Catch as catch can: markets, availability, and fishery closures drive distinct responses among the U.S. West Coast coastal pelagic species fleet segments

Felipe J. Quezada [a,b], Desiree Tommasi [a,b], Timothy H. Frawley [a,b], Barbara Muhling [a,b], Isaac Kaplan[c], and Stephen Stohs [b]

[a]Institute of Marine Sciences' Fisheries Collaborative Program, University of California, Santa Cruz, CA, USA; [b]Fisheries Resources Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla, CA, USA; [c]Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA, USA

Corresponding author: **Felipe J. Quezada** (email: fequezad@ucsc.edu)

Abstract

Fishers often target multiple species. More diverse harvest portfolios may reduce income risk, increasing resilience to climate-driven changes in target species' spatial distributions and availability. Moreover, different effects can be observed across vessels in response to the same shocks and stressors, as fishers are heterogeneous. Evaluation of climate risk across different vessel groups within a particular fishery requires consideration of heterogeneous climate impacts on the availability of multiple target species and how such changes may impact substitution behavior. Here we analyze how historical climate-driven changes in forage species distribution and the closure of the Pacific sardine fishery affected landings per vessel of three coastal pelagic species (CPS): Pacific sardine (*Sardinops sagax*), market squid (*Doryteuthis opalescens*), and northern anchovy (*Engraulis mordax*) targeted by the U.S. West Coast CPS fleet from 2000 to 2020. Using cluster analysis, we grouped vessels into different fleet segments and estimated heterogeneous responses by fleet segment and port area. Our results show that considering heterogeneity is essential in the development of equitable and effective adaptation policies designed to mitigate the impact of changes on species availability in these fisheries.

Key words: climate change, fish landings, cluster analysis, closures, coastal pelagic species

1. Introduction

The distribution and abundance of marine species are shifting in response to ocean warming (Poloczanska et al. 2013) and are expected to continue to do so in response to future climate change (Cooley et al. 2022). To maintain their livelihoods, fishers can either follow the fish and move to new fishing grounds or shift target species and broaden their fishing portfolio (Liu et al. 2023). Indeed, fishing portfolios have been an essential mechanism to safeguard fishers' livelihoods when contending with variable marine environments and stock productivity (Frawley et al. 2021b; Powell et al. 2022). Diversification strategies are increasingly associated with reduced income variability and enhanced resilience (Kasperski and Holland 2013; Sethi et al. 2014; Cline et al. 2017), with vessels with broader portfolios more resilient to climate shocks (Cline et al. 2017; Fisher et al. 2021) and interannual oceanographic variability (Aguilera et al. 2015; Finkbeiner 2015). Thus, diversification might be an effective adaptation strategy to climate change (Young et al. 2018). However, diversification is not always possible (Beaudreau et al. 2019). Switching between species can be limited and costly if new or different skills, fishing gears, or permits are required (Frawley et al. 2021b; Powell et al. 2022). Even though fishers may have the flexibility to switch between species, port infrastructure, markets, and regulations may limit opportunities (Kasperski and Holland 2013; Powell et al. 2022). In that case, fishers can adopt other adaptation strategies, such as reducing or reallocating fishing effort or changing their fishing locations (Gonzalez-Mon et al. 2021). In the worst-case scenario, they will pursue alternative employment (Powell et al. 2022). Furthermore, studying the effect of changes in species distribution and regulations is not straightforward, as different responses can be observed across vessels in response to the same conditions. Fishers are heterogeneous (Zhang and Smith 2011; Jardine et al. 2020; Powell et al. 2022) and react in different ways to external drivers of change based upon different goals, strategies, assets, and scales of operations (Gamito et al. 2016; Frawley et al. 2019).

This article focuses on three of the most valuable and highly interdependent (in social and economic terms) (Aguilera et al. 2015) species harvested by the U.S. West Coast coastal pelagic species (CPS) fleet: Pacific sardine (*Sardinops*

1

sagax), market squid (*Doryteuthis opalescens*), and northern anchovy (*Engraulis mordax*). On the U.S. West Coast, market squid was the second largest fishery with an average revenue of US$69MM from 2010–2014, behind only Dungeness crab (US$186MM). Over the 2010–2014 period, Pacific sardine had an average revenue of US$13MM, while average northern anchovy revenue was US$0.8MM.

While in recent years, the number of studies concerning climate-driven changes in species availability, fisheries catches, and landings has increased (Young et al. 2018; Dubik et al. 2019; Selden et al. 2019; Smith et al. 2021; Powell et al. 2022), the effect of climate-driven changes in availability in a multiple-species fishery context (Aguilera et al. 2015; Rogers et al. 2019) and its potential impact on interactions between target species remains poorly understood. Here we investigate the effects of changes in target species availability and the implementation of fisheries closures, as mediated by the diverse behaviors and vessel characteristics that comprise the U.S. West Coast CPS fleet, on landings per vessel and species substitution across multi-species fisheries. The U.S. West Coast CPS fleet presents a valuable study system to assess fishers' responses to changing species availability in a multi-species context, as the composition of the forage complex in this region can shift dramatically over time and space in response to variability in oceanographic conditions (Santora et al. 2017; Thompson et al. 2019).

In particular, we assessed how the recent decline and closure of the Pacific sardine fishery (PFMC 2020), a booming northern anchovy population (PFMC 2020), and the decline of market squid availability in Southern and Central California (Van Noord and Dorval 2017) have affected landings per vessel and substitution between these three species. The environmental underpinnings of these fluctuations (see Chasco et al. (2022) for squid, Koenigstein et al. (2022) for sardine, and Swalethorp et al. (2022) for anchovy) suggest that climate change may lead to strong shifts in the future availability of CPS to U.S. West Coast fisheries. During past sardine population busts (i.e., fishery crashes), such as the infamous crash in the 1940s on the U.S. West Coast, heterogeneous responses were observed across the purse seine fleet, with some vessels switching gears to target alternate fisheries, others focusing on alternate species that could be caught by purse seine, such as anchovy, squid, Pacific mackerel, and tuna (Uber and MacCall 1990; Herrick et al. 2006), and many exiting the fishery entirely (Uber and MacCall 1990; Herrick et al. 2006). In other small pelagic fisheries worldwide, fishers generally have adapted to busts impacting their main target species availability by switching to other species capable of being targeted by the same gear, such as the switch from sardine to mackerel for the Portuguese purse seiners (e.g., Gamito et al. 2016), the switch from anchovy to tuna and seabass for French pelagic trawlers operating in the Bay of Biscay (Daurès et al. 2009), or the switch from anchovy to mackerel and tunas for the Spanish purse seiners in the Bay of Biscay (Andrés and Prellezo 2012). However, even among vessels utilizing the same gear, individuals are known to respond heterogeneously. For instance, different sectors of the Spanish purse-seine fleet showed different adaptive capac-

ities despite using similar technologies (Andrés and Prellezo 2012).

Our unique approach first characterizes heterogeneity in the CPS fleet fishing strategies using cluster analysis, a tool gaining popularity as a means of understanding the nature and extent of behavioral heterogeneity within a fishery (O'Farrell et al. 2019; Frawley et al. 2021a; Liu et al. 2023), before using those results to inform the development of a Bayesian model of landings per vessel that considers the interrelation between species and heterogeneity between vessels. By analyzing the drivers of historical landing dynamics using a multiple-species targeting framework, our results will contribute to understanding how U.S. West Coast CPS vessels and other multi-species forage fish targeting fleets around the globe might adapt to projected climate-driven changes in species availability.

2. Materials and methods

2.1. Study system

Vessel landings are affected by a range of factors, including permits, quotas, alternative employment opportunities, gear, weather, vessel capital, fishing methods, skipper skills, and processing capacity, as well as species availability and market conditions (e.g., price). Therefore, here we first provide an overview of the regulatory and operational context for the CPS fishery.

Since 2000, U.S. West Coast catches of CPS (Pacific sardine, northern anchovy, Pacific (chub) mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*), and market squid) have been federally managed (PFMC 2020) through the CPS Fisheries Management Plan (CPS FMP). The CPS FMP requires a limited entry permit for vessels catching CPS finfish south of $39°$ N if a vessel lands more than five metric tons of CPS in a trip. Vessels operating north of $39°$ N do not require federal permits, but state regulations authorize issuing permits to limit the number of vessels targeting CPS. Vessels landing market squid are exempt from the federal CPS finfish permit requirement but require a permit from the California Department of Fish and Wildlife (CDFW) when operating in California (CDFG 2005).

The fishery is also subject to federal, coast-wide, species-specific quotas. Pacific sardine is managed using a Harvest Control Rule that limits coast-wide commercial catches of the northern subpopulation of Pacific sardine and also specifies that directed commercial fishing is closed when the estimated biomass falls below a biomass cutoff. Critically, the directed Pacific sardine fishery has been closed for the whole U.S. West Coast since 2015, as the spawning stock estimated biomass is below this biomass cutoff point of 150,000 metric tons. For market squid, the majority of landings (99.2% from 2000 to 2020) occur in California, and the California Fish and Game Commission (CFGC) implemented a catch limit of 125,000 U.S. tons for this state in 2001. Later, in 2005, the CFGC implemented the market squid FMP, which reduced the limit to 118,000 U.S. tons and incorporated a weekend closure to allow uninterrupted spawning (PFMC 2020). For this species, vessel permits allow vessels to attract squid with

light and use purse seine for harvest, brail permits allow vessels to attract squid with light and use brail gear, and light boat permits only allow vessels to attract squid with light. A key distinction between the catch limit allocated to the market squid fishery and the catch limit allocated to the Pacific sardine fishery is that the latter is adaptively managed, changing every season depending on different factors (e.g., biomass and recruitment). In contrast, the catch limit allocated to the market squid fishery is fixed. The northern and central subpopulations of northern anchovy are also subject to a Harvest Control Rule that sets an annual catch limit based on 25% of the maximum sustainable yield (PFMC 2020). The northern subpopulation of northern anchovy is targeted by vessels in Oregon and Washington, while vessels in California target the central subpopulation. In recent years, there has been no reduction capacity for the northern anchovy fishery in California (i.e., there are no operational factories capable of processing large volumes of anchovy catch into fish meal or oil). Anchovy is principally harvested in the Monterey Bay area as a substitute for sardine and squid when both are unavailable (PFMC 2020). In Washington, the northern anchovy fishery has been restricted from developing into a high-volume fishery to protect the traditional bait fishery for this species. By contrast, the Oregon northern anchovy fishery is currently under an open-access regime, though harvesting is restricted to the use of lampara net, hook and line, or purse seine gears on inland waters and purse, lampara, and round haul seine gears in the Columbia River area (PFMC 2020; ODFW 2023).

