Vol. 741: 47–70, 2024
https://doi.org/10.3354/meps14319

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 30[§]

Contribution to the Theme Section 'Small pelagic fish: new research frontiers'

Trophoscapes of predatory fish reveal biogeographic structuring of spatial dietary overlap and inform fisheries bycatch patterns

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ABSTRACT: Trophic interactions are proximate drivers of ecosystem function, including predator–prey dynamics, and their spatio-temporal variability may reflect ecosystem shifts and changes in trophic transfer. We investigated biogeographic structuring of trophic interactions by analyzing multi-decadal time series of diet for Pacific hake *Merluccius productus* and Chinook salmon *Oncorhynchus tshawytscha* from a large marine ecosystem. We compared our predictions for spatio-temporal variability of hake and salmon trophoscapes (i.e. spatially explicit predictions of trophic relationships) to inform ecosystem dynamics and fishery bycatch patterns. We have 3 inter-related findings pertaining to the spatial coherence of the trophoscapes and the potential consequences to juvenile and sub-adult (i.e. after the first year at sea but prior to maturation) salmon when sharing foraging areas with Pacific hake. First, the spatial scale of Pacific hake diet represents coastwide variability, and the spatial variability of Chinook salmon diets differs across regions and demonstrates a broad diet. Second, the expectation for increased diet and spatial overlap of Pacific hake and Chinook salmon during low productivity periods (e.g. periods with low krill biomass, suboptimal upwelling) can inform fishery management challenges. In this regard, we explore the role of shared foraging habitats on increased predation, and consequentially reduced recruitment, by Pacific hake on juvenile salmon during sub-optimal upwelling conditions. Third, we show that above-average bycatch of sub-adult Chinook salmon was associated with later spring transition, potentially as a result of both Pacific hake and salmon sharing foraging areas and prey species on the shelf and shelf break.

KEY WORDS: Bycatch · Trophic dynamics · California Current · Pacific hake · *Merluccius productus* · Chinook salmon · *Oncorhynchus tshawytscha*

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[§]Advance View was available July 6, 2023

1. INTRODUCTION

Ecosystem structure and processes are largely a consequence of trophic interactions, including predator and prey dynamics, and their spatio-temporal variability may reflect ecosystem shifts and changes in trophic transfer (Hanley & La Pierre 2015). Knowledge of spatio-temporal variability in foraging habitats can provide retrospective and prospective insights into the variability of the seascape and the responsive behavior of predators. Within the California Current Ecosystem (CCE), an Eastern Boundary Upwelling Ecosystem, quantifying spatio-temporal variability in diet provides a basis for assessing risks associated with varying predator and prey distributions and negative interactions with fisheries (e.g. whale entanglements in fixed-gear fisheries, significant predation on juvenile salmon, and anomalous mortality events for marine mammals; McClatchie et al. 2016, Wells et al. 2016, 2017, Santora et al. 2020). Due to similar positions in the marine food web, seabird, fish, and marine mammal predator diets strongly covary with prey availability in the CCE (e.g. Wells et al. 2012, Thayer et al. 2014, McClatchie et al. 2016, Santora et al. 2021). For example, observations of the seascape and forage species assemblages informs distribution patterns and behavior of central-place foraging dynamics of seabirds and marine mammals within the CCE (Weise et al. 2006, Santora et al. 2014, Wells et al. 2017, Amador-Capitanachi et al. 2020, Lowry et al. 2022). Further, examination of predator diets elucidates processes underpinning ecological dynamics and improves risk mitigation of interactions related to predator and fishery distributions and consumptive demands. We quantified trophoscapes of predator fish diet (derived from multi-decadal diet databases) using models to predict the spatio-temporal variability and classification of diet cluster area and persistence. Trophoscapes are simply classified areas of specific trophic interactions informed by modeling predator diets. Importantly, the prediction of trophoscapes is based on diet observations and does not include covariates for oceanographic variables or climate indices because including those variables may add prediction biases due to unidentified ecosystem processes. Classification of trophoscapes in consideration of what is known regarding environmentally driven prey dynamics (e.g. Santora et al. 2017a, Auth et al. 2018, Friedman et al. 2018) improves our understanding of the scale at which population and ecosystem dynamics are dependent and may benefit fishery management considerations. Namely, quantifying the spatial coherence of feeding dynamics provides context on the spatial coherence of ecological responses to large- and regional-scale ecosystem variability and management actions.

We examined and modeled multi-decadal time series of diet for Pacific hake *Merluccius productus* and juvenile and sub-adult (i.e. after the first year at sea but prior maturation) Chinook salmon *Oncorhynchus tshawytscha* to characterize spatio-temporal variability and similarity of their diets and evaluate overlap in foraging habitats. Chinook salmon are a cultural icon, a species of high fishery importance, and important forage for higher trophic level predators such as Southern Resident Killer Whales (Ward et al. 2009, Warlick et al. 2020). Pacific hake are the most abundant finfish and support the largest non-shellfish fishery in this ecosystem by both volume and value (National Marine Fisheries Service 2023). Chinook salmon tend to concentrate on the continental shelf, often nearer natal rivers (Weitkamp 2010, Satterthwaite et al. 2013), while Pacific hake are densely concentrated along the outer slope, where their principal prey item (euphausiids) are most abundant and persistent (Santora et al. 2011, 2018, Malick et al. 2020a). There is the potential for these species to interact on the shelf and shelf break, especially when oceanographic conditions are conducive to increased availability of shared prey in this location. For example, shared prey between Pacific hake and Chinook salmon, including juvenile rockfishes *Sebastes* spp., juvenile flatfishes (Pleuronectiformes), smelt (Osmeridae), juvenile Pacific hake, and shrimp (Pandalidae), are common on the shelf and shelf break off of Oregon and Washington, USA, during periods of lower productivity, including late, weak upwelling or downwelling conditions (Buckley & Livingston 1997, Emmett & Krutzikowsky 2008, Auth et al. 2018, Friedman et al. 2018, Riddell et al. 2018).

Chinook salmon are migratory but also display variable ocean distributions depending on region of origin and ocean environmental conditions (e.g. sea surface temperature) (Weitkamp 2010, Satterthwaite et al. 2013, Shelton et al. 2019). CCE resident sub-adult Chinook salmon from some stocks reside on the shelf, feeding within their natal bioregion for most or all of their ocean life, while more migratory stocks pass through CCE shelf bioregions early and late in their ocean life. These bioregions include central California Current from Monterey Bay (37° N) to approximately Cape Mendocino (40° 26′ N), between Capes Mendocino and Blanco (42° 8′ N), and north of Cape Blanco (to 48° 13′ N; Checkley & Barth 2009, Gottscho 2016). Variability in Chinook salmon forage availability follows these bioregions, with significant differences in prey assemblages between them (Friedman et al. 2018). Some studies have demonstrated that salmon feeding matches fairly well with variability in the regional seascape and has been shown to relate directly to salmon survival and body condition (Daly et al. 2013, Dale et al. 2017, Sabal et al. 2020). Specifically, juvenile Chinook salmon survival is associated with increased availability of lipid-rich diets and increased availability of alternate prey for predators (Daly & Brodeur 2015, Litz et al. 2017, Wells et al. 2017). Both juvenile and sub-adult Chinook salmon diets are diverse and indicate a capacity to adapt to forage variability. Chinook salmon prey include crustaceans such as krill and crab larvae and several important forage fish taxa (Pacific herring *Clupea pallasii*, northern anchovies *Engraulis mordax*, smelt), with the latter increasing in importance as salmon grow (Brodeur et al. 1987, 2014, Hunt et al. 1999, Daly et al. 2009, Thayer et al. 2014, Hertz et al. 2015). What has not been explored in detail is the geospatial distribution of Chinook salmon diets along the CCE and inshore of (and at) the shelf break, which may provide insights into their population dynamics (e.g. survival, growth, distribution) that depend on biogeographic seascape structure.

Pacific hake are migratory and undergo a large-scale spring and summer northern feeding migration from the southern CCE (~34° N) to the northern CCE (in some years ~49–50° N), with the extent of the migration dependent on the demographic structure of the population and basin-scale oceanographic conditions (Dorn 1995, Agostini et al. 2006). Specifically, larger, older hake typically migrate much further north, and the northward extent of the distribution is also highly variable from year to year in response to ocean conditions, extending farther north with increasing ocean temperature and, likely, forage availability (Ressler et al. 2007, Malick et al. 2020a,b). Pacific hake diets are generally narrower than those of Chinook salmon, with a substantial reliance on krill and a more limited number of forage fishes (Brodeur et al. 1987, 2014, Tanasichuk et al. 1991, Buckley & Livingston 1997). The total biomass of Pacific hake has ranged from 1–10 million metric tons over the past 50 yr, and hake are the most abundant finfish in the CCE (Edwards et al. 2022). Consequently, the abundance and distribution of Pacific hake have long been associated with ecosystem impacts on other components of the food web (Hannah 1995, Ware & McFarlane 1995, Field et al. 2006, Harvey et al. 2008) and may be among the most consequential predators on forage fishes in the northern CCE (Brodeur et al. 2014). Therefore, trophic interactions between Pacific hake and trophically equivalent species are likely to be substantial, particularly when seasonal oceanographic variability leads to distributional changes (principally onshore shifts) among and within bioregions.

Where shared foraging habitat exists between Pacific hake and Chinook salmon, both juvenile and sub-adult Chinook salmon could be negatively affected. When spring oceanographic conditions are warmer and, specifically, the spring transition to the upwelling season is later, Pacific hake are observed in greater abundance feeding on the northern CCE shelf, intersecting with juvenile and sub-adult Chinook salmon foraging areas (Dorn 1995, Emmett et al. 2006), with both likely feeding, in part, on shared forge taxa (Buckley & Livingston 1997, Riddell et al. 2018). Importantly, Pacific hake abundance on the northern CCE shelf has been related to the survival of Chinook salmon, indicating that predation on juveniles in spring and summer may be a significant determinant of Chinook salmon recruitment (Emmett et al. 2006). Additionally, during operation of the mid-water trawl fishery for Pacific hake on the shelf, bycatch of sub-adult Chinook salmon (~80% are 30–50 cm in fork length) is greater (Otto et al. 2016, Bellinger et al. 2009).

Here, we elucidate the spatio-temporal variability of trophoscapes (i.e. spatially explicit predictions of trophic relationships) for Pacific hake and Chinook salmon and compare results to ascertain potential drivers of ecosystem dynamics. We explore the hypothesis that the spatial coherence of Pacific hake diets will represent coastwide variability while Chinook salmon diets will represent variability at regional scales, with each matching the understood biogeography of their prey. We discuss the significance of the spatio-temporal scale at which Pacific salmon and Chinook salmon diets vary. Further, based on previous work (e.g. Emmett et al. 2006, Hertz et al. 2015), there is likely a spatio-temporal similarity of foraging habitats and a subset of shared prey resources on the shelf for Pacific hake and Chinook salmon. We discuss the potential ramifications of physical overlap between Pacific hake and Chinook salmon foraging habitats in regard to Pacific hake predation pressures on juvenile Chinook salmon. We also explore increased sub-adult Chinook salmon bycatch in the Pacific hake fishery during years of late initiation of spring upwelling when Pacific hake are more abundant in the north and on the shelf (Emmett et al. 2006) and the availability of shared forage between Pacific hake and Chinook salmon is greater (e.g. Auth et al. 2018, Friedman et al. 2018).

