**Oregon Department of Fish and Wildlife**
**Marine Resources Program**
**Semi-annual update on Oregon Dungeness Crab Commission Fishery Improvement (FIP) work plan**
**Assessment Period: February 2023 – July 2023**
**Report Date: August 2023**

| Goal/Performance Indicator | Actions | Due Date | Responsibilities | Progress |
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| 2. Identify the main non-target species and provide information on the status of these species.<br><br>PI 2.1.3, 2.2.3 | A. Assess the amount (weight) of bait used by species in the fishery each year and identify which species are actively managed (i.e. for management targets such as an LRP). | Feb 2024 | Troy Buell (ODFW) | A and B - ODFW continues to process and enter crab logbook data which provides information on bait use in the fishery. ODFW has developed and finalized a bait survey questionnaire targeted at crab bait dealers. ODFW met with ODCC and WCSPA staff to discuss the questionnaire and get input on specific contacts in the industry to reach out to for bait information. ODFW made initial email contact with each of the bait dealers letting them know about the project and plans to reach out to them soon to get more specific information about the species and quantities of crab bait that they sell for use in the Oregon commercial crab fishery. |
| | B. Provide available stock status information on bait species that account for 5% or more of the total catch (by weight) in the fishery. | Feb 2024 | Troy Buell (ODFW) | |
| | C. Provide encounter rates and/or catch data (numbers) for out of scope species (non-ETP amphibians, reptiles, birds, mammals, e.g. orange sea pen, pelagic cormorant). | Aug 2024 | Troy Buell (ODFW) | C – ODFW is on track to complete assessment of in-house crab fishery bycatch data collected during pre-season and in-season ride-along trips, by August 2024. |
| 3. Demonstrate that the main non-target species are above biological based limits<br><br>PI 2.1.1, 2.2.1 | A. For species that account for 5% or more of the total catch (if any) and have management targets (such as an LRP), provide annual stock status information over the past 10-15 years relative to the target. | ~~Aug 2023~~ Proposed Feb 2024 | Troy Buell (ODFW) | A and B - ODFW continues to process and enter crab fish ticket data which documents all species commercially landed during operation of the fishery. ODFW was not able to complete this task as planned for Aug 2023 due to multiple staffing changes affecting the crab program and the need to focus the limited crab staff capacity on other priorities, many of which |

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| | B. For species that account for 5% or more of the total catch (if any) and do not have management targets and all out of scope species, provide available abundance trend information (catch or CPUE data, observer data, abundance surveys, etc). | Aug 2024 | Troy Buell (ODFW) | are associated with performance indicators 5, 6 and 10.<br><br>ODFW can complete these assessments by February 2024 (A) and August 2024 (B). |
| 4. Demonstrate that there is a strategy in place that is designed to maintain the main non-target species at sustainable levels.<br><br>PI 2.1.2 and 2.2.2 | A. For species that account for 5% or more of the total catch (if any) describe the strategy used to maintain these species at or above biological based limits or if none, develop and implement such a strategy.<br>B. For species that account for 5% or more of the total catch (if any) provide an objective rationale and evidence for why the above strategy will work based on some direct information the UoA and/or species involved. | Aug 2025<br><br><br><br><br><br><br>Aug 2025 | Troy Buell (ODFW)<br><br><br><br><br><br><br>Troy Buell (ODFW) | A and B - ODFW continues to process and enter crab fish ticket data which documents all species commercially landed during operation of the fishery. ODFW is on track to complete assessment by August 2025. |
| 5. Provide evidence that the fishery does not hinder recovery of ETP species.<br><br>PI 2.3.1 | A. Continue to participate in and support the Oregon Whale Entanglement Working Group and/or the Crab Advisory Group (OWEWG) to develop short- and long-term options for reducing whale entanglements in Dungeness crab fishing gear. | Ongoing (through Aug 2025) | Executive Director (TBD) (ODCC) | A - ODFW convened a meeting of the Oregon Entanglement Advisory Committee (OEAC), a stakeholder advisory group, in March 2023. The purpose of the group is to provide ODFW with information and broad perspectives from a range of stakeholders on strategies to support the co-occurrence of economically viable fixed gear fisheries and thriving marine life populations off Oregon. The purpose of the March meeting was to discuss the newly published OR whale distribution modeling efforts and the evaluation of the late-season marine life risk reduction measures adopted in 2020. All information from this meeting is on our website here. |

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| | B. Continue research to monitor whale distribution off the Oregon coast to identify whale hotspots. | Ongoing (through at least Aug 2021) | Leigh Torres (OSU) | B – Within this reporting period, ODFW and OSU's manuscript on factors influencing overlap between the fishery and rorqual whales was published in the journal of Biological Conservation found here. This was the second published paper resulting from the first Section 6 Species Recovery Grant funded project to investigate the co-occurrence of large whales and the crab fishery. ODFW and OSU also have been working on a final progress report to NMFS that summarizes all the work done throughout the first phase of this project which will be submitted to NMFS by October 28, 2023.<br><br>Also in this reporting period, ODFW and OSU continued work on a second Section 6 grant funded project to continue the aerial whale surveys and expand on the initial modeling efforts for investigation of co-occurrence of whales and the crab fishery off Oregon. The most recent progress report to NMFS summarizing this work is included as Attachment A. |
| | C. Continue to develop the Conservation Plan for endangered and threatened whales. | Aug 2025 | Executive Director (TBD) (ODCC) and Troy Buell (ODFW) | C – ODFW developed a regulatory exhibit to the Oregon Fish and Wildlife Commission proposing maintaining and enhancing Oregon's primary marine life entanglement risk reduction measures. These measures are the foundation of the department's Conservation Plan to reduce the risk of endangered and threatened whale entanglement in Oregon crab gear. All the materials for the exhibit are located here. |

