Multi-scale relationships between humpback whales and forage species hotspots within a large marine ecosystem

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Open Research: Marine mammal data (Henry et al. 2020; Moore 2021) are available from OBIS-SEAMAP at https://seamap.env.duke.edu/dataset/2147. Echosounder data (Stierhoff et al. 2019; NOAA SWFSC 2022a,b) used to quantify prey are available in NCEI at https://www.ncei.noaa.gov as EK60 data at https://doi.org/10.25921/j7n9-2q77 and EK80 data at https://doi.org/10.25921/2gmv-xn83 under the OMAO cruise name RL1807. Collection Archive: doi:10.7289/V5HT2M7C/.

Key words/phrases: California Current Ecosystem, prey hotspot, humpback whale, predator-prey, endangered species, coastal pelagic fish, ecosystem-based management, prey hotspots
ABSTRACT

Fluctuations in prey abundance, composition, and distribution can impact predators, and when predators and fisheries target the same species, predators become essential to ecosystem-based management. Because of the difficulty in collecting concomitant predator-prey data at appropriate scales in patchy environments, few studies have identified strong linkages between cetaceans and prey, especially across large geographic areas. During summer 2018, a line-transect survey for cetaceans and coastal pelagic species was conducted over the continental shelf and slope of British Columbia, Canada and U.S. West Coast, allowing for a large-scale investigation of predator-prey spatial relationships. We report on a case study of humpback whales (*Megaptera novaeangliae*) and their primary prey—Pacific herring (*Clupea pallasii*), northern anchovy (*Engraulis mordax*), and krill—using generalized additive models to explore the relationships between whale abundance on 10-km transect segments and prey metrics. Prey metrics included direct measures of biomass densities on segments and an original hotspot metric. For each prey species, segments in the upper 5th percentile for biomass density (across all segments) were designated hotspots, and whale counts on a segment were evaluated for their relationship to number of hotspot segments (species-specific and multi-species) within 25, 50, or 100 km. Whale abundance was not strongly related to direct measures of biomass densities, whereas models using hotspot metrics were more effective at describing variation in whale abundance, underscoring that evaluating prey at relevant and measurable scales is critical in patchy, dynamic marine environments. Our analysis highlighted differences in the distribution and prey availability for three humpback whale Distinct Population Segments (DPSs) as defined under the U.S. Endangered Species Act, including Threatened and Endangered DPSs that forage within the California Current Large Marine Ecosystem. These linkages provide insights into
which prey species whales may be targeting in different regions and across multiple scales, and
consequently, how climatic variability and anthropogenic risks may differentially impact these
distinct predator-prey assemblages. By identifying scale-appropriate prey hotspots that co-occur
with humpback whale aggregations, and with targeted, consistent prey sampling and estimations
of potential consumption rates by whales, these findings can help inform the conservation and
management of humpback whales within an ecosystem-based management framework.
INTRODUCTION

Spatiotemporal relationships among predators and prey are foundational to studies of ecology. In marine environments, changes in prey abundance, composition, and distribution can directly impact the survival, growth, and reproductive success of apex predators such as seabirds (e.g., Anderson et al., 1982; Davis et al., 2005; Ainley et al., 2018), pinnipeds (e.g., Soto et al., 2004; McClatchie et al., 2016; Lowry et al., 2017), and cetaceans (e.g., Le Boeuf et al., 2000; Meyer-Gutbrod et al., 2021). Understanding trophic linkages is beneficial for implementing ecosystem-based management strategies, especially if predator populations are threatened or endangered. Further, these assessments provide context for understanding increasing risk or predator response to climate-driven shifts in prey and the environment (Poloczanska et al., 2013; Silber et al., 2017), mitigating adverse effects of harvesting forage species by commercial fisheries (Surma & Pitcher, 2015; Koehn et al., 2020), and other anthropogenic threats such as entanglement in fishing gear (Santora et al., 2020) and ships strikes (Meyer-Gutbrod et al., 2021).

It has been historically difficult to model the relationship between cetacean predators and their prey. Coinciding observations of non-cetacean predator and prey data increases the explanatory strength of predator-prey models (e.g., Rose & Leggett, 1990; Fauchald et al., 2000; Benoit-Bird et al., 2011), but due to logistic constraints of working in offshore marine environments, data are often not collected this way. Studies including cetaceans that did not find strong correlative linkages between predators and their prey were compromised by mismatches in measured and observed processes, i.e., data were collected at different temporal and spatial scales, with different resolutions and coverages (e.g., Fauchald et al., 2000; Torres et al., 2008).
In addition to coincident data collection, collecting predator or prey data at the appropriate spatial or temporal scales is a challenge. For example, data collected at finer scales provide insight to a foraging predator’s perspective (e.g., Hazen et al., 2009; Kirchner et al., 2018; Miller et al., 2019; Cade et al., 2021), but inferences may be limited to a subset of the population, especially for highly mobile predators that are more broadly distributed. Finding the appropriate scale becomes more complicated with multi-species research, where the relevant scales for one species might differ from another. Therefore, a multi-scale assessment may enhance understandings of ecosystem function and inform ecosystem-based management.

Several studies have examined predator-prey relationships across multiple scales, most notably involving seabird observations and acoustics to sample their prey (e.g., Schneider & Piatt, 1986; Russell et al., 1992; Logerwell & Hargreaves, 1996; Logerwell et al., 1998; Mehlum et al., 1999; Fauchald et al., 2000). On coarser scales (e.g., 100s of km), predator and prey densities tended to be positively correlated, while at finer scales (e.g., 10s of km) correlations tended to be negative, hypothetically resulting from prey depletion, behavioral patterns (e.g., diel vertical migration), or predator avoidance response by prey (Haury et al., 1978; Logerwell & Hargreaves, 1996; Fauchald et al., 2000). Heterogeneity of prey aggregations occurs at every scale, with finer-scale relationships hierarchically nested within coarser ones (Fauchald et al., 2000). The strength of scale-dependent relationships will vary depending on how prey heterogeneity is incorporated in predator-prey models. Furthermore, predator-prey linkages may be better quantified using prey metrics that integrate information about prey availability, aggregation, quality, or combinations of these (Hooker & Gerber, 2004; Gende & Segler, 2006; Hazen et al., 2013; Santora et al., 2017). Therefore, in this study we examine functional relationships between a highly mobile and generalist predator and multiple prey species, using
both density and counts of prey species hotspots (areas of high concentration), across fine,
regional, and large ecosystem scales.

