






Original Article

Temperature and upwelling dynamics drive market squid (*Doryteuthis opalescens*) distribution and abundance in the California Current

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Market squid (*Doryteuthis opalescens*) constitute one of California's largest fisheries by landings and are an essential prey item for numerous top predators in the California Current ecosystem. However, extreme fluctuations in market squid abundance inhibit our ability to forecast local recruitment. We generate a species distribution model for market squid with data from an annual survey to examine the mechanisms behind the variability in their regional abundance and occurrence. Our results indicate juvenile market squid abundance was controlled by local recruitment in connection with sea surface temperature and upwelling dynamics, with finer spatial variability connected to the extent of upwelling dominated regions. Recent changes in these environmental factors also appear to contribute to the recent northward range expansion of market squid. Our spatiotemporally explicit model estimates of juvenile market squid abundance predicted the occurrence and abundance of older market squid in the diet of California sea lions (*Zalophus californianus*) and California fishery landings with as much skill as regional survey indices, suggesting the models are robust. Collectively, we provide mechanisms driving market squid variability throughout California's waters and an ecosystem assessment of this economically and ecologically critical species.

Keywords: fisheries, market squid, predator-prey interactions, recruitment, species distribution model.

Introduction

Forage species are an important trophic link from bottom-up processes to higher trophic levels and fisheries. Market squid (*Doryteuthis opalescens*) are important forage for fish, seabirds, and ma-

rine mammals throughout the California Current Ecosystem (CCE; Lowry and Carretta, 1999; Becker *et al.*, 2007; Glaser *et al.*, 2014; Warzybok *et al.*, 2018) and often are California's largest fishery by landings (Heine, 2017). Market squid are a predominately shallow water (~10–100 m), coastal semi-pelagic species that aggregate in

large spawning shoals and have been targeted by fisheries since 1863 (Fields *et al.*, 1965). With the decline of Pacific sardine (*Sardinops sagax*) biomass since 2010, the California wetfish fleet has shifted from a multispecies fishery to one focused primarily on market squid (Aguilera *et al.*, 2015). Annual ex-vessel value of market squid has exceeded \$70 million several times from 2010 to 2020, making it a species of great economic importance (Free *et al.*, 2022). Despite the combined observations of high variability in abundance and landings and its considerable commercial importance, market squid ecology is relatively understudied. This is both a regional and global management challenge, as high variability in catches, abundance, and distribution, often assumed to be largely driven by environmental factors, is typical of most of the world's largest cephalopod fisheries (Rodhouse *et al.*, 2014; Arkhipkin *et al.*, 2015; Sobrino *et al.*, 2020; Moustahfid *et al.*, 2021). The increasing reliance of the commercial fishery on market squid, their role as forage for predators such as California sea lions (*Zalophus californianus*), and their changing distribution has resulted in a need to better understand the causes of fluctuations in their abundance and distribution throughout California's waters (Chasco *et al.*, 2022).

Market squid are unique among coastal pelagic forage species of the southern and central CCE because they are extremely short-lived and semelparous, living 6–9 months and undergoing benthic egg deposition during spawning (Fields *et al.*, 1965; Butler *et al.*, 1999; Macewicz *et al.*, 2004). The species typically ranges from 25°N to 50°N within the CCE (Roper *et al.*, 1984), with most of the biomass of the species predominately occurring between 32°N and 38°N (Zeidberg *et al.*, 2006). However, the range of the species has fluctuated dramatically recently, with an episodic expansion up to the Gulf of Alaska (Chasco *et al.*, 2022). The population structure of market squid along this latitudinal gradient remains an open question, with the species currently treated as a single population that spawns throughout the year during appropriate environmental conditions (Reichow and Smith, 2001). Recent genetic research supports this consideration while also indicating that there is potential for “micro-cohorts” (in which there are greater genetic similarities over small temporal scales, e.g. 1–2 months) throughout the range of market squid (Cheng *et al.*, 2021).

Market squid abundance—and their corresponding prevalence in predator diets and the magnitude of commercial landings—exhibit a large degree of variability due to their short lifespan and high sensitivity to environmental conditions (Jackson and Domeier, 2003; Lowry and Carretta, 1999; Dorval *et al.*, 2013; Ralston *et al.*, 2018). Documented drivers of abundance and fishery landings include El Niño Southern Oscillation (ENSO) cycles influencing survival at the paralarval stage (Perretti and Sedarat, 2016), variability in benthic egg deposition and survival (Zeidberg *et al.*, 2011, 2012; Van Noord and Dorval, 2017), and prey availability (Ralston *et al.*, 2018). Understanding the effect of these combined environmental drivers on squid recruitment has been of increasing interest due to the recent range expansion of market squid to more northern CCE areas (e.g. increased abundance off Oregon, periodic observations in Alaska; Burford *et al.*, 2022; Chasco *et al.*, 2022). Increasing fishing pressure has also coincided with increased variability of landings (Ralston *et al.*, 2018). The leading predictor of market squid variability has been temperature in the upper 20 m, which appears to have contributed to the brief range expansion during a marine heatwave (Chasco *et al.*, 2022). However, temperature alone is unable to explain the interannual variability in landings and abundance of market squid within its core range of Monterey Bay

(~37°N) to the Southern California Bight (~32°N), of which the latter has oceanographic dynamics generally distinct from the rest of the CCE (Checkley and Barth, 2009). This has collectively resulted in a need to synthesize the multiple known drivers of variability in market squid abundance and explore new hypotheses to predict their range and abundance fluctuations.

Species distribution models (SDMs) can elucidate the relationships between a species' occurrence and abundance with environmental conditions. SDMs have been used in multiple case studies throughout the CCE to better understand fisheries catch anomalies of swordfish *Xiphias gladius* (Brodie *et al.*, 2018) and the essential habitat of important prey species (Muhling *et al.*, 2019; Cimino *et al.*, 2020). An advantage of SDMs is their ability to predict species occurrence in areas and time periods that surveys miss, allowing for refined estimates of species abundance despite uneven sampling in space and time (Thorson *et al.*, 2020; Elith and Leathwick, 2009; Guisan and Thuiller, 2005). However, most species distribution models do not incorporate indices of recruitment or mechanisms driving recruitment variability despite the strong effects these may have on both the probability of occurrence and the local abundance of a species (Thorson *et al.*, 2021). Incorporation of these processes is essential for garnering a mechanistic understanding of the drivers of a species' distribution, abundance, and catchability for fisheries and predators (Selden *et al.*, 2020; Muhling *et al.*, 2020). Identifying these mechanisms can also allow models to better perform in novel spatiotemporal domains which is essential for a species with a shifting range and high sensitivity to environmental conditions (Burford *et al.*, 2022; Chasco *et al.*, 2022).

The short life span and high fecundity of market squid lead to little autocorrelation in local annual abundance indices (Ralston *et al.*, 2018; Santora *et al.*, 2021) and notable “boom-bust” variability throughout California coastal waters (Figure 1). While the Southern California Bight constitutes their core range—and the area of greatest fishing intensity and landings—localized abundance and landings of market squid in more northerly areas such as Monterey and Half-Moon Bay can rival those to the south in certain years (Ralston *et al.*, 2018). However, the timing of these landings differs, with squid fishing in the regions north of the Southern California Bight peaking in May through August, while southern California landings occur predominantly in October through January (Free *et al.*, 2022). Given this seasonal separation, the fishing season spans multiple cohorts (seasonal pulses of recruitment or productivity) each year, resulting in a need to understand mechanisms driving squid recruitment and abundance for each region and season (Cheng *et al.*, 2021). Market squid also serve as critical forage for California sea lions in the Southern California Bight, who consume market squid at a greater frequency than almost any other prey item (Lowry and Carretta, 1999; Lowry *et al.*, 2022). California sea lion populations have been recovering from historical exploitation and culling since the 1970s (Laake *et al.*, 2018), thus predation pressure on market squid by sea lions (and likely other predators) has been steadily increasing as well. Improved understanding of the drivers of market squid abundance is thus a priority given their economic and ecological value within the CCE.

Here, we use a long-term epipelagic micronekton survey throughout California's coastal waters in spring/summer to assess the drivers of market squid abundance and distribution using a combination of oceanographic influences on recruitment and contemporaneous oceanographic model estimates. Specifically, we hypothesize that thermal conditions and upwelling dynamics during the early life stages of market squid, including benthic egg depo-

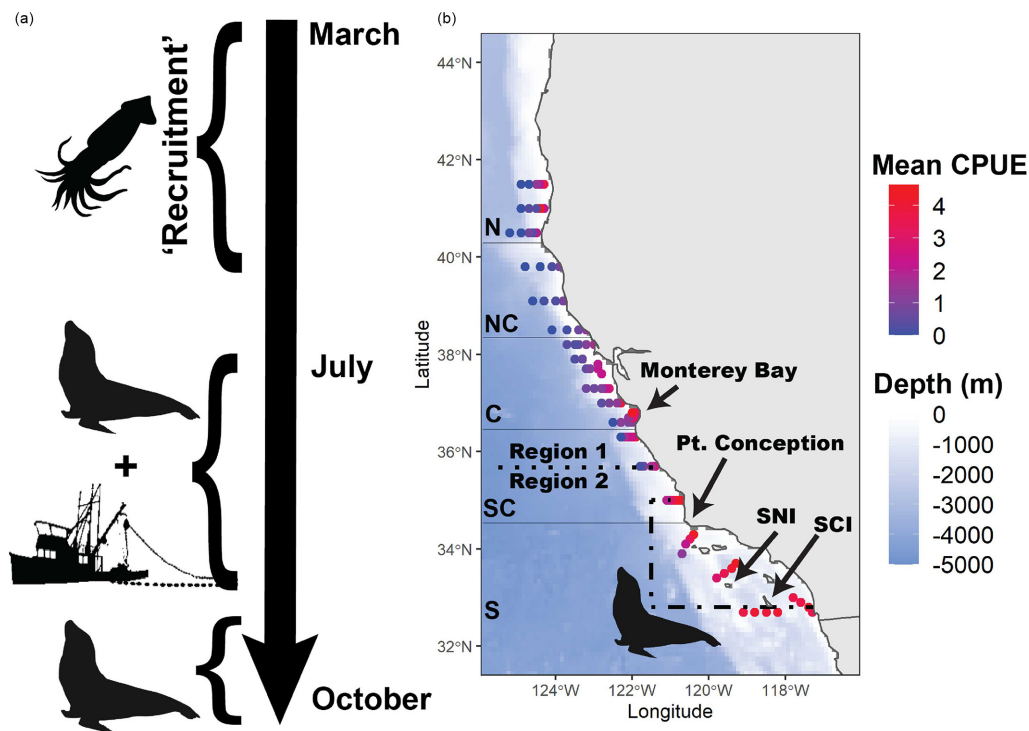


Figure 1. (a) Schematic diagram of the modelling method used in this work, with a recruitment and hurdle model generated based on conditions before and during a spring/summer fishing-independent survey. Model estimates are subsequently validated against California sea lion diets in the summer and fall and fishing landings in the summer. (b) Map of Rockfish Recruitment and Ecosystem Assessment Survey stations with mean catch-per-unit-effort (CPUE; log-scale) for each fixed station location from 1998 to 2021 (exact sampling may occur within ~ 1 nm of these locations). Boundary used to compare with California sea lion diets in dashed line with the two rookeries used for diet comparison (SNI = San Nicolas Island; SCI = San Clemente Island). The dotted line indicates the latitudinal boundary used to separate Region 1 and Region 2 for fishery landings. Strata boundaries are indicated by thin solid lines (N = North, NC = North Central, C = Core, SC = South Central, S = South).

sition, drive regional abundance of the juvenile squid observed in the survey. We also hypothesize that the distribution and abundance of market squid on smaller (~ 10 km) scales is driven by both their overall recruitment during spring/summer and local environmental conditions such as temperature, chlorophyll-*a*, and bottom depth. We evaluate and compare our model estimates of juvenile market squid distribution to survey data not used in model training and to the distribution of larger size classes observed in summer market squid landings and the diet of California sea lions in the summer and fall (Figure 1a). Our work provides an improved understanding of market squid dynamics throughout the southern and central CCE, serving as an integrated portfolio product that combines inference from an SDM with assessment of predator and fishery responses.