In general, vessels targeting CPS leave and return to port on the same day to prevent fish spoilage. This constraint may increase vessels' cost of adapting to changes in target species availability as they may not be able to shift fishing grounds without changing the landing port or fishing community. Non-CPS such as Pacific bonito (*Sarda lineolata*) and Pacific bluefin tuna (*Thunnus orientalis*) are also captured by the CPS fleet (PFMC 2020). Some CPS vessels also switch seasonally to troll or pot gears to pursue albacore (*Thunnus alalunga*), Dungeness crab (*Metacarcinus magister*), California spiny lobster (*Panulirus interruptus*), and different species of Pacific salmon. Switching between CPS is comparatively straightforward. Vessels that use purse seine nets as gear, common in this fishery, only require changing net sizes to target a different CPS. Oftentimes, the local viability of potential alternative target species depends on the available port infrastructure for landings and processing.

In summary, coastwide or state-level factors such as quotas, port-level factors such as processor capacity, and vessel-level factors likely influence captains' or owners' choice of target species. Below, we include these aspects and additional covariates in our landings per vessel model.

2.2. Input data

2.2.1. Fisheries data

Daily vessel-level landings records (i.e., fish tickets) were obtained from the Pacific Fisheries Information Network (PacFIN) for the period 2000–2020. The data include all vessels that had commercial landings of species with a PacFIN Coastal Pelagic Management Group code (CPEL) or that used purse seine, encircling nets, half rings, drum purse seine, lampara net, dip net, or hook and line fishing gear at least once. The raw data include 1,048,106 fish tickets submitted by 2,891 vessels.

We filtered the data to only include vessels that targeted a species from the CPS complex or targeted albacore and used northern anchovy as bait at least three times from 2005–2014. We chose this subset of years because it comprises a relatively stable regulatory regime from the change in the sardine quota allocation framework (i.e., from an area-based to a coast-wide seasonal release) and the implementation of the market squid FMP to the closure of the directed Pacific sardine fishery. We defined the target species as the dominant species on a fish ticket in terms of revenues. Moreover, we only included entries of the following removal category types: commercial (direct sales) (0.14% of the entries), exempted fishing permit (EFP) (8.73% of the entries), and commercial (non-EFP) (88.82% of the entries), excluding personal use, research, and unspecified. Our final dataset for analysis comprises 149,950 fish tickets submitted by 265 vessels.

2.2.2. Species distribution models

Species distribution models (SDMs) were built upon those described by Muhling et al. (2019, 2020). For sardine and anchovy, we trained and validated binomial generalized additive models in R (Wood 2017; R Core Team 2020) using presence/absence data for CPS caught in fishery-independent trawl surveys conducted by NOAA Fisheries. Sardine and anchovy were sampled in surface waters at night using a Nordic 264 trawl in a survey primarily targeting sardine, anchovy, and other finfish CPS, which has been running since 2003 (Zwolinski and Demer 2012). Sampling effort in this survey covers waters from southern California to British Columbia and includes months from March through October, with the most effort from April to August. A randomly sampled 50% of the data were used in model training, and the other 50% was withheld for validation.

Environmental covariates used to predict sardine and anchovy presence included sea surface temperature, sea surface height, mixed layer depth, an estimate of water column stratification (buoyancy frequency averaged over the top 200 m) that were available daily at 0.1 degree resolution from a data assimilative configuration of the Regional Ocean Modeling System (Neveu et al. 2016; oceanmodeling.ucsc.edu), and 8-day surface chlorophyll-a at an aggregated 0.25° resolution from a satellite reanalysis developed by the Ocean-Colour Climate Change Initiative (Sathyendranath et al. 2019). More details on the complete predictor suite are contained within Brodie et al. (2018) and Muhling et al. (2019, 2020). Annual indices of spawning stock biomass for sardine and anchovy were also included as covariates to account for higher probabilities of occurrence within environmentally suitable habitat at larger stock sizes (Muhling et al. 2020). Predicted habitat suitability was generated for every day from 1998 to 2020 at 0.1 degree spatial resolution for the California Current

domain (30°–48° N and inshore of 134° W). SDM skill was fair (area under the receiver operating characteristic curve (AUC) = 0.71) for sardine and good (AUC = 0.84) for anchovy when models were tested against the withheld observations not used in model training.

Squid fishers are believed to target spawning aggregations during squid harvest (Vojkovich 1998; Butler et al. 1999). Therefore, we used a benthic spawning habitat model to delineate locations where fishable aggregations were likely present. No large-scale survey data are available for squid spawning habitat or egg masses. Following Zeidberg et al. (2012) and Navarro et al. (2018), we therefore assumed that suitable spawning habitats were 10–100 m deep on sandy substrates, where bottom temperatures were 9 °C–15 °C and bottom oxygen concentration was >160 mol. Water depths were obtained from the ETOPO 1 arc-minute global relief model (Amante and Eakins 2009). Bottom temperature was extracted from the GLORYS12V1 physics reanalysis at daily 0.08333 degree resolution (European Union-Copernicus Marine Service 2018a), and bottom oxygen was extracted from the Mercator-Ocean biogeochemistry hindcast at daily 0.25 degree resolution (European Union-Copernicus Marine Service 2018b), both hosted by the Copernicus Marine Environmental Monitoring Service. Benthic habitat was extracted from a variety of sources covering subsets of the ROMS domain. We primarily used habitat classifications from the Oregon State University's Surficial Geologic Habitat Map, version 4.0 (Romsos et al. 2007), from the California State Waters Map Series catalog (Golden 2013), and from substrate characteristics data for central California from the Monterey Bay National Marine Sanctuary (NOAA 2006). Locations within the ROMS domain not covered by these data sources were then assigned a benthic habitat type using figures digitized from Arafeh-Dalmau et al. (2017; for northern Baja California), and from georeferenced sediment point data collected under the usSEABED program (Buczkowski et al. 2020), converted to Theissen polygons in ArcMap 10.7.1. Depth, substrate, and environmental data were re-gridded using the *raster* package in R (Hijmans 2022) to match the 0.1 degree resolution of the ROMS outputs, using bilinear interpolation. Squid SDM values were a mean of suitable (1) and unsuitable (0) pixel values once interpolated to 0.1 degrees.

We used either the probability of presence (sardine, anchovy) or mean suitable pixels (squid) obtained from SDMs as an explanatory variable in our landings per vessel model. We followed the same procedure as Smith et al. (2021) to associate SDM outputs with port areas. We computed the average probability of presence within a radius around the port for each species. The radii were defined based on the average distances traveled by vessels plus two standard deviations computed from available logbook data provided by the California, Oregon, and Washington Departments of Fish and Wildlife (CDFW, ODFW, and WDFW, respectively). Logbooks contain logs of fishing locations during a vessel trip by species. From Chebyshev's inequality, we know that at least 75% of the observations would be within two standard deviations of the mean. This agrees with Selden et al. (2019), who use the 75th quantile of the travel distances made by vessels to define the availability of species associated with a port. Specifically, for

Pacific sardine, the radius was set to 60 km, which coincides with the radius used by Smith et al. (2021), while for market squid and northern anchovy, the radius was set to 90 and 20 km, respectively. These species-specific fishing radii were confirmed by members of the commercial fishing industry during stakeholder workshops designed to vet preliminary results (Quezada et al. 2023). SDM outputs were available from January 1998 to August 2019 for Pacific sardine and northern anchovy and from January 1993 to December 2019 for market squid.

2.3. Cluster analysis

Recognizing that fishing strategies can be variable (Aguilera et al. 2015; Frawley et al. 2021b) and that such heterogeneity may influence vessels' adaptive response to changes in target species availability (Fisher et al. 2021; Liu et al. 2023) and other drivers, we performed a cluster analysis designed to group vessels in fleet segments based on common strategies and attributes (O'Farrell et al. 2019; Frawley et al. 2021a, 2022).

To conduct our clustering analysis, we used landings data from 2005–2014, reducing the number of fish tickets from 149,950 to 79,038. We computed five inputs to characterize CPS vessels: average annual revenue, the latitudinal center of gravity (LCG), inertia (I), CPS income diversification, and the percentage of revenue coming from CPS landings. We removed two other variables with a variance inflation factor value larger than 2.5, as they were highly correlated with other variables included as inputs (correlation higher than 0.5). More specifically, average annual landings and average number of months fishing CPS were highly correlated with average annual revenue. For each vessel, LCG was defined as the mean latitude of landings (Woillez et al. 2009; Richerson and Holland 2017):

$$(1) \quad \text{LCG} = \frac{\sum_{p=1}^{P} l_p z_p}{\sum_{p=1}^{P} z_p}$$

where l_p is the latitude of the port of landing $p \in (1,\ldots, P)$, where P is the total number of ports, and z_p is the total revenue received by the vessel at port p. Inertia, a measure of dispersion, was defined as the variance of the landing latitude (Woillez et al. 2009; Richerson and Holland 2017):

$$(2) \quad I = \frac{\sum_{p=1}^{P} \left(l_p - \text{LCG}\right)^2 z_p}{\sum_{p=1}^{P} z_p}.$$

Using the coordinates of the first principal axes of inertia, we transformed our inertia metric to kilometers. CPS income diversification was calculated using the Herfindahl–Hirschman index (HHI), also called the Simpson diversity index (Richerson and Holland 2017):

$$(3) \quad \text{HHI} = \sum_j \delta_j^2$$

where δ_j is the percentage of revenue from CPS j. To facilitate interpretation, we computed the inverse of this index,

so higher values indicate greater diversification (Holland and Kasperski 2016).

All input variables were rescaled between 0 and 1 to produce a standardized comparison and then combined in a distance matrix using Euclidean distances. We conducted our cluster analysis using partitioning around meoids (PAM) clustering in the R package *cluster* (Kaufman and Rousseeuw 1990; Frawley et al. 2022). We used the average silhouette method to choose the optimal number of clusters. Once clusters were defined, we built a random forest model in the R package *randomForest* (Breiman 2001; Liaw and Wiener 2002) to compute the relative importance of input variables in determining clusters.

Vessel groupings into clusters were iterated and refined using expert knowledge provided by representatives of the California and Washington Departments of Fish and Wildlife (CDFW and WDFW). Subsequently, clusters were described and validated by using the results of a principal component analysis to plot them in two-dimensional space using all the input variables described before and computing intra- and inter-cluster metrics using the R package *clv* (Nieweglowski 2020). Specifically, we used complete and average intracluster diameter with an average intercluster linkage to assess relative uniformity within clusters and similarity between clusters, where complete intracluster diameter calculates the distance between the two most remote objects within a cluster, average intracluster diameter calculates the average distance between all samples within a cluster, and average intercluster linkage calculates the average distance between two clusters using all samples. Finally, we labeled each cluster based on their input averages, the ports where they land, and the average composition of their catch. The final groupings resulting from this analysis were referred to as fleet segments.