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| 6. Demonstrate that there is a strategy in place that is designed to ensure the fishery does not pose a risk of serious or irreversible harm to the habitats.<br><br>PI 2.4.2 | A. Develop and implement new technologies to monitor crab vessel locations and compliance with closed areas. | Aug 2025 | Executive Director (TBD) (ODCC) | A - ODFW worked to extend the contract with a software developer in this reporting period to enhance the integrated vessel tracking electronic logbook system based on ODFW and user feedback from the initial pilot of the product during the 2022-23 crab season. The extension of this contract is through June 2023 and the enhanced software application and data flow will be piloted in the upcoming 2023-24 crab season.<br><br>ODFW remains committed to working with industry to test electronic monitoring (EM) systems for vessel tracking and developing procedures for how systems can be used to provide near real-time fishery data by the 2026-27 crab season (see Section 5.3.3.3 starting on page 94 of the draft CP titled "Electronic Monitoring"). |
| 7. Demonstrate that Information is adequate to determine the risk posed to the habitat by the fishery.<br><br>PI 2.4.3 | A. Continue research and monitoring of coastal habitats identified in the Oregon Nearshore Strategy, including:<br>• Survey of seafloor structures and habitat composition<br>• Examination of species, communities, and habitat relationships to habitat monitoring priorities. | Ongoing (through Aug 2025) | Scott Marion (ODFW) | A - ODFW conducted a fishery-independent survey of habitat condition and fish and invertebrate communities in an important commercial fishing region. Transects were conducted using a stereo video sled in the recently re-opened bottom trawl RCA (Rockfish Conservation Area) in the vicinity of Heceta Bank.<br><br>Additionally, nearshore shallow rocky reef habitats in previously un-mapped regions near Seal Rock were surveyed using a multibeam sonar system. Finally, video transect surveys assessing fish and invertebrate habitat utilization were conducted in the Cascade Head Marine Reserve and associated comparison areas using a small ROV. |
| 10. Demonstrate that monitoring, control and surveillance | A. Develop and implement new technologies to streamline logbook submittals and to | Aug 2025 | Executive Director (TBD) (ODCC) Troy Buell (ODFW) | A - ODFW worked to extend the contract with a software developer in this reporting period to enhance the integrated vessel tracking |

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| mechanisms ensure the management measures in the fishery are enforced and complied with.<br><br>PI 3.2.3 | monitor compliance with closed or restricted fishing areas (marine reserves).<br><br><br><br><br><br><br><br><br><br><br><br><br><br><br><br><br>B. Work with fishermen to educate them on the importance of reporting whale entanglements. | | | electronic logbook system based on ODFW and user feedback from the initial pilot of the product during the 2022-23 crab season. The extension of this contract is through June 2023 and the enhanced software application and data flow will be piloted in the upcoming 2023-24 crab season.<br><br>ODFW remains committed to working with industry to test electronic monitoring (EM) systems for vessel tracking and developing procedures for how systems can be used to provide near real-time fishery data by the 2026-27 crab season (see Section 5.3.3.3 starting on page 94 of the draft CP titled "Electronic Monitoring").).<br><br>B. In this reporting period, ODFW convened a meeting of the Oregon Entanglement Advisory Committee (OEAC), a stakeholder advisory group, in March 2023. The purpose of the group is to provide ODFW with information and broad perspectives from a range of stakeholders on strategies to support the co-occurrence of economically viable fixed gear fisheries and thriving marine life populations off Oregon. The purpose of the March meeting was to discuss the newly published OR whale distribution modeling efforts and the evaluation of the late-season marine life risk reduction measures adopted in 2020. All information from this meeting is on our website here.<br><br>ODFW developed and widely distributed a marine life fleet advisory in May 2023 due to the anticipation of elevated fishery effort into May. This notice is on our website here. |

# ATTACHMENT A

## NOAA Species Recovery Grant Semi-Annual Progress Report

Grant number: NA22NMF4720105

Project title: Enhancing Co-occurrence Assessment of Whales and Fishing Gear in Oregon Waters through Incorporation of Prey Data and Residency Analysis

Grantee name: Oregon Department of Fish and Wildlife

Contact information for project managers:

Troy Buell
troy.v.buell@ odfw.oregon.gov
541-861-8135

Kelly Corbett
kelly.c.corbett@odfw.oregon.gov
541-270-5083

Dates of the award period: 7/1/2022-6/30/2025

Dates covered by the progress report: 1/1/2023-6/30/2023

Description of the tasks scheduled for the reporting period and tasks accomplished during the reporting period:

As described in the project proposal, the Oregon Department of Fish and Wildlife (ODFW) planned for most of the work under this award to be conducted by Oregon State University (OSU) under an Intergovernmental Agreement (IGA) establishing a contractual relationship between the two parties, which was executed on August 5, 2022. This report addresses tasks scheduled during the reporting period as outlined in *Figure 3. Milestone timeline of proposed project* of the project proposal.