Material and methods

Survey data and market squid collections

We estimated the abundance and distribution of juvenile market squid from collections by the National Oceanic and Atmospheric Administration-National Marine Fisheries Service Rockfish Recruitment and Ecosystem Assessment Survey (RREAS). The survey began in 1983 as a “pre-recruit” survey of pelagic young-of-the-year rockfish (and other groundfish) sampling from late April through June to inform stock assessments with indices of incoming year

class strength and to provide insights for recruitment process studies (Ralston and Howard, 1995, Ralston *et al.*, 2013). Sampling was limited to a “core” region (36.5°N – 38.3°N) between 1983 and 2004, at which point sampling expanded to cover the majority of California coastal waters, leading to the addition of three more strata: “north central” (38.3°N – 40.2°N), “south central” (34.5°N – 36.5°N), and “south” (32.5°N – 34.5°N). The final stratum, “north” (38.3°N – 41.5°N), was added in 2013. Fixed trawl sampling stations are typically sampled two to three times each year (hauls), resulting in 80 hauls per year on average from 1998 to 2003 (time period used for “core” stations only), and a mean of 119 hauls per year for 2004–2021 (except 2020 when sampling was reduced, see Santora *et al.*, 2021; Figure 1b; Supplementary Table S1).

Collections were made using a modified Cobb midwater trawl with a 9.5 mm cod-end liner, fished at a 30 m headrope depth, corresponding to a swath of water column between a depth of 30 and 45 m (Ralston *et al.*, 2013; Sakuma *et al.*, 2016). All trawling was conducted during hours of total darkness to minimize net avoidance. The standard tow duration is 15 min, and nearly all micronekton collected—including market squid—were reliably enumerated starting in 1990 (Sakuma *et al.*, 2016). This survey provides an informative estimate of juvenile market squid abundance for individuals generally in the range of 20–50 mm mantle length in late spring (Ralston *et al.*, 2018; Supplementary Table S2). The midwater trawl, and the general design of the survey, followed that of

Table 1. Hypotheses for each variable used in the formation of three squid models [recruitment, presence(P)/absence(A), and abundance].

Model	Variable	Units	Hypothesis	Reference
Recruitment	Mean March–June SST	°C	Spawning habitat, growth, and survival	Vidal <i>et al.</i> , (2002); Zeidberg <i>et al.</i> , 2011, 2012
	Mean March–June meridional current	m s ⁻¹	Advection of individuals and upwelling	Cimino <i>et al.</i> (2021)
	Relaxation events	Count	Transport of primary production shoreward	Supplementary Material
	Intermediate upwelling days	Num. Days	Generation of primary production without excessive turbulence	Cury and Roy (1989)
	January, February, March Oceanic Niño Index (JFM ONI)	°C	Shifts in productivity and thermal dynamics prior and during spawning	Perretti and Sederat (2016)
	Mean March–June wind stress curl	N m ⁻³	Generation of “slow” upwelling and production	Ryckazewski <i>et al.</i> (2008)
	Spring transition index in Biologically Effective Upwelling Transport Index (BEUTI)	Day of Year	Initiation of regional net production altering timing of growth	Jacox <i>et al.</i> (2018); Bograd <i>et al.</i> (2009)
	Mean March–June chlorophyll-a	mg m ⁻³	Productivity during growth period affecting growth and survival	Wheeler <i>et al.</i> (2017)
P/A and Haul-specific abundance	Recruitment estimate	Mean abundance	Drives overall abundance leading to variable interannual occurrence	Suca <i>et al.</i> (2021)
	Sea surface temperature (SST)	°C	Thermal preference	Muhling <i>et al.</i> (2019, 2020); Brodie <i>et al.</i> (2018)
	Std. Dev. of sea surface temperature (SST_sd)	°C	Indicator of thermal fronts	Muhling <i>et al.</i> (2019, 2020); Brodie <i>et al.</i> (2018)
	Sea surface height (SSH)	m	Indicator of divergence and convergence	Muhling <i>et al.</i> (2019, 2020); Brodie <i>et al.</i> (2018)
	Std. Dev. of sea surface height (SSH_sd)	m	Indicator of fronts	Muhling <i>et al.</i> (2019, 2020); Brodie <i>et al.</i> (2018)
	Total kinetic energy (TKE)	m ² s ⁻²	Preference for strength of current regimes	Muhling <i>et al.</i> (2019, 2020); Brodie <i>et al.</i> (2018)
	Wind stress curl	N m ⁻³	Generates localized divergence and convergence	Muhling <i>et al.</i> (2019, 2020); Brodie <i>et al.</i> (2018)
	Depth	m	Depth association	Muhling <i>et al.</i> (2019, 2020); Brodie <i>et al.</i> (2018)
	Rugosity	m	Association with shifts in bathymetry such as sea mounts	Muhling <i>et al.</i> (2019, 2020); Brodie <i>et al.</i> (2018)
	Coastal Upwelling Transport Index (CUTI)	m ² s ⁻¹	Aggregation/disaggregation in response to upwelling	Benoit-bird <i>et al.</i> (2019); Jacox <i>et al.</i> (2018)

an earlier survey that was developed and designed to sample coastal pelagic fishes as well as market squid (Mais, 1976, Show and Hill, 2021).

The timing of market squid spawning varies substantially in space, with spawning in the Southern California Bight taking place largely between October and May, while in central California, spawning generally begins in April and ends in October (Butler *et al.*, 2003, CDFG, 2005). However, both spawning activity and fishing catches are highly variable in both regions, and both can take place at any time of the year (CDFW, 2005; Jackson and Domeier, 2003, Navarro *et al.*, 2018). The survey thus captures a subset of the spawning output of market squid for a given year, with this spawning output representing a varying proportion of total reproductive output within a given year.

Model formation

Framework

We modelled the abundance and distribution of juvenile market squid using a three-step modelling approach: a stratum-specific recruitment model; a presence/absence model; and a haul-specific abundance model (the latter two comprising a traditional hurdle model; Potts and Elith, 2006; Steel *et al.*, 2013). Each component is complementary while simultaneously representing different processes of market squid dynamics: (1) recruitment preceding the survey; (2) suitability of habitat allowing a squid to occupy a location; and (3) localized aggregation behaviour that modulates haul-specific catch observations. An advantage of the three-step approach is that model output for each step may have utility for different comparisons, including population-scale dynamics (recruitment), predicted shifts in habitat occupancy (presence/absence), and local catchability (haul-specific abundance; Suca *et al.*, 2021). The stratum-specific recruitment model serves to identify the drivers of overall abundance of market squid in a survey stratum linked to interannual variability in spawning and paralarval and juvenile growth/survival conditions leading up to and during the sur-

vey. This component of the model serves to account for larger scale environmental and biological processes that drive overall abundance. This is particularly important for species with large abundance fluctuations, such as coastal pelagic species (including semi-pelagic species like market squid), that can exhibit a decoupling of habitat suitability and occurrence (Suca *et al.*, 2021). We note that we call this model component “recruitment” to represent the abundance of juvenile squid (typically, <50 mm dorsal mantle length; Ralston *et al.*, 2018) in the CCE during the time of the survey. This is different from recruitment to the fishery, which nearly exclusively targets spawning adults (120–150 mm dorsal mantle length) using purse or drum seine gear (Roper *et al.*, 1984; Macewicz *et al.*, 2004). The presence/absence component of the framework identifies survey stations where shoals of market squid are likely to occur, which is linked to the overall abundance of market squid as well as oceanographic conditions in each region (Suca *et al.*, 2021). The haul-specific model predicts squid abundance at positive stations using environmental drivers and overall abundance in the stratum from the recruitment model, both of which are assumed to influence squid shoaling dynamics. The combination of these modelling components was ultimately used to predict juvenile market squid abundance throughout California coastal waters. Estimates of stratum-specific “recruitment” were used as predictors within the presence–absence and haul-specific abundance models, which combined represent a traditional hurdle model. Our analyses spanned 1998–2021 as these years match the start of the SeaWiFS satellite chlorophyll record.

Environmental predictors

Environmental predictors for squid models are derived from a data-assimilative Regional Ocean Modeling System (ROMS) built for the CCE (Moore *et al.*, 2011; Neveu *et al.*, 2016). The model contains 42 vertical-terrain-following layers and spans the range from 30°N to 48°N and shore to 140°W at 0.1° horizontal resolution. Predictors vary by model component and were constrained to surface variables (both hydrographic and derived; Table 1) due to poor agreement among subsurface model estimates and survey observations (Supplementary Methods; Supplementary Figure S1).

The RREAS collects *in situ* environmental data, which have been used in prior assessments of juvenile rockfish abundance and micronekton biodiversity (Schroeder *et al.*, 2014, 2019; Santora *et al.*, 2017). Extensive evaluation of RREAS collections has been made with physical oceanographic variables from both *in situ* sampling and ROMS, demonstrating the utility of the model for monitoring the variability of micronekton (Schroeder *et al.*, 2014). Therefore, we used ROMS fields to incorporate additional variables and greater spatiotemporal coverage to investigate squid distribution and abundance. Daily ROMS environmental predictors were matched based on sampling time and location (at the 0.1° by 0.1° spatial scale and daily level) in the presence/absence and haul-specific abundance models (Cimino *et al.*, 2020). We considered a suite of predictors that can collectively describe the mesoscale oceanography and interannual variability of the CCE: SST, sea surface height, wind stress curl, total kinetic energy, standard deviation (*SD*) of SST, and *SD* of sea surface height (Table 1). The exception to the spatial matching scale is for *SD* of sea surface height and SST, which were taken at the 0.3° by 0.3° level, and wind stress curl, which was re-gridded to a 0.5° by 0.5° grid to generate agreement between a ROMS historical re-analysis (1980–2010) and a ROMS near real-time product

(2011–present) (Brodie *et al.*, 2018). These were combined with the Garver–Siegel–Maritorena (GSM) model surface chlorophyll-*a* estimates from the GLOBcolour database using level 3 fields at 4 km resolution (Fanton d’Anton *et al.*, 2009). This model merges data from various satellites when available and provides the best fit to *in situ* chlorophyll-*a* observations (Maritorena and Siegel, 2005). We also used static variables, including depth-related variables derived from the ETOPO1 Global Relief Model: bottom depth and rugosity (defined as *SD* of depth at a 0.3° by 0.3° scale; Table 1).

Derivations of daily upwelling dynamics were used as predictors, namely metrics derived from the coastal upwelling transport index (CUTI) and the biologically effective upwelling transport index (BEUTI; Jacox *et al.*, 2018). CUTI represents the balance of wind-forced upwelling combined with the effects of geostrophic flow along the coast, representing a more accurate index of coastal upwelling relative to the Bakun Index (Jacox *et al.*, 2018). In the case of BEUTI, transport is scaled according to nitrogen upwelling to represent the amount of nutrients available to primary producers (Jacox *et al.*, 2018). Both CUTI and BEUTI are calculated in 1° latitudinal bins.

Three derivations of upwelling conditions were predictors in the “recruitment” model. The first is the spring transition index, representing the day of the year in which integrated BEUTI (starting from January 1) reaches its minimum and thus represents the day in which upwelling transitions to a positive regime in terms of available nutrients (Bograd *et al.*, 2009). The second derivation is the number of upwelling “relaxation” events, where a “relaxation” event occurs when a daily CUTI exceeding 1.0 m² s⁻¹ is followed by three or more consecutive days of CUTI values <0.5 m² s⁻¹. Relaxation events are proposed to serve as a mechanism for enrichment, concentration, and retention of chlorophyll and other biogenic materials (Lasker, 1981; Bakun, 1996). The third metric was defined as the proportion of days in which CUTI values fall between 2.0 and 0.5 m² s⁻¹, representing the frequency of days with “moderate” upwelling, which may allow for sufficient primary productivity while not generating too much turbulence or offshore transport such that production is disrupted or pushed away from the coast (i.e. optimal environmental window hypothesis; Cury and Roy, 1989).