2.4. Landings per vessel models

2.4.1. Estimation sample

For the landing per vessel models, we aggregated our filtered fisheries data monthly by vessels, species, and port areas. We expected that monthly data would allow us to observe seasonality in fishers' behavior while reducing the risk of losing general behavior when data are disaggregated on a finer temporal scale. All the vessels included in our estimation sample were associated with a fleet segment.

We dropped rows where landings were N/A or equal to zero. Therefore, the dataset only includes vessel-level positive landings, allowing us to model landings produced by vessels actually participating in the fishery for that species during a particular month, consistent with our focus on how landings of squid, sardine, and anchovy of a vessel already participating in the CPS fishery during a specific month are affected by species availability and other factors. We also dropped rows with zero revenue, as they might correspond to bycatch. We only used observations for months when the corresponding fishery was completely open (i.e., did not close at any point during the entire month), resulting in the exclusion of 19 out of 158 months in the case of sardine, 3 out of 241 months in the case of squid, and none in the case of anchovy. We fil-

tered our data further by selecting fleet segments with more than 5% of their average annual revenue coming from the corresponding species (Table S1).[1] We also subsetted the data for fleet segments and port area combinations where we had enough observations relative to the sample size to compute random coefficients (more than 4% of the total observation after filtering by fleet segments in the case of squid and 2% in the case of sardine and anchovy—see Table S2).

The two fleet segments identified in the cluster analysis that were not included in the estimation model, as they do not target CPS or exceed the threshold described above, were the "Southern CCS small-scale CPS opportunist" and the "Pacific Northwest (PNW) albacore-crab generalist" fleet segments (see Fig. 1). The networks presented in Fig. 1 were constructed using the methods described by Fuller et al. (2017) and Frawley et al. (2021b), with the following parameter specifications: only nodes (i.e., fishing metiers) that accounted for more than 1% of the total revenue generated by that fleet segment over the time period were displayed. Nodes were sized according to their percentage contribution to total revenue generated by each fleet segment during each time period. Edge-weight thickness (i.e., the width of the lines connecting the nodes) was sized according to the percentage of vessels in each fleet segment participating in each pair of fisheries, with participation defined as a vessel earning more than 10% of their revenue during the time period from that metier.

Finally, we screened the data for the non-stationarity of explanatory variables. See Section D in the online supplementary material for more details about the non-stationarity tests.

2.4.2. Empirical model

Our empirical model was estimated using a hierarchical Bayesian framework (Hobbs and Hooten 2015). We chose this approach for several reasons: First, it allowed us to consider process uncertainty, treating all parameters as random variables. Second, Bayesian modeling allowed us to include multilevel (hierarchical) effects for each parameter, estimating random coefficients at different levels, including port areas and the vessel segments identified from our cluster analysis. Third, Bayesian models treat group-level effects as parameters instead of part of the error component (Fox and Weisberg 2011; Bürkner 2017). Finally, we could incorporate previous knowledge as a prior, such as the effect of SDMs on Pacific sardine landings, based on the results obtained by Smith et al. (2021).

In general, our hierarchical Bayesian landings per vessel model has the following structure:

$$(4) \quad \left[\boldsymbol{\beta}_{cj}, \boldsymbol{\delta}, \sigma_q^2, \sigma_\beta^2, q_{itj}^s\right] \propto \left[q_{itj}^s \,\middle|\, \boldsymbol{\beta}_{cj}, \sigma_q^2\right]\left[\boldsymbol{\beta}_{cj} \,\middle|\, \boldsymbol{\delta}, \sigma_\beta^2\right]\left[\boldsymbol{\delta}\right]\left[\sigma_q^2\right]\left[\sigma_\beta^2\right]$$

where the bracket notation $[z|y]$ means the distribution of z conditional on y. q_{itj}^s is the observed landings of the related species $s \in (1,\ldots, S)$ by vessel $i \in (1,\ldots, L)$ at month t in the

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[1] Tables and Figures denoted with a prefix S are available in the online supplementary material (Sections A and B, respectively).

Fig. 1. Participation networks for each fleet segment before and after the sardine closure. CPS-associated metiers are shown in blue with their labels bolded; everything else is shown in beige. Nodes represent fishing metiers, and their size represents their percentage contribution to total revenue generated by each fleet segment during each time period. The width of the lines connecting the nodes represents the percentage of vessels in each fleet segment participating in each pair of fisheries.
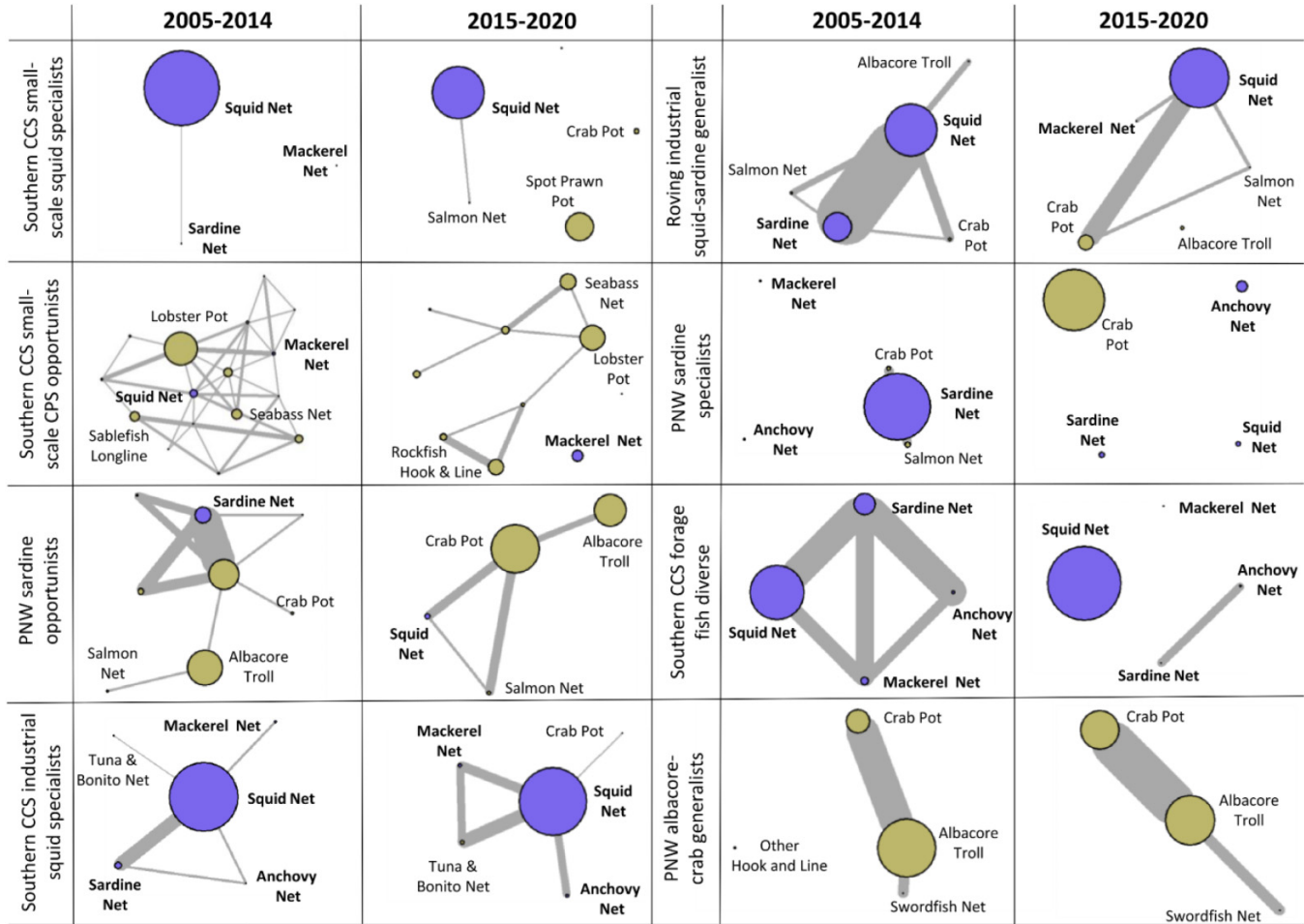
port area $j \in (1,\dots,J)$, S is the total number of species, L is the total number of vessels, and J is the total number of port areas. $\boldsymbol{\beta}_{cj}$ is a vector $k \times 1$, where k is the number of explanatory variables that contains the random coefficients to be estimated by port areas j and fleet segments $c \in (1,\dots,C)$, where C is the total number of fleet segments, σ_q^2 is the variance of the model predictions to be estimated, δ is a vector $k \times 1$ that contains the mean of the random coefficients to be estimated, and $\boldsymbol{\sigma}_\beta^2$ is a vector $k \times 1$ that contains the variances of the random-coefficients to be estimated. The hierarchical structure reflects that observed landing levels are conditional on the random coefficients, which in turn are conditional on the mean δ, the population-level coefficient, and the variance σ_β^2, which captures the coefficient variability by fleet segment and port area combinations.

We assume that the probability density function of landings $\left[q_{itj}^s | \boldsymbol{\beta}_{cj}, \sigma_q^2 \right]$ follows a lognormal distribution

(5) $\qquad \left[q_{itj}^s | \boldsymbol{\beta}_{cj}, \sigma_q^2 \right] \sim \text{lognormal} \left(\mu_{q_{itj}^s} \left(\boldsymbol{\beta}_{cj} \right), \sigma_q^2 \right)$

where $\mu_{q_{itj}^s} = \boldsymbol{X}\boldsymbol{\beta}_{cj}$ is the mean of the distribution and $\boldsymbol{X}$ is a vector of explanatory variables that explain landings. Our estimation framework allowed for modeling the correlation between random coefficients. All models of landings per vessel were estimated using the *brms* package in R developed by Bürkner (2017).