2. MATERIALS AND METHODS

2.1. Diet data sources

We used diet composition data to explore spatiotemporal variability in diets. Diet composition data for Chinook salmon (<50 cm, mixed-stocks) and Pacific hake were extracted from the California Current Trophic Database (Bizzarro et al. 2023), which contains multiple data sets for each species, collected at varying times and locations between southern California and British Columbia. Weight-based diet data were fitted as a double-marked point process, which uses diet information to infer the thinned density of available prey by treating their distribution as a point process with marks representing prey taxa (Thorson et al. 2022). The thinning rate represents the proportion of local prey that are attacked, captured, and present in available diet sampling data. We assume that thinning rates vary both spatially and over time, such that stomach samples are not interpreted as representing underlying densities of prey species. Instead, we assume that thinned densities of prey in stomach samples are proportional to the consumption of prey per predator at a given place and time, such that they represent patterns in prey utilization across the seascape. This thinned and double-marked point process was then fitted using a multivariate spatio-temporal model using the vector autoregressive spatio-temporal (VAST; Thorson 2019) R package (more details on this approach are provided in Section 2.5). We fit stomach contents and predicted 'diet densities' across space and time, where predicted densities then represent the per-predator stomach contents that would occur at a given place and time if a stomach were sampled there. Weight-based diet data, when unavailable for Chinook salmon, were augmented with a relatively limited amount of volumetric data (90% of Chinook salmon diet examined was weight-based) since comparative analyses indicated high correlations between these metrics ($r > 0.90$). Finally, numerical data were also analyzed separately because weight-based data were unavailable for Pacific hake during recent years, and a comparison between reasonably long overlapping time series of Chinook salmon and Pacific hake could not be accomplished otherwise. Unfortunately, due to the extremely diverse taxa represented in the diets, conversion to weights based on known relationships was unreasonable.

Weight-based diet data for individual Chinook salmon were available north of Cape Mendocino ($n = 9532$) and in the central region ($n = 551$). Numerical Chinook salmon diet data were available north of Cape Mendocino ($n = 9532$) and south of Cape Mendocino ($n = 1719$). We restricted our samples to those less than 50 cm to ensure that a similar size range was covered across latitudes (Fig. 1). This size range covers the first year of ocean life and into the second (1 winter at sea). Thus, we enveloped the first period at sea when Chinook salmon are most vulnerable to predation as well as the subadult period during which they also become vulnerable to bycatch in the Pacific hake fishery. Weight-based diet data for individual Pacific hake were examined north of Cape Mendocino ($n = 9946$) and south of Cape Mendocino ($n = 2634$). We also used numerical Pacific hake diet data spatially trimmed to match the distribution of Chinook salmon north of Cape Mendocino ($n = 6690$) and south of Cape Mendocino ($n = 1199$). Specific collection years for each taxon and region can be seen in Table 1.

Weight-based and numerical diet data sets for each species were grouped into generalized prey categories for analysis (see Table 2). These categories included the top 10 prey taxa for each species by aggregate weight, plus the critical taxa krill (Chinook salmon, Wells et al. 2012; Pacific hake, Buckley & Livingston 1997), Dungeness crab *Metacarcinus magister* (Chinook salmon, Wells et al. 2012), and a catch-all category for all additional prey taxa ('other'). Pacific hake and Chinook salmon diet composition, respectively, for each species was then calculated for both weight and numerical metrics on an individual basis as a basis for VAST analysis.

2.2. Hake catch and stomach analysis

Pacific hake samples were obtained from a number of data sources. Pacific hake stomach samples were collected by bottom trawl surveys along the Pacific Coast continental shelf and upper continental slope conducted by the National Oceanic and Atmospheric Administration (NOAA) Alaska Fisheries Science Center (AFSC), 1980–2001 (Buckley & Livingston 1997, Buckley et al. 1999). All diet data used in Emmett et al. (2006) is included for fish collected during 1998–2003 from the Washington and Oregon shelf and shelf break with a 264 Nordic rope pelagic trawl (NET Systems) (Harding et al. 2011, 2021). Pacific hake were incidentally caught during NOAA Southwest Fisheries Science Center (SWFSC) midwater trawl surveys conducted in 1987 and 1988 (Buckley et al. 1999, Sakuma et al. 2016) and during NOAA Northwest Fisheries Science Center (NWFSC) surface trawls

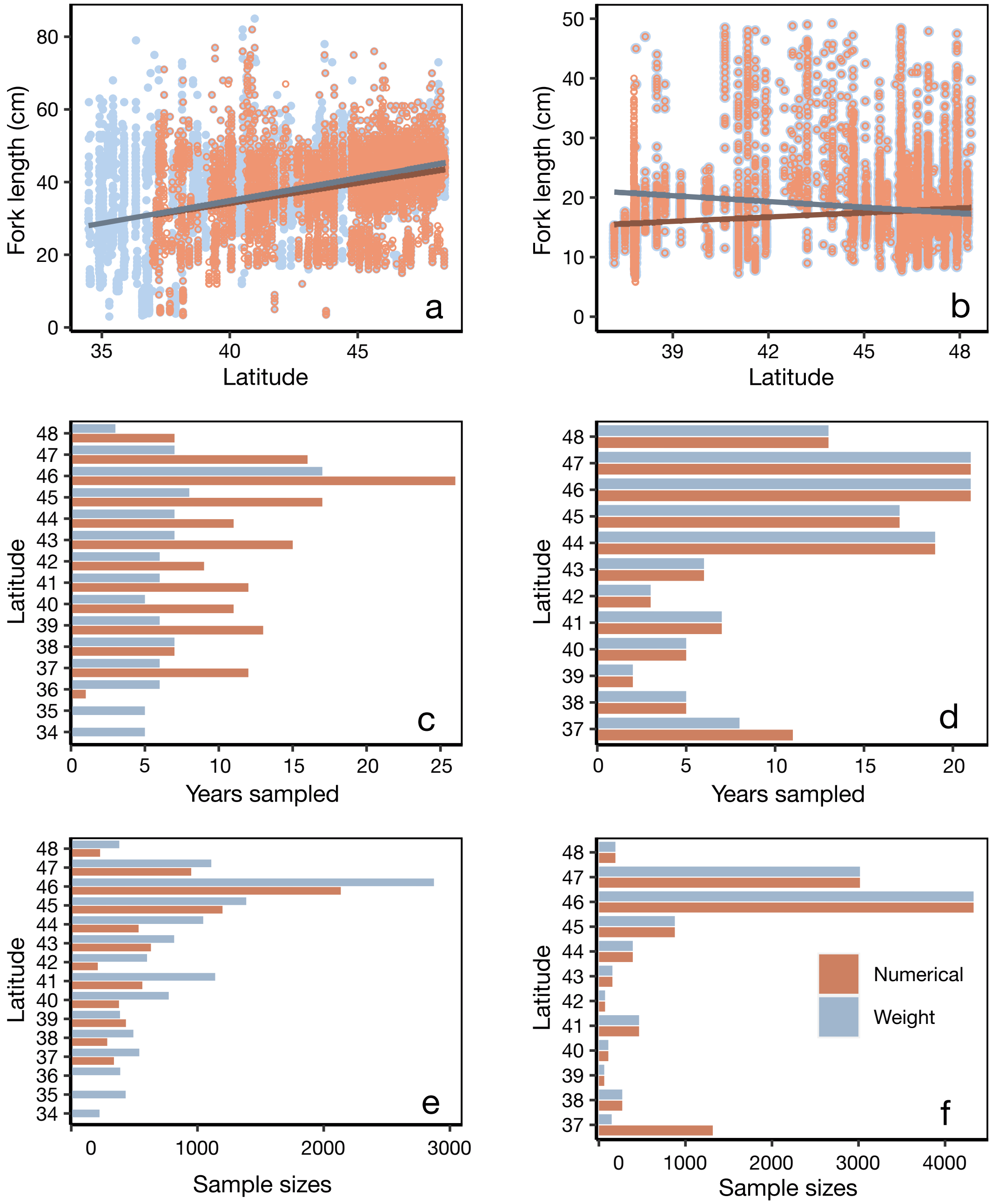

Fig. 1. Length of (a) Pacific hake from weight-based (1987–2007, blue) and spatially trimmed numerical data sets (1980–2019, orange) and (b) Chinook salmon (1998–2018) related to latitude for weight-based and numerical data. Number of years during which (c) Pacific hake and (d) Chinook salmon diet were analyzed at each latitude for weight-based and spatially trimmed numerical data. Number of samples of (e) Pacific hake and (f) Chinook salmon for which diet was analyzed at each latitude for weight-based data and trimmed numerical data

conducted in 1998–2018, described below for Chinook salmon collections. In addition, following 2005, additional Pacific hake stomachs were collected during the Joint US–Canada Integrated Ecosystem and Pacific Hake Acoustic Trawl Survey. This biennial survey is conducted jointly by NOAA NWFSC and Fisheries and Oceans Canada, although the stomachs for this analysis were collected by NOAA. The survey takes place on the West Coast of the USA from June through September. The net used was an Aleutian Wing Trawl (NET Systems) with a 32 mm codend liner. In all cases, prey were identified to the lowest taxonomic category possible. For each predator, when possible, the associated fork length measures were taken.

Table 1. Years during which weight-based and numeric diet data was used south and north of Cape Mendocino for Pacific hake and Chinook salmon. Sample sizes are shown in each cell

Year	Pacific hake				Chinook salmon			
	Weight		Numerical		Weight		Numerical	
	South	North	South	North	South	North	South	North
1980			74	111				
1981			13	55				
1982								
1983								
1984								
1985								
1986								
1987	111		65					
1988	438	793	57	326				
1989	279	1957	147	824				
1990	5	300		6				
1991	130		113					
1992		74		74				
1993								
1994								
1995	353	1388	115	957				
1996		58		39				
1997	387	145	73	72				
1998	657	3696	417	2722		223	117	223
1999	274	359		121	1	515	148	515
2000		46		17	2	750	164	750
2001		132		65		269	149	269
2002		116		95		1037	299	1037
2003		126		47	2	539	296	539
2004		2		2		352		352
2005		256		241		307		307
2006		297		271		607		607
2007		201		180		507		507
2008						851		851
2009			9	51		352		352
2010					72	491	72	491
2011			21	53	143	630	143	630
2012			36	64	48	495	48	495
2013			20	84	218	231	218	231
2014					65	130	65	130
2015			22	130		245		245
2016						468		468
2017			2	35		86		86
2018						447		447
2019			15	48				
	N = 2634	N = 9946	N = 1199	N = 6690	N = 551	N = 9532	N = 1719	N = 9532

2.3. Chinook catch and stomach analysis

Chinook salmon were collected during June to early July surface-trawl surveys conducted by NWFSC in Oregon and Washington from 1998–2018, and SWFSC in California from 2010–2014. Each study used a sampling grid that included transects aligned perpendicular to the coast (typically 30–50 km apart) with along-transect stations spaced 5–8 km apart. The trawl net was a 264 Nordic rope pelagic trawl (Harding et al. 2011, 2021). At predetermined sampling stations, the net was towed during daylight hours for 30 min at a ship speed of approximately 6 km h^{-1}. Additionally, from 1998–2003, Chinook salmon collected by midwater trawling at the point of entry into the central CCE were included in the examination (see methods in MacFarlane & Norton 2002). In the laboratory, the stomachs were removed and preserved. For trophic analysis, prey items in the stomachs were identified to the lowest possible taxonomic category using a dissecting scope, counted, and weighed to the nearest 1 mg.

2.4. Sample characterization

Linear regression indicated there was a significant, weakly positive, size-dependent slope with latitude for Pacific hake length samples, likely resulting from smaller hake in southern latitudes that were rare in the north (Fig. 1a,b). A positive trend in fork length (when recorded) between northern and southern collections of Pacific hake was significant (weight-based regression, $p < 0.0001$, df = 10 870, numerical-based regression: $p < 0.0001$, df = 6678). For weight-based analyses, 5–17 years of collections were available from each latitude minus 48° N, for which there were only 3 years of data (Fig. 1c). There was more representation of numerical data for Pacific hake, with typically 10+ years of data from each latitude, with exceptions including 36, 38, 42, and 48° N (Fig. 1c). Sample sizes for Pacific hake were greater in the north (Fig. 1e). For Chinook salmon, years of collections and sample sizes were more represented in the north (Fig. 1d,f). Numerical and weight-based diet data were equitable across the California Current and years of sampling. For Chinook salmon collections, there was a very shallow but significant negative linear slope between size and latitude for weight-based data ($p < 0.0001$, df = 10 028, ~10 cm difference) and a positive slope for numerically based data ($p < 0.0001$, df = 11 196, ~5 cm difference).