In 2018, the National Oceanic and Atmospheric Administration (NOAA) Southwest
Fisheries Science Center conducted a joint stock assessment survey (California Current
Ecosystem Survey; CCES) for commercially important fish stocks, concurrently with visual
surveys for marine mammals (Stierhoff et al., 2019; Henry et al., 2020). The fish stocks, referred
to as “coastal pelagic species” or CPS, comprised Pacific sardine (*Sardinops sagax*), Pacific
mackerel (*Scomber japonicus*), jack mackerel (*Trachurus symmetricus*), northern anchovy
(*Engraulis mordax*), and euphausiids (hereafter, “krill”). The survey sampled a large portion of
the summer distribution of humpback whales (*Megaptera novaeangliae*); including biologically
important areas (BIAs) for feeding humpback whale populations (Fig. 1; Calambokidis et al.
2015; Federal Register, 2021). Thus, we use humpback whales as a case study within the
California Current Large Marine Ecosystem (CCLME) to address challenges of modeling
predator-prey relationships to provide context to benefit fishery and protected resources
management at regional and large marine ecosystem scales.

Here, we use multi-scale data collected in 2018 over a large spatial extent throughout the
CCLME to explore and evaluate several different modeled predator-prey relationships between
synoptically surveyed humpback whales and their three dominant prey species in this
ecosystem—herring, anchovy, and krill. Specifically, our investigation considered: (1) a prey
hotspot approach to defining clusters of prey aggregations (segments with mean prey density
>95th percentile of values across all segments); (2) incorporating species-specific prey hotspots
or one multi-prey hotspot metric; and (3) from local to regional spatial scales (i.e., number of
prey hotspots within 25, 50, and 100 km of each segment). Key questions for this study were: (1)
Can we successfully model predator-prey relationships across a large marine ecosystem using hotspot prey metrics? and, (2) What are the functional relationships for humpback whales and their most common prey in the CCLME?

Due to effects of grazing, behavioral patterns, and predator avoidance, we expected to see similar weak or negative association of predators and prey hotspots at smaller scales and positive association as larger scales (Haury et al., 1978; Logerwell & Hargreaves, 1996; Fauchald et al., 2000). We also anticipated stronger positive relationships using a multi-prey hotspot metric because of the prey switching ability and high mobility of humpback whales. Although we did not include environmental drivers of prey (i.e., prey accessibility), combining prey removes some of the variability, allowing us to assess the relationship of humpback whales as a generalist feeder to prey as “total food”.

We discuss our modeling results as implications for regional and large ecosystem scale management for Distinct Population Segments (DPSs) for humpback whales, as defined under the Endangered Species Act. A multi-regional assessment of the relationship between humpback whales and prey hotspots is relevant because DPSs are distributed in different, partially overlapping regions, feeding at local hotspots with varying prey species composition (Wright et al., 2015, 2016; Witteveen et al., 2015). Enhancing our understanding of the relationships between humpback whales and their prey can improve the sustainable management of a protected-species at risk of entanglement (Santora et al., 2020), ship strikes (Dransfield et al., 2014), exposure to anthropogenic noise (Redfern et al., 2017), and pollution (Elfes et al., 2010) and commercially important fisheries from local scales (humpback whale DPSs and stock-specific prey) to regional scales (all humpback whales as a feeding group and species-specific prey).
METHODS

Case Study – Humpback Whale Populations and Prey in the California Current

The CCLME is a large, dynamic, and spatially heterogeneous marine environment spanning Vancouver Island, British Columbia, Canada to Baja California, Mexico. It is an eastern boundary upwelling system with areas of seasonally high primary productivity that relates to the formation and maintenance of trophic hotspots relative to upwelling strength and transport dynamics. These hotspots enhance predator-prey interactions by attracting resident krill, forage fish, seabirds, and marine mammals (Nur et al., 2011; Sigler et al., 2012; Santora et al., 2017, 2018). Humpback whales switch prey throughout the CCLME. Depending on which prey is most abundant or accessible, these foraging generalists (Witteveen et al., 2015; Fleming et al., 2016) may feed on krill or small schooling forage fish (Nemoto, 1957, 1959; Rice, 1963; Pauly et al., 1998). During spring (Mar–Apr), humpback whales migrate from discrete calving areas off Hawaii and the coasts of Mexico and Central America to feed in the CCLME. These whales are managed as Distinct Population Segments (DPS; Federal Register, 2016). Whales coming from Hawaii (a DPS not at risk under the U.S. Endangered Species Act) forage primarily in northern British Columbia and Southeast Alaska. Whales coming from the coasts of Mexico and Central America calving areas comprise two DPSs listed under the U.S. Endangered Species Act. While the two DPSs can be further classified into migratory herds or demographically independent populations (Martien et al., 2020, 2021; Taylor et al., 2021; Curtis et al., 2022), broadly the Threatened Mexico DPS spends winter off northern mainland Mexico and the Revillagigedo Islands. These whales forage along a wide range of North American coastline, from California to the Bering Sea (Calambokidis et al., 2008; Barlow et al., 2011; Bettridge et...
The Endangered Central America DPS winters off southern Mexico and Central America, as far south as Panama, and forages predominantly off California and southern Oregon (Calambokidis et al., 2008; Barlow et al., 2011).

Ecosystem Conditions

In 2018, ocean climate and ecosystem conditions in the CCLME were recovering from an unprecedented three-year (2014–2016) marine heatwave (Frölicher et al., 2018)—a combination of the warm water “blob”, attributed to strongly positive sea level pressure anomalies over the Gulf of Alaska (Bond et al., 2015) and El Niño, linked with extratropical Pacific Ocean atmospheric variability (Jacox et al., 2016). While still relatively warm in some areas, such as off southern California (Wells et al., 2017; Thompson et al., 2018), cooler than average areas formed in the summer off Washington, Oregon, and central California. Indicators of upwelling (i.e., vertical volume transport and nitrate flux) in 2018 were close to their respective long-term averages. The ecosystem conditions in 2018 also supported a stable northern stock of northern anchovy (north of Cape Mendocino), an increasing central stock of northern anchovy (south of Cape Mendocino), and a stable biomass of Pacific herring (Stierhoff et al., 2019).