## <u>Data collection and compilation</u>

### Step 1: Vessel-based endangered species survey and prey data collection

Several ship-based surveys were conducted during this reporting period. Data were also acquired a posteriori from other cruises conducted by OSU's Marine Mammal Institute (MMI) in 2022 and 2023. Ship-based survey methods are described by Derville et al. 2022.

One marine mammal observer (Craig Hayslip) was onboard the R/V *Bell M. Shimada* for the May Northern California Current (NCC) cruise as part of OSU's collaboration with NOAA (chief scientist: Jennifer Fisher) and funded by this award. The cruise totaled 13 days of survey and 126 baleen whale groups observed (including 102 validated sightings on-effort). Validated sightings of baleen whales included (in number of individuals): 17 fin whales, 123 humpback whales, and 28 unidentified baleen whales. Among the photos that were collected during this cruise and processed so far, 7 humpback whales were photo-identified.

Moreover, OSU/MMI supplemented the dataset currently available for this project with distance sampling data collected as part of the MOSAIC project (Marine Offshore Species Assessment to Inform Clean Energy; funded by the US Department of Energy). MOSAIC cruises are led by the MMI of OSU and cover continental shelf and slope waters of Oregon and northern California. These cruises were conducted onboard the R/V *Pacific Storm* in August 2022 (10 days), October 2022 (6 days) and April 2023 (10 days), for a total of 26 days of effort. Among the many cetacean species observed across these three surveys, a total of 520 baleen whale groups were observed (including 475 validated sightings on-effort). Validated sightings of baleen whales include (in number of individuals): 48 fin whales, 41 blue whales, 413 humpback whales, 11 gray whales, one Sei whale, and 197 unidentified baleen whales. Over these cruises, 36 humpback whales were photo-identified.

Finally, OSU conducted three days of effort at sea onboard the R/V *Pacific Storm* as part of the STEM at Sea cruises (funded by Oregon Sea Grant and NOAA award NA22NMF4690373). Surveys were conducted on the continental shelf and slope off Newport, OR. During portions of the cruises when distance sampling effort was conducted, 21 baleen whale groups were observed, including 20 validated sightings. Validated sightings of baleen whales include (in number of individuals): 2 fin whales, 10 humpback whales, one gray whales, and 10 unidentified baleen whales. Over all three days of survey (including but not limited to distance sampling survey), fourteen humpback whales were photo-identified during these cruises and will provide data for the steps 17 and 18.

### Step 2: Endangered species helicopter transects

Monthly helicopter surveys of Oregon coastal waters were continued through a partnership with the United States Coast Guards (USCG) during this reporting period. Four 150 nm transects were planned to be flown each month out of USCG stations in North Bend (NB), Newport and Astoria/Warrenton, weather permitting. Survey methods are described by Derville et al. 2022.

A total of 17 cetacean surveys have been conducted aboard USCG helicopters since January 1, 2023 (Table 1). As of June 30, 2023, OSU conducted the following number of complete surveys: NB-South = 3 (3.3 hours of effort); NB-North = 3 (4.7 hours of effort); Newport = 6 (9.3 hours of effort); Warrenton = 5 (5.8 hours of effort).

During these surveys, a total of 6 different species of cetaceans were recorded: fin whales, gray whales, humpback whales, northern right whale dolphins, pacific white-sided dolphins, and Risso's dolphins. A total of 46 sightings of these species were recorded, which amounts to observation of 194 individuals once group size at each sighting is accounted for. After filtering out the off-effort or unsuitable sightings, pacific white-sided dolphins were observed in greatest numbers (75 individuals, 4 groups), followed by humpback whales (27 individuals, 13 groups), northern right whale dolphins (25 individuals, 1 group), and gray whales (11 individuals, 7 group). Eleven sightings (including 19 individuals) were qualified as "unidentified baleen whales."

Table 1. Dates of cetacean surveys conducted aboard USCG helicopters off the Oregon coast, by month, and transect, since January 2023. Grey boxes indicate that the transect was not surveyed during that month, due to weather, helicopter maintenance, limited scheduling opportunities, search and rescue operation, and/or personnel availability (see details at the end of this report).

| | | NB, South | NB, North | Newport | Warrenton |
|---|---|---|---|---|---|
| 2023 | January | 21-Jan | 22-Jan | 17-Jan | 19-Jan |
| | February | | 12-Feb | 17-Feb | 28-Feb |
| | March | 5-Mar | 26-Mar | 25-Mar | 21-Mar |
| | April | | | 7-Apr | |
| | May | | | 28-May | 16-May |
| | June | 18-Jun | | 18-Jun | 27-Jun |

These newly acquired ship-based and helicopter-based distance sampling data were processed as per Derville et al., (2022) to derive counts of whale groups and individuals per 5-km long segments. Several minor revisions were applied to streamline and improve the R code workflow that processes these data before inclusion in a density surface model. For instance, these revisions include removing sections of survey made in conditions considered too poor for whale detection (i.e., when sightability was scored "Very Bad" or Beaufort Sea State reached 6).