2.5. VAST modeling

Diet data for each Chinook salmon and Pacific hake were not collected equally across all cells between years; thus, we were required to use an analytical approach that estimated the diet composition in cells during years for which diet was not observed (Fig. 1). We fitted spatio-temporal models using VAST (Thorson & Barnett 2017; scale: 25 km^2), where prey for a given predator are treated as separate categories in a multivariate model (i.e. one category per prey taxon). We specifically fit sampled prey densities in each stomach-content sample as a response; modeling prey densities in this way is an approximation to the multivariate Tweedie distribution that has been used recently for stomach-content analysis in other ecosystems (Grüss & Thorson 2019, Thorson et al. 2022).

We fitted a series of multivariate spatio-temporal models that differed in terms of (1) which predator's stomach contents were modeled, (2) whether prey density was measured in weight or numerical abundance, and (3) what spatial extent was defined during model fitting and spatial extrapolation. In each case, we fitted a Poisson-linked delta model (Thorson 2018) with a gamma distribution for positive catches based on previous research suggesting that its expected performance is more similar to a design-based estimator (Thorson et al. 2021). We estimated a 'separate-and-equal' structure for the spatial and spatio-temporal covariance among prey species (i.e. using the same value for spatial and spatio-temporal variance parameters across all prey species). By default, we estimated both spatial and spatio-temporal variation in both linear predictors of the delta model, where annual intercepts and spatio-temporal components both follow a first-order autoregressive process over time. In cases where the estimated variance parameter approached zero, we refitted the model, fixing these at zero to avoid statistical issues arising when parameters approach their bounds. VAST estimates fixed effects while using Template Model Builder to implement the Laplace approximation for integrating across random effects (Kristensen et al. 2016). VAST uses a conventional gradient-based nonlinear minimizer to identify maximum-likelihood estimates and then applies a generalization of the delta-method to calculate standard errors (Kass & Steffey 1989). After identifying the maximum likelihood estimate of fixed effects, we fixed random effects at their empirical Bayes estimates and then predicted prey-specific stomach contents across the modeled spatial domain in each year. We extracted these spatio-temporal predictions and applied a hierarchical clustering algorithm to identify 4 biogeographic strata that represent different prey communities. Applying cluster analysis to multivariate spatio-temporal density estimates has been used previously to identify stock structure based on age-specific survey data (Lindegren et al. 2022) but has not, to our knowledge, been used to quantify landscape-level foraging habitats.

For the weight-based diet analysis, we used all available data for both individual Pacific hake and Chinook salmon. This allowed us to estimate foraging habitats across the CCE, but we did not have a long enough time series to examine many years of overlap between the 2 (overlap between 1998 and 2007 was available). To extend overlapping time series, we used enumerated diet data which provided a comparison between the years 1998–2018. The numerical analysis used all available data for Chinook salmon, but Pacific hake data were trimmed to match the distribution of Chinook salmon (Fig. 1). In doing so, direct comparisons of foraging habitats could be made between Pacific hake and Chinook salmon during overlapping years. The same prey taxa were used for weight-based and numerical analyses.

2.6. Graphical representation and classification of trophoscapes

Output from the modeling approach is voluminous and requires consolidation of results in a meaningful way to enable both visual and quantitative interpretations. For each 25 km^2 grid cell resulting from the VAST analysis, classification of diet by area and persistence (i.e. diet clusters are trophoscapes) was determined from model output in each year of our analysis for Pacific hake and Chinook salmon. We provide, geographically, the mode value of classifications for each grid cell, thus providing the most common diet classification in each cell across modeled years. For interpretation of results, we rely on consistent colors for diet classifications to represent those commonly identified on the shelf (i.e. orange), typically offshore (i.e. green), and a mix of coastal (i.e. light blue, dark blue) habitats along the CCE. These colors should not be considered to represent similarities between the diets of Pacific hake and Chinook salmon but, rather, similarities in foraging habitats. To assess the modeled persistence of a given diet cluster in each grid cell, we quantified the proportion of occurrences across years that the grid cell was the mode value (Santora et al. 2017a, 2018). In doing so, we provide a spatio-temporal characterization of the persistence of diet types across the CCE. Variability in the size (areal coverage) of a given diet classification in the CCE was also reported across the years. The combined approach of showing model results of the most common diet classifications, the persistence of those classifications, and the areal coverage of each classification across the CCE provides context for coastwide and regional variability in trophoscapes.

2.7. Spatio-temporal bycatch data

We explored VAST-predicted diet clusters for Pacific hake and Chinook salmon to the bycatch of Chinook salmon to improve our understanding of the role and potential process of environmental pressures on bycatch probability. The Pacific hake fishery uses midwater trawl gear to target Pacific hake. Though bycatch rates in the fishery are generally low, the fishery does encounter Chinook salmon, rockfish, and other bycatch species. The high-volume nature of the fishery means that total bycatch can be a cause for concern, as closure of the non-tribal fisheries is among the potential consequences of exceeding bycatch limits. The industry uses a number of strategies to avoid bycatch, including information sharing, night fishing restrictions, closed areas, move-on rules, and test tows (Hamel et al. 2015, Holland & Martin 2019).

We used observer data from the At-Sea Hake Observer Program from 2002–2018 and examined variability of bycatch observations with upwelling dynamics (N = 42 544 hauls). Vessels in the at-sea hake fishery catch and process hake at sea, and though bycatch rates are typically low, the high-volume nature of the fishery means that bycatch of Chinook salmon is often a major concern for the fleet (Lomeli & Wakefield 2019). All processing vessels carry 2 observers, and virtually every haul is sampled for species composition, including Chinook salmon. To visualize patterns in fishing effort and Chinook salmon bycatch, we gridded observer data into 0.2° cells for Pacific hake catch-per-unit-effort (CPUE; metric tons per tow hour) and Chinook salmon bycatch-per-unit-effort (BPUE; individuals per tow hour) across all years of data. Any cells where fewer than 3 vessels were represented were not used for confidentiality reasons. We did not include data from the Tribal at-sea hake fishery, which was active from 2002–2012. In addition, for simplicity, we did not include data from the shoreside Pacific hake fishery, which also targets Pacific hake but delivers the catch to shoreside processors instead of processing at sea. Though all shoreside Pacific hake vessels carry either an observer or electronic monitoring equipment, catch is typically not sorted at sea, and any bycatch is quantified after landing. Therefore, attributing bycatch to a particular spatial location is more difficult.

We focused on the at-sea Pacific hake fishery sectors without inclusion of the shoreside sector. However, both the shoreside and at-sea sectors generally operate off the coasts of Oregon and Washington (Somers et al. 2022). While there may be some potential for the shoreside sector to fish slightly closer to Oregon and Washington ports, both fleets tend to fish where Pacific hake are abundant, and effort is generally widespread over broad temporal and spatial scales as a result. The fact that our analysis included only data from the at-sea sector should preclude any possible temporal bias that might have resulted had we used mixed-fishery data for some but not all years that were included in our analysis.

Following Emmett et al. (2006), who showed that there are more Pacific hake on the shelf during later spring transitions, and Auth et al. (2018) and Friedman et al. (2018), who demonstrated increased abundance of shared forage taxa between Pacific hake and Chinook salmon (Buckley & Livingston 1997, Hertz et al. 2015) on the shelf during similar conditions, we examined the likelihood of resulting increases in CPUE of Pacific hake and bycatch of Chinook salmon. We used the values of the spring transition dates for 2002–2018 averaged between 45 and 48° N. Spring transition data were obtained within the California Current Integrated Ecosystem Assessment data portal. The date of spring transition was calculated as the date at which cumulative upwelling is at a minimum (Bograd et al. 2009). This is an indicator of the initiation of the upwelling season, which can have implications for forage availability (Auth et al. 2018, Friedman et al. 2018), and the functionality, phenology, and productivity of coastal ecosystems (Emmett et al. 2006, Bograd et al. 2009).

3. RESULTS

3.1. Diets

The dominance of our top diet taxa used in this analysis and the remaining taxa (i.e. ‘other’) indicated diet similarities and differences between Pacific hake and Chinook salmon. Pacific hake diets were narrower than Chinook salmon diets, even though 7 of the most represented species were shared between the 2 predators (Table 2). Pacific hake diets were dominated in weight by krill (euphausiids) and juvenile Pacific hake (cumulatively 50 % of the diet). Pacific herring represented 17 % of the diet by weight. The remaining diet included prey taxa typically observed at bottom depths greater than 250 m (i.e. Myctophidae, Oegopsida) and shelf environments <250 m (i.e. eulachon, *Thaleichthys pacificus*, northern anchovy, Pacific sardine, juvenile rockfishes, and smelt). Approximately 32 % of Chinook salmon diet comprised juvenile rockfishes, krill, and northern anchovy. Cumulatively, by weight,

Table 2. Weight-based and numerical data sets for each species, grouped into generalized prey categories for analysis (Bizzarro et al. 2023). These categories included the top 10 prey taxa for each species by summed weight plus, due to demonstrable importance (Buckley & Livingston 1997, Wells et al. 2012), krill and Dungeness crab. We also include a conglomerate category for all other prey taxa (‘other’). Diet composition for each species was then calculated for both metrics on an individual basis for VAST analysis. The top 10 taxa for weight-based analysis for Pacific hake and Chinook salmon are shown, listing the summed weight across samples. Also shown are summed numerical values of these top 10 taxa in the diets for Pacific hake and Chinook salmon. The ‘other’ category represents all items not within the taxa-specific categories. For Pacific hake, other prey was dominated by weight by bony fishes (Actinopterygii = 80 %), the majority of which were unidentified (76.0 %). Among identified bony fishes, Clupeiformes (13.9 %) were most commonly consumed. Crustaceans of the class Malacostraca (10.99 %) also contributed substantially. For Chinook salmon, the ‘other’ prey category was highly diverse, with 307 taxa; however, most contributed trivial amounts by weight. Bony fishes (Actinopterygii) represented 78 % of other prey, with the majority unidentified (96.0 %) to lower taxa. Malacostracan crustacean prey (11.7 %) also was well documented. No other phylum or class accounted for >1 % of this category by weight

Prey category	Pacific hake				Chinook salmon			
	Weight (g)	Weight (%)	Number	Number (%)	Weight (g)	Weight (%)	Number	Number (%)
Dungeness crab					73	0.8	2182	1.59
Eulachon	230	0.2	68	0.03				
Flatfish	1887	1.9	260	0.11	338	3.7	2720	1.98
Market squid					135	1.5	182	0.13
Myctophid	1091	1.1	226	0.09				
Northern anchovy	4920	5.1	401	0.16	861	9.4	1471	1.07
Northern ronquil					42	0.5	343	0.25
Oegopsida	943	1.0	158	0.06				
Pacific hake	23448	24.1	281	0.12				
Pacific herring	16213	16.6	414	0.17	370	4.1	132	0.10
Pacific sandlance					416	4.6	1653	1.20
Pacific sardine	2685	2.8	54	0.02	58	0.6	188	0.14
Rockfish	1087	1.1	46	0.02	806	8.8	1444	1.05
Sculpin					434	4.8	2851	2.08
Smelt	2184	2.2	548	0.23	513	5.6	860	0.63
Krill	25348	26.0	228435	94.52	1261	13.8	25052	18.24
Other	17376	17.8	10784	4.46	3825	41.9	98267	71.54

Dungeness crab larvae, market squid *Doryteuthis opalescens*, and primarily juvenile fishes, including flatfishes, northern ronquil *Ronquilus jordani*, Pacific herring, Pacific sand lance *Ammodytes hexapterus*, sculpin (Cottidae), and smelt represented 26 % of the diet. The 'other' category represented those prey taxa not considered directly in the analysis; for Chinook salmon, this category comprised 42 % of the diet by weight, and for Pacific hake, only 18 %. This difference indicates our selection of Pacific hake prey was fairly representative of the Pacific hake diets, yet Chinook salmon diets were considerably broader. Shared significant forage items between Pacific hake and Chinook salmon represent shelf and shelf break taxa (i.e. flatfishes, northern anchovy, Pacific herring, Pacific sardine, rockfishes, smelt, and krill).