Survey and Data Collection

From June 26 through September 23, 2018, the CCES spanned the west coasts of Vancouver Island, Canada, and the continental U.S., from ~ 30-m depth to ~200 nautical miles offshore. Data were collected aboard the NOAA ship Reuben Lasker. Prey data were collected via paired acoustic and net tow sampling (NOAA SWFSC 2022a,b). The acoustic trawl method is described in detail by Stierhoff et al. (2019). Briefly, multi-frequency and wideband
transceivers measured volume backscatter strength (dB re 1 m² m⁻³) along predetermined tracklines continuously throughout the survey. A surface trawl was deployed at night in up to three areas where acoustic echoes from probable CPS schools were observed that day. The acoustic survey included 127 east-west transects spanning a total of 11,304.6 km and included 169 nighttime trawls. Stierhoff et al. (2019) describes biomass conversions in detail. Briefly, catches of target species were sorted, weighed, and enumerated to estimate the proportion of each species and their lengths in each night’s collection, or “cluster”, of trawl catches. Acoustic backscatter was apportioned to CPS and krill in 5 m depth bins over 100 m intervals and the net tow data were used to convert the echo data to estimated biomass densities (kg m⁻²) of northern anchovy and Pacific herring. Krill species and lengths were insufficiently sampled, so krill area backscattering coefficient (ABC; m² m⁻²), a proxy for biomass density, was estimated along the same 100-m transect intervals.

Visual surveys of marine mammals were conducted concomitantly with acoustic sampling for a total of 80 days between 26 June and 23 September 2018 (Moore, 2021). The marine mammal survey spanned 12,857 km. The standard line-transect-survey method is described in detail by Henry et al. (2020). Briefly, the ship traveled at ~10 knots while marine mammal observers sighted animals from the vessel’s flying bridge using 25x150 mounted binoculars. Sighting information (e.g., species and group size) and environmental conditions (e.g., weather, visibility, glare, swell height, and Beaufort sea state) were recorded. Only standardized sighting data collected along daytime track lines in sea state ≤5 were included.

Predator-Prey Data
For the marine mammal sightings data, contiguous “main” transect lines (up to 136 km long) were divided into nominal 10-km transect segments [swfscDAS package v 0.5.2.9; (Woodman, 2021) in R (v 4.1.0, R Core Team, 2021)]. This segment length was chosen as a tradeoff of various factors affecting modeling performance. Longer segments minimize between-segment sampling variance and spatial autocorrelation in sighting rates, whereas shorter segments better match the spatial resolution of environmental gradients of interest (Hedley & Buckley, 2004; Buckland et al., 2001, 2004). Main transect lines did not exist in exact multiples of 10 km, so dangling segments <5 km were appended to an adjacent 10 km segment along the main transect, while those between 5 and 10 km were considered their own segment and chosen randomly along the main transect, following the methods described in detail by Becker et al. (2010). If the entire main transect was <10 km, it was treated as a separate segment regardless of length. The resulting dataset contained a total of 1,650 segments, with 38.5% equal to the target length of 10 km, 38.5% with a length of 5-10 km or 10-15 km, and 23% with a length of <5 km. Any 100 m CPS transect interval within a 5 km radius of a segment’s geographical midpoint (relative to the vessel’s position) was paired with that segment. Herring and anchovy biomass densities (kg m⁻²) and krill ABC (m² m⁻²; a proxy for biomass density) were averaged across all the 100-m intervals along each segment. Humpback whale sightings were summed along each segment. Only segments with both marine mammal sighting effort and prey effort were retained for the analysis, resulting in 697 segments (Fig. 1).

**Predator-Prey Modeling**

Generalized Additive Model (GAMs; Hastie and Tibshirani, 1990) were developed in R with the mgcv package (v 1.8-34; Wood, 2004). Using humpback whale counts along each
segment as the response variable, we constructed models using either direct measures of prey (i.e., biomass density) or derived prey hotspot metrics as explanatory variables. On a segment mean biomass density (across 100-m intervals in that segment) was used for herring and anchovy, and krill ABC was used for krill. Prey hotspot metrics were based on the number of prey hotspots within 25, 50, and 100 km of each transect segment to represent varying scales (see next paragraph). Following the methods described in Becker et al., (2020), effective area searched (EAS) was estimated for each segment as a product of the length of the effort segment (L), two times the effective strip half-width (ESW), and the probability of detection on the trackline (g(0)):

\[
EAS = 2 \cdot L \cdot ESW \cdot g(0)
\]

Encounter rate variance was modeled using a Tweedie distribution to account for overdispersion, fit using restricted maximum likelihood (REML), thin plate regression spline with the penalty modified toward shrinkage, and natural log of the effective area searched as an offset. Prey hotspots were identified for each species. Any segment with mean prey density greater than the 95th percentile of values across all segments in the dataset was designated as a hotspot for that prey species. We then separately quantified, for each segment, the total number of herring, anchovy, krill hotspots separately within 25, 50, and 100 km, i.e., local to regional scales (Fig. 1). We also tallied, for each segment, the total number of hotspots of any prey type within 25, 50, and 100 km of that segment, which we refer to as multi-species prey hotspots.

Model performance was evaluated using explained deviance, Akaike’s Information Criteria (AIC; Akaike, 1970), REML value, area under the receiver operating characteristic
curve (AUC; Fawcett, 2006), true skill statistic (TSS; Allouche et al., 2006), and root mean squared error (RMSE). Models with lower AIC and REML values are considered parsimonious. AUC, which is calculated from receiver operating characteristic (ROC) curves, measures the accuracy of predicting observed presences and absences (between 0 to 1) with >0.5 indicating better than random skill. TSS (Sensitivity + Specificity - 1) accounts for false negative and positive errors (between -1 to +1) with +1 indicating perfect agreement. The ROCR package (v. 1.0-11, Sing et al. 2005) was used to estimate TSS and AUC. For the purposes of this study, we used TSS and AUC as goodness-of-fit metrics.