We estimated the following base model for the landings of species s:

(6) $\qquad \mu_{q_{itj}^s} = \beta_{0,cj} + \beta_{1,cj}\text{SDM}_{jt}^s + \beta_{2,cj}\text{Price}_{jt}^s + \beta_3\text{Length}_i$

$\qquad\qquad + \beta_{4,cj}\text{SDM}_{jt}^k \times \text{Open}_t^k + \beta_{5,cj}\text{SDM}_{jt}^s \times \text{SDM}_{jt}^k$

$\qquad\qquad\qquad \times \text{Open}_t^k + \beta_{6,cj}\text{PSDN.Closure}_t$

where SDM_{jt}^s is the standardized probability of the presence of species s in port area j during month t, Price_{jt}^s is the average price of species s in port area j during month t, Length_i is the length of the vessel i, SDM_{jt}^k is the probability of the presence of species k, where $s \neq k$, in the port area j during the month t, Open_t^k indicates the fraction of the month t that the species k fishery was open, and PSDN.Closure_t is a binary vari-

able that takes the value of one when the Pacific sardine fishery closed after July 2015, and zero otherwise. If prices at the port area level were missing, we replaced the average species' price in the port for all vessels in the corresponding year. If we still had missing values, we used the average monthly price at the port code, then at the port area, then at the state, and then considering the whole continental U.S. West Coast. Note that we estimated random coefficients for all the regressors, including the constant, except for length. Therefore, for the variable length, we only estimate a population parameter (i.e., the variance $\sigma^2_{\beta_3}$ was set equal to zero), while for the other regressors, we estimated population parameters and variance, and using these two parameters, we computed specific coefficients by port area and fleet segment combination. The coefficient estimated for the intercept can be interpreted as catchability for fleet segment c and port area j. The intercept could also capture different degrees of participation (or effort) by port area and fleet segment. The SDM outputs are a proxy for availability, while length is a proxy for effort capacity. The SDM outputs enter as a direct term and as an interaction to capture changes in relative abundance. Except for SDM outputs, all variables were standardized (z-values). Note that the effects of other species' probability of presence on species s landings (conditional on species s probability of presence), SDM^k_{jt} and $SDM^s_{jt} \times SDM^k_{jt}$, were weighted by the fraction of the month t that the fishery k was open. If the fishery k was closed for half of the month, the effect of the interaction would be reduced by half during that month. Note that SDM^s_{jt} is not adjusted by the fraction of the month that the species s fishery was open because, as we mentioned earlier, we only used observation of landings when the species in consideration is completely open during the month. For the Pacific sardine equation, we also include a binary variable that controls for the sardine closure in Washington from 1 January to 31 March.

If significant interaction effects were found in a model, to better interpret these results, we computed and plotted the effect of species k probability of presence on species s landings, conditional on the level of species s probability of presence. This effect was estimated by taking the derivative of eq. 6 with respect to SDM^k_{jt} to deriving the slopes of the lines to be plotted:

$$\frac{\partial \ln\left(q^s_{itj}\right)}{\partial SDM^k_{jt}} = \beta_{4,cj}Open^k_t + \beta_{5,cj}SDM^s_{jt} \times Open^k_t.$$

An identification challenge in our landings per vessel model was that the price might be endogenous, resulting in biased and inconsistent parameter estimates (Greene 2008). We used an instrumental variables (IV) approach to address this. In a Bayesian context, this requires estimating a multivariate model for both landings and prices using an instrument (i.e., exogenous variable) as a regressor in the endogenous variable equation (McElreath 2020). Moreover, it requires allowing for residual correlation between equations that arise from the unobservable confounder. In our case, the residual correlation between equations came from unobserv-

able demand shocks that affected both quantity supplied and prices.

The multivariate model expanded eq. 6 to incorporate the IV approach, and followed the form:

$$\begin{bmatrix} \ln\left(q^s_{itj}\right) \\ Price^s_{jt} \end{bmatrix} \sim MVNormal\left(\begin{bmatrix} \mu_{q^s_{itj}} \\ \mu_{Price^s_{jt}} \end{bmatrix}, \Sigma\right)$$

$$\mu_{q^s_{itj}} = \beta_{0,cj} + \beta_{1,cj}SDM^s_{jt} + \cdots + \beta_{6,cj}PSDN.Closure_t,$$

$$\mu_{Price^s_{jt}} = \alpha_{0,j} + \alpha_{1,j}Fish.Meal.Price_t$$

$$\Sigma = \begin{bmatrix} \varepsilon_{q^s_{itj}} & 0 \\ 0 & \varepsilon_{Price^s_{jt}} \end{bmatrix} \Phi \begin{bmatrix} \varepsilon_{q^s_{itj}} & 0 \\ 0 & \varepsilon_{Price^s_{jt}} \end{bmatrix}$$

$$\Phi = \begin{bmatrix} 1 & \rho \\ \rho & 1 \end{bmatrix}$$

where Σ is the error covariance between landings and prices and Φ is the corresponding correlation matrix. For all species, we used the world's fishmeal price as an instrument for prices, as this variable should be correlated with CPS prices but is likely not to be affected by demand shocks. In preliminary estimations of our landings per vessel model, we included diesel price by port as a proxy of the marginal cost of effort, but this variable was highly correlated with the fishmeal price ($r \geq 0.7$) and, consequently, highly correlated with the instrumented species price. Therefore, we dropped it from our analysis. Similarly, we estimated a model including quarterly wages by state for finfish fishery, but due to its correlation with fish meal prices, estimates for prices became negative. Thus, we decided to exclude this variable as well. For the population-level parameters, we assumed a flat prior for both intercepts, a normal prior for the interaction, the direct effect of other species SDM and the Pacific sardine closure coefficients, and a lognormal prior for length, species price, fishmeal price, and our own SDM coefficients:

$$\beta_4, \beta_5 \text{ and } \beta_6 \sim Normal(0, 1)$$

$$\beta_1, \beta_2, \beta_3 \text{ and } \alpha_1 \sim LogNormal(0, 1)$$

$$\varepsilon \sim Exponential(1)$$

$$\rho \sim LKJ(2).$$

We ran each model using four chains of 2,000 iterations each, half of which were warm-up iterations. The effective sample size (ESS) was large enough, so no additional iteration was needed to run the model. Convergence was checked based on the number of divergent transitions, the R-hat statistics, and the ESS (Bürkner 2017). Specifically, we use an R-hat lower than 1.1 and an ESS larger than 10% of the total sample size as thresholds to define convergence (Bürkner 2017). Additionally, we used the Monte Carlo standard error as a robustness check for this purpose (Vats and Gupta 2021). Our final sample for estimation comprised the period from January 2000 to August 2019.

See Section C in the online supplementary material for links to our GitHub repository with the code used to conduct the analyses presented in this article.

Fig. 2. Inputs contribution to each cluster. Bars show the mean of the standardized input value (z-value) within each fleet segment. Black lines show 95% confidence intervals. CCS, California current system; LCG, latitudinal center of gravity; CPS, coastal pelagic species.
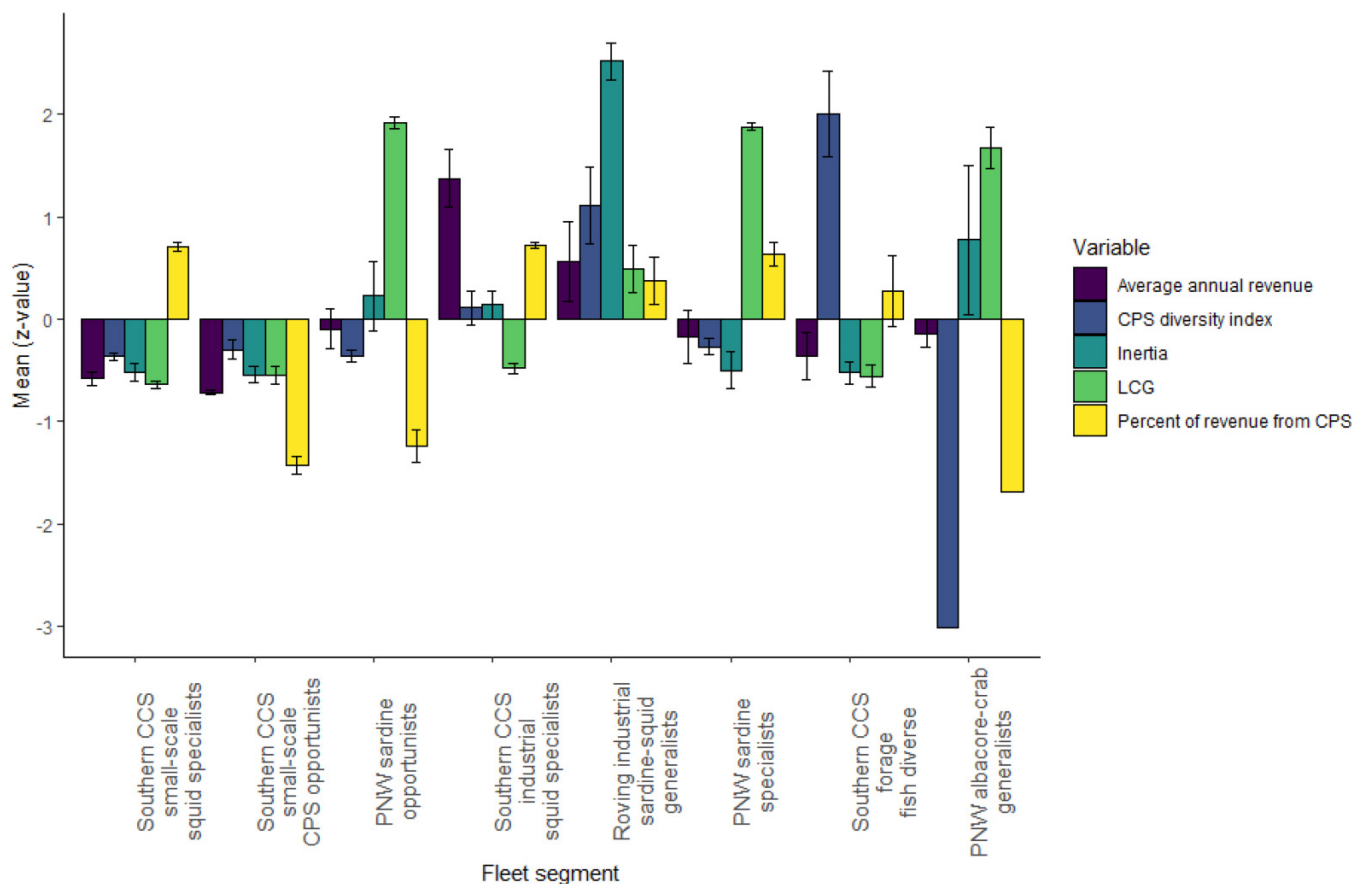
3. Results

3.1. Cluster analysis

3.1.1. Clustering algorithm

We conducted the PAM clustering algorithm using eight clusters, which was suggested to be optimal by the average silhouette method (Fig. S1). The random forest algorithm indicated that the most important variable for partitioning vessels into clusters was the percentage of revenue that comes from CPS landings (Fig. S2), followed by the LCG, the average annual revenue, and then the CPS diversity index. The least important variable was inertia. The input contribution to each cluster is shown in Fig. 2.

3.1.2. Cluster labeling

We assigned unique labels to each of the eight clusters (Table 1). The labels indicate scale of operation ("small scale" or "industrial"), landing ports ("Southern CCS", "PNW", or "Roving"), and degree of specialization ("specialist", "generalist", "diverse", or "opportunist").[2] The main targeted species

and gear used (i.e., fishing métiers) by each cluster are shown in Fig. 1.