3.2. Predicting trophoscapes

We used a default output of 4 diet clusters for Pacific hake, 1987–2007, along the CCE that provided insight into the spatio-temporal coherence of their diets (Fig. 2). We represent the commonality of each diet classification at each 25 km^2 grid cell by reporting the mode value (Fig. 2a), the persistence of each classification by showing the proportion of years each cell was that mode value (Fig. 2b), and the areal extent of each classification across the years of

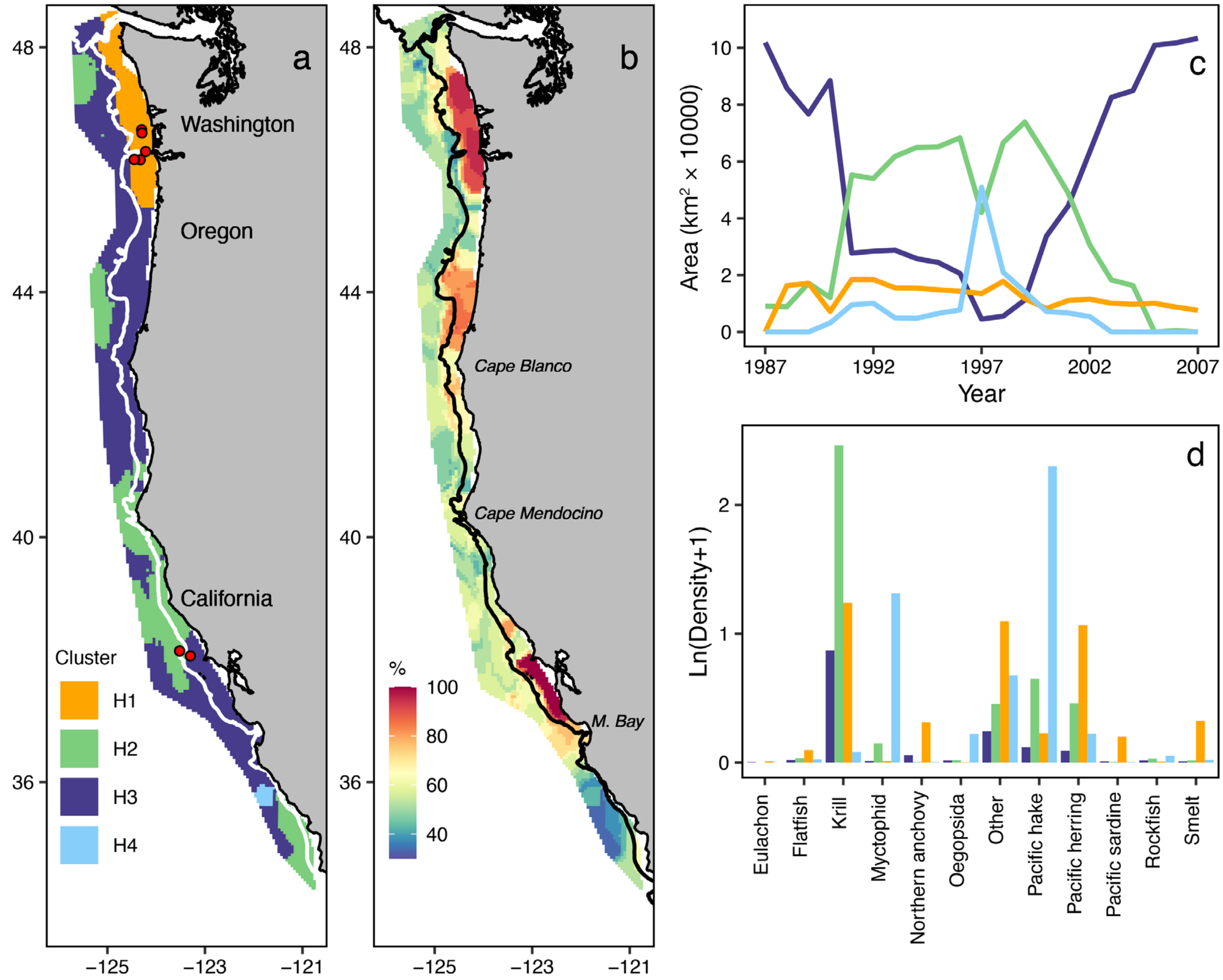

Fig. 2. (a) Spatial extent of Pacific hake diet clusters (H1, H2, H3, H4) identified for a given location for the largest number of years, 1987–2007, when clustering spatio-temporal density estimates across those years. Red circles: 10 locations where Chinook salmon were found in hake guts (2 locations have multiple salmon in a given gut) (b) Percentage of years 1987–2007 when a location was classified as that modal cluster in (a). Contours represent 250 m. (c) Area of each diet cluster identified in (a) over time. (d) Estimated prey densities associated with each of those 4 clusters, using the same colors as (a) to identify the prey composition for each cluster

sampling (Fig. 2c). There were 3 interspersed spatially dominant diets of Pacific hake feeding along the California Current, including krill, Pacific hake, and Pacific herring, with myctophids being a significant but irregular contributor (Fig. 2a,c,d, dark blue, green, light blue). There was a fourth shelf-oriented diet off Oregon and Washington dominated by krill, Pacific herring, northern anchovy, smelt, Pacific sardine, juvenile flatfishes, and other forage fish (Fig. 2d). Importantly, while not a dominant prey item, it is within this fourth shelf-oriented foraging area where all northern predation events on juvenile Chinook salmon were observed (Fig. 2a).

The spatial coverage of the Pacific hake diet types varied across years except on the shelf and shelf break (~250–300 m depth) at central California and Oregon/Washington where diets were persistent (Fig. 2b). Along the coast, juvenile Pacific hake and herring in the diet were more dominant in 1991–2001 (Fig. 2c, green) largely replacing a diet of krill and returning to krill in 2002 (Fig. 2c, dark blue). There was a significant increase in the spatial representation of juvenile Pacific hake and myctophids in diets during 1997 and 1998 (Figs. 2c,d & 3, light blue). There was also dramatic switching between dominant trophoscape states (Fig. 2c). This can be observed between 1988 and 1992, during which there was a significant switch in the offshore diet assemblage to one dominated by krill, Pacific hake, and Pacific herring (Figs. 2c,d & 3). In addition, the extensive spatial extent of myctophids and juvenile Pacific hake in the diet is apparent in 1997 (Figs. 2c,d & 3). In later years, a coastal diet was again represented largely by krill, with a reduced representation of juvenile Pacific hake and Pacific herring and increased representation of the 'other' classification (Figs. 2d & 3). From 1987–2007, inshore along Oregon/Washington and central California represented a stable diet composition of krill and fishes, respectively. However, diets within the remaining California Current were variable (Figs. 2b & 3).

Chinook salmon diets from 1998–2018 were dominated by 3 shelf-oriented diet clusters: (1) central California (37° N), (2) northern California (37–42° N), and (3) Oregon and Washington (42–48° N). Further, there was an offshore (>250 m) diet cluster (4) at Oregon and Washington (Fig. 4a, green). Central and northern California Current shelf diets were dominated by krill, squid, young-of-the-year rockfishes, northern anchovy (in the north), and other (Fig. 4a,d, light blue and orange, respectively). Inshore at Washington and Oregon there were a number of minor diet contributors (i.e. other) and a diverse collective of fishes including smelt, juvenile rockfishes, Pacific sand lance, northern anchovy, juvenile flatfishes, and krill, all of which (minus Pacific sand lance) are shared with Pacific hake when in the region. (Figs. 3d & 4d, orange). Salmon diet on the Oregon and Washington shelf was broader and had more influence from juvenile rockfishes than diets from central California. The offshore diet cluster was dominated by juvenile rockfishes, juvenile flatfishes, sculpin, and other (Fig. 4a, green). The spatio-temporal variability of these clusters differed little over the years except at their margins (Fig. 4b,c).

3.3. Comparison of Pacific hake and Chinook salmon trophoscapes

There was a longer time series of diet for Pacific hake from numerical diet data compared to weight-based diet data and, therefore, more recent comparisons with Chinook salmon diets are based on numerical diet data. Given the abundance of krill in Pacific hake and Chinook salmon diets, much of the signal in the trophoscapes is attributed to krill; however, diets of fishes remain common inshore and offshore at Oregon and Washington (Fig. 5a,b, orange and green). Namely, notable shared taxa between Pacific hake and Chinook salmon on the shelf included juvenile flatfishes, northern anchovy, and smelt; a similar result as that estimated from weight-based diet analyses (43–48° N; Fig. 5a,c, orange). Offshore diets of Pacific hake were characterized by krill and myctophids (Fig. 5b,c, green) and for Chinook salmon included juvenile flatfishes, juvenile rockfishes, and sculpin.

Trophoscapes based on numerical diet data for both Pacific hake and Chinook salmon across their shared distribution were largely stable through the years 1998–2018. There was a dramatic increase in myctophids observed in Pacific hake diets in 2009 (Fig. 6, green). The increase in myctophids resulted in a maintained modest shift upward in the representation of that diet component in 2008–2018 (Fig. 6c). This variability indicates less stability in Pacific hake diets from the offshore region of Washington and Oregon (Fig. 6a).

3.4. Bycatch of Chinook salmon in the Pacific hake fishery

The greatest BPUE of Chinook salmon occurred on the shelf and shelf break of Washington and Oregon, where Pacific hake fishing effort was relatively low

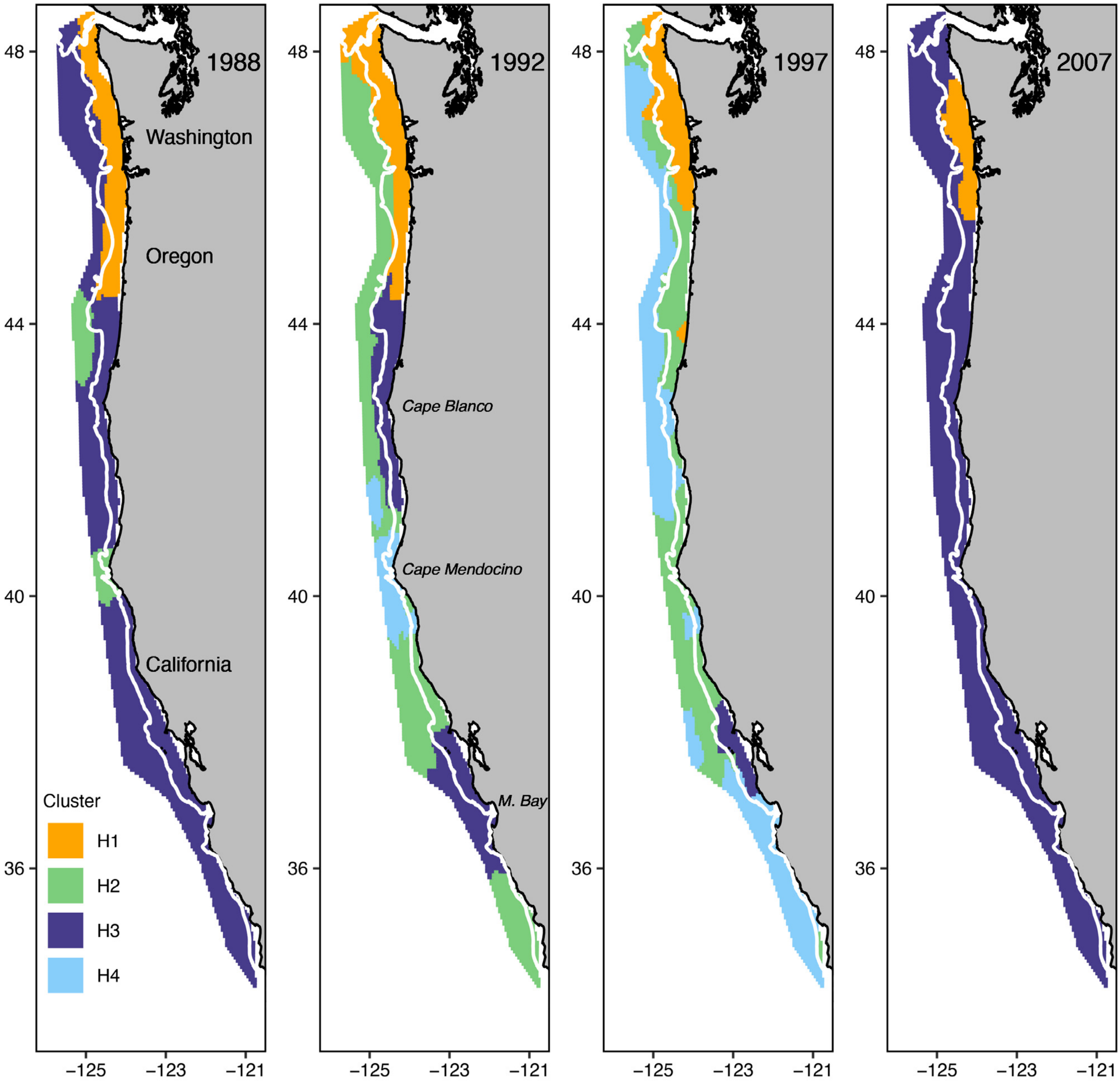

Fig. 3. Coast-wide spatial variability in the Pacific hake trophoscape (area of diet clusters H1, H2, H3, and H4) demonstrated across 4 years (1988, 1992, 1997, and 2007). Contours represent 250 m. See Fig. 2c–d for additional information on diet cluster classification