**Step 3: Fishery effort mapping**

ODFW continued to collect and enter logbooks from Dungeness crab and other fixed gear fisheries. Data entry was completed for two additional crab seasons (2021-22 and 2015-16), and QA/QC was completed for 2015-16. This data will be available to update fishery effort maps in the next reporting period.

**Step 4: Small boat surveys**

One small boat survey funded by this award was conducted off Newport on June 2, following observations of humpback whales aggregating on the continental shelf. Groups of one to three humpback whales were observed. Some of these groups were observed foraging in the area. Of the 11 individuals observed, nine were photo-identified, seven were biopsied and one fecal sample was collected.

**Step 5: Compilation of environmental predictor variables**

Compilation of environmental variables continued over this reporting period, building off previous work that included environmental conditions up to September 2021 (Derville et al., 2022). Daily remotely sensed chlorophyll-a layers were downloaded from September 2021 onwards. Regional Ocean Modeling System (ROMS) variables could not be updated due to technical issues on the server's end; ROMS technicians at UC Santa Cruz are currently addressing this issue.

**<u>Outreach and Engagement</u>**

**Step 6: Promote reporting of whale sightings**

The reporting of whale sightings continues to be promoted during public outreach events and OSU's website home page (https://mmi.oregonstate.edu/gemm-lab). Moreover, fishermen engaged in another related research project led by OSU/MMI (SLATE: https://mmi.oregonstate.edu/gemm-lab/slate) are directly reporting whale sightings through custom made data sheets. ODFW promoted reporting of whale sightings with WhaleAlert in the annual crab newsletter, mailed to all permit holders in January 2023 and posted to ODFW's website.

**Step 7: Develop and manage fleet alert system**

Since the month of April, OSU communicated monthly summaries to ODFW to report on the monthly distribution of whales and upwelling conditions as measured by the Cumulative Upwelling Transport Index (CUTI) and Pacific Decadal Oscillation (PDO) that were found to be potential indicator of entanglement risk (Derville et al., 2023). Following the observation of an aggregation of humpback whales within 40 fathoms off Astoria and ODFW's assessment that May fishery effort would be well above normal, a fleet advisory was issued for May 2-31. The advisory was distributed via the ODFW website, email to advisors, and the ODFW GovDelivery commercial crab listserv which has over 14,000 subscribers. ODFW also began exploration of distribution channels to reach other fixed fishery participants. Finally, seven derelict crab gear sets detected by OSU/MMI during boat-based surveys in May and June and were reported to ODFW and locations were posted on the ODFW website to inform vessels interested in recovering derelict gear.

**Step 8: Develop R shiny app to predict whale distribution on a weekly scale**

This task was not prioritized during this reporting period and OSU has no progress to report. OSU anticipates this work to primarily occur toward the end of the project, once whale predictive models are being finalized.

**Step 9: Raise awareness of issue and project**

The context, process, and value of this project have been communicated by OSU through diverse outreach efforts during this reporting period. On February 27, a research presentation shared preliminary results of concurrent whale-krill analyses to the OSU College of Earth, Ocean, and Atmospheric Sciences graduate students, staff, and faculty (approximately 25 people). Other efforts have been aimed at local Oregon classrooms. On March 22, two virtual presentations at Valley Catholic Middle School's Women in STEM Day shared about methods of studying krill and whales, the experience of seagoing fieldwork, and a basic overview of species distribution modeling to approximately 60 students. On March 3, a kindergarten class at Bessie Coleman Elementary School learned about Oregon whales and krill, looked at photographs from the field, and passed around dried krill samples (approximately 20 students).

In addition, two paid undergraduate interns who joined the project during the summer of 2022 have continued working on krill identification, microscopy, and krill caloric sample processing during this reporting period. One wrote a blog post about her experience[1], and the other wrote about the process of caloric analysis[2]. Another blog post shared about Project OPAL through the lens of adaptive, ecosystem-based management[3].

Outreach regarding entanglement issues and related whale research off the coast of Oregon was also conducted as part of the Marine Science Day (April 8) at the Hatfield Marine Science Center and during STEM at Sea cruises (May 9, 11, 12) run by Oregon Sea Grant onboard the R/V *Pacific Storm.* Students from Molalla High School, Tillamook

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[1] https://blogs.oregonstate.edu/gemmlab/2023/05/01/navigating-the-research-rollercoaster/

[2] https://blogs.oregonstate.edu/gemmlab/2023/01/09/a-glimpse-into-the-world-of-marine-biological-research/

[3] https://blogs.oregonstate.edu/gemmlab/2023/01/30/a-matter-of-time-adaptively-managing-the-timescales-of-ocean-change-and-human-response/

High School, and Blanchette Catholic School shared a day at-sea with OSU scientists (funded by NOAA award NA22NMF4690373) to learn about whale survey techniques, ecology and conservation (Figure 1).