3.1.3. Cluster validation

Intra-cluster metrics results (Fig. 3 and Table S6) show that the "Southern CCS industrial squid-specialist" and the "Roving industrial sardine-squid generalists" fleet segments are the most heterogeneous clusters, with the highest values of complete (5.70 and 4.56, respectively) and average intra-cluster diameters (1.64 and 2.16, respectively), while the "Southern CCS small-scale squid specialists" fleet segment is the most homogeneous according to these metrics (2.08 for complete intra-cluster diameters and 0.62 for average intra-cluster diameters). Inter-cluster metrics (Fig. 3 and Table S7) indicate that the "Southern CCS small-scale squid specialists" and the "Southern CCS small-scale CPS opportunists" fleet segments are closely related, with the lowest distance between them (2.5), while the "Southern CCS small-scale squid specialists" fleet segments and the "PNW albacore-crab generalists" fleet segments are the most different, with the highest distances between each other (8.4).

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[2] More detailed descriptions of these categories are provided in Section E in the online supplementary material.

8

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Table 1. Cluster labels (i.e., fleet segments).

Cluster label	Region of operation	Gear used	Principal source of revenue	Limited entry CPS permit?	Other description
Southern CCS small-scale squid specialists	Mostly in Los Angeles (LA) (Table S3), showing a small range of latitudes in landings (i.e., inertia)	Usually seine and dip nets (Table S4)	Principal source of revenue is market squid (Table S1)	Only 7.25% of the vessels own a limited entry permit	48% of the vessels are light brail boats
Southern CCS small-scale CPS opportunists	South of San Francisco, focusing on a single port (small inertia)	Commonly use crab and lobster pot, pole, and longline. Occasionally use dip net and seine	Variety of non-CPS (e.g., lobster), but they harvest CPS, such as squid and mackerel occasionally	None of the vessels have a limited entry permit	24% are light brail boats
PNW sardine opportunists	Washington and Oregon, moving between close ports	Commonly use crab pot, troll, and seine	Crab and albacore, but they also target sardine. Switching between crab and albacore might depend on the season, fishing crab in the winter	N/A	To catch albacore, they use anchovy as bait (Table S5)
Southern CCS industrial squid specialists	South of San Francisco	Mainly use seine	Market squid	More than half (51.9%) of the vessels own a limited entry permit	Average vessel revenue over 1 million USD
Roving industrial sardine-squid generalists	Range over all the CCS, landing in ports from LA to North Puget Sound	Commonly use seine or other net gears	Switch between sardine and squid	20.8% of the vessels have a limited entry permit	Large annual revenues
PNW sardine specialists	Pacific Northwest, from Astoria (CLO), the principal port, to Westport (CWA), but they have low inertia	Commonly use seine or other net gears	Mainly from sardines	N/A	Considerable portion of revenue from bait fishery
Southern CCS forage fish diverse	Mostly operate between LA and Monterey, focusing on a single port	Mainly seine	Harvest a diverse list of CPS	23.8% have a limited entry permit	14% of vessels are light brail boat
PNW albacore-crab generalists	Located in the PNW	Common gear is troll	Seasonally switch between crab and albacore; do not land CPS	N/A	Use anchovy as bait for albacore

Fig. 3. Principal component analysis of fleet segments (i.e., clusters). Fleet segments are enclosed by ellipses. Metrics included in the principal component analysis are average annual revenue, the latitudinal center of gravity (LCG), inertia (I), coastal pelagic species (CPS) income diversification, and the percentage of revenue coming from CPS landings.
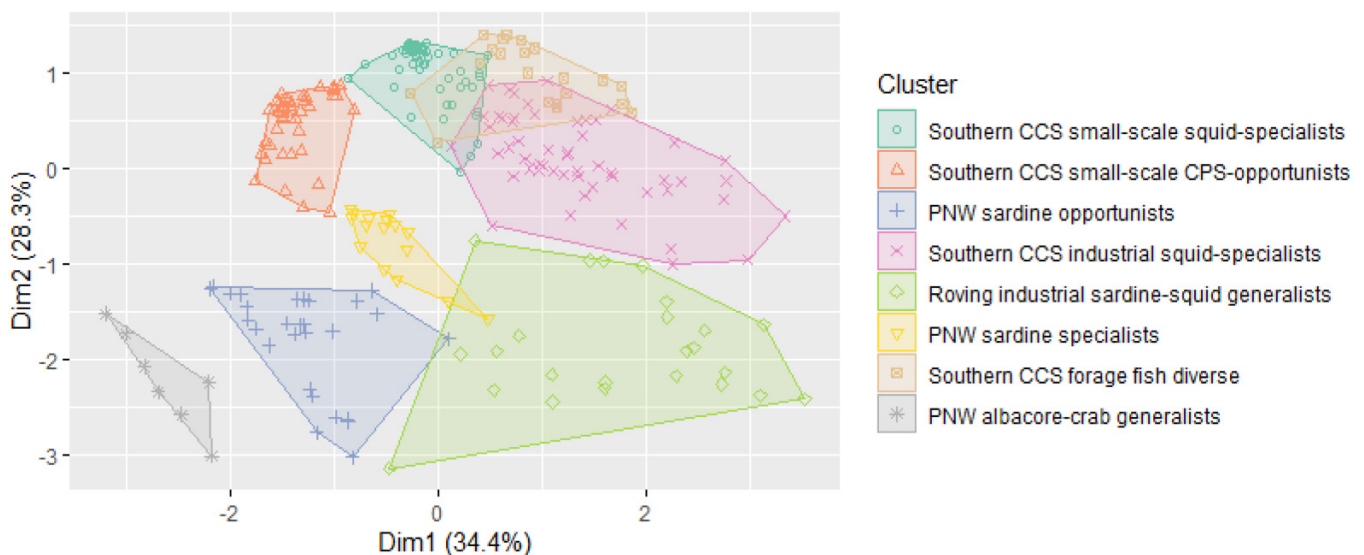
Fig. 4. Spatial distribution of fleet segments and port areas used in each landing per vessel model. Each dot represents a fleet segment and port area combination that was included in the corresponding model and for which we estimated a coefficient. Base map (WGS84 datum) and boundaries were obtained from Natural Earth (naturalearthdata.com) using the R packages *rnaturalearth* (South 2017) and *maps* (Becker et al. 2018).
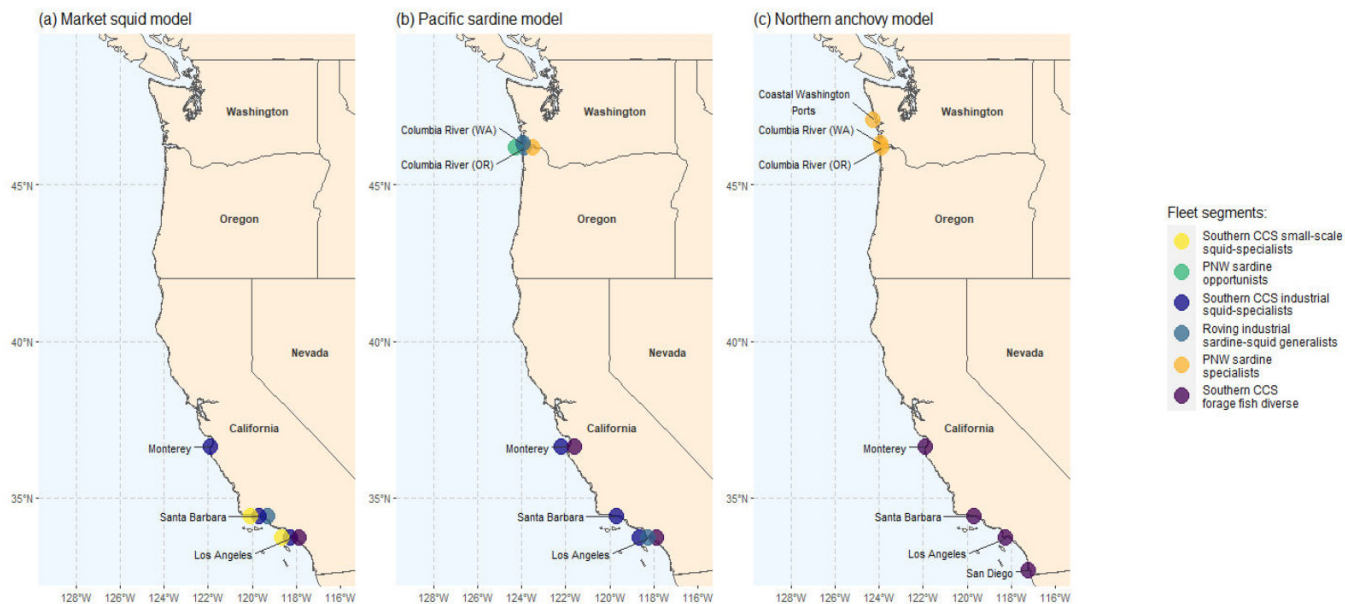
3.1.4. How did fleet segments change after the Pacific sardine closure?

The only fleet segments that increased their average annual revenue per vessel after the closure were the "Southern CCS small-scale squid specialists", the "Southern CCS small-scale CPS opportunist", and the "PNW sardine opportunists" fleet segments, where the latter had the more significant annual revenue increase per vessel (+US$110,582; Table S8). Meanwhile, the "Southern CCS industrial squid-specialists" had the highest loss in average annual revenue per vessel after the closure (−US$614,441), followed by the "Roving industrial sardine-squid generalists" fleet segment (−US$289,147). In addition, the only two fleet segments that we observed an increase in total annual revenue for after the closure were the opportunist fleet segments ("Southern CCS small-scale CPS opportunists" and "PNW sardine opportunists").

Many vessels identified as CPS-targeting from 2005–2014 stopped fishing entirely after the closure of the Pacific sardine fishery in July 2015. When we consider new entrants, the "Southern CCS small-scale CPS-opportunists", the "Southern CCS industrial squid specialists", and the "PNW sardine opportunists" fleet segments are the only ones that experienced an increase in the average number of active vessels per year post-closure (Table S8 and Section F in the online supplementary material). It is noteworthy that the majority (52%) of new entrants coming into the CPS post-sardine closure belonged to the opportunist clusters. In contrast, the "Southern CCS small-scale squid-specialists" fleet segment saw the highest level of attrition following the sardine closure (Table S8). Some vessels exited the CPS fishery after the sardine closure in 2015 and continued to operate in completely different fisheries. This is observed mostly for vessels belonging to the two "opportunist" fleet segments, where more than 50% of the vessels in these fleet segments do not have a CPS ticket after 2015 but are still active in other fisheries (Table S9).