(Fig. 7a–c). There is a potential for overlap in Pacific hake and Chinook salmon foraging (both diet and distribution) in this region as indicated by the weight-based diet analysis (Figs. 2a & 3a, orange) and supported by the numerical analysis (Fig. 5a,b, orange). The years of greatest Pacific hake CPUE on the shelf and shelf break co-occurred with increased BPUE of Chinook salmon (Fig. 7c). Further, there were 6 years of above-average bycatch, 5 of which occurred during periods of later initiation of spring upwelling (Fig. 7d). The greatest CPUEs of Pacific hake were associated with near-average or above-average dates of spring transition (Fig. 7d). Importantly, salmon bycatch was greatest where the Chinook salmon inshore diet cluster extended toward and intersected the shelf break at ~42–45° N (Fig. 8, orange). An exception, 2009, was characterized by early spring transition; however, this year was anomalous with the significant inshore expansion of the offshore foraging habitat, reflected in increased abundance of myctophids in Pacific hake diets (Fig. 5a,c, green; Fig. 6c, green; Fig. 8d, green).

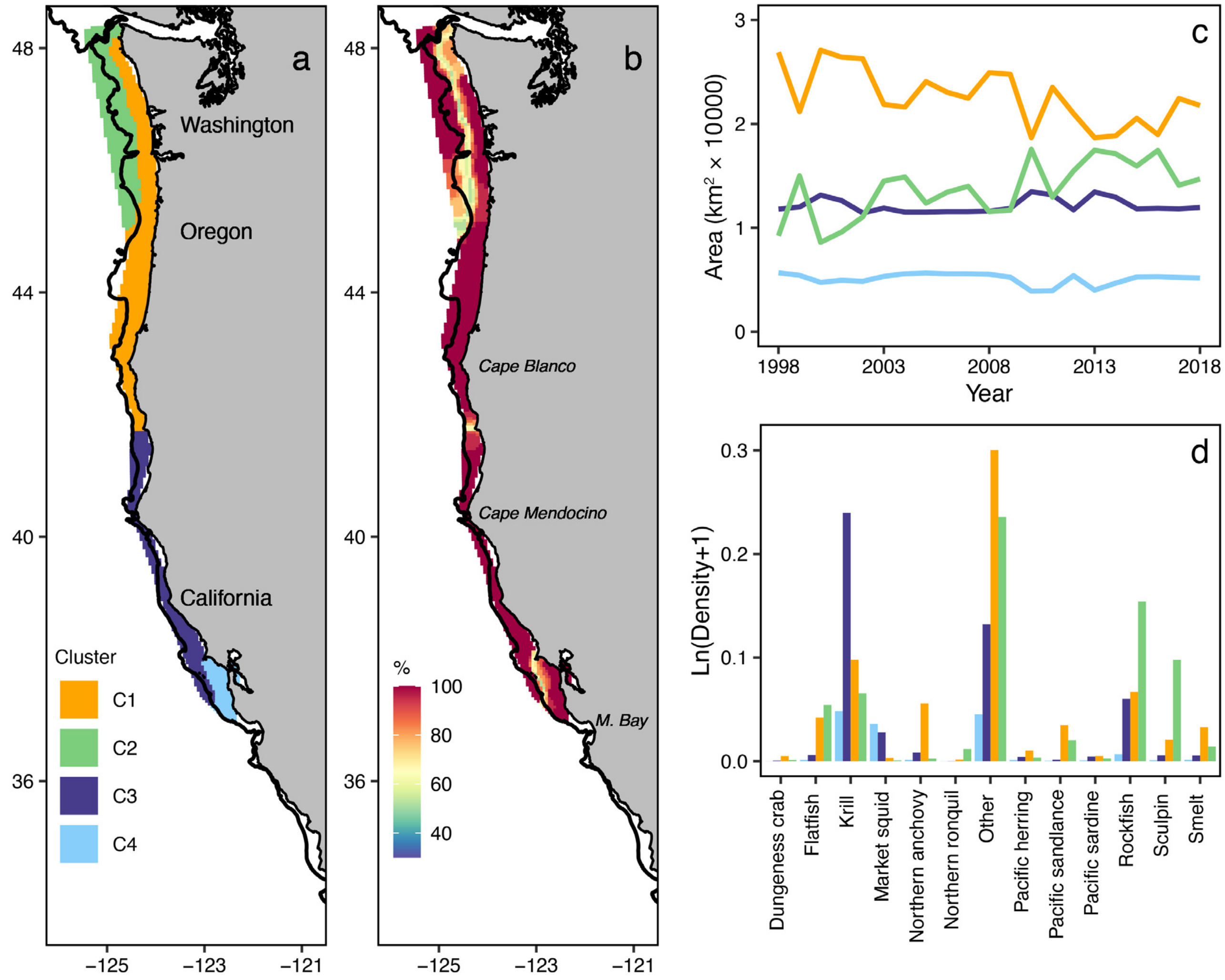

Fig. 4. (a) Spatial extent of Chinook salmon diet clusters (C1, C2, C3, and C4) identified for a given location for the largest number of years, 1998–2018, when clustering spatio-temporal density estimates across those years. (b) Percentage of years 1998–2018 when a location was classified as that modal cluster in (a). Contours represent 250 m. (c) Area of each diet cluster (identified in a) over time. (d) Estimated prey densities associated with each of those 4 clusters, using the same colors as (a) to identify the prey composition for each cluster

While our methodology is multivariate, there is value to exploring the spatio-temporal patterns of individual dominant forage taxa estimated to be in the diets of Chinook salmon on the shelf and shelf break during 5 years of increased bycatch in the region (2003, 2005, 2012, 2014, and 2015). Namely, the estimated density anomalies, based on weight-based diet analysis of Chinook salmon, for juvenile rockfishes and juvenile flatfishes were positive — especially in the regions where bycatch was greatest — indicating they may be particularly influential in the interaction of Chinook salmon and the Pacific hake fishery on the shelf and shelf break (Fig. 9b,d). Northern anchovy and smelt had modestly inflated representation in the diets on the shelf by the Columbia River, while krill in diets were estimated to be generally below average in the region except for small positive anomalies north of 47° N (Fig. 9a,c,e). Pacific herring and sardine had the least representation in Chinook salmon diets and the range of anomalies was small (Figs. 4d, 5d & 9f,g). The diverse assemblage of the ‘other’ taxa, representing minor prey, demonstrates an increased representation in diets in the southern area as well as near the area of greater bycatch (Fig. 9h).

4. DISCUSSION

Combining long-term predator diet studies with geospatial modeling, we defined simplified diet-based trophoscapes, including measures of their area

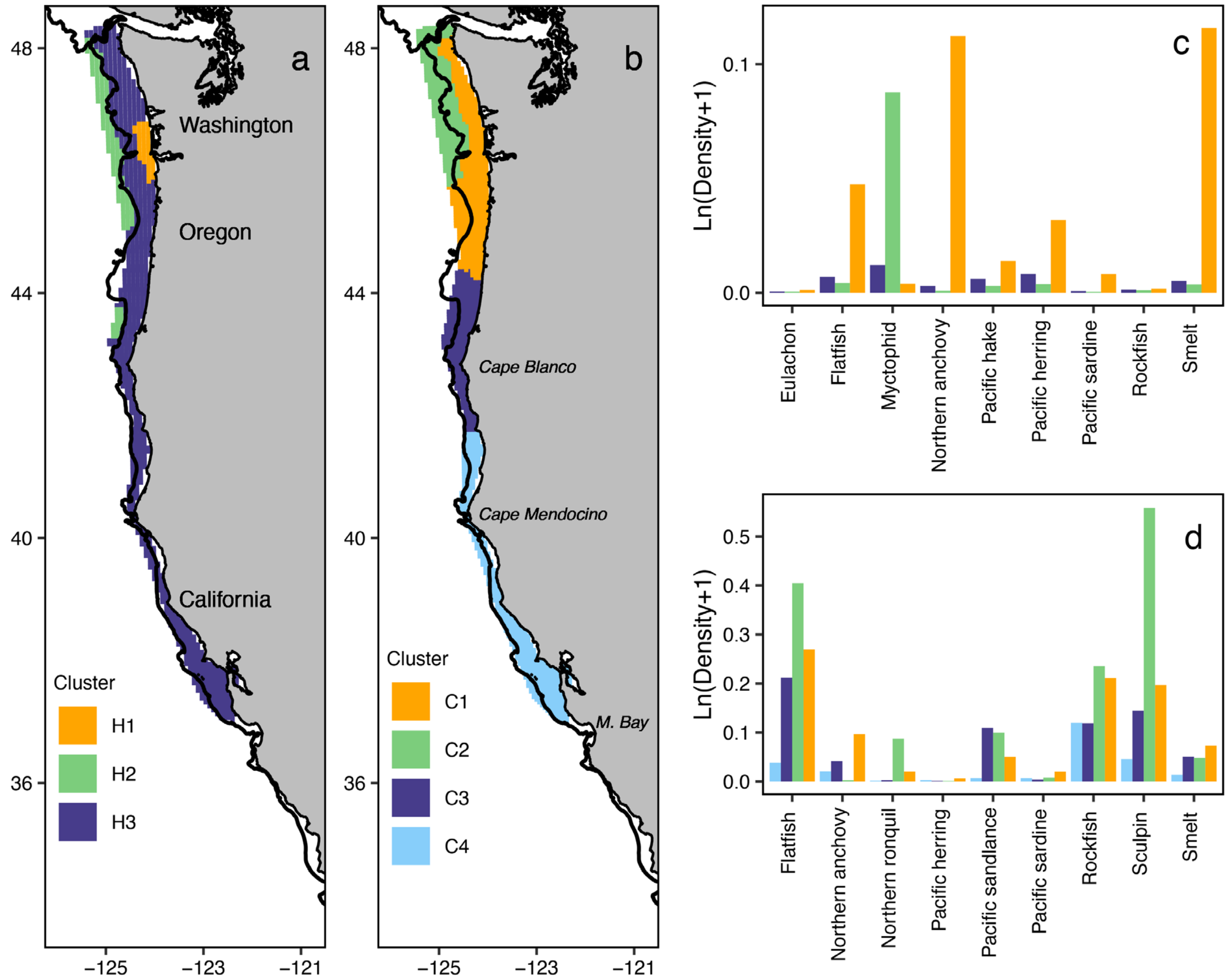

Fig. 5. (a) Pacific hake (H1, H2, and H3) and (b) Chinook salmon (C1, C2, C3, and C4) diet clusters using Chinook salmon distribution as a footprint and abundance (numerical) of taxa in diet; (a) and (b), run independently for Pacific hake and Chinook salmon, respectively, represent the spatial extent of each of their diet clusters. Colors represent different regions identified in this study and can be used to explore the potential for foraging overlap of Pacific hake and Chinook salmon within these regions. For example, while the 2 maps should not be directly compared for diet itself, they represent the spatial extent of an on-shelf (H1 and C1, orange) feeding area based on overlapping years and space of collection. Plots include the most commonly classified diet clusters for (a) Pacific hake spatially, 1998–2018 (only 3 clusters were present in the clipped numerical analysis) and (b) Chinook salmon spatially, 1998–2018. The estimated density of fish in the diets of (c) Pacific hake for each cluster shown in (a) (signal was dominated by krill and other) and (d) Chinook salmon for each cluster shown in (b). In this analysis, diet taxa were chosen independently for Pacific hake and Chinook salmon from the previous analyses based on weight in diet

and frequency of occurrence, to better understand the feeding ecology of Pacific hake and Chinook salmon. Despite the fact that no oceanographic covariates were included in diet models, the distribution, structure, and variability of diet-informed trophoscapes were remarkably similar to the known biogeographic regionalization of forage in the CCE (e.g. Thompson et al. 2019, Friedman et al. 2018). We found that Chinook salmon have a broad diet that is regionally coherent, while Pacific hake diets are narrow and generally coherent coastwide offshore. Pacific hake diets reflect interannual switching between different prey guilds offshore along the CCE, and the shelf region in the north may provide an array of nutrient-rich fish taxa on which to forage and adapt to or mitigate less productive conditions offshore of the shelf break (Litz et al. 2010, Daly & Brodeur 2015). Having explored the shared forage taxa in the shelf diet clusters of Pacific hake and Chinook salmon on the northern shelf region (i.e. juvenile rockfishes, juvenile flatfishes, smelt, northern anchovy, Pacific sardine, and krill), we argue that negative conse-