**RESULTS**

**Predator-Prey Distributions**

The abundance, composition, and distribution of prey species varied across the entire survey area (Table 1, Fig. 2a-b). Herring were found mostly off Vancouver Island but extended southward to Oregon. Mean herring biomass density was larger on the continental slope, but the largest herring biomass density on a single segment was observed on the shelf off Vancouver Island. High krill-ABC values were distributed throughout the entire survey area, with largest values off Vancouver Island to northern Washington, and between Cape Blanco and Cape Mendocino. Lower krill-ABC values spanned from San Francisco to Southern California. The segment with the largest krill-ABC value was found off Vancouver Island, just south of the segment with the largest herring biomass density. Mean krill-ABC was larger on the slope, but there was also more variability in krill-ABC on the slope. Anchovy were present off Washington and south of Point Conception, but the largest biomass densities spanned from San Francisco to Monterey Bay. Mean anchovy biomass density across all segments was larger on the shelf, but
the largest anchovy biomass density on a single segment was observed on the continental slope
of the Monterey Submarine Canyon.

Humpback whale distribution superficially resembled the collective distributions of
herring, krill, and anchovy (Table 1, Fig. 2c-d), with the largest counts off southern Vancouver
Island, between Cape Blanco to Cape Mendocino, and off San Francisco and Monterey Bay. A
total of 749 humpback whales were counted in 431 sighting events. Whale counts were summed
along each 10 km segment, resulting in 175 segments with whale sightings. Counts on a segment
ranged from 1 to 26 ($\bar{x}$=4, SD=5) whales. Whale density (Fig. 2d), which was calculated as
counts per latitude (for illustrative purposes) divided by effective area searched (see Predator-
Prey Modeling), mirrored the trend seen with the count data, indicating counts were influenced
by effort and sighting conditions during surveys. The largest number of humpback whale
sightings occurred just south of San Francisco (20% of sightings) followed by off Monterey Bay
(15% of sightings). The total number and range of humpback whales on the shelf (n=379, range
1-25) were close to the number and range of humpback whales on the slope (n=370, range 1-25).

**Predator-Prey Hotspot Distributions**

We identified 35 segments considered hotspots for herring, krill or anchovy based on our
cutoff, i.e., these segments were in the upper 5th percentile of values across 10-km segments.
(Fig. 3a). For herring, any segment with a biomass density greater than 3.64x10^{-4} kg m^{-2} was
defined as a hotspot. For krill, any segment with area backscatter greater than 4.66x10^{-5} m^{2} m^{-2}
was defined as a hotspot. For anchovy, any segment with a biomass density greater than 2.39x10^{-2} kg m^{-2} was defined as a hotspot. The distribution of the prey hotspots visually mirrored the raw
distribution of prey densities (Fig. 3b).
Herring hotspots were identified off Vancouver Island (n=30), around the mouth of the Columbia River (n=3), and north of Cape Blanco (n=2). Of the 35 hotspots, herring hotspots on the shelf were identified off Vancouver Island (n=14), around the mouth of the Columbia River (n=3), and north of Cape Blanco (n=1). The remaining hotspots on the slope were identified on the slope off Vancouver Island (n=16) and north of Cape Blanco (n=1).

Krill hotspots were identified off southern Vancouver Island (n=17), north of the Columbia River (n=3), from Cape Blanco to Cape Mendocino (n=12), and from San Francisco to Monterey Bay (n=3). Of those 35 krill hotspots, more were distributed on the slope than on the shelf. On the slope, krill hotspots were identified off southern Vancouver Island (n=11), north of the Columbia River (n=3), from Cape Blanco to Cape Mendocino (n=8), and from San Francisco to Monterey Bay (n=1). On the shelf, krill hotspots were identified off southern Vancouver Island (n=6), from Cape Blanco to Cape Mendocino (n=4), and from San Francisco to Monterey Bay (n=2).

Two anchovy hotspots were identified around the mouth of the Columbia River and the remaining 33 were identified off San Francisco (n=28) and Southern California (n=5). Most of the 35 anchovy hotspots were distributed on the slope near the mouth of the Columbia River (n=1), from San Francisco to Monterey Bay (n=23), and in and Southern California (n=4). A smaller number of hotspots were found on the shelf, near the mouth of the Columbia River (n=1), off San Francisco (n=5), and in Southern California (n=1).

The locations of the prey hotspots generally corresponded spatially with the locations of higher counts of humpback whales (Fig. 3b). Of the 174 segments with whale sightings, 48 (27.6%) were segments with hotspots. Of the 522 segments with no whale sightings, only 77 (14.8%) were segments with hotspots.
Models of Humpback Whale Counts vs. Prey Biomass

The GAMs using biomass density (for herring and anchovy) or ABC (for krill) along 10-km transect segments resulted in flat functional response for herring and decreasing functional response for krill, suggesting that these models did not adequately describe spatial overlap between humpback whales and prey (Fig. 4). The functional plots suggest no relationship between humpback whales and herring and krill densities, but a slightly positive relationship between humpback whales and anchovy density. Deviance explained by the model for direct measures of prey biomass density was 8.76 percent (Table 2). AIC and REML were lower for the density model compared to the null model; AUC was 0.67; TSS was 0.3; RMSE was 2.91.

Models of Humpback Whale Counts vs. Species-Specific Prey Hotspots

The species-specific prey hotspot models indicate prey- and scale-specific relationships with humpback whale counts (Fig. 5a). The functional plots suggest a positive relationship between humpback whales and the number of herring hotspots within 25, 50, and 100 km of each segment. For krill and anchovy, the relationships were more complex but suggested that whale densities increased as the number of hotspots within 25, 50, or 100 km of a segment increased from zero to some positive number. For krill, whale density plateaued as the number of krill hotspots within 25 km approached 2 but then whale density continued to increase as the number of krill hotspots within 50 km increased. Whale density decreased as the number of hotspots within 100 km increased from 10 to 15 hotspots, but then whale density increased again as the number of krill hotspots at this scale increased beyond 15. For anchovy, whale density increased with the number of prey hotspots within 25, 50, or 100 km increased, although as the number of
anchovy hotspots approached their maximum values at the larger distance scales, whale counts decreased. Deviance explained by the separate prey hotspot models was variable, ranging from 15.48 to 26.28 percent (Table 3). The model using number of separate prey hotspots within 100 km of each segment had the lowest AIC and REML, and the model using the number of separate prey hotspots within 50 km of each segment had the highest AUC and TSS. RMSE values ranged from 2.74 to 2.87. The species-specific prey hotspot models improved at larger scales.