Recruitment model

Recruitment was defined as stratum-specific mean log abundance and was modelled as a Tweedie distributed variable. This value, ln(catch + 1), was deemed catch-per-unit-effort (CPUE) following previous studies using these data (Santora *et al.*, 2012; 2017). We used generalized additive models (GAM) with thin-plate regression splines using the *mgcv* package (Wood 2006) in R (version 4.0.4), with each stratum/year combination treated as an observation. Predictor variables were restricted to mean values over March–June as this corresponds to the likely time of spawning and growth for squid collected in the survey (Ralston *et al.*, 2018). Predictors included hydrographic variables (SST), upwelling indicators (relaxation events, spring transition index, moderate upwelling days), chlorophyll-*a*, and climate indices (e.g. Oceanic Niño index). Each predictor included corresponds to a potential hypothesis for fluctuations in market squid recruitment and regional distribution throughout California’s coastal waters (Table 1). All predictors, except those for upwelling, were averaged from the shore to the maximum distance from the shore sampled by the survey (~100 km from the nearest land, including the Channel Islands)

and bounded by the maximum and minimum latitude sampled for the given strata from March to June. This spatial extent corresponds to that of the response variable (stratum-specific abundance) and the spawning and growth window of squid collected in the survey.

A suite of eight candidate models representing alternative hypotheses were formed and each possible combination of predictors within those models was fit using the dredge function within the *MuMIn* R package (Table 2; Barton and Barton, 2015). The foundation of the eight models originated from hypothesized mechanisms driving squid recruitment based both on existing studies on market squid or other coastal pelagic taxa. The differences in individual models represent the possible combinations of non-collinear predictor variables ($r < 0.6$). Region-specific by-smooths were included for SST and wind stress curl. Primary productivity is likely to respond differently to these drivers within the Southern California Bight versus the region north of Point Conception due to differences in hydrography across this boundary (Hickey, 1979; Parrish et al., 1981; Checkley and Barth, 2009). Thus, regions for these by-smooths were defined as north and south of Point Conception.

Each candidate “recruitment” model (Table 2) followed the following general formula:

$$\begin{aligned} CPUE_{ij} &= tw(\mu_{ij}, P_{ij}) \\ \log(CPUE_{ij}) &= \alpha + f_1(Env. Pred._{1ij}) + f_2(Env. Pred._{2ij}) \dots \\ &+ f_n(Env. Pred._{nij}) + \varepsilon_{ij} \\ \varepsilon_{ij} &\sim Gamma(1, \nu), \end{aligned} \quad (1)$$

where mean *CPUE* in a given stratum *i* and year *j* is treated as a variable following a tweedie distribution with mean μ and a tweedie power parameter P . f_n represents a thin plate regression spline for environmental predictor *n*. ε represents the Gamma noise parameter with mean 1 and scale parameter ν .

Models were ranked using the AIC, where models with a $\Delta AIC < 2$ from the best fit model were considered to have substantial support (Burnham and Anderson 2002). Predictions from models with a $\Delta AIC < 2$ were then averaged to account for uncertainty in variable selection using the *model.avg* function within the *MuMIn* R package (Barton and Barton, 2015).

Models were trained using 1998–2016 collections and tested on collections from 2017 to 2021, representing $\sim 75/25$ test-train split. Strata with < 5 hauls each year (3 of 80 strata/year combinations) were excluded from model formation to avoid bias in variable selection through the inclusion of these under-sampled strata (Supplementary Table S1). Predictions using the model ensemble were then compared to strata-specific abundance estimates from 2017 to 2021 (“test” set) to assess the model’s out-of-sample predictive capability. Model performance was evaluated through the R^2 and root-mean-square-error (RMSE) of the model’s predictions over 2017–2021. Due to the low number of predictors and models used in the ensemble, variable importance was evaluated through ΔR^2 and $\Delta RMSE$ for the training and test sets, as the SW would be unable to discern variable importance (see below).

Presence/absence model

Juvenile market squid presence/absence (*P/A*) was modelled as a binomially distributed variable using GAMs with thin-plate regression splines where individual hauls represent observations. Lunar illumination was included as a predictor due to the nighttime sampling scheme of the survey and the documented effects of lunar illu-

mination on the catchability of numerous species (Bos and Huamano, 2012; Scales et al., 2017). Predictions from the recruitment model were also included as predictors to account for variability in overall abundance and drive presence. Splines for this predictor were constrained to three knots as opposed to six for other environmental predictors, to force a biologically plausible response.

Eight candidate models were formed, and each possible combination of predictors within those models was fit using the dredge function within the *MuMIn* package (Barton and Barton, 2015; 1.46.0; Table 3). Sea surface height and SST ($r = 0.64$), total kinetic energy, and *SD* of sea surface height ($r = 0.63$), and CUTI and wind stress curl ($r = 0.69$) were collinear. The eight different models thus represent each possible combination of non-collinear predictor variables. We used multi-model averaging for models whose $\Delta AIC < 2$ different from the “best” fit model.

Each candidate model for the *P/A* component (Table 2) followed the following general formula:

$$\begin{aligned} PA_{ijk} &= binomial(n_{ijk}, p_{ijk}) \\ \text{logit}(PA_{ijk}) &= \alpha + f_1(\widehat{CPUE}_{ij}) + f_2(Env. Pred._{1ijk}) \\ &+ f_3(Env. Pred._{2ijk}) \dots \\ &+ f_n(Env. Pred._{nij}), \end{aligned} \quad (2)$$

where *PA* (presence–absence) within stratum *i*, year *j*, and haul *k* are treated as binomially distributed variables with a number of trials (hauls) *n*, and a number of successes (presence) *p*. f_n represents a thin plate regression spline for environmental predictor *n*. \widehat{CPUE} represents the estimate of mean *CPUE* in stratum *i* and year *j* (“recruitment”) from Equation (1) for the given year and stratum that each haul occurs.

As with the recruitment models, presence/absence models were trained using 1998–2016 collections and tested on collections from 2017 to 2021, representing $\sim 75/25$ test-train split. Predictions using this multimodel ensemble were then compared to presence/absence data from 2017 to 2021 (“test” set) to assess the model’s out-of-sample predictive capability. Model performance was evaluated through receiver operating characteristic curves, namely the area under the curve (AUC). AUC values range from 0 to 1, with values close to 1 indicating high model skill and values of 0.5 indicating a model no better than random chance. The Northwest Fisheries Science Center Pre-Recruit Survey data (same mid-water trawl and sampling schema) were also used as an evaluation set (dataset description in supplement) to test the model’s predictive skill in a novel spatial domain (NWFSC, 2022).

Variable importance was evaluated using Akaike weights through the following formula:

$$w_i = \frac{\exp\left[-\frac{1}{2}\Delta_i\right]}{\sum_{i=1}^n \exp\left[-\frac{1}{2}\Delta_i\right]}, \quad (3)$$

where Δ_i represents the difference in AIC of a particular model from the model with the lowest AIC. The sum of these values for each variable was then calculated, resulting in the “sum of Akaike weights” (SW hereafter), with values close to 1 indicating high variable importance and those close to 0 representing low importance (Giam and Olden, 2016).

Table 2. Candidate models and minimum Akaike Information Criterion (AIC) within the combinations of each candidate model for the “recruitment” model.

Model	Mean SST	SST by region	Mean BEUTI	BEUTI by region	BEUTI STI	Relax. events	Mean chl-a	Mean WSC	Mean WSC by region	Int. upwelling	JFM ONI	Min. AIC
1	X				X	X	X	X		X	X	166.93
2		X			X	X	X	X		X	X	168.43
3		X			X	X	X		X	X	X	169.50
4	X				X	X	X		X	X	X	169.33
5			X		X	X	X	X		X	X	176.79
6				X	X	X	X	X		X	X	174.62
7				X	X	X	X		X	X	X	175.11
8			X		X	X	X		X	X	X	177.06

Xs indicate the variable was included in the given model. Abbreviations correspond with those presented in Table 1. Note minimum AIC may correspond to a model fit using a subset of predictors within the given candidate model.

Table 3. Candidate models and minimum AIC within the combinations of each candidate model for the presence/absence and haul-specific abundance components of the full hurdle-model.

Component	Model	Recruitment	SSH	SST	SSH SD	SST SD	WSC	Chl-a	TKE	CUTI	Depth	Rugosity	Lunar illum.	Lon, Lat	Min. AIC
P/A	1	X		X	X	X	X	X			X	X	X	X	1 611.80
	2	X	X		X	X	X	X			X	X	X	X	1 603.55
	3	X		X		X	X	X	X		X	X	X	X	1 612.94
	4	X	X			X	X	X	X		X	X	X	X	1 605.51
	5	X		X	X	X		X		X	X	X	X	X	1 631.66
	6	X	X			X		X		X	X	X	X	X	1 617.32
	7	X		X		X		X	X	X	X	X	X	X	1 634.58
	8	X	X			X		X	X	X	X	X	X	X	1 621.79
Abundance	1	X		X	X	X	X	X			X	X	X	X	9 814.16
	2	X	X		X	X	X	X			X	X	X	X	9 805.84
	3	X		X		X	X	X	X		X	X	X	X	9 810.29
	4	X	X			X	X	X	X		X	X	X	X	9 803.55
	5	X		X	X	X		X		X	X	X	X	X	9 839.06
	6	X	X		X	X		X		X	X	X	X	X	9 828.72
	7	X		X		X		X	X	X	X	X	X	X	9 822.57
	8	X	X			X		X	X	X	X	X	X	X	9 816.67

Acronyms are defined in Table 1.

Haul-specific abundance model

Juvenile market squid haul-specific abundance in units of catch per tow was modelled as a negative-binomially distributed variable with GAMs using thin-plate regression splines. Individual tows where market squid were caught represented observations (i.e. positive stations only). Predictor variables and candidate models followed exactly those of the presence/absence models (Table 1).

Each candidate model for the haul-specific abundance component (Table 3) followed the following general formula:

$$\begin{aligned}
 Catch_{ijk} &= Neg. binomial(\mu_{ijk}, \theta_{ijk}) \\
 \log(Catch_{ijk}) &= \alpha + f_1(\widehat{CPUE}_{ij}) + f_2(Env. Pred._{1,ijk}) \\
 &\quad + f_3(Env. Pred._{2,ijk}) \dots \\
 &\quad + f_n(Env. Pred._{n,ijk}) + \varepsilon_{ijk} \\
 \varepsilon_{ijk} &\sim Gamma(1, \theta),
 \end{aligned}
 \tag{4}$$

where catch for haul *k* within stratum *i* during year *j* is treated as a negative binomially distributed variable with a mean μ , and dispersion parameter θ . f_n represents a thin plate regression spline for environmental predictor *n*, along with error ε . \widehat{CPUE} represents

the estimate of mean CPUE in stratum *i* and year *j* (“recruitment”) from Equation (1) for the given year and stratum that each haul occurs. ε represents the Gamma noise parameter with mean 1 and dispersion parameter θ .

Models were trained, tested, and averaged using the same time windows and thresholds as the presence/absence model. The Pre-Recruit Survey data (for the Oregon and Washington areas) were not used due to the limited number of stations with market squid presence and a larger size distribution of squid captured in this survey relative to the RREAS collections (Supplementary Figure S2). Model performance was evaluated through the R^2 and RMSE of the model’s predictions over 2017–2021 (data that was outside of the time window used for model formation and selection).