Catch composition differed before and after the closure. There is an abrupt reduction in market squid share in the "Southern CCS small-scale squid specialists" fleet segment (Fig. 1). Some vessels in these fleet segments moved to other non-CPS, such as spot prawns (*Pandalus platyceros*). Vessels in the "Southern CCS industrial squid-specialists" fleet segment expanded effort into mackerel, anchovy, and tunas after the closure, while the "Southern CCS forage fish diverse" and the "Roving industrial squid-sardine generalists" fleet segments became more exclusively reliant on squid. The latter, together with the "PNW sardine opportunists", increased their reliance on the Dungeness crab fishery after the closure, while most vessels in the "PNW sardine specialist" fleet segment now exclusively target crab. In addition, coincident with a recent observed shift in market squid distribution (Chasco et al. 2022), some vessels in PNW fleet segments began participating in an emerging Oregon-based squid fishery that has remained open-access, while the "PNW sardine specialists" fleet also allocated more effort to northern anchovy.

3.2. Landings per vessel model

After filtering our data, we end with a subgroup of fleet segments and port area, for which we estimate differentiated coefficients. The spatial distribution of the subset of fleet segments and port areas included in each landing per vessel model is presented in Fig. 4. We rejected non-stationarity for all variables included in the three landing models (Table S10). A description of each variable used in our models is presented in Table S11, while population parameter estimates are pre-

Fig. 5. Price effect on landings per vessel by fleet segment and port area. Dots represent estimated coefficients and black lines show credible intervals at the 95% level.
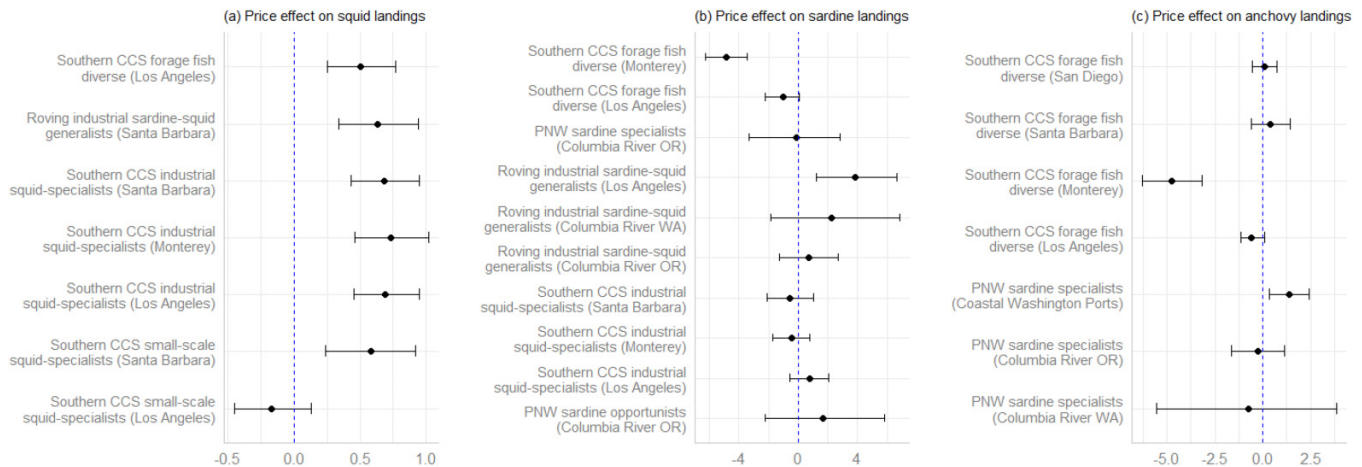
sented in Table S12.[3] Our estimated models for squid, sardine, and anchovy landings per vessel have a Bayesian R-squared (Gelman et al. 2019) of 0.19, 0.49, and 0.61, respectively.[4] As a reminder, we are estimating models of landings per vessel, conditional on vessel participation during a specific month.

3.2.1. Price effect

The results for the squid model indicate that all fleet segments and port areas are responsive to variations in squid prices, except for the "Southern CCS small-scale squid specialist" fleet segment landing in Los Angeles (Fig. 5). In the case of sardine and anchovy, most effects are non-significant. We only found a significant positive effect of sardine prices on sardine landings for the "Roving industrial sardine-squid generalist" fleet segment in Los Angeles and a positive effect of anchovy prices on anchovy landings for the "PNW sardine specialist" fleet segment in the Coastal Washington Port area. Unintuitively, we found a negative and significant effect of price on sardine and anchovy landings in Monterey for the "Southern CSS forage fish diverse" fleet segment. We do not have a clear understanding of what is driving these negative coefficients, though we hypothesize it may be attributable to omitted variable bias. For instance, the prices of sardine and anchovy might be correlated with the prices of other more valuable species in the Monterey area, causing a shift in effort allocation to the other more valuable species when prices increase.

3.2.2. Own probability of presence

We did not find any significant effect of the own probability of presence on squid and anchovy landings per vessel (Fig. 6). In the case of sardines, we found a significant and positive effect in 7 out of 10 fleet segments and port areas. The only fleet segments and port areas for which we did not find a significant effect were the "Southern CCS industrial squid specialists" fleet segment in Santa Barbara, the "PNW sardine specialists" fleet segment in the Columbia River at Oregon, and the "Southern CCS forage fish diverse" fleet segment in Monterey.

3.2.3. Pacific sardine closure

The Pacific sardine closure coincided with a negative and significant effect on (i) squid landings per vessel for the "Southern CSS industrial squid-specialists" fleet segment at Santa Barbara and Los Angeles areas (Fig. 7), and (ii) anchovy landings per vessel for the "Southern CCS forage fish diverse" fleet segment that lands at San Diego and Monterey areas. Moreover, we found a significant and positive effect of the closure on (i) squid landings per vessel for the "Southern CCS small-scale squid specialist" fleet segment at Los Angeles and (ii) anchovy landings per vessel for the "PNW sardine specialists" fleet segment at Columbia River in Washington. Note, however, that these estimates should be discussed with care as they might reflect other non-observable effects that are not captured by the other covariates.

3.2.4. Other species probability of presence

Effect on market squid landings per vessel

Landings of squid in all "squid-specialists" fleet segments and port areas, except at Monterey, either industrial or small-scale, were lower when the probability of sardine presence was high (Panel (a); Fig. S3). By contrast, landings by "squid-specialist" vessels in Monterey were significantly and negatively affected by the probability of anchovy presence. The decrease observed in both cases suggests that there might be some substitution between squid and anchovy for "squid-specialists" in Monterey and between squid and sardine for "squid-specialists" operating in other ports when anchovy or sardine, respectively, become more available (i.e., their prob-

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[3] A discussion about the convergence of each landings model is discussed in Section G in the online supplementary material.

[4] Bayesian *R*-squared by fleet segment and port areas are presented in Table S13.

Fig. 6. Own species SDM effect on landings by fleet segment and port area. Dots represent estimated coefficients and black lines show credible intervals at the 95% level.
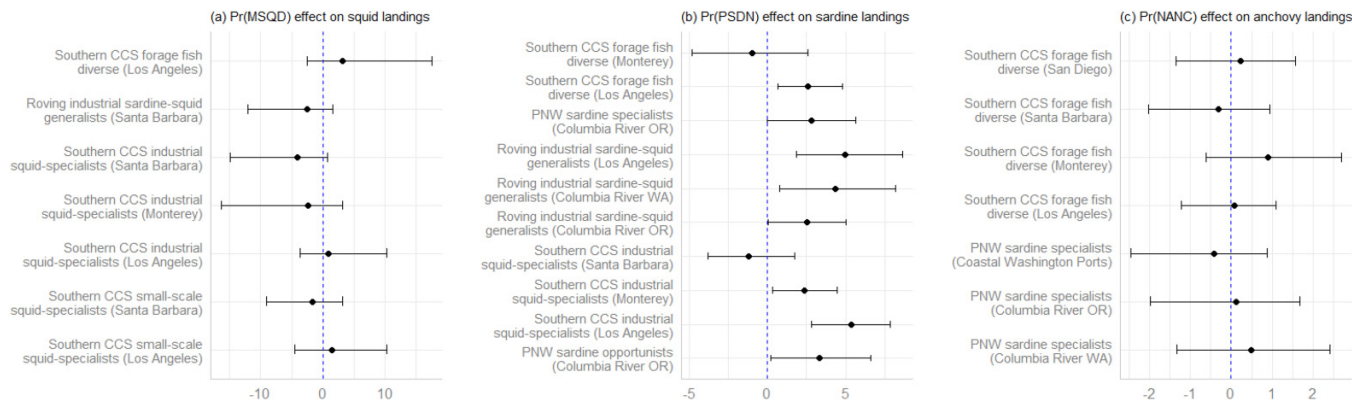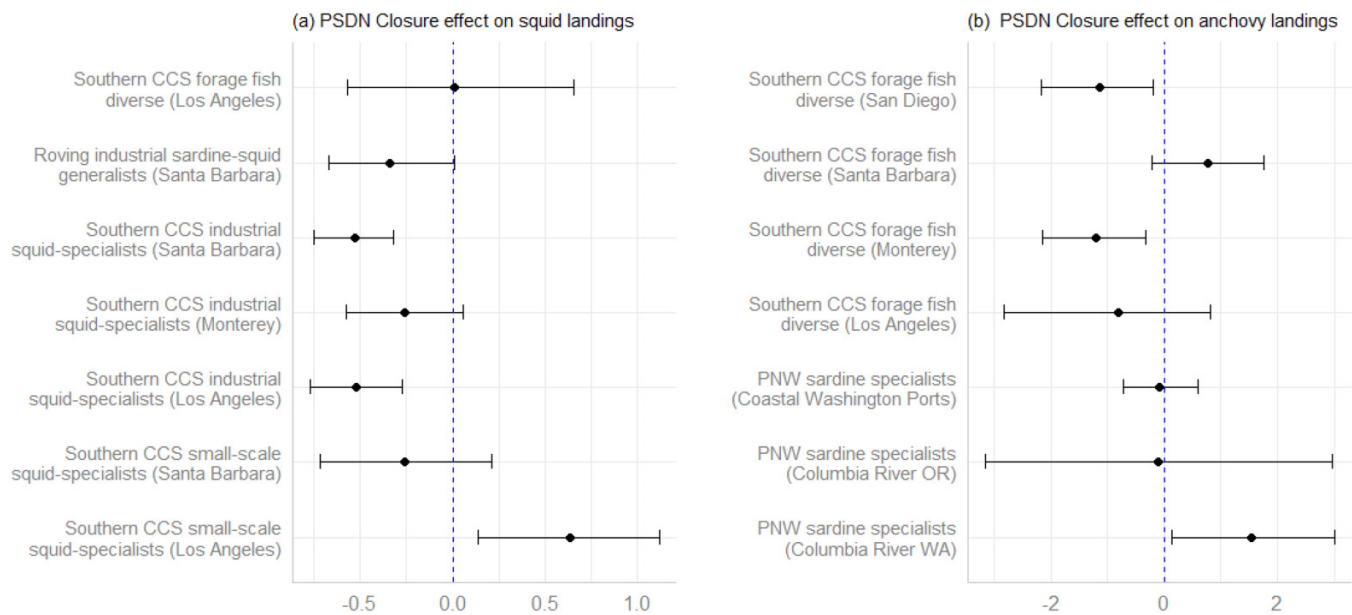

Fig. 7. Pacific sardine closure effect on landings per vessel by fleet segment and port area. Dots represent estimated coefficients and black lines show credible intervals at the 95% level.

ability of presence is high). However, note that the results in this section should be interpreted with caution, as they do not say anything about what happens to anchovy or sardine landings, and their availability may be correlated with the availability of other target species (e.g., mackerels and tunas) and with the distinct types of oceanographic conditions and/or regimes thought to favor these other target species as compared to other CPS. Therefore, the model might be capturing substitution for other species whose availability is correlated with that of anchovy or sardine.