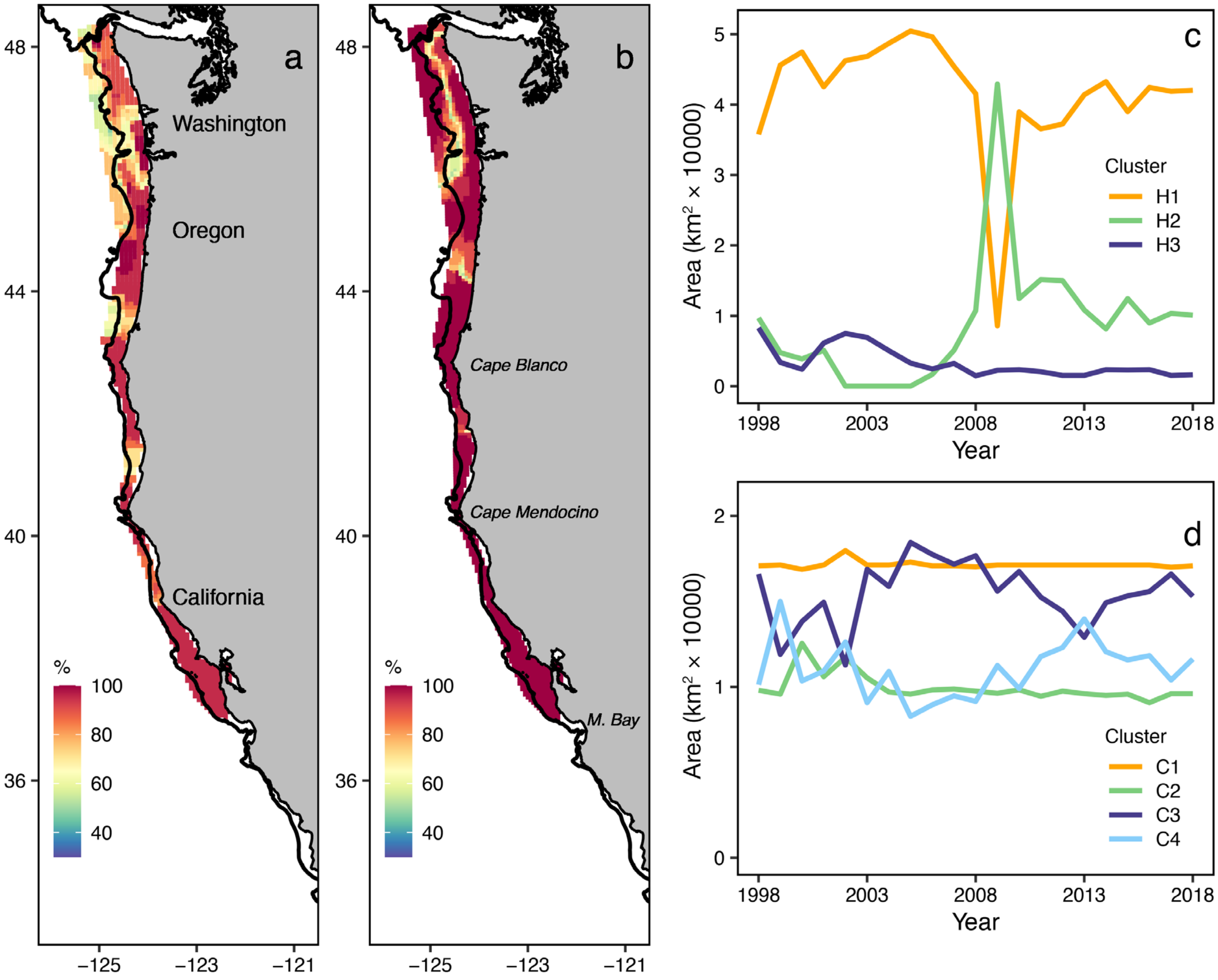

Fig. 6. Persistence of (a) Pacific hake and (b) Chinook salmon diet clusters using Chinook salmon distribution as a footprint and abundance (numerical) of taxa in diet, 1998–2018. Specifically, (a) and (b) show the percentage of time a cell was classified as the mode in Fig. 5a,b for Pacific hake and Chinook salmon, respectively. Area of each cluster shown in (c) in Fig. 5a over time for Pacific hake (H1, H2, and H3) and (d) Fig. 5b over time for Chinook salmon (C1, C2, C3, and C4)

quences to juvenile and sub-adult Chinook salmon could be synergistic. Namely, both species feed on aggregations of shared forage taxa, potentially leading to greater predation of juveniles by Pacific hake. Similarly, we showed that increased bycatch of sub-adult Chinook salmon typically occurs during periods of late spring transition, likely as a result, again, of both Pacific hake and Chinook salmon feeding on the same prey and their aggregations in a shared habitat.

4.1. Considerations

Our analysis is challenged by a number of constraints. For example, diet samples were not equally distributed; there was a greater number of both years and samples in the northern CCE. Chinook salmon diets were also observed at finer spatio-temporal variability in the north. In selecting the most-represented prey taxa, the list was weighted toward northern forage availability. However, Chinook salmon had a diverse diet across the CCE as indicated by the influence of the ‘other’ category. We sampled Chinook salmon from the earliest period at sea through their first year and into their second (Riddell et al. 2018). Chinook salmon rely considerably on krill and crustaceans upon emigration to sea but quickly transition to include fish in their diets (Daly et al. 2009, Wells et al. 2012). Although this study does not include robust diet data on larger, older Chinook salmon, the species composition of diets reported in

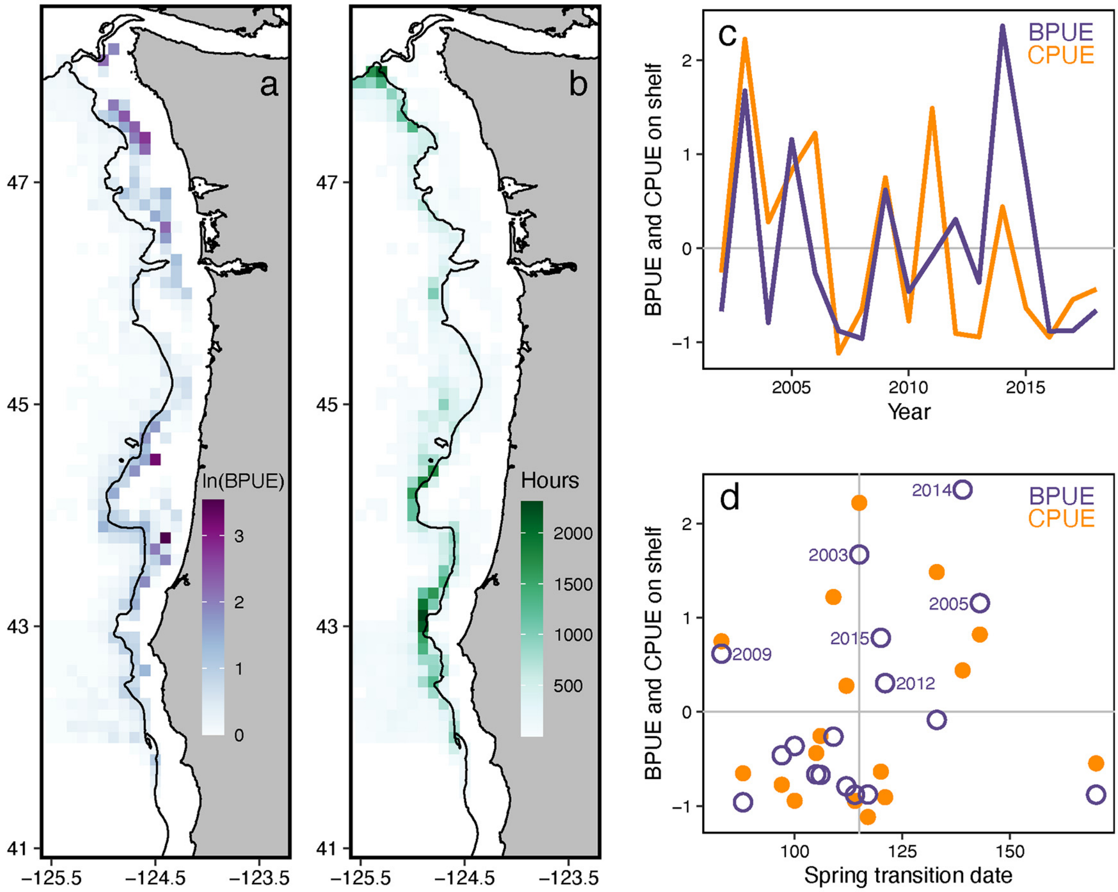

Fig. 7. (a) Abundance of Chinook salmon bycatch per unit of haul time (BPUE) for the Pacific hake fishery, 2002–2018, and (b) hours of fishing for Pacific hake (2002–2018). Contour is 250 m (shelf). Note that the region with spatially overlapping forage guilds (Figs. 2, 4, & 5), the shelf of Washington and Oregon coast, is an area of limited effort (b), yet the greatest bycatch of individual Chinook salmon per unit (hour) of effort during 2002–2018. (c) Anomaly times series, 2002–2018, of BPUE (purple) and catch per unit effort of Pacific hake (CPUE, orange) on the shelf and shelf break (<250 m). (d) Anomalies of Chinook salmon BPUE (purple) and Pacific hake CPUE (orange) on the shelf and shelf break (<250 m) relative to the date (day-of-the-year) of spring transition. Grey lines in (c) and (d) represent averages

other studies of sub-adult and adult salmon is consistent with our results (e.g. Thayer et al. 2014). As added confidence, our results for Chinook salmon matched very well with the biogeography of forage observed from independent surveys along the CCE (Friedman et al. 2018). Such results indicate that Chinook salmon are opportunistic foragers and that our sample coverage was sufficient to capture this dynamic. The spatial consistency of the Chinook salmon trophoscapes is further evidence of the robustness of our approach and highlights the importance of regional and diverse salmon diets (Fig. 4b,c). It is important to recognize that post-smolt salmon (those recently having entered the ocean), juveniles, and sub-adults behave differently. We acknowledge that post-smolts are most likely to use the shelf near shore while older salmon can move further north, south, and offshore. From the perspective of predation of juveniles by Pacific hake, we restricted our interpretations and samples to the shelf region and, hence, more on post-smolts, juveniles, and stocks that use the shelf more commonly. Similarly, we restricted our bycatch analysis to the shelf, where sub-adults from more coastally dependent stocks may make up a larger portion of the bycatch (Bellinger et al. 2009).