We recognize that utilizing previous model estimates as data has the potential to introduce bias, result in compounding errors that may reduce model fit, and produce estimates whose statistical uncertainty is under-estimated. To understand the sensitivity of our model to using model estimates as if they were raw data, we compared the model fit of both the presence/absence and hurdle models using “recruitment” point estimates to model fit using the upper 95% estimate, lower 5% estimate, point estimate + standard error, and point estimate—standard error. For the presence/absence com-

ponent, AUC was used as the metric of model fit. R^2 and RMSE were used as metrics of model fit for the hurdle model. We also assessed the potential effects of random error in recruitment estimates on model fit. We randomly sampled a value for the recruitment estimate within the 95% CI for each stratum and year and recorded the model's AUC (P/A), R^2 , and RMSE. We repeated this process 100 times to generate 100 AUC, R^2 , and RMSE values. We report the minimum, mean, and maximum metrics of model fit based on these approximations of error to represent the presence/absence and hurdle model's sensitivity to uncertainty in the recruitment estimate.

Trends with time

We computed the linear trend in habitat suitability (presence/absence model) and predicted abundance (log-scale; hurdle model) for each 0.1° by 0.1° grid cell throughout California's coastal waters to identify regions of greatest change. Annual estimates were taken for each grid cell from June to October, with 1998 representing the first year and 2021 the final year of model estimates. Individual grid slopes were calculated with linear regression.

External data comparison and model evaluation

California sea lion diet comparison

Historical observations have shown that market squid form a major component of California sea lion diets in the Southern California Bight (Lowry and Carretta, 1999). A comparison of the model predictions with diet information was thus an opportunity to assess whether the modelled market squid distribution and abundance were reflected in predator foraging ecology. Hurdle model estimates of CPUE [$\ln(\text{catch} + 1)$] and mean probability of occurrence estimates were compared to observations of California Sea lion diet from San Nicolas and San Clemente Island rookeries (SNI and SCI, respectively). We use CPUE rather than expected catch due to the large degree of variability in the observed catch of market squid, as is common with small pelagic species (Suca et al., 2021). Diet estimates come from a time series of scat collections from sea lion rookeries on each of these islands (Lowry et al., 1990, 1991, 1999, 2022). Scat samples were collected with at least quarterly resolution from each island from 1981 onward, representing prey consumed within the 1–3 d prior (Orr and Harvey, 2001; Sweeney and Harvey, 2011). Collections occurred primarily in areas occupied by females and juveniles, though some male collections occurred. Observation of prey in the scat included identification, enumeration, and measurement of hard parts, specifically beaks in the case of market squid.

Hurdle model estimates of CPUE [$\ln(\text{catch} + 1)$] and mean probability of occurrence estimates within the feeding ranges of each rookery were averaged over July–August and October, matching the time window of summer [mean number of scats per year for years used: SCI = 49.44 (31–61), SNI = 100.1(89–104)], and fall [mean number of scats in years used: SCI = 49.25 (38–55), SNI = 100.1(96–104)] scat collections, respectively (Figure 1). We used contemporaneous environmental predictors during these time windows for comparisons, while the “recruitment estimates” were intra-annually static. We aimed to see if juvenile habitat was able to reflect the habitat of subsequent adult squid, which the California sea lions were feeding on. The feeding ranges for both islands were bounded by $32.8\text{--}35^\circ\text{N}$ and waters east of 121.5°W , corresponding with the predominant range of feeding sea lions from these rookeries (Briscoe et al., 2018; Melin Pers. comm.). For each

rookery, mean hurdle model estimates of CPUE and mean probability of occurrence were compared with the frequency of occurrence of squid beaks in scats using beta regression in the *betareg* R package (version 4.0.4; Zeileis et al., 2016). The mean number of squid per scat sample was also compared to mean hurdle model estimates of CPUE and mean probability of occurrence through log-normal regression, due to skew in the data.

A major advantage of SDMs is their ability to provide indices of abundance in regions and times when survey data are not available. We therefore compared the ability of an index of abundance for the southern stratum generated from station level catches of market squid in the RREAS (Ralston et al., 2018) versus our hurdle model to predict the mean number of squid per scat sample, and the frequency of occurrence of squid beaks. Briefly, the index of abundance was generated using a delta-GLM with year and station as the main effects and represents our best index of local squid abundance to date (Ralston et al., 2018). This comparison allows us to see if the model can provide a robust representation of market squid abundance, and subsequent consumption by California sea lions, when survey data are not available. Quality of fit to the California sea lion diet data was determined through R^2 and p -values (significance at $\alpha = 0.05$).

Distribution of market squid landings

Market squid landings from the California Department of Fish and Wildlife (CDFW) were summed from July to September (quarter 3) for regions north and south of 35.67°N (Figure 1b; Supplementary Table S3). Landings data were recorded at both the port scale (where the squid are landed) and at the fishing block scale (where the squid were caught). We used landings data aggregated at the port-scale due to confidentiality clauses leading to discrepancy in total landings when looking at block level data.

Model predictions of abundance from the hurdle-model within each CDFW region were averaged from July to September for each year to compare with quarter 3 landings from 1998 to 2019, following the lag between the survey and expected landings used in previous research (Ralston et al., 2018), and aiming to test the same logic as using the comparison of model estimates with California sea lion diet data. While total landings by region were utilized as the response variable, model values were only considered for in-shore fishing blocks that averaged >5 landings per year. We chose these filters so as to not skew model estimates by including areas that largely go unfished and to exclude areas in which landings are reported but are too far offshore—in waters too deep—to plausibly represent areas in which market squid fishing occurs (Supplementary Figure S3). We also grouped CDFW's Region 3 landings into Region 2 as the majority of market squid caught in Region 3 is landed in Region 2, thus Region 3 blocks need to be included to accurately recreate Region 2 port-scale landings (Supplementary Figure S4).

Mean estimated market squid CPUE by CDFW region was compared with the interannual variability in quarter 3 landings of each region through log-normal linear models. We also analysed spatial shifts in relative landings through a comparison of the proportion of landings occurring in Region 1 compared to cumulative landings with the equivalent fraction of model estimated CPUE within

Table 4. Models used for averaging within each model component and measures of fit from the model ensembles.

Model stage	Model	AIC	Model avg. train R^2 (AUC)	Model avg. train RMSE	Model avg. test R^2 (AUC)	Model avg. test RMSE
Recruitment	Mean SST, relaxation events, JFM ONI	166.93	0.724	0.894	0.758	0.773
	Mean SST by region, relaxation events, JFM ONI	168.43				
	Mean SST, relaxation events, JFM ONI, wind stress curl	168.90				
Presence/Absence	Recruitment estimate, SSH, lunar illum., depth, wind stress curl, SST sd, SSH sd, longitude \times latitude	1603.55	0.890		0.865	
	Recruitment estimate, chlorophyll- <i>a</i> , SSH, lunar illum., depth, wind stress curl, SST sd, SSH sd, rugosity, longitude \times latitude	1604.74				
	Recruitment estimate, SSH, lunar illum., depth, wind stress curl, SST sd, SSH sd, rugosity, longitude \times latitude	1604.77				
	Recruitment estimate, chlorophyll- <i>a</i> , SSH, lunar illum., depth, wind stress curl, SST sd, SSH sd, longitude \times latitude	1604.85				
Haul-specific abundance	Recruitment estimate, chlorophyll- <i>a</i> , SSH, lunar illum., depth, wind stress curl, SST sd, longitude \times latitude	1605.53	0.323	2.145	0.167	2.337
	Recruitment estimate, chlorophyll- <i>a</i> , SSH, lunar illum., depth, wind stress curl, SST sd, TKE, rugosity, longitude \times latitude	9803.55				
Hurdle model	P/A avg \times haul-specific avg		0.478	2.167	0.389	2.409

R^2 and RMSE used for recruitment and haul-specific abundance models. Area under receiver operating characteristic curve (AUC) used for presence–absence models.

Table 5. Difference in model fit without each component predictor of the recruitment model for both the training set (1998–2016) and test set (2017–2021).

Variable	ΔR^2 train	Δ RMSE train	ΔR^2 test	Δ RMSE test
Sea surface temperature	0.294	0.386	0.423	0.493
Relaxation events	0.090	0.132	0.000	0.032
Ocean Nino Index	0.234	0.322	– 0.108	0.035
Wind stress curl	0.037	0.068	0.057	0.098

Region 1 through the following equation:

$$\log \frac{P(Landings_{R1})}{1 - P(Landings_{R1})} = \beta_0 + \beta_1 * P(Model CPU E_{R1}) + \epsilon, \tag{5}$$

where $P(Landings_{R1})$ represents the proportion of landings occurring in Region 1, treated as a beta-distributed variable, and $P(Model CPU E_{R1})$ represents the proportion of modelled CPUE within Region 1 compared to the full California coastline.

We also compared models fit to regional landings using indices of squid abundance from the south stratum for Region 2, and a mean of the north central and core strata for Region 1, with those fit from hurdle model estimates to understand if our model is better able to predict regional landings than survey indices alone. The quality of fit to the regional landings data was determined through R^2 and p -values.

Results

Recruitment model

Three models, containing four total variables, resulted in $\Delta AIC < 2$ values. These models were averaged and used to generate predictions of recruitment (Table 4). Changes in R^2 and RMSE values showed mean SST as the most important variable, followed by the January–March Ocean Niño Index, relaxation events, and

mean wind stress curl (Table 5). The model fit to the training set ($R^2 = 0.72$; RMSE = 0.89) and test set ($R^2 = 0.78$; RMSE = 0.78) was strong (Figure 2).

Mean SST had a linear positive effect on stratum-specific recruitment at values between 10 and 16°C (Figure 3a). High values of January–March ONI (strong El Niño events) had a negative effect on stratum-specific recruitment, with no pattern present for large negative January–March ONI values (strong La Niña events; Figure 3b). The frequency of upwelling relaxation events had a positive, linear effect on stratum-specific recruitment, although the effect size was lower than that of mean SST (Figure 3c). High levels of mean wind stress curl had a negative effect on stratum-specific recruitment, though uncertainty was high and the effect size was low (Figure 3d).

Presence/absence model

The presence/absence model ensemble was composed of eight component models (Table 4). Variables included, in decreasing order of importance by SW, were as follows: “recruitment” estimate, longitude and latitude tensor product, wind stress curl, sea surface height, depth, lunar illumination, SD of SST, chlorophyll-*a*, rugosity, and SD of sea surface height (Table 6). Model fit to training and test data were both high, with AUC values of 0.887 and 0.867, respectively. Model fit to the NWFSC Pre-Recruit Survey was fair (AUC = 0.748).

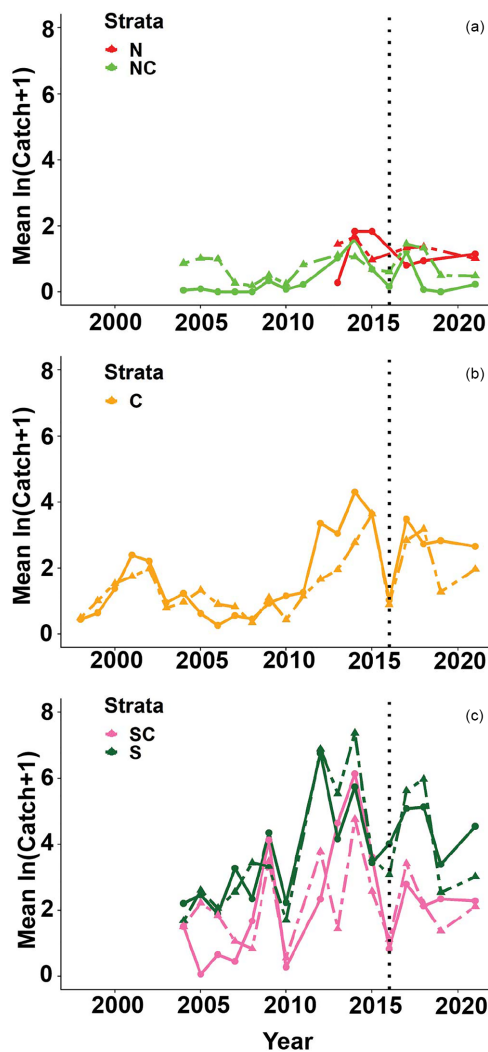


Figure 2. Comparison of strata-specific abundance from the survey (solid lines) and results from the recruitment model estimates (dashed lines) through time for (a) north and north-central strata, (b) core stratum, and (c) south and south-central strata. A vertical dotted line indicates separation between training and test data sets.