For the "Southern CCS industrial squid-specialists" and the "Roving industrial squid-sardine generalists" fleet segments in Santa Barbara, there was also a significant interaction effect between squid and sardine probabilities of presence (Panel (c); Fig. S3). We can observe that, for these two fleet segments, the effect of the sardine's probability of presence on market squid landings is positive for values above 0.1 for the probability of presence of squid (Fig. S4). For the "Southern CCS industrial squid-specialists" fleet segment, this is in

contrast to the negative direct effect of sardine availability on squid landings described above that does not consider the interaction effect (Fig. S3). This effect is stronger as the squid's probability of presence increases and suggests that complementarity between market squid and sardine for these fleet segments in Santa Barbara increases when there is high availability of squid. Note that in our model, the probability of presence for sardine is treated as zero during the closure of the Pacific sardine fishery, and thus the effect of the probability of presence for sardine on squid landings is no longer in place during the closure years of 2015 onwards.

Effect on Pacific sardine landings per vessel

We did not find any significant direct or interaction effect of the squid probability of presence on sardine landings. We only found one positive and significant direct effect of the anchovy's probability of presence on sardine landings for the "Southern CCS industrial squid-specialist" fleet segment at Santa Barbara (Fig. S5). This is one of the few fleet segments

and port areas where the sardine's own probability of presence does not have a significant effect on landings.

By contrast, sardine landings in Los Angeles for the "Southern CCS industrial squid-specialist" and the "Southern CCS forage fish diverse" fleet segments were negatively impacted by an increase in anchovy probability of presence, but only when sardine probability of presence was high (Fig. S6). The main effect of the sardine SDM showed that, at a high probability of the presence of sardines, landings of sardine for these fleet segments in Los Angeles are higher (Fig. 6). Likely, there is an incentive for vessels to allocate effort to catching sardines when it is easier to find them. Nevertheless, results for the interaction term suggest that as anchovy availability increases, vessels reduce targeting of sardine, even if sardine availability is still high. However, as noted above, these results should be interpreted with caution, as they do not say anything about what happens to the other species (in this case, anchovy) landings. Targeting efforts might actually switch to other species, such as mackerels and tunas, whose availability may be positively correlated with anchovy availability. Indeed, currently, the Southern CCS fleets do not target anchovy as there is a limited market for this fishery in California (K. Lynn, CDFW (personal communication, 9 May 2023)).

By contrast, when the sardine probability of presence is low, there is no negative effect of anchovy availability on sardine landings (Fig. S6). This suggests that any effort allocated to targeting anchovy does not impact sardine landings, as there is no incentive to target sardine given their low availability, and the trade-off no longer exists. At low sardine availability, we only observe a small positive slope with increasing anchovy availability that we attribute to by-catch from targeting anchovy or other species.

Effect on northern anchovy landings per vessel

We only found two negative and significant direct effects of the sardine probability of presence on anchovy landings. These effects are for the "Southern CCS forage fish diverse" fleet segment landings at San Diego and Monterey (Fig. S7). Note that these two fleet segments and port areas are the same, for which we found a negative effect of the Pacific sardine closure. Thus, when the sardine fishery was no longer available, the negative direct effect of sardine availability on anchovy landings was no longer in place, increasing landings and counteracting the negative effect of the binary variable PSDN.Closure. As the average sardine availability is around 0.33, it seems that both effects cancel out, and no significant changes in anchovy landings per vessel were observed after the sardine closure for these two fleet segments and port areas. We did not find any significant effect of the interaction terms on anchovy landings.

4. Discussion

The fleets we analyzed represent a diverse set of over two hundred vessels targeting fishing grounds across 2,080 km of the U.S. West Coast with distinct motivations and operating considerations. The results obtained from our model of ex-vessel landings show that vessel heterogeneity and landing port are important in explaining vessel responses to shifts in species availability and other market drivers. Also, the measured effects differ by species, suggesting that the decision process influencing CPS targeting reflects factors that vary over economic markets and ecological characteristics unique to different species.

Though it is clear that landings classified by fleet segment and port area respond distinctively to different drivers, two major generalizations are evident. First, the landing model suggests that market squid landings per vessel are driven mainly by market conditions, such as prices, and do not respond to changes in squid's habitat suitability (i.e., the availability of squid to port areas). This relationship was clearest for the higher volume fleet segments (i.e., industrial fleet). This is consistent with the argument by Powell et al. (2022) that market prices would affect fishers' willingness to travel further distances to target squid. It should be noted, however, that the Bayesian *R*-square for the squid landings per vessel model was lower than for other species, suggesting that other variables, in addition to prices but not its own habitat suitability, affect landings. For statistical reasons (i.e., collinearity), we did not include other variables that might have improved the estimation of the landings per vessel model for this species, such as trip cost (e.g., fuel and distances to fishing grounds, or crew wages), other species availability (besides the ones included in the model), and variables that are proxies of fishing risks, such as ocean conditions. For instance, including finfish quarterly wages by states did improve prediction for market squid landings per vessel, but worsened other species landing predictions. However, its inclusion also affected the implementation of our IV regression by making the estimates for prices negative, as wages are correlated with fishmeal prices.

Squid habitat suitability being an imperfect index of squid availability may also be a potential reason for the lower explanatory power of the squid landings model and the lack of a relationship between habitat suitability predictions and squid landings. Unlike the anchovy and sardine SDMs, which include annual indices of spawning stock biomass to account for lower availability at lower stock sizes, the squid model represents suitable and unsuitable spawning habitat based on environmental covariates and shows increasing habitat suitability in recent years when landings were decreasing (Fig. S8) and squid paralarvae abundance in southern California was low (Van Noord 2020). Ralston et al. (2018) show that a pre-recruit index based on trawl survey catches of small (30–50 mm mantle length) squid was correlated with commercial landings several months later. As the SDM used in this study was based on the spatial extent of benthic spawning habitat, it is likely that recruitment of squid is related to processes other than habitat suitability (Suca et al. 2022).

The second major generalization from the results is the importance of sardine availability (habitat suitability) in determining sardine landings per vessel, consistent with Smith et al. (2021). This was particularly evident for the higher-volume fleet segments. In contrast, landings per vessel of anchovy were not correlated with predictions from the anchovy SDM or with market prices (with limited exceptions to this). This is likely due to a lack of market, as reduction capacity has de-

creased to almost zero (PFMC 2020), and so anchovy is not the main target species of any of the CPS fleet segments. Thus, it seems that anchovy per vessel landings are driven instead by conditions observed for Pacific sardine. For instance, more anchovy landings occurred for the "PNW sardine specialists" during the sardine closure and for the Monterey and San Diego "Southern CCS forage fish diverse" fleet segment during periods of low sardine abundance.

Species availability over historical fishing grounds is expected to shift under climate change, putting fishing communities at risk (e.g., Rogers et al. 2019). Our analysis of the response of different fleet segments in the CPS fleet to the 2015 sardine fishery closure provides insights on the impact of a dramatic shift in availability on different fleet segments and their potential vulnerability to future changes in fishing opportunities. We show that opportunist fleet segments that possessed broad harvest portfolios (i.e., containing other non-CPS species) prior to the closure were more resilient to the loss of sardine fishing opportunity and revenue. In the PNW, where sardine dependence was high, growth in crab, squid, and anchovy fisheries represented valuable opportunities for substitution, while in southern California, lobster, seabass, and groundfish fisheries continued to anchor small-scale opportunist harvest portfolios despite declining sardine revenue. However, in both the PNW and Southern CCS, it was only the opportunist fleets with the capacity to shift fishing gears and/or target species (i.e., "PNW sardine opportunists" and "Southern CCS small-scale CPS opportunists") that were able to mitigate sardine-associated losses by taking advantage of alternative fisheries. These opportunist fleet segments may have been able to draw upon their previous experience with other gears (i.e., an economic diversity asset sensu Mason et al. 2022) to contend with the sardine closure. These findings support evidence from other fisheries and regions that diversification strategies are associated with enhanced resilience and might be an effective adaptation strategy to climate change (Cinner et al. 2012; Kasperski and Holland 2013; Sethi et al. 2014; Gamito et al. 2016; Cline et al. 2017; Fisher et al. 2021).

For other fleet segments, the sardine closure resulted in a higher degree of specialization, which may reduce their resilience to future climate shocks and stressors. For instance, most vessels in the "PNW sardine specialist" fleet segment now exclusively target crab, while the "Southern CCS forage fish diverse" and the "Southern CCS small-scale squid-specialists" fleet segments increased their reliance on squid. All these fleet segments had losses in terms of revenues per vessel after the closure (Table S8). Likewise, after the closure, the "Southern CCS industrial squid specialists" also did not switch fishing gears (except for a small number that entered the crab fishery), but directed more effort towards anchovy, mackerels, and tunas, other purse seine fisheries that supplemented their primary dependence upon squid. This is a similar response to that observed among purse seiners in Portugal impacted by environmental variation, which were found to be willing to fish new species when their main target declined dramatically only if they could target them with purse-seine gear (Gamito et al. 2016). The "Southern CCS industrial squid specialists" fleet segment also saw a considerable de-

cline in their average annual revenue per vessel, but unlike the "Southern CCS small-scale squid-specialists", it did not experience any attrition (Table S8). The response observed post closure for these high squid-dependent fleet segments coincides with Powell et al. (2022), who found that fishers would switch to other species if low squid abundance was observed, but if fishermen were highly dependent on market squid for revenue and these revenues were large, the probability of switching would be lower.