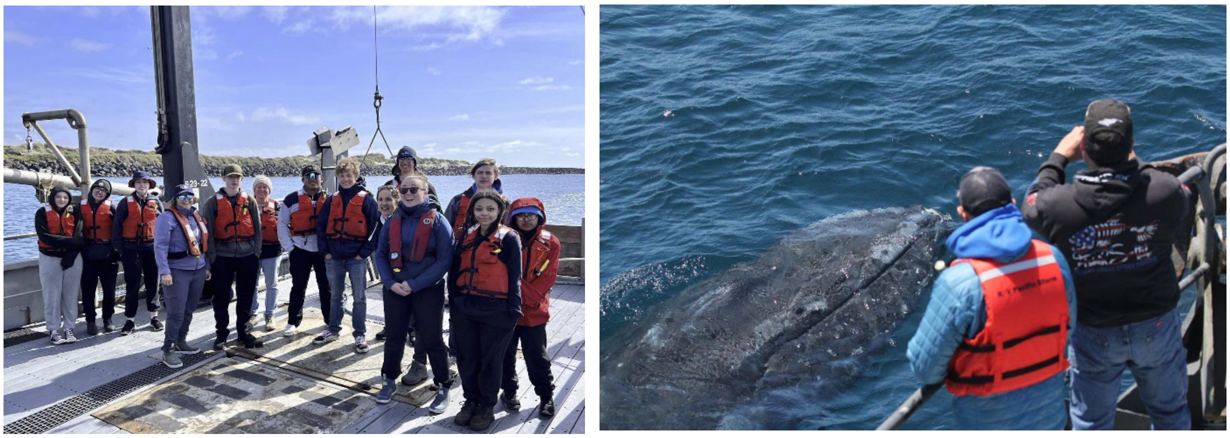

Figure 1: Students and OSU scientists onboard the *R/V Pacific Storm* during the May STEM cruises (observers' time funded by NOAA award NA22NMF4690373).

## Spatial and ecological analysis of prey and whales

### Step 11: Analysis of krill data

*Acoustic data processing* – During the NCC cruises onboard the R/V *Bell M. Shimada,* acoustic backscatter data were collected via hull-mounted Simrad EK60 (2018) and EK80 (2019-2022) echosounders operating at multiple frequencies (18, 38, 70, 120, and 200 kHz). Acoustic data were processed by OSU using Echoview version 13.1 (Echoview Pty Ltd, Hobart, Australia) following the workflow described in Phillips et al., (2022). Various filtering steps were applied to remove background noise and omit seafloor echoes and bottom intrusion. Data within 30 m of the water surface were omitted as well as below a depth of 300 m. Data are reported in relative units of abundance using Nautical Area Scattering Coefficient (NASC, $m^2nmi^{-2}$), which is a proxy for biomass. Frequency differing was used to identify the acoustic signal of krill and calculate krill NASC layers at a 10 m resolution. Methods are detailed in (Kaplan et al., In review; see Appendix).

*Krill distribution model* – Using the NASC data derived from echosounder data collected across NCC cruises 2018-2022, OSU conducted preliminary analyses of krill distribution relative to seabed topography. Daytime daily NASC values summed over the whole water column (30 m to 300 m deep) were aggregated over grids of 5 km resolution (matching rorqual whale models) and environmental variables were extracted for each grid cell. NASC was modelled with a Tweedie distribution in a Generalized Additive Model including three topographic variables: seabed depth, seabed slope and distance to canyons. This model had a deviance explained of 21 % and suggested significant multimodal relationships between krill and seabed topography (Figure 2).

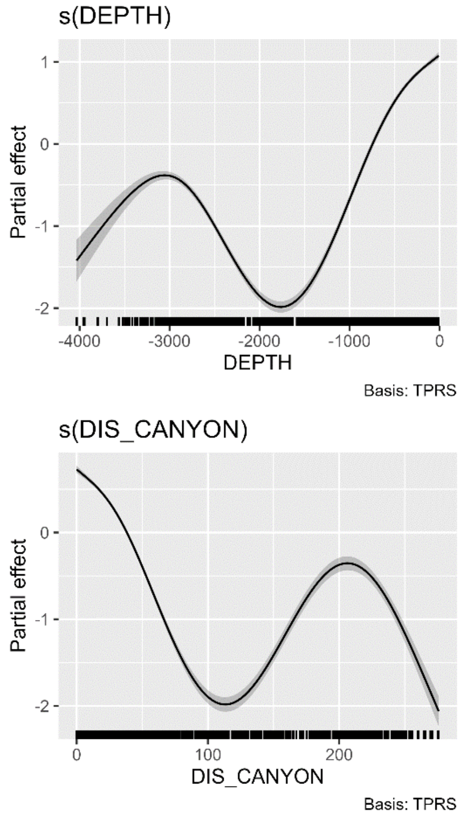


Figure 2: Krill NASC relationships to topographic variables fitted with a Generalized Additive Model generated using 4 years of NCC cruise echosounder data (2018-2022). Solid lines represent the marginal effect of each variable relative to krill NASC. Shaded areas represent the 95 % confidence intervals. Predictors include: DIS_CANYON = distance to canyons (in km), DEPTH = seabed depth (in meters), SLOPE = seabed slope (radians).

*Caloric analysis -* Bomb calorimetry is the gold standard for the caloric analysis of prey species, including krill. In September 2022, individual krill were collected for caloric analysis aboard the R/V *Bell M. Shimada* (n=160). These krill were processed for their caloric content during winter and spring 2023 using bomb calorimetry. Preliminary analyses suggest that in the fall (September), the caloric content of *Thysanoessa spinifera* krill is higher than that of *Euphausia pacifica*, but that in the spring (May), the caloric content of these two species is not significantly different (Figure 3).