Table 6. SW for each predictor within the presence/absence and haul-specific abundance models.

Variable	P/A SW	Haul-specific SW
Recruitment	1	1
Chlorophyll- <i>a</i>	0.461	1
Wind stress curl	1	1
SSH	1	1
SSH SD	0.527	NA
SST SD	1	1
Depth	1	1
Rugosity	0.561	1
TKE	NA	1
Lunar illum.	1	1
Lon, Lat	1	1

All variables other than chlorophyll-*a*, rugosity, and *SD* in sea surface height were highly important ($SW > 0.9$). Recruitment estimates had a positive, log-linear effect on the probability of occurrence (Figure 4a). Wind stress curl had a positive relationship with the probability of market squid occurrence (Figure 4b). Sea surface height had a negative linear relationship with the probability of occurrence (Figure 4c). The probability of occurrence was highest at shallow depths, with no observable effect at depths > 500 m (Figure 4d). High values of lunar illumination (full moon) had a negative effect on the probability of occurrence of market squid, indicating decreased catchability (Figure 4e). The probability of market squid occurrence peaked near intermediate values of *SD* of SST (Figure 4f).

Haul-specific abundance model

The haul-specific abundance model was a single model and not an ensemble (no other models had a $\Delta AIC < 2$; Tables 4, 6). Variables included in this model are “recruitment” estimates, longitude and latitude tensor products, lunar illumination, chlorophyll-*a*, sea surface height, wind stress curl, rugosity, *SD* in SST, total kinetic energy, and depth (Table 6). Model fit was poorer than recruitment for both the training set ($R^2 = 0.324$; RMSE = 2.141) and the test set ($R^2 = 0.167$; RMSE = 2.337). Combined hurdle estimates (probability of occurrence \times abundance estimates) fit the training ($R^2 = 0.478$; RMSE = 2.167) and test sets ($R^2 = 0.389$; RMSE = 2.409) similarly.

Recruitment estimates had a similar partial effect within the abundance model to that of the presence/absence model, with a log-linear relationship levelling off at ~ 4 mean CPUE (Figure 5a). Increasing chlorophyll-*a* values had a positive effect on haul-specific catch from ~ 0 to 8 mg m^{-3} , decreasing afterward (Figure 5b). Sea surface height had a negative linear relationship with catch (Figure 5c). Catch was highest at shallow depths, with no observable effect at depths > 500 m (Figure 5d). Lunar illumination showed a decreasing effect on haul-specific catch at values > 0.6 (Figure 5e). Catch had a positive relationship with the *SD* of SST, wind stress curl, and total kinetic energy (Figure 5f, g, and i). Catch had a bimodal positive relationship with rugosity around values of 300 and 800 m (Figure 5h).

Model fit for both the presence/absence model and the hurdle model was nearly insensitive to simulated error in the recruitment estimate (Supplementary Table S4). The poorest model fit occurred when using the upper 95% estimate of recruitment as a predictor, with R^2 declining to 0.41, RMSE increasing to 3.01, and AUC only declining to 0.88. Model fit metrics for randomly sampled error within recruitment estimates generally produced model fit metrics close to the model created with point estimates, with a mean (range) AUC of 0.87 (0.86–0.89), R^2 of 0.43 (0.39–0.47), and RMSE of 2.39 (2.27–2.52; Supplementary Table S4).

The spatial climatology of hurdle model predictions estimated high abundances of market squid throughout the Southern California Bight and in coastal regions to the north, such as Monterey Bay, with little to no predicted abundance in offshore waters or northern coastal waters outside of prominent bays (Figure 6a). Hurdle model estimates had minimal average monthly variability in estimated abundance (Supplementary Figure S5) but notable spatiotemporal variability interannually, particularly from 2013 to 2017. Abundance anoma-

Recruitment

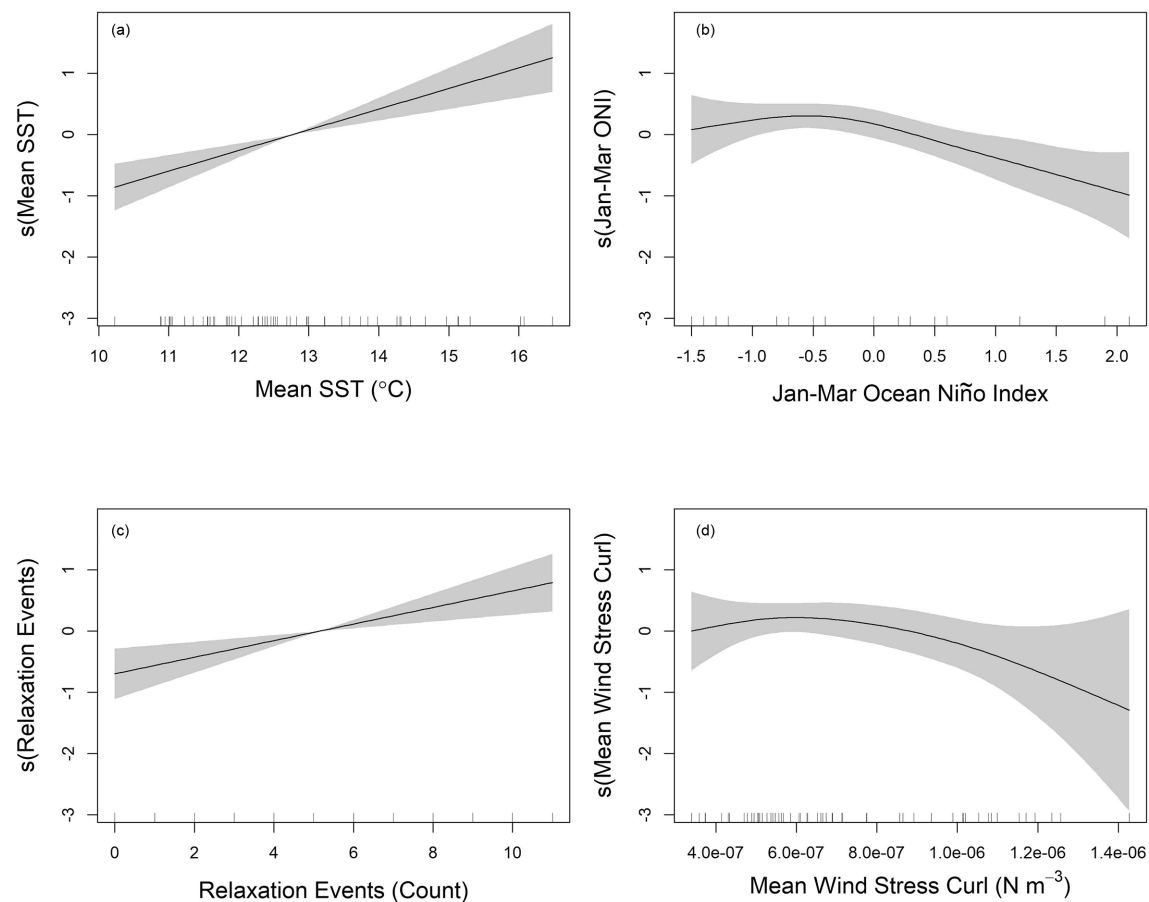


Figure 3. GAM response curves for variables included in the recruitment model: (a) March–June SST, (b) January–March Oceanic Niño Index, (c) March–June count of relaxation events, and (d) March–June mean wind stress curl.

lies peaked for much of the area in 2014 and reached a minimum in 2016 (Figure 6b and f).

Market squid abundance and habitat suitability increased through time throughout much of California's coastal waters (Figure 7). Central California and the offshore waters of southern California had the greatest increase in both habitat suitability and estimated abundance (Figure 7).

Comparison with California sea lion diet

Hurdle model estimates of market squid CPUE and mean probability of occurrence had significant, positive relationships with the frequency of occurrence of market squid in the diet of California sea lions from SNI in the summer and fall, and in the summer for SCI (Table 7; Figure 8).

Both the hurdle model estimates of market squid CPUE and mean probability of occurrence had significant positive relationships with the mean number of squid per diet sample of California sea lions for both San Nicolas Island and San Clemente Island in the summer and San Nicolas Island in the fall (Table 7; Figure 8).

Comparisons of hurdle model estimates with survey indices indicated that model estimates had stronger and more frequently significant relationships with California sea lion diet metrics in five of eight cases (two metrics \times two seasons \times two rookeries). Only the

frequency of occurrence of market squid in the diet of California sea lions in the summer on San Nicolas Island, the mean number of market squid in the summer on San Clemente Island, and the frequency of occurrence of market squid in the fall on San Clemente Island had stronger fits to survey data (Supplementary Table S5).

Comparison with California market squid landings

Region 1 landings for quarter 3 were significantly correlated with the interannual variability in model estimated CPUE ($R^2 = 0.28$, $p = 0.02$; Figure 9a), and Region 2 ($R^2 = 0.25$, $p = 0.05$; Figure 9b). The years 2017 and 2018 represented anomalies in both comparisons despite good model fit to survey data in those years (Figure 2). Model estimates of squid CPUE outperformed the survey index in predicting landings for Region 1 and Region 2, but differences were slight (Supplementary Table S6). The proportion of landings in Region 1 was significantly related to the proportion of model estimated CPUE in Region 1 (Pseudo- $R^2 = 0.26$, $p < 0.01$; Figure 9c; Table 8) for quarter 3.

Discussion

Our work identifies potential mechanisms for variability in market squid abundance throughout California's coastal waters in the