The highly CPS specialized fleet segments ("PNW sardine specialist", "Southern CCS forage fish diverse", and "Southern CCS small-scale squid-specialists") were also the only ones showing an increase in inertia (i.e., range of fishing grounds) following the closure (Table S14), meaning their landings were dispersed over more ports than prior to the closure. For specialized vessels, increased mobility may be an effective adaptation strategy in the face of changing target species availability (Young et al. 2018), but it did not appear to be an effective adaptation measure here. The success of any one adaptation strategy, like increased mobility, will be limited by context-dependent factors, such as the availability of adequate port and processing infrastructure and other interdependent socio-economic, governance, and ecological attributes (Mason et al. 2022).

Specialization might be a response to the high price observed for squid and crab in recent years. As Finkbeiner (2015) found for small-scale fishers in Mexico, specialization may allow fishers to maximize revenue under favorable market conditions. However, to increase fishers' resilience to climate change, diversification is required (Aguilera et al. 2015; Finkbeiner 2015; Cline et al. 2017; Fisher et al. 2021). Thus, targeted policies to encourage diversification, such as the development of new markets, infrastructure investments, and flexible permits that make diversification appealing, may be warranted. Also on the U.S. West Coast, Liu et al. (2023) found that diversification, together with an increase in spatial mobility, improved Dungeness crab fishers' adaptation capacity to a marine heatwave. Indeed, measures that increase diversification of species captured, fishery added value, and gear/license diversification have been suggested to increase the adaptive capacity of the purse-seine fleet in Portugal, which is highly dependent on sardines (Albo-Puigserver et al. 2022). Future work could further investigate how socio-economic, ecological, and governance attributes, for example those proposed by Cinner et al. (2018) and Mason et al. (2022), as well as contextual considerations, facilitated diversification and resilience in some fleet segments but not others.

In summary, other factors in addition to main target species availability, such as the availability of other species in a vessel's portfolio, regulations, and market conditions, need to be considered to understand vulnerability to climate-driven changes in ex-vessel landings and to foster effective adaptation measures. The strong relationship found for sardine between availability and per-vessel landings cannot be generalized to squid and anchovy. Thus, the definition of climate risk for the U.S. West Coast CPS fleet will not only need to consider exposure (i.e., shifting habitats over fishing grounds), but also limitations to the adaptive capacity of fish-

ing communities in terms of markets and port infrastructure, a similar conclusion found by Selden et al. (2019) for U.S. West Coast groundfish. Indeed, marketing adjustments, such as diversification of marketing channels and improved access to high-value markets, have been put forward as an important climate adaptation measure for fisheries (OECD 2011; Ibarra et al. 2013; Karadzic et al. 2014; Ho et al. 2016; Lindegren and Brander 2018; Ojea et al. 2020). Within the context of the U.S. West Coast CPS fishery, policy and investment designed to build the infrastructure required to process anchovy will be of critical importance in increasing the resilience of participating fishers.

Additionally, our landing models reveal that no universal truth can be applied across fisheries in terms of their response to changing species availability. We have found some generalizations as well as some heterogeneous drivers of landings for most high-volume CPS fleet segments and ports. For certain fleet segments and ports, particularly for mid- and low-volume CPS fleets (e.g., the PNW sardine specialists and the Southern CCS forage fish diverse fleets), motivations and drivers of landings are less clear. For these lower-volume fleets, even if landing models do not provide full insight, grouping vessels into distinct fleet segments represents an advance upon previous distinctions in the literature made on gear-type and vessel size alone, or by catch profile (Ruiz et al. 2021), allowing us to classify vessels into a more realistic set of heterogeneous groups, or "fishing behavioral types" (O'Farrell et al. 2019). This is relevant as heterogeneous fishing strategies can emerge even when vessels use similar technologies (Andrés and Prellezo 2012; Frawley et al. 2021a). Different actors within a given fishery will respond to the same shocks and stressors in different ways based on things we can measure (e.g., the size of their boats, the permits they have, the infrastructure and markets available to them) and other factors not widely considered in traditional bioeconomic modeling approaches (e.g., preferences, traditions, culture, etc.). Taking into consideration this variation within fisheries is relevant when we want to consider equity dimensions in the development of adaptation strategies to the impact of projected changes on species distribution (see, e.g., Jardine et al. 2020), or the implementation of new regulations.

Our finding that there is a lack of a universal truth predicting U.S. West Coast CPS fishery landings is reflected in other regions of the world as well as other fisheries. For instance, in the Bay of Biscay, the anchovy stock collapsed and the fishery was closed from 2005 to 2009. Closure impacts and adaptive capacity were heterogeneous, depending on the fleet segment (Andrés and Prellezo 2012). In Portugal, Gamito et al. (2016) found that the vulnerability of vessels to climate change varied depending on the gear used and the fishing grounds. Purse-seine vessels and the south coast of Portugal are the most vulnerable to climate change, while trawlers and multi-gear vessels are the least vulnerable (Gamito et al. 2016). In Peru, Bertrand et al. (2004) found significant differences in fishing behavior among and within vessels targeting anchoveta (*Engraulis ringens*). Fisheries targeting groups other than CPS also demonstrate heterogeneous responses. For instance, in the reef-fish fishery in the Gulf of Mexico, Zhang and Smith (2011) found heterogeneous responses to the creation of marine protected areas.

Our analysis predicts monthly landings per vessel. We can predict aggregate landings by fleet and port by multiplying the average landings per vessel for each port and fleet segment by the observed number of participating vessels. When we add them across fleet segments and ports, our model closely follows the total landings of squid and sardines (Bayesian R-squared of 0.89 and 0.91, respectively), suggesting that knowing the number of participating vessels is important to accurately predict aggregate landings. In our case, by construction, we only considered vessels that we knew from landing observations participated in the squid, sardine, or anchovy fishery during a month at a particular port. Given that the drivers of participation decisions may be different from those underlying how much participating vessels catch, aggregate landings are often computed by combining results from a participation model of how many vessels are participating with a landings per vessel model (e.g., Smith 2002). Alternatively, a simpler model can be estimated using an equation for aggregate landings (e.g., total monthly landings across all vessels at a port, as in Smith et al. (2021)) that implicitly incorporates individual participation and landing decisions. Developing a participation model was outside the scope of this work, but this analysis provides a valuable first step towards the development of a future modeling framework to predict aggregate landings that combines structural models of participation and landing per-vessel decisions. The use of a per-vessel landings model, such as the one presented here, to forecast future aggregate landings at the fleet or port levels will require investigation into the drivers of vessel participation at the port level during a specific period of time. Using the results of our work, together with the results from a participation model, would allow researchers and policymakers to predict the impact of climate change or closures on landings at an aggregate level.

4.1. Caveats

Our analyses rely in large part on SDM outputs, which are imperfect predictors of species availability to fishers. Our SDMs predicted the presence or absence of CPS, but abundance (which is more relevant for predicting landings) is influenced by fine-scale oceanographic features such as fronts, schooling behavior, and other processes at spatial scales too fine for us to model at the spatial resolution of our SDMs (0.1 degrees). Market squid has a particularly complex life cycle, and they are primarily fished when they aggregate to spawn. The lack of explanatory power of the squid SDM may suggest that our benthic spawning habitat model did not adequately represent availability to fishing fleets from this aggregation behavior, and thus the squid SDM could not predict landings well. A potential impact of imperfect observation of species availability in our model estimates is that the coefficients can be biased (Aigner 1973) if the reported value is correlated with the measurement error (Hyslop and Imbens 2001), as the measurement error becomes part of the error term of the regression. Future refinement of SDM models from presence/absence to density to better represent target

species availability may help improve the explanatory power of our landings model.

Another drawback of our models is that the vessels used in our cluster analysis, and then in our landing model, were identified as those targeting CPS during 2005–2014. New vessels targeting CPS could have entered after 2015 but were not considered in our landings model. This new vessel set can include experienced CPS fishers that could have bought a new vessel to replace their old, or new entrants. Consequently, our model does not consider any new entrant behavior that these vessels brought to the fishery.

5. Conclusions

This study analyzed how historical changes in forage species distribution, price, and the closure of the Pacific sardine fishery affected landings per vessel of three CPS: Pacific sardine, market squid, and northern anchovy that are targeted by the U.S. West Coast Coastal Pelagic Fleet during the period 2000–2020. Using cluster analysis results, we identified eight different CPS fleet segments, which differ in terms of their dependence on the CPS fishery, the average location of their landings, the number of species they target from the CPS groups, their revenue, and how much they travel. Our landing models estimate heterogeneous responses by fleet segment and port areas to different variables such as prices, own and other species' probability of presence, and the closure of the Pacific sardine fishery. In general, we found that squid landings are mainly driven by market conditions, while sardine landings are driven by habitat suitability and anchovy landings by the state of the sardine fishery. In terms of vessels targeting the same species, we found that distinct fleet segments and port areas respond differently to the same drivers. Our results support the idea that the implementation of new regulations and climate change adaptation strategies developed to reduce the impact of climate change should consider the heterogeneity in responses that exist between target species, fleet segments, and port communities.

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Article information

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Notes

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Data availability

Vessel-level landings collected by the Pacific Fisheries Information Network (PACFIN), CDFW, ODFW, WDFW, and the NOAA National Marine Fisheries Service are confidential U.S. government data. The raw data cannot be made public under the Magnuson–Stevens Fishery Conservation and Management Reauthorization Act of 2006, Section 402(b), 16 U.S.C. 1881a. Additionally, CDFW acquires data from its own fisheries management activities and from mandatory reporting requirements on commercial and recreational fisheries pursuant to the Fish and Game Code and the California Code of Regulations. These data are constantly updated, and data sets are constantly modified. CDFW may provide data upon request but, unless otherwise stated, does not endorse any particular analytical methods, interpretations, or conclusions based upon the data it provides. To request access to U.S. West Coast vessel-level landings data, please contact Brad Stenberg (BStenberg@psmfc.org).

Author information

Author ORCIDs

Felipe J. Quezada https://orcid.org/0000-0002-9594-0403
Desiree Tommasi https://orcid.org/0000-0003-4027-6047
Timothy H. Frawley https://orcid.org/0000-0003-4477-6567
Barbara Muhling https://orcid.org/0000-0002-4555-6382
Stephen Stohs https://orcid.org/0000-0002-6118-4515

Author contributions

Conceptualization: FJQ, DT, THF, BM, IK, SS
Data curation: FJQ, THF, BM
Formal analysis: FJQ, THF, BM
Funding acquisition: DT, BM, IK
Investigation: FJQ
Methodology: FJQ, THF, BM, SS
Project administration: DT
Resources: BM
Software: FJQ, THF

Supplementary material

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17

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19