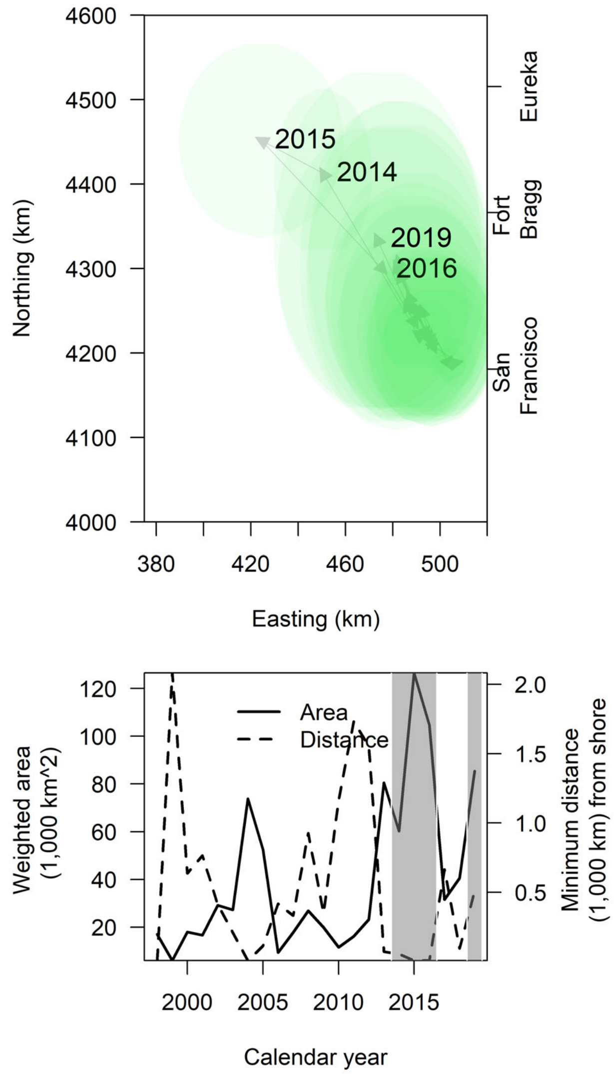

FIGURE 5. Estimated shifts in the center of gravity (COG; UTM northing and easting coordinates) for market squid surveyed between San Francisco Bay, California, and Cape Flattery, Washington, from 1998 to 2019 (upper panel); and estimates of the area and distance from shore for marine heatwaves (lower panel). Arrowheads (upper panel) represent the maximum likelihood estimates for the COG, and ellipses represent the confidence intervals of 1 SD. The gray shaded region in the lower panel highlights years with large deviations from the average COG in the upper panel, associated with extreme marine heatwaves. Descriptions of marine heatwave size and distance from shore can be found at the NOAA's California Current Marine Heatwave Tracker (https://www.integratedecosystemassessment.noaa.gov/regions/california-current/cc-projects-blobtracker).

DISCUSSION

After accounting for the temporal and spatial biases for two fisheries-independent surveys conducted over the last 22 years between Pigeon Point, California, and Cape Flattery, Washington, we found that the index of squid abundance has increased fivefold. While survey indices increased over the entire spatial domain, the largest relative increases occurred in the Oregon and Washington strata. Based on the increased indices and the EAO, market squid appear to be responding positively to warmer sea surface temperatures across the entire spatial domain rather than radiating outward from core habitat due to density-dependent processes (Figure 5). Furthermore, despite spatial differences in the increased densities across strata, we found warmer ocean conditions to be correlated with shifts in the COG; however, conditions during the MHWs appeared to amplify the environmental effects in the northern strata, leading to larger shifts in the squid distribution. Similarly, other surveys and models of squid density for the entire California coast have shown a marked increase in squid catches and density since 2004, and the catch for the northern portion of the state has risen steadily (Ralston et al. 2018).

Climate change is predicted to have major impacts on the distribution of marine resources and the communities