Presence/Absence

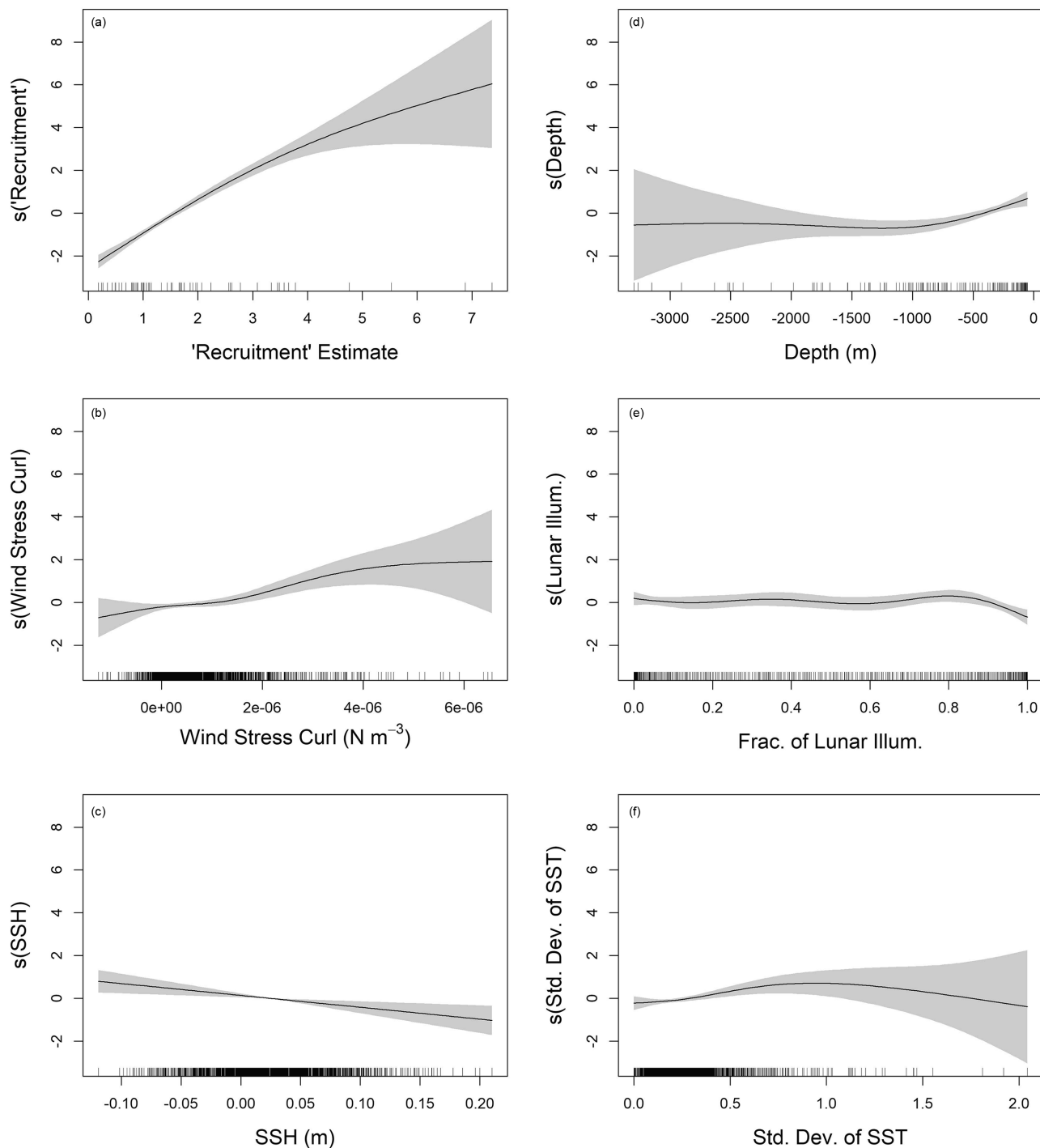


Figure 4. GAM response curves for variables with high importance ($SW > 0.9$) in the presence/absence model ensemble: (a) “recruitment” estimate, (b) wind stress curl, (c) sea surface height, (d) depth, (e) lunar illumination, and (f) SD of SST.

summer and early fall. We evaluate these estimates with independent data sources to confirm the utility of the model for estimating market squid abundance in unsampled regions and times. Importantly, our model estimates can recreate regional fluctuations in market squid abundance and the emergence of increased mar-

ket squid abundance in central and northern California following the 2014–2016 marine heatwave. Our work thus provides potential mechanisms behind this expansion beyond temperature—specifically, variability in upwelling dynamics during the early life stages of market squid and the availability of upwelling-influenced

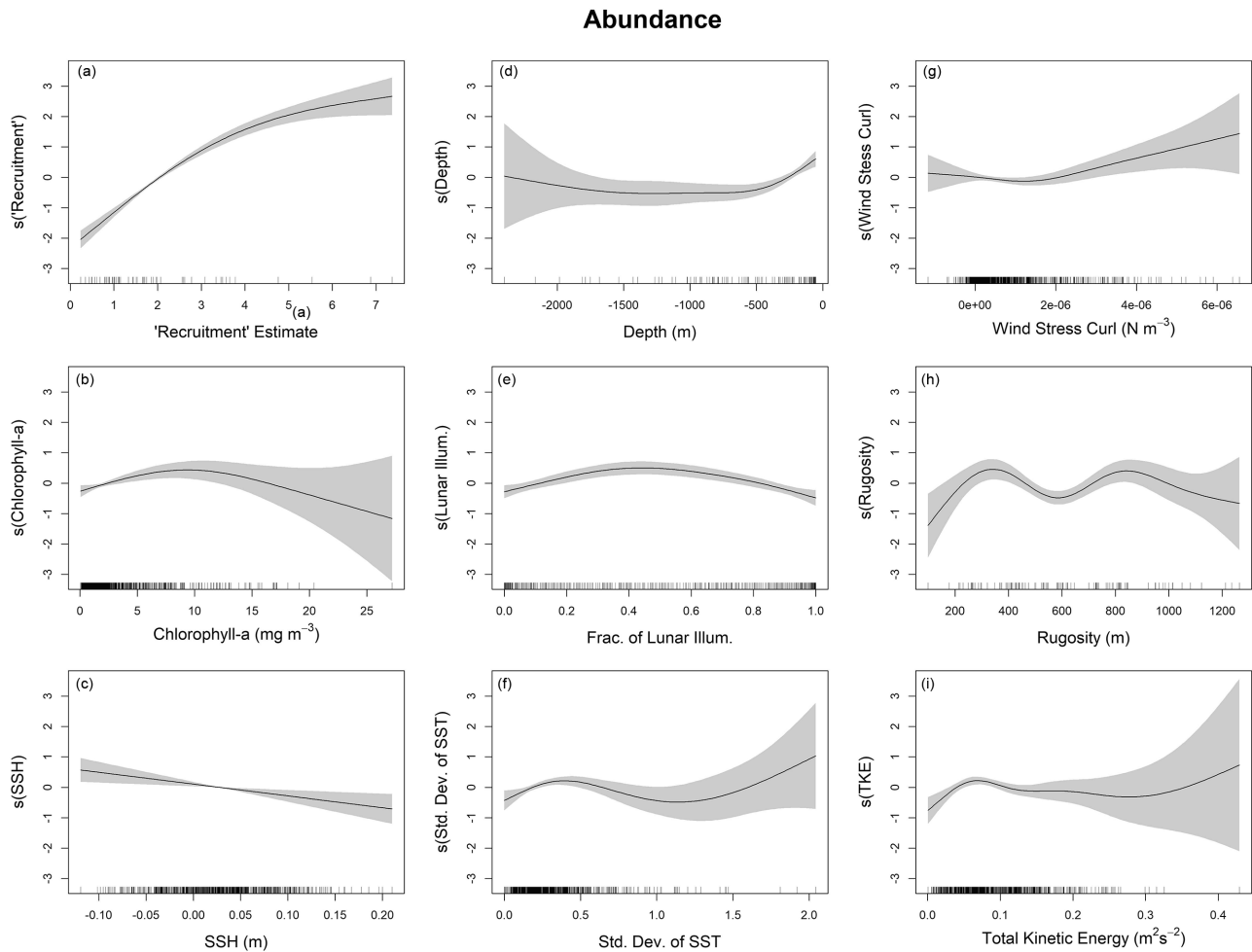


Figure 5. GAM response curves for variables included within the haul-specific abundance model: (a) “recruitment” estimate, (b) chlorophyll-a, (c) sea surface height, (d) depth, (e) lunar illumination, (f) SD of SST, (g) wind stress curl, (h) rugosity, and (i) total kinetic energy.

Table 7. Fit of regressions of market squid model estimates of occurrence and abundance with the frequency of occurrence and mean number of market squid in the scats of California sea lions from two rookeries in two seasons.

Rookery	Season	Response	Predictor	Model form	Slope estimate	Efron-pseudo-R ²	p-value
San Nicolas Island	Summer	Freq. Occurr.	Abundance	Betaregression	0.425	0.270	0.040
	Summer	Freq. Occurr.	Prob. Occurr.	Betaregression	3.120	0.264	0.041
	Summer	Num. squid	Abundance	Log-normal	0.817	0.794	<0.001
	Summer	Num. squid	Prob. Occurr.	Log-normal	6.504	0.801	<0.001
	Fall	Freq. Occurr.	Abundance	Betaregression	0.587	0.145	0.006
	Fall	Freq. Occurr.	Prob. Occurr.	Betaregression	4.459	0.162	0.004
	Fall	Num. squid	Abundance	Log-normal	0.302	0.488	0.003
	Fall	Num. squid	Prob. Occurr.	Log-normal	2.358	0.508	0.002
	Summer	Freq. Occurr.	Abundance	Betaregression	0.462	0.315	0.022
San Clemente Island	Summer	Freq. Occurr.	Prob. Occurr.	Betaregression	3.512	0.327	0.017
	Summer	Num. squid	Abundance	Log-normal	0.349	0.313	0.011
	Summer	Num. squid	Prob. Occurr.	Log-normal	2.610	0.310	0.012
	Fall	Freq. Occurr.	Abundance	Betaregression	0.244	0.152	0.138
	Fall	Freq. Occurr.	Prob. Occurr.	Betaregression	1.670	0.133	0.166
	Fall	Num. squid	Abundance	Log-normal	0.398	0.336	0.011
	Fall	Num. squid	Prob. Occurr.	Log-normal	2.976	0.317	0.015

Bolded p-values indicate significance.

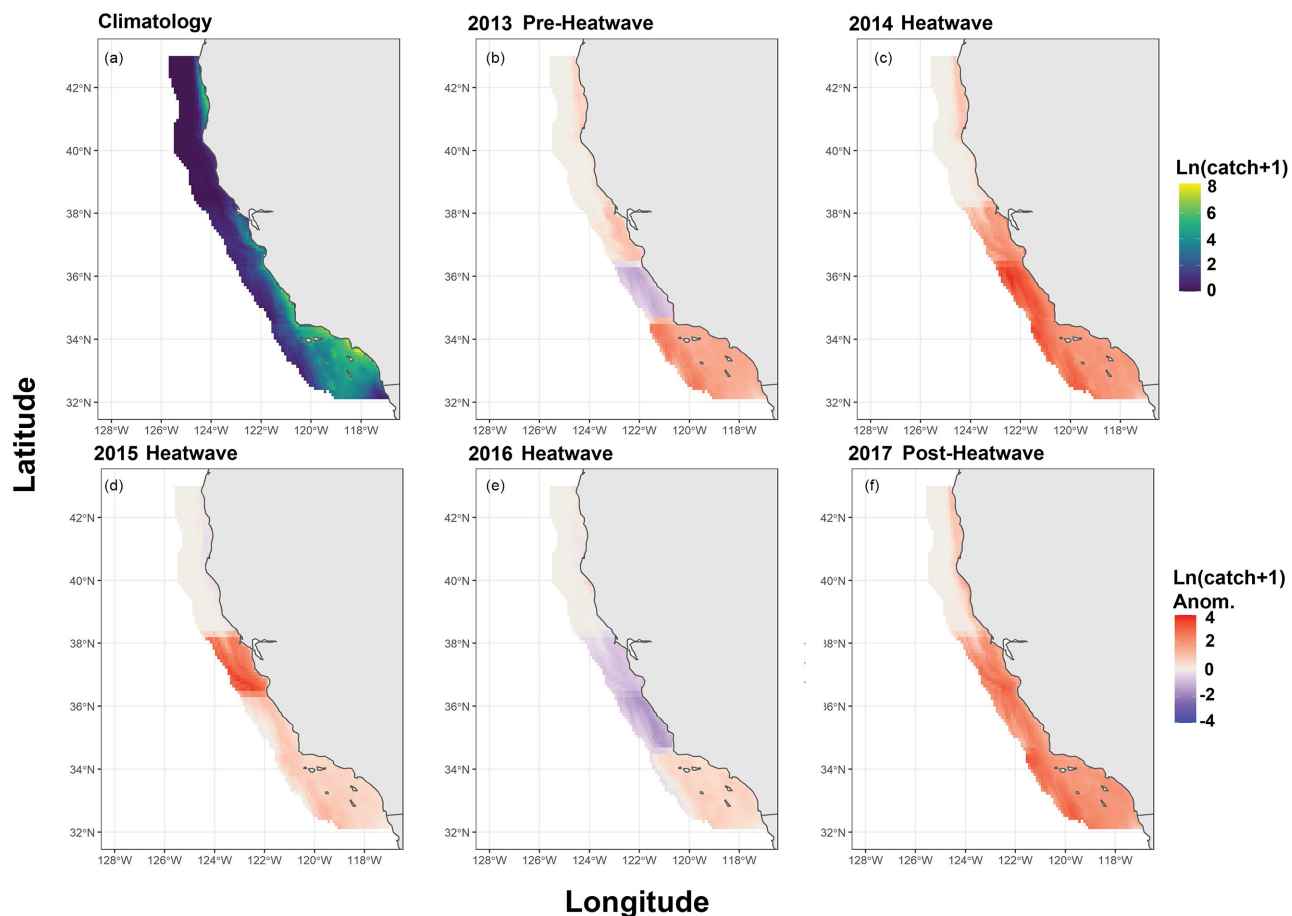


Figure 6. Hurdle model estimates of log market squid abundance (a) averaged from 1998 to 2021 and anomaly from the climatology for years preceding, during, and immediately after a marine heatwave, 2013–2017 (b–f).