Models of Humpback Whale Counts vs. Multi-Species Prey Hotspots

The multi-species prey hotspot models, which tallied the total number of hotspots across all prey (Fig. 5b), suggests a positive increase in humpback whale counts as the number of prey hotspots within 25, 50, and 100 km of each segment increases. This relationship indicated a plateau followed by an increase with the number of hotspots. Deviance explained by the multi-species prey hotspot models ranged from 11.68 to 16.98 percent (Table 3). The model using the number of prey hotspots within 50 km of each segment had the lowest AIC and REML, and the model using number of prey hotspots within 25 km of each segment had the highest AUC. TSS values ranged from 0.25 to 0.40 and the RMSE values ranged from 2.77 to 2.87. At 50 and 100 km, the separate prey hotspot model outperformed the combined prey hotspot models in terms of model performance metrics, but at 25 km, the combined prey hotspot model and separate prey hotspot model were similar.

DISCUSSION

We investigated associations between highly mobile humpback whales and their herring, anchovy, and krill prey using direct metrics of prey biomass and derived metrics of prey hotspots
at multiple spatial scales. Concurrent survey data allowed for investigation of predator-prey spatial relationships involving multiple species of fishery management interest. Accounting for heterogeneity of predator-prey aggregations by using the number of hotspots within spatial scales relevant to humpback whales (25, 50, and 100 km) explained the geospatial variability of whale-prey associations to inform generalist foraging patterns of humpback whales.

Models using Direct Measures of Prey Biomass Density

Similar to some previous studies, our models relating coincident measures of predator and prey biomass on a segment did not perform well at predicting humpback whale distributions (e.g., Torres et al., 2008). Some other recent studies, however,—conducted at much finer scales than our study—have identified relationships between coincident measures of predators and prey. For example, mean krill volume backscatter and density were reasonably good predictors of blue whale (*Balaenoptera musculus*) presence/absence at spatial scales of 4 km (Barlow et al., 2020) and 10-40 km (Miller et al., 2019), perhaps reflecting the relative ease of modeling the simpler trophic chain of krill-feeding blue whales (Nemoto, 1970) compared to predators that feed on multiple fish and krill species. Their models also selected prey metrics that added information about prey quality (e.g., number, height, width, and depth of aggregations). Hazen et al. (2009) found the surface feeding behavior of tagged humpback whales was correlated with high sand lance (*Ammodytes* spp.) mean volume backscatter within 500 m.

Models using Derived Prey Hotspot Metrics

In our study, humpback densities were better predicted by the number of prey hotspots within some region around a segment than by the amount of prey on the segment itself. The
species-specific prey hotspot models performed better than the multi-species hotspot, particularly as scales increased. Herring hotspots were always positively associated with humpback whale counts while the relationship with krill and anchovy became more variable with increasing scale. As spatial scales increased, some models became non-linear or decreased as hotspots increased. The largest concentrations of predators are not always associated with the largest concentrations of prey (e.g., Hammond et al., 2013; Benoit-Bird et al., 2013; Boyd et al., 2020; Fall et al., 2021) and at certain levels of prey density, functional response curves level off (Mehlum et al., 1999). This suggests a potential density-dependent relationship with the number of prey hotspots in an area limiting the number of predators that can exploit that prey at any given time.

Humpback whales were typically observed on the periphery of hotspots (see Fig. 3b). One possible explanation for this is predator-avoidance behavior by prey, which has been hypothesized as the cause of negative correlations between predators and prey at very fine scales (Haury et al., 1978; Logerwell & Hargreaves, 1996; Fauchald et al., 2000). Additionally, there may also be some threshold above which the abundance of prey becomes unimportant for predators (i.e., saturation), resulting in stronger or at least equally strong relationships between whales and hotspots of intermediate size (e.g., Hunt et al., 1990; Piatt & Methven, 1992; Benoit-Bird et al., 2013). Oceanographic features (e.g., fronts, slicks, and shallow canyon heads) can facilitate the concentration of krill, forage fishes, and their predators. Therefore, the offset between whales and greatest number of hotspots may also reflect lack of additional oceanographic features in the models.

Finally, variability in species-specific prey hotspot models may also be due to whales responding differently to different prey types within the same regions in ways not specified by our models. Prey switching may play a role in regions where there were fewer aggregated
hotspots of preferred (or potentially more energetically beneficial) prey. Prey switching may have been the reason Rockwood et al. (2020) found no strong overlap between krill hotspots and humpback whales off northern California. These different prey types may also occupy different habitats within a region, some of which may be more accessible by predators, and this may have influenced the non-linear or negative relationships we found. However, our models did not include depth or distance to significant features that have been shown to link both predator and prey abundance or density (e.g., Becker et al., 2020; Barlow et al., 2020; Derville et al., 2022).

Regional Variability in Abundance of Prey and Predator-Prey Relationships

Prey hotspots differed among regions, corresponding with distinctive northern, central, and southern biogeographic areas of the California Current. Herring was overwhelming found in the north, anchovy in the south, and krill throughout the CCE. These prey are managed as separate stocks (e.g., Stierhoff et al., 2019) and have been shown to be affected differently by interannual and decadal environmental variability, marine heatwaves, climate change, and past and ongoing fishing pressure (Enticknap et al., 2011). For example, herring in British Columbia increased from 1951 to 2012 (Thompson et al., 2017) while declining in San Francisco Bay from 1979 to 2017 (Thayer et al., 2020). The central stock of anchovy crashed between 2009 and 2015 (MacCall et al., 2016; Sydeman et al., 2020) then rapidly recovered (Stierhoff et al., 2020; Weber et al., 2021), while the stock off Washington and Oregon has remained small (Stierhoff et al., 2020). Krill display high variability (Cimino et al., 2020; Fiechter et al., 2020; Rastetter et al., 2021), declining followed by rapid recovery during some El Niño and marine heatwaves but increasing during others (Brinton & Townsend, 2003; Lilly & Ohman, 2021).
Assemblages of the humpback whale DPSs differ among these distinctive biogeographic areas. Although the Hawaii, Mexico, and Central America DPSs overlap in portions of their summer feeding areas, there are differences in the proportions of whales from each DPS at foraging locations spanning British Columbia and the U.S. West Coast (Calambokidis et al., 2008, 2000; Barlow et al., 2011; Wade et al., 2016). We hypothesize that at the time of our study, animals from the Mexico DPS off British Columbia, Washington, and Oregon were more likely targeting herring, krill, and anchovy, whereas the Central America DPS off California were more likely targeting anchovy and krill. Humpback whales have demonstrated the ability to shift their foraging patterns in the CCE in response to interannual ecosystem fluctuations (Fleming et al., 2016). They also display extremely strong site fidelity to feeding areas (Steiger et al., 1991; Calambokidis et al., 1996, 2000, 2001; Rasmussen et al., 2012; Baker et al., 2013; Witteveen & Wynne, 2017; Martien et al., 2021). Therefore, from a bottom-up perspective, the loss of prey at region-specific foraging ground could impact the DPSs differently in terms of energy acquisition needed for survival, growth, reproduction, migration, and other normal life functions.