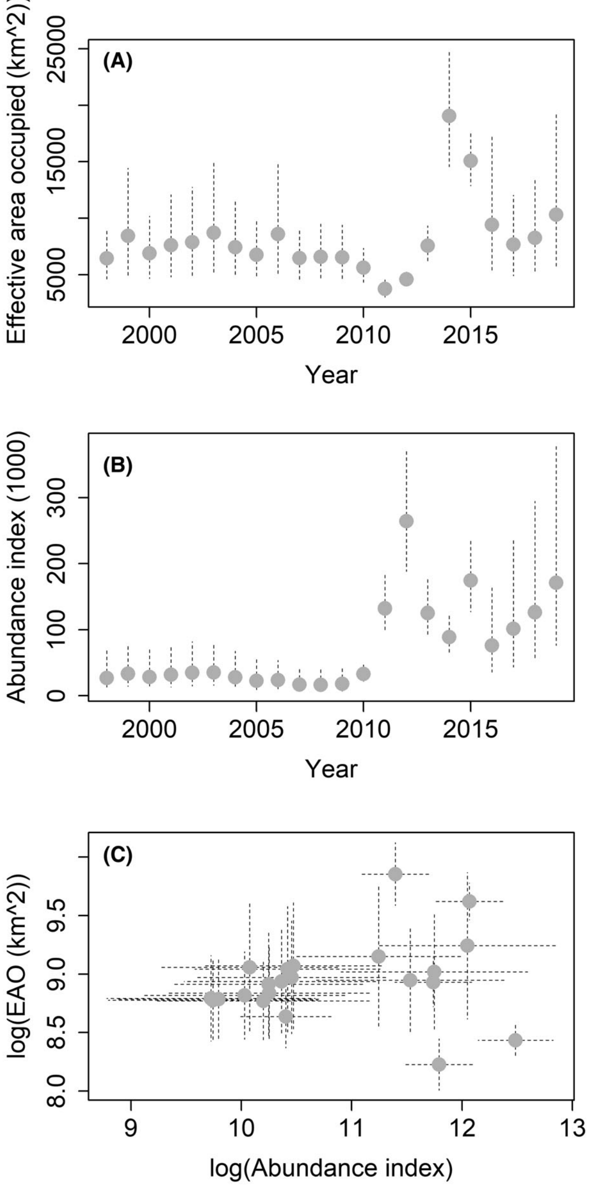

FIGURE 6. Annual estimates of **(A)** the effective area occupied (EAO; km^2) and **(B)** the index of abundance (thousands) for market squid collected during fisheries-independent surveys (Juvenile Salmon and Ocean Ecosystem Survey and Southwest Fisheries Science Center survey) between 1998 and 2019 in the nearshore waters of California, Oregon, and Washington; and **(C)** the relationship between the EAO and the abundance index. Uncertainty for the EAO and abundance index is represented by 1 SD (horizontal and vertical dashed lines).

they support (Pinsky et al. 2018; Rogers et al. 2019). Although much of the work on climate-induced distribution shifts has focused on habitat changes for demersal and reef species, our research demonstrates that at the margins of their distribution, small pelagic species like the market squid may be experiencing shifts (i.e., COG) or boundary expansions during extreme climate events, such as MHWs. Marine heatwaves are characterized by an intense amplification and duration of anomalously high sea surface temperatures over a large area (Di Lorenzo and Mantua 2016; Hobday et al. 2016). The shift in the COG for market squid during MHWs is not surprising given the documented northward shift in fish and other marine nekton in the CCE (Cavole et al. 2016; Morgan et al. 2019; Sanford et al. 2019). However, unlike the habitat models for demersal and reef fishes, it remains unclear whether the estimated COG shifts for pelagic species are due to changes in survival in response to changes in habitat or due to the redistribution of the population in response to ocean currents. Understanding the mechanism of the market squid population's response to MHWs is an important consideration for future research, as the frequency of extreme warming events is likely to increase with future carbon emissions levels (Frölicher et al. 2018), which will make MHWs an important component of fisheries management scenarios.

Shifts in market squid distribution could have real consequences for fisheries and coastal communities along the U.S. West Coast. The market squid fishery is routinely the largest fishery in California economically (PacFIN, no date); thus, population shifts could have large economic impacts on the state and region. Historically, the market squid fishery catches in California have decreased during periods of warm ocean conditions, such as strong El Niño events (Zeidberg et al. 2006). This trend has continued with recent El Niños: a strong El Niño event in 2015–2016 was followed by two weak events in 2017–2018 and 2018–2019, resulting in lower squid landings in California. The MHW that began in 2014, coupled with early El Niño signals, also decreased landings in southern California and pushed squid landings northward in California (PFMC 2020). Conversely, the Oregon fishery for market squid has been sporadic; periods of strong El Niños have coincided with increases in fishery activity in Oregon as well. Temporal indices of abundance for California in our model may not coincide directly with decreased catches during each of the previous El Niño events due to the spatial coverage of our survey (Figure 4A); however, increases in the estimated indices for Oregon and Washington do appear to coincide strongly with increased catches and fishery participation (PFMC 2019).

The squid fishery in Oregon appears to be increasing effort in response to the long-term increases in squid densities and short-term fluctuations. While no commercial landings of squid occurred in Oregon during 2015, they increased from 1,260 metric tons in 2016 to a record 4,667 metric tons in 2020. The ex-vessel revenue for this fishery exceeded \$1.1 million dollars in 2016 and reached almost \$6 million dollars in 2020 (PacFIN, no date). Although the California market squid fishery remains more economically significant, with ex-vessel revenues averaging \$34.4 million between 2015 and 2020, continued landings in

Oregon could support a rapidly growing fishery for market squid (PacFIN, no date).