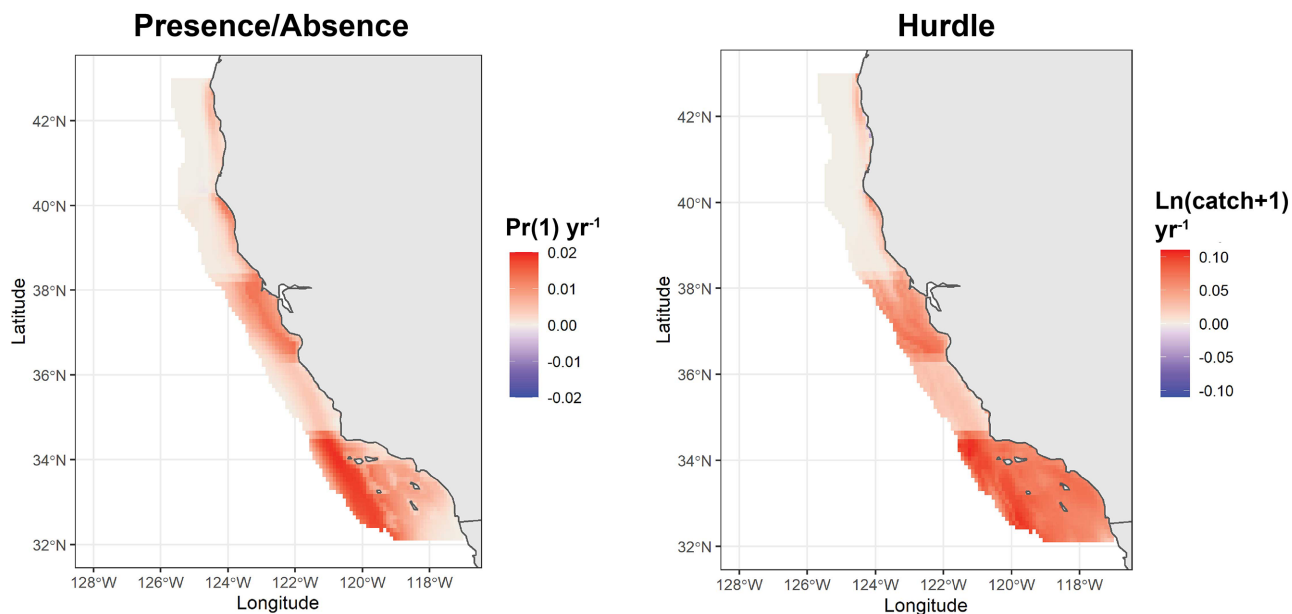


Figure 7. Linear trend in probability of occurrence and log of CPUE of market squid from 1998 to 2021 for each 0.1° by 0.1° grid cell within 100 km from land.

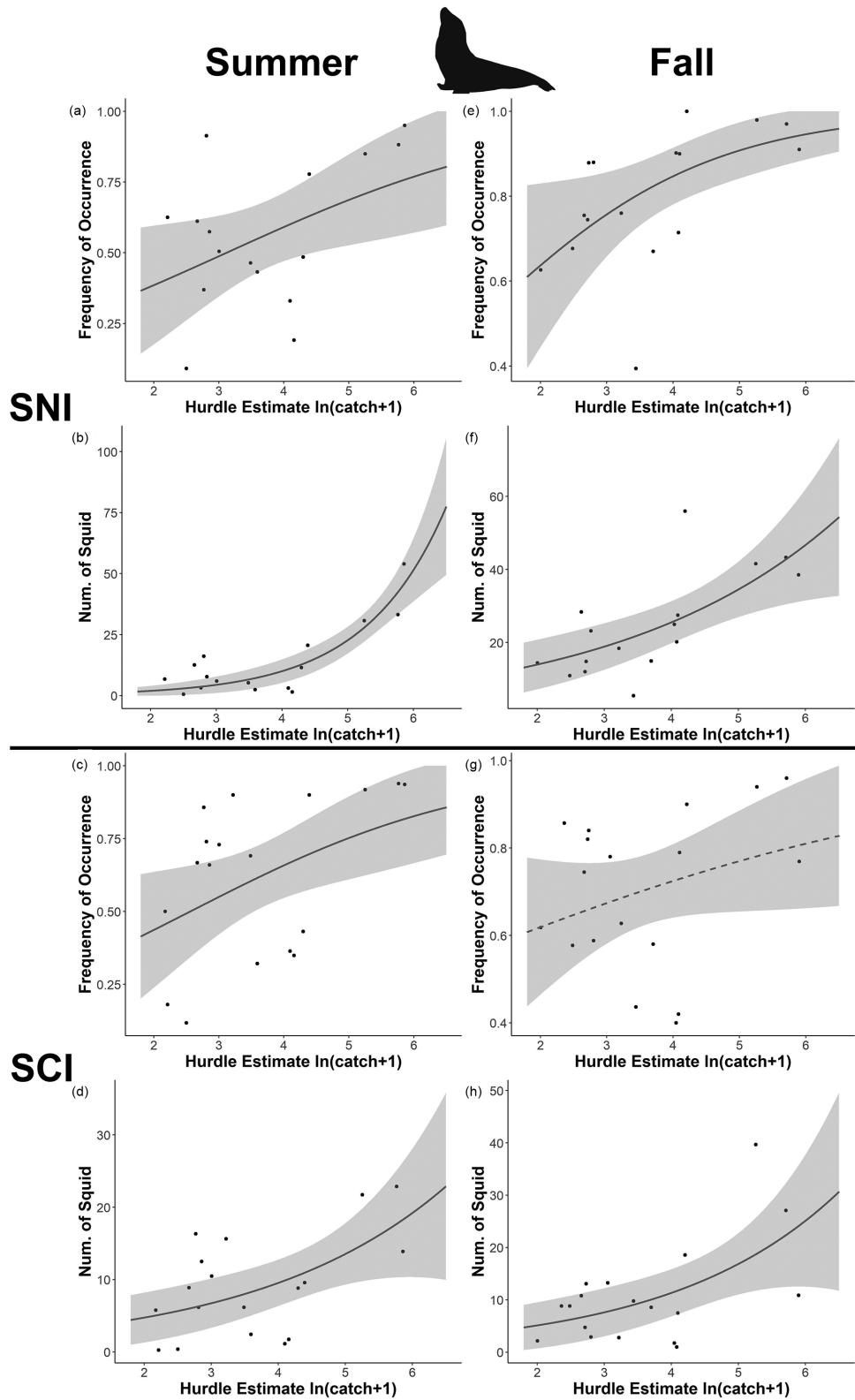


Figure 8. Regressions between hurdle model estimates of squid abundance and frequency of occurrence of market squid in California sea lion diet in the summer and fall for San Nicolas Island (a, e), San Clemente Island (c, g), and for mean number of prey in scats collected for summer and fall for San Nicolas Island (b, f) and San Clemente Island (d, h). Solid lines indicate significant relationships ($p < 0.05$), while dashed lines indicate non-significant relationships.

Table 8. Fit of regressions of market squid model estimates of abundance with the landings of market squid in Region 1 (central and northern California), Region 2 (southern California), and the proportion of landings occurring in Region 1 for July–September.

Season	Region	Model form	Efron-pseudo-R ²	p-value
July–Sept	1	Log-normal	0.276	0.023
	2	Log-normal	0.250	0.047
	Proportion	Betaregression	0.262	0.003

water during the summer. These results suggest variability in spawning and survival of juveniles have much stronger effects on overall distribution and abundance than small spatial scale variability in habitat suitability. Our inclusion of recruitment-related drivers beyond simply temperature in a species distribution modelling framework has the potential to be utilized for other short-lived, highly fecund species that exhibit large fluctuations in distribution and abundance.

Environmental drivers of market squid distribution

One outcome of this work is an improved understanding of the drivers of market squid abundance and distribution. Our results corroborate previous studies that suggest temperature plays a major role in determining the location of market squid and their spawning environment throughout the CCE and Gulf of Alaska (Burford et al., 2022; Chasco et al., 2022), as SST explained the most variance within our “recruitment” model. Fluctuations in temperature, relaxation events, and wind stress curl (and subsequent “slow upwelling”; Rykaczewski and Checkley, 2008), may have allowed for market squid abundance to shift northward, particularly allowing for a pocket of high market squid abundance in the “core” stratum near Monterey Bay in 2015 (Figures 6 and 7). This is corroborated by observations within regions of upwelling-influenced waters and the relatively high abundance and diversity of many forage species in this region during the 2014–2016 marine heatwave (Sakuma et al., 2016; Santora et al., 2017). Given that the most important predictors in the presence/absence model and haul-specific abundance models were those that correspond with typical upwelling-influenced water (low SSH, high wind stress curl, and moderate chlorophyll), these localized regions of compressed upwelling habitat may serve as essential habitat for market squid during times of otherwise high SST, such as those observed during the marine heatwave (i.e. thermal refugia; Santora et al., 2020). The higher occurrence and catch at elevated *SD* of SST and total kinetic energy further indicate that upwelling associated frontal features may specifically represent the habitat occupied by juvenile squid.

While our recruitment model attempts to elucidate mechanisms beyond broad-scale climate indices, we were unable to isolate a group of predictors that could replace the Oceanic Niño Index. Previous work has indicated that variability in this index is an important correlate of squid abundance and distribution throughout California’s waters, including leading to notable declines in landings after strong El Niño events (Zeidberg et al., 2006). El Niño events have also been associated with lower growth rates and smaller size at age (Jackson and Dormier, 2003), decreases in paralarvae survival (Koslow and Allen, 2011; Perretti and Sedarat, 2016), and decreased market squid in the diet of California sea lions (Lowry and Carretta, 1999). Our recruitment model corroborates these findings, as Ocean Niño Index values only begin to have a notable negative

effect during strong El Niño conditions, with little observed effect during La Niña. This is likely due to the positive effects of La Niña patterns being captured in other aspects of the models, particularly upwelling dynamics such as relaxation events and wind stress curl. However, the exact mechanisms behind the pattern of notable declines in abundance during strong El Niño conditions remain unclear. We used the Oceanic Niño Index from January to March as this value was not collinear with the March–June average SST. This time window corresponds to the Oceanic Niño Index during the adult stages of the parents of market squid collected in the RREAS. One possibility is the role of strong El Niño events in reducing the availability of productive, upwelling-influenced waters. Our collective model indicates that upwelling-influenced water is an important habitat for juvenile market squid, even if they can have large recruitment events during periods of relatively warm SST. Given that El Niño events are manifested both by generally warm offshore conditions and coastally trapped Kelvin waves, it may not be temperature specifically that is deleterious to market squid, as their range includes regions such as Baja California where surface conditions can exceed 30°C (Fields, 1965). Coastally trapped Kelvin waves generate positive sea surface height anomalies, leading to decreased upwelling and productivity as they move northward along the California coast (Amaya et al., 2022). Given that these Kelvin waves are frequent in the months following strong El Niño events (~2–3 month lag; Enfield, 1989; Myers et al., 1998; Amaya et al., 2022), it is possible that these events can result in frequent or large enough coastally trapped Kelvin waves to effectively remove available market squid habitat during the juvenile or adult life stages throughout the California coast, resulting in a decrease in subsequent spawning, recruitment, and landings. This hypothesis warrants further exploration given the need to move beyond climate indices in our understanding of species distribution and recruitment. However, other possibilities remain, including trophic shifts driven by El Niño events. Declines in productivity may lead to decreased zooplankton abundance for adult market squid, resulting in decreased growth, parental condition, and spawning output (Jackson and Domeier, 2003; Zeidberg et al., 2006). The trophic effects of El Niño events may also be less direct, such as non-linear shifts in food chain length and trophic efficiency (Ruiz-Cooley et al., 2017). However, it is important to note that the role of density-dependence in market squid recruitment is not well understood, thus decreases in spawning habitat may not necessarily lead to decreases in recruitment. Indeed, research on the cephalopod *Octopus vulgaris* indicates strong density-dependence in the stock-recruitment relationship can lead to boom–bust cycles from even small environmentally driven or fishing induced disturbances (Roa-Ureta et al., 2021). Additional research is needed to identify which of these hypotheses have support and how they may interact to manifest in the deleterious effect of El Niño events on market squid abundance.