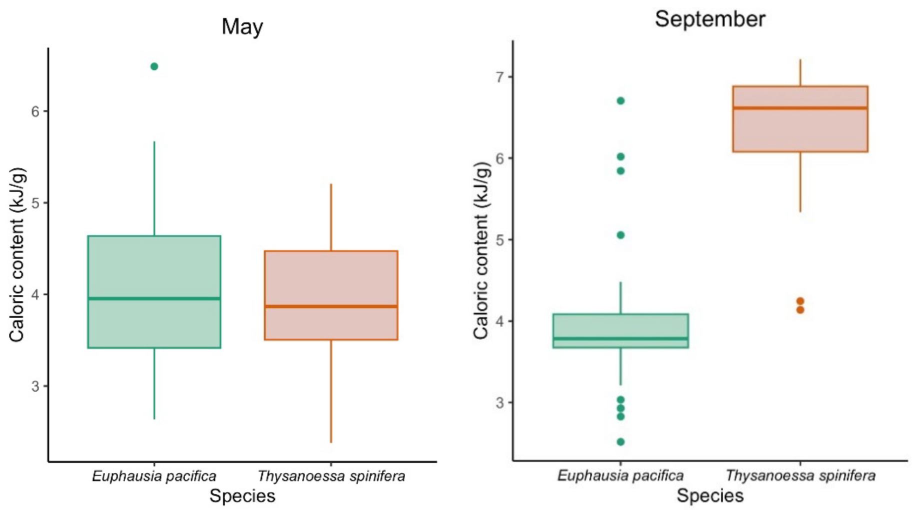


Figure 3: Preliminary analyses indicate that *Thysanoessa spinifera* krill has higher caloric content than *Euphausia pacifica* in September (One-way ANOVA, $p < 0.05$), and that the species do not have significantly different caloric content in May (One-way ANOVA, $p > 0.05$).

**Step 12: Assess fish distribution with whale densities**

*Relationships between fish and whales* – Daily predictions of anchovy, sardine, and herring occurrence at 0.1 ° resolution were provided by B. Muhling et al. (https://coastwatch.pfeg.noaa.gov/erddap/griddap/FRD_CPS_SDMs.html). Predictions of fish occurrence were derived from Generalized Additive Models that were trained with fishery independent sampling combined with a variety of environmental variables (Muhling et al., 2019). Layers were processed along with other environmental layers used for this project: these layers were averaged at a weekly scale, expanded to include very nearshore pixels, projected in a UTM coordinate system, and resampled at 5 km resolution (e.g., Figure 4).

Fish occurrence values were extracted at the centroid of each 5-km segment of whale survey effort (including all USCG helicopter and ship platforms). Similar to the approach taken to model whale densities based on ROMS variables in (Derville et al., 2022), fish variables were computed at a weekly scale, with daily values averaged over the 7 days prior to any given survey day included in the data. Generalized Additive Models were fitted to the number of whales per segment with a negative binomial distribution and a logarithmic link function, using the *mgcv* R package (Wood, 2011). Offsets and weights were used to account for detection and availability bias. Fish explanatory variables were modeled with penalized thin-plate regression splines with basis size limited to 5 to prevent overfitting (Wood, 2017). Variable selection was conducted with a shrinkage approach implemented in the *mgcv* R package, which adds an extra penalty to each smoother and penalizes non-significant variables to zero (Marra & Wood, 2011). Models were generated by season (April-July or August-November) and by species (blue whales, fin whales, and humpback whales, as well as all these species grouped together with unidentified rorqual whales).