Management Implications

The Central America DPS remains listed as Endangered, while the Mexico DPS has been downlisted to Threatened (Federal Register, 2016). The estimated Central America DPS abundance is 1,494 (CV=0.167) and has a slower growth rate (1.8% per year) than the Mexico DPS, whose estimated abundance is 3,479 (CV=0.099) (Curtis et al., 2022). If the different DPSs are targeting different prey in different regions, then the recovery of the Central America DPS may also be negatively impacted by the instability of anchovy and sardine (another possible prey
type for humpback whales, which was largely absent during this study; see: Stierhoff et al., 2020) off California, whereas the Mexico DPS may benefit by also targeting larger more stable, northern populations of herring and krill.

As prey stocks fluctuate within a region (either due to natural variability or climate change), prey accessibility and preference may impact the cross-shore and north-south distribution of foraging humpback whales. Specifically, whales may shift their distributions to match changes in prey, which could exacerbate risk to anthropogenic threats like entanglement in fishing gear (Santora et al., 2020) and ships strikes (Meyer-Gutbrod et al., 2021). Because most entanglements in fishing gear occur in coastal waters where fishing activity is highest (Saez et al., 2013, 2021), whales may be at higher risk of entanglement when foraging on fish on the nearshore continental shelf, which is especially narrow off California, than on whales feeding on krill at the shelf-break and slope associated with submarine canyon habitat (Santora & Reiss, 2011; Fossette et al., 2017; Santora et al., 2018). This may have been the case when humpback whale entanglements spiked in 2015 and 2016 following the onshore concentration of anchovy in Monterey Bay where crab gear was also concentrated (Santora et al., 2020).

In our study, humpback whales and herring hotspots were equally distributed on both the continental shelf and slope, while there were slightly more krill and anchovy hotspots distributed on the continental slope and they were much more aggregated off San Francisco and Monterey Bay. This suggests that the risk of entanglement of whales in the nearshore waters of our study remained. It also suggests differential risk to the different DPSs in terms of their overlap with vessel traffic and fishing activities in these regions (Halpern et al., 2009).

The larger feeding group of humpback whales in the CLME has increased during the past several years (Becker et al., 2020; Calambokidis & Barlow, 2020). This translates to an increased
demand for prey throughout the CCLME, which necessitates a focus on the foraging ecology needs of these growing humpback whale populations. With daily modeled consumption rates of krill at 9,039 kg d\(^{-1}\) (2,104-15,103 kg d\(^{-1}\)) and anchovy at 1,554 kg d\(^{-1}\) (707-2,653 kg d\(^{-1}\)) to 5,353 kg d\(^{-1}\) (2,436-91,41 kg d\(^{-1}\)) (Savoca et al., 2021), this begs the question: is there enough standing forage fish and krill to support the growth in these DPSs? How will climate change broadly change predator and prey distribution and abundance? And will these broader changes further increase anthropogenic threats and/or reveal new threats?

Relevance of our Findings for Ecosystem-based Management

The multi-spatial scale investigation involving multiple prey species demonstrated that there are typically more predators in areas with more prey hotspots, notably off Vancouver Island, from Cape Blanco to Cape Mendocino, and from San Francisco to Monterey Bay. This study included Threatened and Endangered humpback whales and commercial important fish species (PFMC, 2016) protected or managed by NOAA. Understanding these scale-dependent linkages may be useful to consider when implementing ecosystem-based management approaches at different scales, and within the framework of a changing climate (Poloczanska et al., 2013; Silber et al., 2017). Below we describe implications from our study for ecosystem-based management consideration at a variety of scales. However, the patterns we found represent one snapshot in time and predator-prey patterns may shift; therefore, adaptive management strategies will be necessary as more knowledge is gained.

At small scales, the linkages between humpback whales and their prey may better reflect the perspective of individual foraging humpback whales and aggregations of their prey. Smaller-scale relationships, which we discuss above, may reflect complex density-dependent
relationships, prey preferences, and prey accessibility, and density thresholds. For example, few anchovy hotspots and zero krill hotspots despite higher biomass densities of both suggests that density thresholds were not high enough to minimize the energetic cost of foraging (Goldbogen et al., 2011; Hazen et al., 2015) and explain why there were few whales present off southern California. However, the modeled relationship between anchovy hotspots and humpback whale abundance was positively linear at the smallest scale, suggesting that management spanning San Francisco to Monterey Bay, where anchovy hotspots dominated, might be more effective at this scale. Management might not always be feasible at smaller scales, especially scales smaller than this study (<25 km), but knowledge of the relationships, and what may be driving them, may be useful for predicting future predator-prey hotspot aggregations, potentially temporally as well.

At intermediate scales, linkages between humpback whales and their prey reflect assemblages of humpback whale DPSs and distinct prey stocks. This allows for different regions to be managed in terms of the specific concerns in those regions. However, there are a number of differences among the regions that may influence predator and prey abundance and distribution with important implications and considerations for management. For example, the positively linear relationship between herring hotspots and humpback whale abundance at every scale suggests that management, especially off Vancouver Island where herring hotspots dominated, could still be effective at intermediate scales. Management at this scale also allows for a specific focus on areas where prey switching may also increase pressure for commercially important fishes or vice versa (e.g., Surma & Pitcher, 2015; Koehn et al., 2020). Individual krill models were variable at all scales likely due to overlap and prey switching with herring or anchovy. In areas where it is less clear which species humpback whales may be targeting, multi-species prey hotspots metrics may be more appropriate and easier to interpret. This scale is likely the most
effective for management of threatened and endangered humpback whales and their prey. With targeted trawls at consistent time intervals at regions where whales are present may allow for better predictions of whale aggregations. Estimating prey consumption by predators at these intermediate scales may also help manage targeted stocks of small pelagic fish and in turn their marine mammal predators.