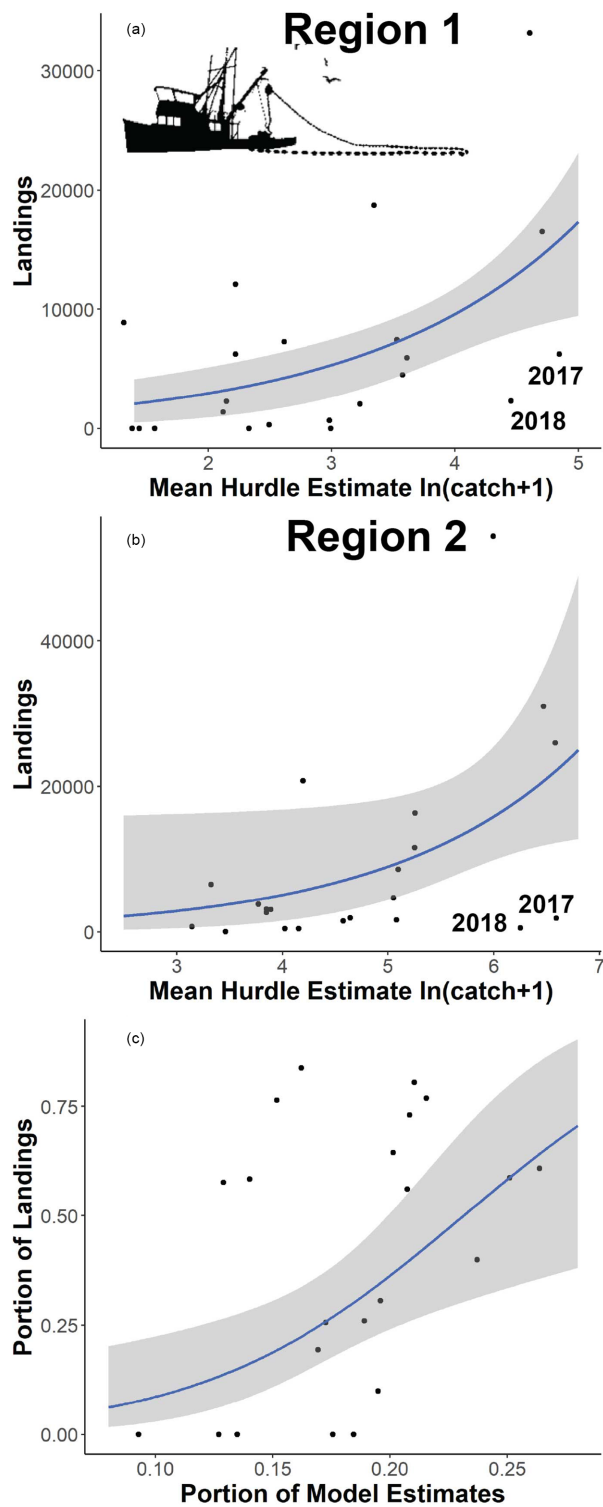


Figure 9. Regression of model estimated log CPUE compared to landings in July–September for Region 1 north of Pt. Conception (a), Region 2 south of Pt. Conception (b), and the proportion of overall landings in Region 1 (c).

Predicting adult squid abundance

In addition to providing possible mechanisms behind market squid abundance and distribution, our model was able to predict California sea lion diet from two rookeries in two seasons in the Southern California Bight and commercial squid landings in central and northern California, suggesting there is potential for the model to serve as an indicator of future market squid abundance in multiple regions of the California Current. This is particularly important for years when survey collections in this region are reduced or missed altogether, as has happened multiple times throughout the span of the RREAS (Santora *et al.*, 2021).

Implications for California sea lions

Previous research indicates market squid are one of the most frequently consumed prey items for California sea lions in the Southern California Bight in both summer and fall (Lowry and Caretta, 1999; Lowry *et al.*, 2022). Thus, moving towards a mechanistic understanding of squid recruitment and abundance is relevant to ecosystem-based fisheries management that accounts for changing ocean conditions and balances commercial fishing with the needs of these central place foragers and other predators, including both protected and fished species. California sea lions have undergone unusual mortality events due to factors such as malnourishment and domoic acid poisoning throughout the past few decades during their long-term recovery, particularly in 1998 and 2013–2016. The 1998 observation matches well with the overall low estimated squid abundance throughout the Southern California Bight during this time and corresponds with a strong El Niño event (Greig *et al.*, 2005). However, the more recent unusual mortality event (UME) occurred during a window of high summertime market squid abundance, especially during the first two years when the model, survey indices, and sea lion diet observations all indicate large numbers of market squid were present in the Southern California Bight (Laake *et al.*, 2018; Ralston *et al.*, 2018). Sea lion diet data from the southern Channel Islands for winter of 2014/15 indicate that squid availability plummeted in this season, when their typical diet is most dominated by squid, potentially contributing to the UME (data for 2015/16 winter are not available) (Lowry *et al.*, 2022). This trophically impactful seasonal shift within a multi-year marine heatwave underscores the importance of a year-round perspective on forage dynamics, as afforded by the quarterly southern Channel Islands sea lion diet time series. Market squid abundance alone may be unable to prevent malnutrition in juvenile sea lions—the lipid content of market squid is lower than other forage taxa such as northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*), so fluctuations in the latter may play an important role in successful reproduction and recruitment of California sea lions (Litz *et al.*, 2010; McClatchie *et al.*, 2016; Burford *et al.*, 2022). Northern anchovy abundance was at very low levels during the 2010 through 2014/15 time period (Santora *et al.*, 2020), yet anchovy in sea lion diet from the Southern California Bight increased to levels not seen since the early 2000s during the summer of 2015 (Lowry *et al.*, 2022). Variation in caloric density within prey species might also play an important role in the population dynamics of predators such as California sea lions (von Biela *et al.*, 2019). A more complete understanding of the pelagic forage dynamics and trophic ecology of California sea lions and other predators is needed for adequate ecosystem-based management of fisheries that considers their requirements.

Comparison of model estimates with market squid landings

Understanding the mechanisms of squid abundance and distribution throughout the central and southern CCE has important implications for the market squid fishery, which has become both increasingly variable and valuable in recent years (Heine *et al.*, 2017; Chasco *et al.*, 2022). Landings have increased in northern California current waters over the past decade, corresponding to the range expansion of market squid observed after the 2014–2016 marine heatwave (Burford *et al.*, 2022; Chasco *et al.*, 2022). Our model estimates of squid abundance correlated with landings throughout California, indicating that the dependencies within the model can help provide context for both the shift in market squid distribution and its fishery. However, our model is restricted to the summer and early fall in terms of its ability to predict adult abundance and is not representative of the full market squid population of California, or even the entire spring spawning population. We are unable to produce reliable estimates of late fall and winter squid abundance when squid can be both ecologically (Lowry *et al.*, 2022) and commercially (Free *et al.*, 2022) important. Estimating squid abundance throughout the year will be essential in improving our understanding of the relationship between fishery and trophic dynamics and squid abundance. This will also allow for year-round estimates of spawning stock biomass. Acquiring estimates of seasonal to monthly biomass of market squid would allow for an exploration of potential stock-recruitment relationships, further improving our understanding of and ability to manage this species. The quarterly sea lion diet data from the southern Channel Islands might provide a useful long-term index for this purpose for the Southern California Bight.

The lack of complete seasonal model predictions specifically limits our capacity to understand market squid fishery dynamics in Region 2, the Southern California Bight, as the majority of annual landings in this region occur in the fall and winter (quarters 1 and 4). This is likely the primary reason for the poorer match between model estimates and landings for Region 2 compared to Region 1, as the fishery in this region is unlikely to be as driven by availability during the summer as in Region 1, where the primary fishing season overlaps with our model's seasonal prediction window (Ralston *et al.*, 2018). Survey indices also fit poorly to landings for Region 2, emphasizing the need for the development of models that can be expanded to incorporate all seasons to understand the population dynamics of the species and the fishery.

Considerations for future research

Future modelling efforts need data that encompasses the full set of environmental conditions experienced by market squid to ensure they are constrained appropriately. A limitation in our study is that the response curve for market squid recruitment and temperature in our model is linear, indicating that increasingly warm temperatures should increase recruitment. However, this is unlikely to be true for market squid in the fall and is an improbable response shape for most species, as concave thermal niches are nearly universal (Magnuson *et al.*, 1979; Stuart-Smith *et al.*, 2017). The inability of our model to constrain the upper limit of market squid's response to SST can serve as an additional warning for extrapolating species distribution models beyond the parameter space in which they were constructed (Conn *et al.*, 2015; Muhling *et al.*, 2020). Temperature is of particular importance as it is the most important predictor in our recruitment model, and a predictor which we know is unlikely

to have a linear response across the full range of conditions experienced by market squid. Climate change projections for the CCE show temperatures warming beyond the ranges of historical variability (King *et al.*, 2011; Pozo Buil *et al.*, 2021). The lack of an upper temperature constraint not only limits the capacity for the model to be used reliably in climate change scenarios but may also limit its utility in expanding to warmer months of the year that may naturally exceed the realized thermal niche of market squid. Indeed, the paralarval abundance of market squid has been shown to decrease in temperatures exceeding those used in our study, corroborating this concern (Van Noord and Dorval, 2017). Responses to upwelling-related phenomena may also have limits, but it is plausible that increasing areas of upwelled water and prey availability may lead to continually increased recruitment. Therefore, in addition to ensuring adequate sampling across a species' thermal niche, considering which predictors to include in predictive models and whether any should be shape-constrained is important to ensure model predictions are able to provide useful and realistic results for both seasonal and climate scale forecasting. Models like ours are effective within the parameter space in which they were constructed but will need updating and refitting as climate and phenological shifts continue in the coming decades.

Conclusion

Overall, our results provide new insights into the drivers of market squid abundance and distribution throughout California's coastal waters. We both corroborate a northward movement of market squid habitat during and following the 2014–2016 marine heatwave and emphasize the importance of upwelled waters for market squid habitat. The availability of juvenile habitat as we described here was able to explain variability in commercial fishing landings and the diet of California sea lions, indicating that these mechanisms are likely consistent for the adult market squid that these groups target. Our results can provide resource managers with valuable information on bottom-up mechanisms that drive fluctuations in market squid abundance throughout the southern CCE from late spring through early fall. Future work, including samples spanning the full thermal niche of market squid, is needed to refine the mechanisms described here. It will ultimately be necessary to develop year-round estimates of squid abundance and to project habitat suitability and abundance of market squid into the future. Doing so will provide an opportunity to ensure continued sustainable management of this species to support economically important fisheries and multiple top predators in the CCE.

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Supplementary data

Supplementary material is available at the ICESJMS online.

Conflict of Interest

The authors have no conflicts of interest to declare.

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Data availability statement

ROMS data are available at <http://oceanmodeling.ucsc.edu/ccsnrt/>. RREAS data can be found at https://coastwatch.pfeg.noaa.gov/erddap/tabledap/FED_Rockfish_Catch.html. Code can be found at https://github.com/jsuca18/Market_Squid_CCE/.

Author contributions

All the authors designed the study. JJS led analyses. JAS, JCF, KAC, and BAM contributed to the interpretation and design of the analyses. All the authors wrote the manuscript.

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