Surveys of fishermen in "wetfish" fisheries (e.g., coastal pelagic fishes and squid) along the central coast of California identified early warning systems as a key goal for increasing their adaptability to shifts in species distribution and abundance caused by climate forces (Aguilera et al. 2018). The preparedness of fishing communities to such shifts will require improvements in spatiotemporal forecasting models and the ability to combine information from multiple biological surveys (Maureaud et al. 2021). Evidence from Haltuch et al. (2019) also suggests that including environmental drivers in modeling frameworks will be critical for estimating the strength of marine species' recruitment to commercial fisheries. Our model, which combines data from two fisheries-independent surveys and environmental covariates to make inferences about market squid abundance and distribution, is a step toward achieving that goal of an early warning system for the squid fleet. However, the environmental covariates in our model are treated as catchability covariates that describe the relationship between encounter rates and density due to sampling biases. Future research should consider treating temperature and salinity as habitat covariates that would allow researchers to forecast the distribution and density of market squid on the U.S. West Coast under future climate scenarios. Furthermore, although our model estimates the effects of temperature and salinity on the survey catches for market squid, we only make heuristic comparisons to MHWs, which are likely to affect the density of market squid. Future iterations of squid distribution models should aim to incorporate information on a broader suite of regional drivers to identify the specific mechanisms driving spatiotemporal variability (Thorson 2019a).

The selection of the random walk model (Table 2, model 7) as the most parsimonious fit to the data has important implications for future management scenarios. While treating the annual intercepts for the year effects as random processes to reflect the full uncertainty and estimating temporal correlation are important for improving model fit, we recognize that the ability to estimate the correlation coefficient in fisheries data is difficult for data sets encompassing less than 40 years and is often biased toward extreme values (Johnson et al. 2016).

Given that stock assessment practitioners recommend integrating multiple data streams to make inferences about stock status (ICES 2013; Maunder and Punt 2013), future advice about the expansion of the market squid population should be used cautiously when based on two fisheries-independent surveys designed for juvenile pelagic fishes occurring at the margins of the squid distribution. Market squid are known to have strong diurnal patterns, with spawning adults diving toward the seabed during daylight hours (Forsythe et al. 2004; Zeidberg et al. 2012); the daytime data collected from surface tows during the JSOES and SWFSC survey may be biased toward a specific life stage. Furthermore, the two surveys in our analysis only overlap from 2010 to 2016, which means that the estimates of the squid encounter rates and densities for 1998–2009 and 2017–2019 are based on spatial autocorrelation with the JSOES and environmental covariates (i.e., salinity and temperature). The VAST package has the ability to integrate multiple gear types to improve estimates of fish density (Grüss and Thorson 2019), and future squid assessments might consider other West Coast surveys that capture squid eggs, larvae, and or adults, albeit using different sampling methods (Peterson et al. 2010; Ralston et al. 2018).

Estimates of standardized catch indices are meant to account for biases in the sampling and survey design (Maunder and Punt 2004). For our part, we focused on the spatiotemporal biases in the surveys and effects of a small number of environmental covariates that are likely to influence the catches. Additional biases exist based on the gear, vessel, and crew that were used: the JSOES used the F/V *Frosti* in 18 of the 22 years, while the SWFSC used the R/V *Ocean Starr* to conduct the majority of its surveys. However, during years with vessel changes, overlaps occurred for the science crews and vessel crew leads. Based on our best available knowledge when addressing these potential biases, we chose to assume that there was no crew bias or vessel bias between years. We could compare the spatiotemporal synchrony for the JSOES and SWFSC catches; however, with little spatial overlap and given the small number of years of data for the SWFSC survey, models comparing the temporal synchrony of the two surveys failed to converge during preliminary analyses.

Advancing the understanding of market squid population dynamics is essential to maximize economic gains and effectively manage fishery effort in the CCE as ocean conditions continue to change. Our results corroborate previous findings that squid productivity and distribution can respond rapidly to environmental shifts, especially extreme events such as MHWs, which has also been shown previously for commercially important forage species in the CCE, including Pacific Sardine *Sardinops sagax*, Northern Anchovy *Engraulis mordax*, and Pacific Chub Mackerel *Scomber japonicus* (Checkley et al. 2009; Lindegren et al. 2013). This research only adds to a growing body of work highlighting the biological response of market squid to a changing environment (Dorval et al. 2013; Navarro et al. 2018) and how those responses may affect fisheries (Ish et al. 2004; Ralston et al. 2018). Future avenues of research should include examining the mechanistic drivers of distribution shifts exhibited by market squid and other forage species and should consider how future ocean conditions will shape the availability of squid as both prey to predators and harvest for coastwide fishing fleets.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.