Pacific hake diet samples had higher sample sizes in the northern region, reflecting the fact that surveys of Pacific hake focus their effort during summer and fall, when hake are distributed to the north and the fisheries for Pacific hake are operating. The distribution and ecosystem interactions of Pacific hake in the southern part of their range, during January–March when spawning is taking place, requires additional sampling. While in northern waters, Pacific hake diets are relatively narrower than Chinook

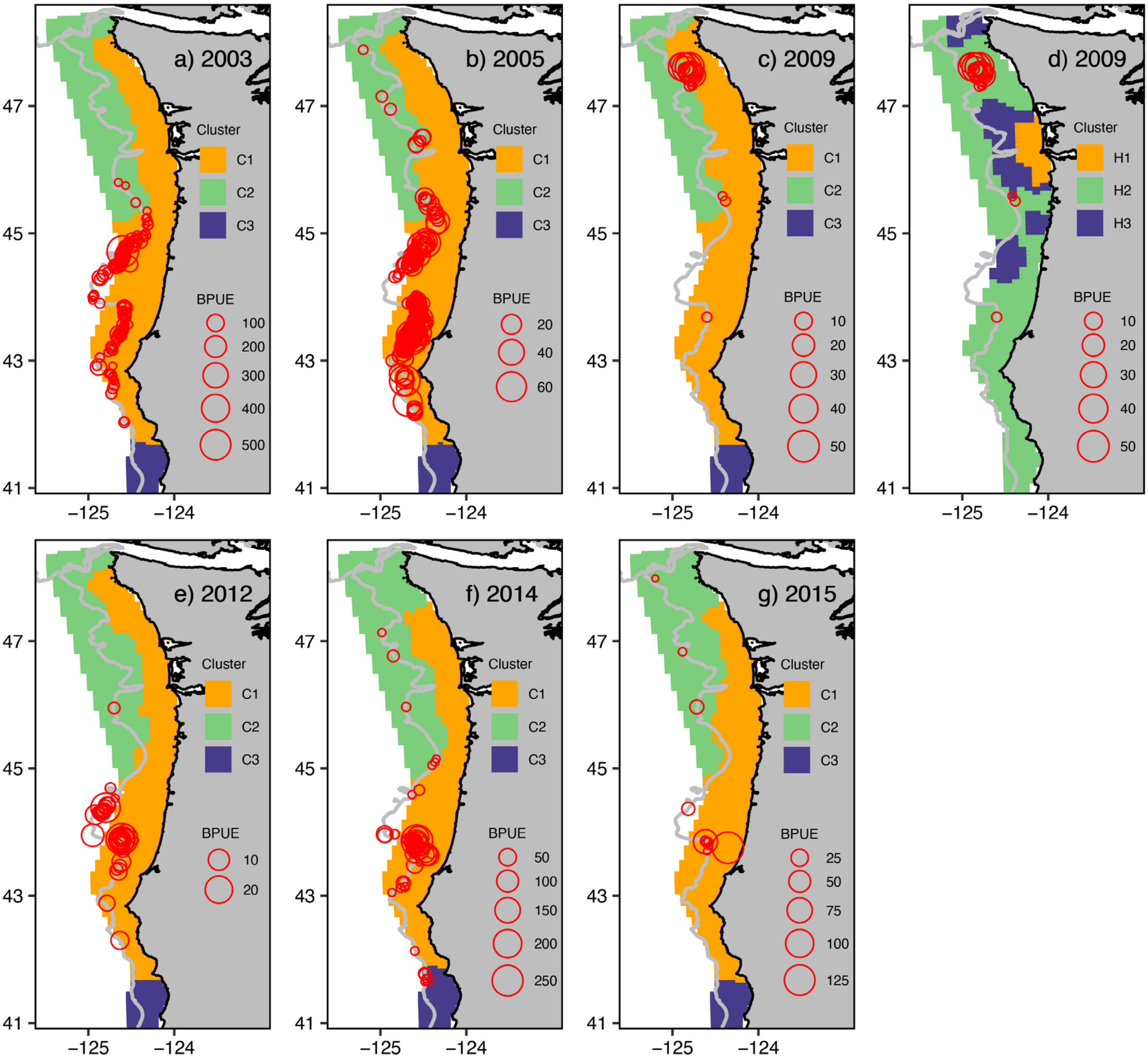

Fig. 8. Distribution of bycatch per unit of haul time (BPUE) and foraging habitats of Chinook salmon (C1, C2, and C3) shown for (a) 2003, (b) 2005, (c) 2009, (e) 2012, (f) 2014, and (g) 2015; group assignments (colors) are the same as in Fig. 4a,c,d. Red bubbles: bycatch locations; bubble size represents magnitude in a given year. (d) BPUE and foraging habitats for Pacific hake in 2009; group assignments (H1, H2, and H3) are the same as in Fig. 5a,c. Importantly, distribution of fishing effort was not distributed equally across the years, in part due to closures following large bycatch (Lomeli & Wakefield 2019); therefore, lack of bycatch does not support a lack of the potential for bycatch in an unfished region

salmon diets and are largely focused on krill along the continental slope, with additional contributions from myctophids and juvenile Pacific hake. When Pacific hake were sampled on the northern CCE shelf, their diets expanded to include, in greater weight, a more diverse diet of other forage fishes. We note that Pacific hake samples show a significant but weak increasing trend in body size related to latitude, resulting from a rarity of smaller Pacific hake captured in northern latitudes. We argue that this does not influence our interpretation, as the size range examined across the CCE was similar and the sample sizes were large; however, it is worth noting that larger Pacific hake generally become much more piscivorous.

We used a combination of weight and numerical diet analyses to examine more years of overlap between Pacific hake and Chinook salmon. The weight-based methodology better represents energy transfer and could indicate prey choice based on a

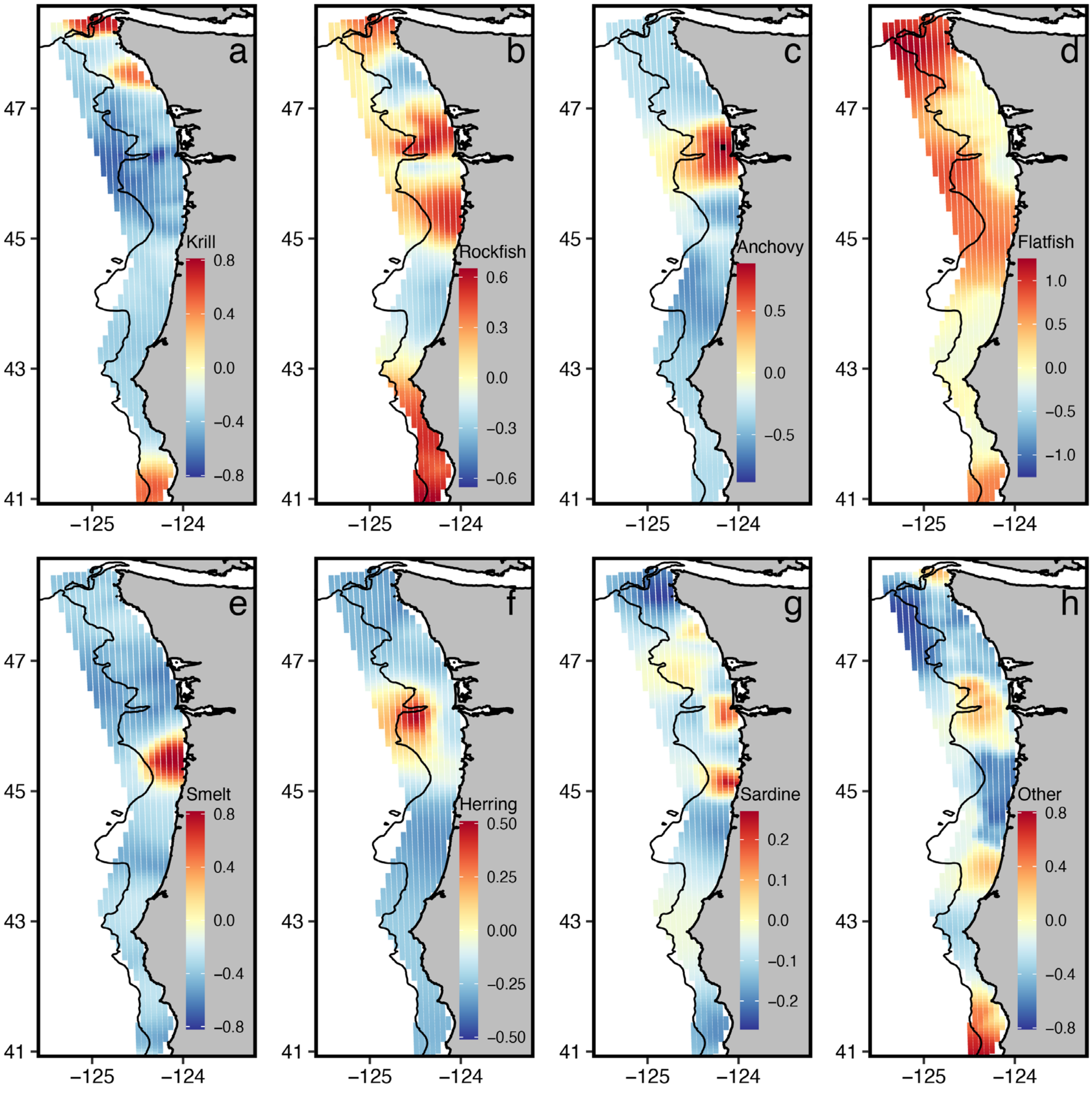

Fig. 9. Estimated anomalies of the weight-based densities for 7 forage taxa in the diets of Chinook salmon on the shelf and the shelf break averaged for 2003, 2005, 2012, 2014, and 2015. These include the shared forage taxa with Pacific hake, including (a) krill, (b) juvenile rockfishes, (c) northern anchovy, (d) flatfishes, (e) smelt, (f) Pacific herring, and (g) Pacific sardine; (h) 'other' represents minor diet taxa

cost–benefit relationship. The numerical analysis was necessary for comparative analysis between Pacific hake and Chinook salmon during overlapping years and foraging areas. Fortunately, the results of the 2 analyses were similar, suggesting that we can rely on similar interpretations. Namely, the results for the Chinook salmon numerical approach were nearly identical to the weight-based analysis, likely resulting from a broad diet of primarily fish. The results between analyses were somewhat different in overlapping years of weight-based diet data for Pacific hake. Any differences were due to the persistent large representation of krill in diets and the trimmed sample distribution. Regardless, in the numerical diet analyses, we observed the same degree of segregation of foraging habitats and types, if only a smaller areal coverage on the shelf (Fig. 5a). Additionally, the numerical diet analysis capably captured temporal shifts in diet at a large scale (e.g. 2009 myctophids in the Pacific hake diet). Therefore, these results are not antithetical between numerical and weight-based diet analyses for Pacific hake or Chinook salmon and provide an examination of their similarity and differences between diets, foraging habitats, and the potential interactions in common areas.

4.2. Biogeographic perspectives

The spatial clusters and prey proportions estimated are similar to past analyses obtained using smaller data sets. While Hertz et al. (2015) explored the geospatial distribution of Chinook salmon diets along the CCE, their data sets were less spatially and temporally comprehensive than those examined here, and the breadth of forage taxa considered was narrower. Data from the CCE used in Hertz et al. (2015) was a subset of the data used here. It is worth noting that even though the Hertz et al. (2015) data sets contained less geographic resolution and fewer years, the results of our study were similar to empirical analysis by Hertz et al. (2015), in which southern Chinook salmon were reliant on krill (~30 % volume) and northern Chinook salmon were reliant on fishes, with northern anchovy being particularly significant (~30 % volume). Modeled Chinook salmon diets along the coast were similarly spatially coherent with their forage community. Specifically, from coastwide micronekton mid-water surveys, Friedman et al. (2018) demonstrated that coherent forage assemblages of approximately 30 prey taxa exist within bioregions, including south of Cape Mendocino, between Capes Mendocino and Blanco, north of Cape Blanco, and an occasional offshore forage assemblage in the northern CCE. This pattern was represented by Chinook salmon diets from these same areas.