At the largest scale, especially at scales larger than this study (>100 km), linkages between humpback whales and their prey hotpots can be considered at the large marine ecosystem level. Humpback whales, though comprising three distinct DPSs, overlap on feeding grounds, forming a larger feeding group through which migration and interchange does occur. Prey at the ecosystem level comprises multiple stocks but is often managed as a group (i.e., coastal pelagic species). While some detail and nuance are lost at this scale (e.g., specific DPSs or prey species), these larger scales may be considered more feasible from a management perspective. However, our study did not find any linkages at this scale (i.e., direct measures of mean prey biomass densities on 10-km segments). Thus, caution should be taken when making management decisions across a large marine ecosystem based solely on direct measures of prey biomass densities within a segment, as this may not be enough to indicate sufficient resources.

Recommendations for Future Work

Future studies might consider including a temporal component to examine how these hotspots change across multiple years. Additionally, due to degrees of freedom in the GAMs from our data, we were unable to explore relationships on the continental shelf versus the slope, regionally stratified relationships, or information about specific DPS distribution. However, by incorporating this additional information and modelling approaches (e.g., number of whale
hotspots correlated with number of prey hotspots), this might reveal stronger predator-prey linkages. Additional scales (both larger and smaller) might be considered as well as additional prey metrics, especially metrics that include information about prey accessibility (e.g., depth specific models of prey), prey quality (e.g., caloric value), stock-specific prey information, and oceanographic aspects of collocated whale and prey hotspots. Additionally, different metrics may be more appropriate for some prey types depending on the aggregation behavior of that prey, which may also vary across different scales. We also did not account for whether whales were actively feeding. Whales sighted during our surveys might have been transiting between concentrations of prey or engaged in other behaviors, such as socialization on resting.

Additionally, we incorporated each humpback whale sighting equally and did not account for group size. This additional information might help account for the effect of density-dependence patterns we saw in some of the models where prey hotspots were kept separate.

ACKNOWLEDGEMENTS

We thank the crew members of NOAA Ship Reuben Lasker, the cruise coordinator, Annette Henry, and the scientists and technicians of the Marine Mammal and Turtle Division and Fisheries Resources Division that participated in data collection. We are grateful to Elizabeth Becker who assisted with data preparation and provided guidance and feedback on data analyses. We also thank Sam Woodman who provided code used to process the data and feedback on data analyses and Kevin Stierhoff who assisted with initial prey-data preparation. Data collection was funded by BOEM (No. M17PG00025), U.S. Navy Pacific Fleet Environmental Readiness Division (IAA No. N00070-18-MP-4C560), Chief of Naval Operations N45, and the NMFS.
National Take Reduction Program. Data analysis was funded by NOAA’s National Protected Species Toolbox Initiative.

CONFLICT OF INTEREST

All authors declare that they have no conflicts of interest.

AUTHORSHIP STATEMENT


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Table 1. Summary statistics (i.e., number of segments, minimum, maximum, mean, and standard deviation (sd)) for mean herring biomass density (kg m$^{-2}$), mean krill area backscattering coefficient (ABC; m$^2$ m$^{-2}$), mean anchovy biomass density (kg m$^{-2}$), and humpback whale counts (number of individuals) spanning the entire study, on the shelf (<= 200 m bathymetric depth; n=193), and on the slope (>200 m bathymetric depth; n=504).

<table>
<thead>
<tr>
<th></th>
<th>Entire Study Area</th>
<th>On the Shelf (&lt;= 200m)</th>
<th>On the Slope (&gt; 200m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>segments</td>
<td>min</td>
<td>max</td>
</tr>
<tr>
<td>Herring</td>
<td>145</td>
<td>2.83x10$^{-8}$</td>
<td>1.91x10$^{-2}$</td>
</tr>
<tr>
<td>Krill</td>
<td>667</td>
<td>9.98x10$^{-9}$</td>
<td>1.07x10$^{-1}$</td>
</tr>
<tr>
<td>Anchovy</td>
<td>263</td>
<td>9.24x10$^{-10}$</td>
<td>2.77x10$^{-1}$</td>
</tr>
<tr>
<td>Humpback Whales</td>
<td>175</td>
<td>0.88</td>
<td>25.5</td>
</tr>
</tbody>
</table>
Table 2. Summary of models predicting whale counts based on mean herring, krill, and anchovy on each segment. Performance metrics included deviance, Akaike’s Information Criteria (AIC), Restricted Maximum Likelihood (REML), area under the receiver operating characteristic curve (AUC), the true skill statistic (TSS), and root mean square error (RMSE).

<table>
<thead>
<tr>
<th>Model</th>
<th>Deviance</th>
<th>AIC</th>
<th>REML</th>
<th>AUC</th>
<th>TSS</th>
<th>RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humpback Whale Counts ~ 1, offset=log(EAS.76), family=tw, method(REML)</td>
<td>0.00</td>
<td>1642.54</td>
<td>819.73</td>
<td>0.50</td>
<td>0.00</td>
<td>3.02</td>
</tr>
<tr>
<td>Humpback Whale Counts ~ Mean Herring + Total Krill + Mean Anchovy, offset=log(EAS.76), family=tw, method(REML)</td>
<td>8.76</td>
<td>1610.92</td>
<td>812.97</td>
<td>0.67</td>
<td>0.30</td>
<td>2.91</td>
</tr>
</tbody>
</table>
Table 3. Summary of models comparing humpback whale counts to various prey hotspot metrics. Performance metrics included deviance, Akaike’s Information Criteria (AIC), Restricted Maximum Likelihood (REML), area under the receiver operating characteristic curve (AUC), the true skill statistic (TSS), and root mean square error (RMSE).