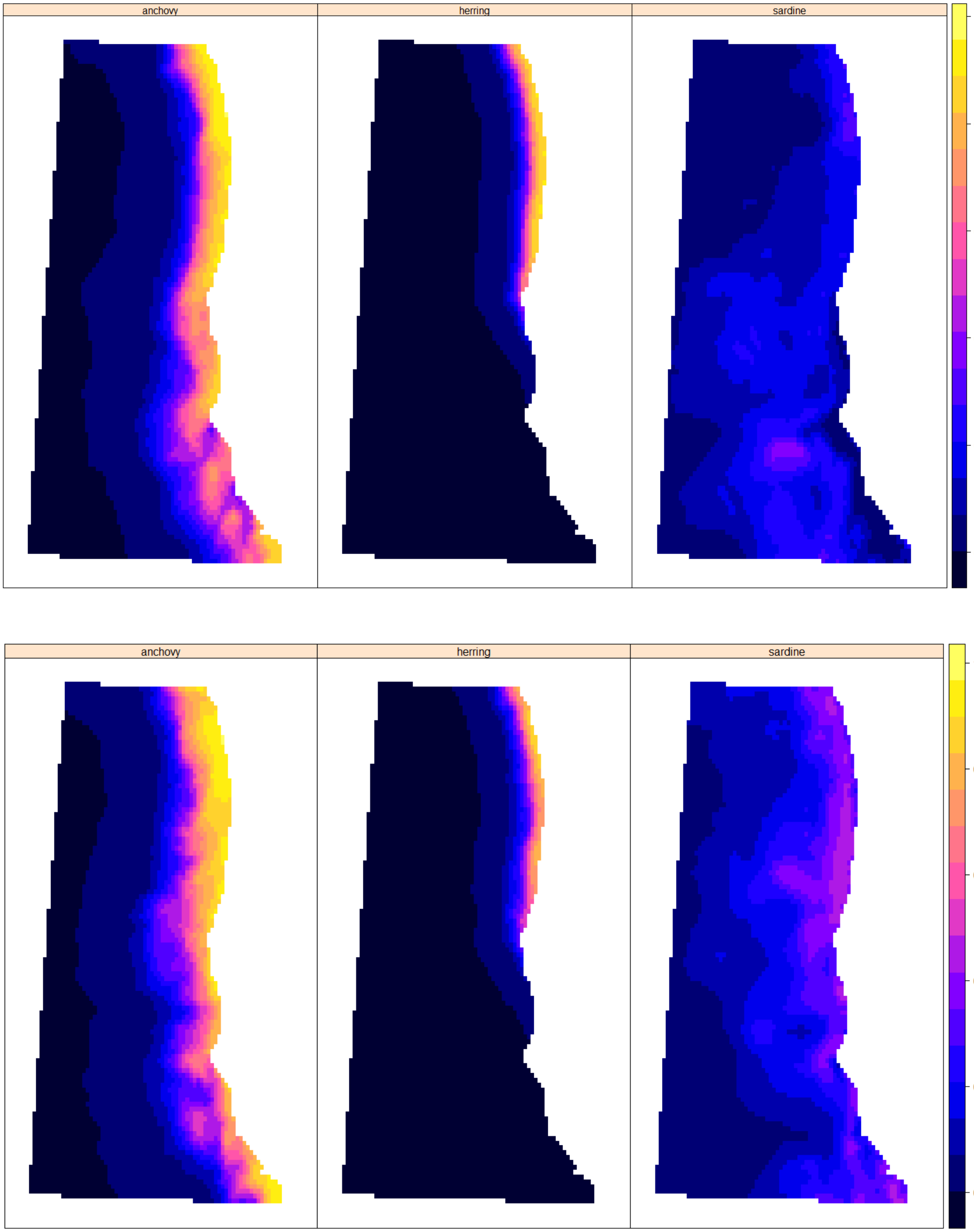


Figure 4: Predicted occurrence of anchovy, herring and sardine in the third week of May (top) and of August (bottom) 2022. Data source: (Muhling et al., 2019).

Fish predicted layers were available until October 2022, hence not yet covering the entirety of the whale survey dataset (which extends through June 2023). Resulting preliminary models of whale distribution suggest generally significant relationships between rorqual whales and anchovy and herring, and to a lesser extent with sardines (Figure 5). Models of humpback, fin, and rorqual whale densities related to fish variables during the two periods of interest (Apr-Jul and Aug-Nov) had relatively high performance, as evaluated with the percent deviance explained that ranged from 16% (Humpback whale Aug-Nov model) to 42 % (Fin whale Aug-Nov model). Anchovy and herring were significant predictors of fin whale and humpback whale densities in both seasons. More surprisingly, sardine, and anchovy were found to be significant predictors of blue whale densities in Aug-Nov (deviance explained 26 %) although blue whales do not feed on fish. This result suggests potential cross-correlation among biotic (fish and krill) and abiotic (seabed topography and ocean conditions) variables, which will be further investigated.