Pacific hake and Chinook salmon diets provide indications of CCE forage availability at coastwide and regional scales as well as providing context for the spatial coherence and extent of the effects of ecosystem variability (sensu Friedman et al. 2018, Thompson et al. 2019). Modeled Pacific hake diets and foraging regions were estimated using data obtained during their northern migration along the coast. Their diets indicate coastwide variability of forage availability, with approximately 3 foraging clusters dominated by krill, myctophids, and juvenile Pacific hake in varying relative importance and areal coverage. Yet localized on the shelves of both central California and off Washington and Oregon, diets are remarkably consistent. This consistency is not necessarily a representation of stable forage availability but rather diet consistency when Pacific hake are present on the shelf. This has implications for assessing the spatial extent of Pacific hake and Chinook salmon trophic interactions across bioregions and within coastal shelf waters. Trophic interactions are likely modulated by interannual variability and secular trends of forage communities that could result in high- and low-frequency spatio-temporal shifts of the trophoscape. Namely, in the face of increasing variability and trends in upwelling dynamics along the CCE (Sydeman et al. 2013, Jacox et al. 2020), trophic models may benefit from assessment of concomitant variability and trends in Pacific hake and, regionally, Chinook salmon distributions and interactions along-, off-, and on-shore. We provide a starting point for process-oriented modeling of these dynamics and greater impacts on the CCE resulting from such variability and trends. For example, our trophoscape approach may be applied to evaluate ecosystem-model performance or provide input layers for climate assessments regarding species interactions and fishery responses to climate change.

4.3. Informing trophodynamics

A closer examination of the diet contributors on the northern shelf demonstrates variability in the availability of forage fishes. The most represented taxa within Pacific hake diets, including myctophids, northern anchovy, Pacific sardine, and juvenile Pacific hake, are typically present on the shelf in increased abundance during periods when upwelling dynamics are suboptimal and onshore transport may be more prevalent (Auth et al. 2018, Friedman et al. 2018). The remaining influential forage fishes, Pacific herring and smelt, reside locally on the shelf and are recurrent in diets (Auth et al. 2018). In the context of Pacific hake feeding behavior, Emmett et al. (2006) demonstrated that during periods of late spring transition to upwelling, typical of both weak upwelling and onshore transport, Pacific hake use the shelf environment to forage. The resulting benefit to Pacific hake is that increased consumption of available fishes inshore could potentially allow them to mitigate or adapt to poorer environmental conditions across the CCE. This is especially true when krill biomass, which is typically concentrated along shelf breaks and within canyons, is reduced during less productive periods such as late or weak upwelling, and feeding inshore may be beneficial (Santora et al. 2011, 2018, 2020).

We provide areal context of the potential impacts of Pacific hake on juvenile Chinook salmon along the shelf of the northern CCE. During periods of weaker and later upwelling and associated reduced productivity and onshore transport, the interactions between Pacific hake and Chinook salmon are potentially greater as each uses the shelf and common prey for foraging (Emmett et al. 2006). It has been asserted that the predation pressure of Pacific hake on juvenile Chinook salmon also increases during these times

(Emmett et al. 2006, Emmett & Krutzikowsky 2008). For the Pacific hake diet data examined in this study, only 10 salmon predation events were observed within the most stable foraging habitats (7 in the north and 3 in central CCE; Fig. 2a). Predation was observed within the area of the Columbia River plume, where juvenile salmon first emigrate to sea and where northern anchovy, Pacific sardine, and Pacific herring (all shared resources) are estimated to have increased presence in Chinook salmon diets and in the regional seascape during suboptimal upwelling periods (Emmett et al. 2006, Auth et al. 2018, Friedman et al. 2018, e.g. Fig. 9). However, few Pacific hake have ever been observed with salmon in their diets. Results from Emmett & Krutzikowsky (2008) and this study, which added an additional ~5000 gut samples, demonstrated ~1 out of 1000 Pacific hake sampled had Chinook salmon in their guts. In agreement with this earlier study, we argue that the cumulative impact of relatively rare predation events for such an incredibly abundant predator could be great. In support of this, Emmett et al. (2006) showed salmon survival is strongly and negatively related to the local abundance of Pacific hake. While this could result from correlative consequences as opposed to processes directly identified here, with both species reacting individually to a warm, unproductive system, predation is considered the primary and proximate determinant of Chinook salmon population survival (Wells et al. 2017, 2020, Riddell et al. 2018). There is increased potential for negative impacts on juvenile Chinook salmon during warmer conditions, when Pacific hake overlap with foraging Chinook salmon. Importantly, the likelihood of Chinook salmon in Pacific hake diets may relate to the abundance of alternative prey, whereby Chinook salmon may simply be an incidental prey taxon with decreasing presence in the diet as the availability of northern anchovy and other prey taxa, including Pacific herring and sardine, increases (Wells et al. 2017). A next step in this research should be to consider the role of increased alternative prey in reducing predation on salmon along with management options to achieve this goal.

4.4. Fishery bycatch

We found that above-average bycatch in the Pacific hake fishery was concomitant with years of later spring transition. Specifically, of 6 above-average years of Chinook salmon bycatch (2002–2018), 5 occurred during periods of later transition. The sixth year (2009) represented an influx of myctophids in the diets of Pacific hake on the shelf (Fig. 8d), likely resulting from the observed intense downwelling and onshore transport events (Bjorkstedt et al. 2010, sensu Pereyra et al. 1969), which could have also resulted in more Pacific hake on the shelf as their offshore habitats and prey species were pushed inshore (Malick et al. 2020b). Similarly, greater CPUE of Pacific hake in the fishery on the shelf occurred during periods of later spring transitions. Together, this indicates that interactions between the Pacific hake fishery and sub-adult Chinook salmon were greater during less-productive, warmer conditions, as Pacific hake were more abundant on the shelf. However, the relationship is not straightforward since both Pacific hake catches and bycatch of Chinook salmon are represented as a per-unit-of-effort basis. Therefore, beyond simply the overlap of foraging areas, during later spring transition conditions there may actually be a change in the way Chinook salmon and Pacific hake interact.

Increased interaction between Chinook salmon and the Pacific hake fishery may occur as a result of their feeding behaviors. We have shown that both are feeding on juvenile rockfishes, juvenile flatfishes, smelt, northern anchovy, and krill, which can aggregate both predators into common higher-density areas (Wells et al. 2017, Auth et al. 2018, Szesciorka et al. 2023). In this regard, Bellinger et al. (2009) showed that the geographic distribution of bycatch off Oregon can be highly clustered (i.e. numerous areas of high density). The distribution of bycatch shown here indicates Chinook salmon may be foraging closer to the shelf break; specifically, where their shelf foraging habitat overlaps the shelf break and the Pacific hake fishery (Figs. 7a,b & 8, orange). This is a marginal area between shelf and offshore diet clusters with relatively low foraging habitat persistence and, during the 5 years of increased bycatch, was estimated to be dominated by juvenile rockfishes, flatfishes, and minor prey taxa (Figs. 4b & 9). Further, Hinke et al. (2005a) demonstrated that during periods of warmer surface water conditions typically associated with later spring transition (Bograd et al. 2009), Chinook salmon use deeper waters to maintain optimal temperatures (8–12°C). In support of this mechanism, the vast majority of bycatch occurs farther offshore near the shelf break at bottom depths of as much as 175 m[1]. Importantly, an additional trophic benefit to Chinook salmon using

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[1] Groundfish management team report on the reinitiation of section 7 consultation regarding the Pacific Fishery Management Council groundfish management plan. Agenda Item H.5.a GMT Report 1, March 2018.

deeper waters is more interaction with juvenile rockfishes and flatfishes that use deeper waters during the day (Lenarz et al. 1991, Sakuma et al. 2001). A dedicated study should be completed in which the seascape, including forage distributions and water column dynamics, is characterized and considered as a backdrop for modeling the horizontal and vertical distributions of Chinook salmon at sea, as estimated from advanced tagging technologies (e.g. Hinke et al. 2005a,b, Hayes et al. 2012), biophysical modeling (Fiechter et al. 2015, Henderson et al. 2019), eDNA (Closek et al. 2019, Shelton et al. 2022), and spatial fishery catch statistics (Satterthwaite et al. 2015). Such results could then be related to spatio-temporal occurrences of Chinook salmon bycatch in the Pacific hake fishery.

4.5. Future applications and modeling

Pacific hake and Chinook salmon diets can indicate, with recognition of selective feeding and sampling, variability in the availability of forage taxa at the coastwide and regional scales, respectively (sensu Santora et al. 2021). At-sea surveys are expensive and additionally restricted in space and time, and thus only provide a snapshot of these predators' spatio-temporal distributions. Supplementing survey results with diet samples from fisheries, port sampling, and opportunistic catches can provide a more substantive and representative indication of conditions in the CCE. For example, clear switches in the modeled trophoscape of Pacific hake along the coast, specifically switches between krill, myctophids, and juvenile Pacific hake in the diets, correspond with larger-scale events such as El Niño and large marine heatwaves, which can have the effect of reducing krill productivity and increasing the availability and reliance on myctophids and juvenile Pacific hake (Santora et al. 2017b, Brodeur et al. 2019). We demonstrated such a shift during 1997 concomitant with an El Niño event. In addition, we showed with the numerical analysis, specifically, sustained inflation of myctophids in the nearshore diets (distribution was restricted to match Chinook salmon) following the extreme year of 2009, during which myctophids increased dramatically in the coastal diet. At a regional scale, variability in Chinook salmon diets represents the availability of prey that are common during productive periods (e.g. krill, smelt) and those representing less productive conditions (e.g. northern anchovy; Auth et al. 2018).

For both Pacific hake and Chinook salmon, these differing forage assemblages provide different nutrient qualities and, for Chinook salmon at least, have demonstrable effects on their growth and condition that relates to the likelihood of being preyed upon (Litz et al. 2010, Daly et al. 2013, Woodson et al. 2013, Daly & Brodeur 2015). Such information regarding growth and survival tied to oceanographic variability provides improved parameterization of ecosystem models and the applications of such models to risk assessment and management strategy evaluations (Collie et al. 2016, Townsend et al. 2019, Tommasi et al. 2021). For example, recent agent-based models on salmon growth and survival have been developed based on a krill-dominated diet (Fiechter et al. 2015, Henderson et al. 2019). These models are now being expanded to represent size-selective mortality and population survival of juvenile Chinook salmon (K. Vasbinder et al. unpubl. data). New insights from this work can be used to account for the potential increases in mortality associated with variability in regional diets and intersection with a potential predator, Pacific hake. Ultimately, we provide a process-oriented context for modeling ecosystem, Pacific hake, Chinook salmon, and fishery dynamics; a substantial improvement over simpler bottom-up parameterization linked to assumed effects on the spatio-temporal variability of trophoscapes.

Data availability. All data used in this analysis can be obtained within the California Current trophic database (CCTD) in the Marine Data Archive (https://doi.org/10.14284/597; Bizzarro et al. 2023). Additional explanation regarding the VAST approach with diet examples can be obtained at https://james-thorson-noaa.github.io/docs/tutorials. Spring transition data were obtained within the California Current Integrated Ecosystem Assessment data portal (https://www.integratedecosystemassessment.noaa.gov/regions/icrozoopl-current/icrozoopl-current-iea-indicators). Pacific hake fishery data (CPUE and BPUE) data used in this analysis are subject to confidentiality requirements set forth in The Magnuson-Stevens Act (MSA) at section 402(b), 16 U.S.C. 1881a(b). This means that raw data are not available to the public except as described in the MSA. For example, an aggregated data set that prevents public disclosure of the identity or business of any person can be requested from the Fisheries Observation Science program at the NWFSC. The text of the MSA is available at https://www.fisheries.noaa.gov/resource/document/magnuson-stevens-fishery-conservation-and-management-act.

Acknowledgements. We thank the researchers who collected diet data used in this analysis. We also thank the contributors to the CCTD. B. Burke and N. Mantua provided helpful comments on an earlier draft of the manuscript. This paper was improved by the assessment of the editor and 3 anonymous reviewers.

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Editorial responsibility: Elliott Hazen,
Pacific Grove, California, USA
Reviewed by: 3 anonymous referees

Submitted: January 17, 2023
Accepted: April 28, 2023
Proofs received from author(s): June 20, 2023