<table>
<thead>
<tr>
<th>Hotspot Range</th>
<th>Model</th>
<th>Deviance</th>
<th>AIC</th>
<th>REML</th>
<th>AUC</th>
<th>TSS</th>
<th>RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>null</td>
<td>Humpback Whale Counts ~ 1, offset=log(EAS.76), family=tw, method=REML</td>
<td>0.00</td>
<td>1642.54</td>
<td>819.73</td>
<td>0.50</td>
<td>0.00</td>
<td>3.02</td>
</tr>
<tr>
<td>25 km</td>
<td>Humpback Whale Counts ~ Herring + Krill + Anchovy, offset=log(EAS.76), family=tw, method=REML</td>
<td>15.48</td>
<td>1577.51</td>
<td>797.69</td>
<td>0.73</td>
<td>0.39</td>
<td>2.87</td>
</tr>
<tr>
<td>50 km</td>
<td>Humpback Whale Counts ~ Herring + Krill + Anchovy, offset=log(EAS.76), family=tw, method=REML</td>
<td>25.98</td>
<td>1523.30</td>
<td>774.84</td>
<td>0.77</td>
<td>0.44</td>
<td>2.76</td>
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<tr>
<td>100 km</td>
<td>Humpback Whale Counts ~ Herring + Krill + Anchovy, offset=log(EAS.76), family=tw, method=REML</td>
<td>26.28</td>
<td>1519.53</td>
<td>772.53</td>
<td>0.75</td>
<td>0.39</td>
<td>2.74</td>
</tr>
<tr>
<td></td>
<td><strong>Species-Specific Prey Hotspots</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25 km</td>
<td>Humpback Whale Counts ~ Combined Prey, offset=log(EAS.76), family=tw, method=REML</td>
<td>15.88</td>
<td>1570.70</td>
<td>791.00</td>
<td>0.72</td>
<td>0.38</td>
<td>2.79</td>
</tr>
<tr>
<td>50 km</td>
<td>Humpback Whale Counts ~ Combined Prey, offset=log(EAS.76), family=tw, method=REML</td>
<td>16.98</td>
<td>1566.36</td>
<td>791.10</td>
<td>0.72</td>
<td>0.40</td>
<td>2.77</td>
</tr>
<tr>
<td>100 km</td>
<td>Humpback Whale Counts ~ Combined Prey, offset=log(EAS.76), family=tw, method=REML</td>
<td>11.68</td>
<td>1593.80</td>
<td>801.78</td>
<td>0.67</td>
<td>0.25</td>
<td>2.87</td>
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<tr>
<td></td>
<td><strong>Multi- Species Prey Hotspots</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
**Figure 1.** Concurrent effort (where marine mammal line transect survey sampling effort was conducted at the same time as acoustic (prey) sampling effort) during the 2018 California Current Ecosystem Survey cruise (June 26-September 23) with humpback whale biologically important areas (Calambokidis et al. 2015; Federal Register, 2021). Red boxes indicate location of two regional insets showing conceptual models from local to regional scales used to enumerate the number of separate prey hotspots within 25, 50, and 100 km of each 10-km transect segment (represented as black lines with mid-point as white circle). Hotspots were defined as any segment with mean herring (orange circles), krill (green circles), and anchovy (purple circles) prey density > 95th percentile of values across all segments. Scale bar represents 200 km.

**Figure 2.** (a) Map of mean herring biomass density (kg m\(^{-2}\); orange circles), mean krill area backscatter (m\(^2\) m\(^{-2}\); green circles), and mean anchovy biomass density (kg m\(^{-2}\); purple circles) on 10-km segments. Segment effort in black. The 200-m isobath in black signifies onshore/offshore designation. (b) Histogram of proportion of total biomass for each prey on 1-degree latitude bins. (c) Map of total humpback whale counts on 10-km segments. Segment effort in black. (d) Histogram of proportion of total whale counts on 1-degree latitude bins (blue bars) with total number of whale counts per bin. Secondary x-axis (upper axis) shows whale density per latitude (counts divided by effective area searched; black dotted line). The 200-m isobath in black signifies onshore/offshore designation.

**Figure 3.** (a) Discrete probability distribution of mean herring biomass density (kg m\(^{-2}\); orange bars), mean krill area backscatter (m\(^2\) m\(^{-2}\); green bars), and mean anchovy biomass density (kg
m$^2$; purple bars) across all segments. Vertical lines indicate 95$^{\text{th}}$ percentile cutoff for hotspot identification. Note the x axes (prey) and y axes (discrete probability distribution) are on different scales. Gaps on y-axis chosen at natural breaks to increase visibility of smaller values.

(b) Humpback whale counts (blue circles, color and size indicate counts) and prey hotspots (defined as greater than the 95$^{\text{th}}$ percentile) colored by prey type (herring as orange circles, krill as green circles, anchovy as purple circles, and no hotspots as small grey circles). Humpback whale and prey data summed along 10-km segments. Corresponding effort segments in black. (c) Inset of San Francisco Bay Area and Monterey Bay area to show predator-prey distribution in finer detail.

Figure 4. Functional plot for models exploring the relationship between humpback whale counts with mean prey biomass densities along the 10-km segments. The x-axis indicates the predictor variable (herring, krill, and anchovy) and the y-axis indicates the smoothing estimator denoted (by the ‘s’) with the predictor variable and estimated degrees of freedom within the parentheses. Note the x axes (mean herring, anchovy, and krill) are on different scales. The y axes (representing the contribution of each predictor variable to the fitted response, centered on zero) are on the same scale, with zoomed herring and anchovy plots above their respective plots to show the smaller-scale relationships.

Figure 5. Functional plot for (a) species-specific prey hotspot models (i.e., herring, krill, and anchovy) and (b) multi-species prey hotspot models exploring the relationship between humpback whale counts and number of prey hotspots within 25 km, 50 km, and 100 km of the 10-km segments. The x-axis indicates the predictor variable (herring, krill, anchovy, and multi-
species prey). The y-axis indicates the smoothing estimator denoted by the ‘s’ with the predictor variable and estimated degrees of freedom within the parentheses. Note the x axes (number of prey hotspots) are on different scales. The y axes (representing the contribution of each predictor variable to the fitted response, centered on zero) are on the same scales within each scale (25, 50, and 100 km, respectively).
0.06
s(Mean Anchovy, 1.71)
-40
-20
20
0 200 400 600

Mean Anchovy

s(Mean Herring, 0)
0 200 400 600

Mean Krill, 3.07

Mean Herring

s(Mean Krill, 3.07)
-40
0
20
0 20 40

Mean Krill

s(Mean Anchovy, 1.71)
-2
0
2
4
0 1^4 2^4 3^4 4^4 5^4 6^4

Mean Anchovy

s(Mean Herring, 0)
-40
0
20
20
0 0