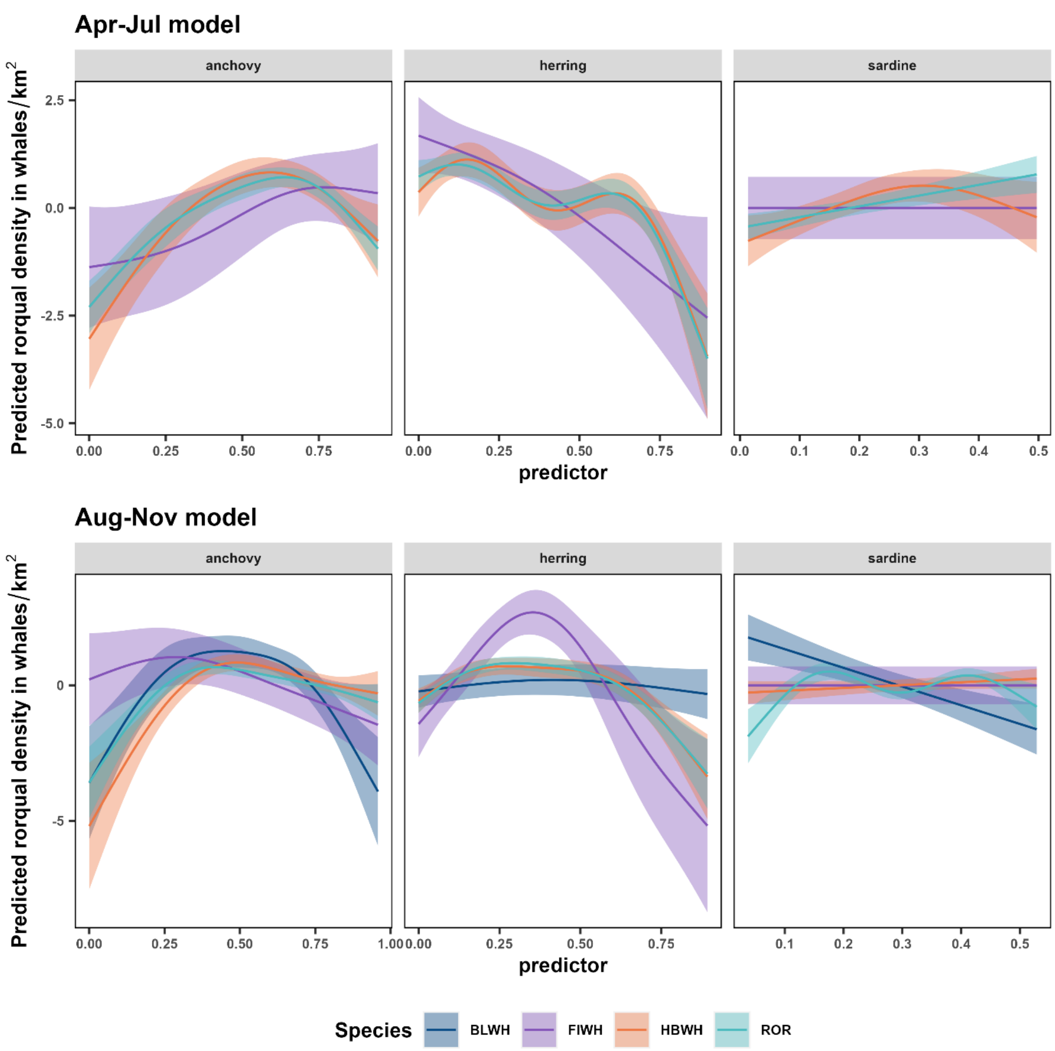


Figure 5: Rorqual ecological relationships modelled over two seasons: April-July and August-November. Functional response curves represent the effect of the smooth function of a selected set of predictor variables (anchovy, herring, and sardine occurrence) upon the trend in rorqual density, with higher values

indicating higher predicted densities. Solid lines represent the marginal effect of each variable relative to rorqual density per season and per species (BLWH = blue whales, FIWH = fin whales, HBWH = humpback whales, ROR = all rorqual whales). Note that the blue whale model was only generated for the months of Aug-Nov because sample size was not large enough in the other season.

### Step 13: Generate rorqual whale SDMs

*Workflow for density surface modeling* – Over this reporting period OSU worked on consolidating R codes to compile ship-based and helicopter-based distance sampling data that allows for efficient and effective density surface modeling of whales. The code pipeline runs in 5 steps: 1) processing of helicopter-based survey effort and observations, 2) processing of ship-based survey effort and observations, 4) merging datasets (Figure 6), assessing unidentified rorquals, counting the numbers of observations by 5 km segments, extracting environmental data at the centroid of segments, 4) estimating the effective strip width in a hierarchical Bayesian framework, and 5) generating density surface models of whales, by season and by species. This pipeline will allow a more effective integration of data as they continue to be collected during this project.

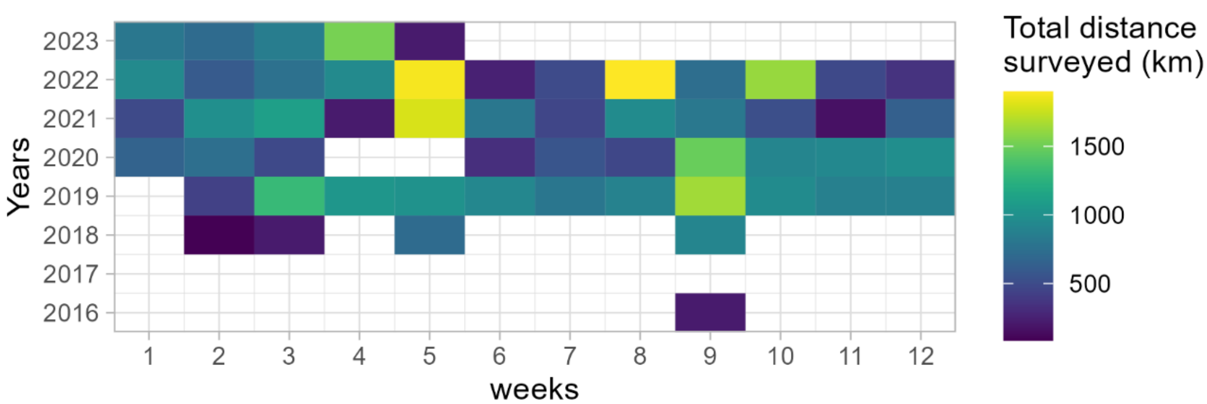


Figure 6: Distance surveyed per month per year from multiple ship-based and helicopter-based platforms (June 2023 effort is not represented in this figure).

*Relationships between krill and whales* – Clarifying the most meaningful spatial scale to analyze relationships between humpback whales and krill, a key prey item, is important to understanding ecosystem function and informing research and management efforts. To examine spatially-explicit relationships between humpback whales and krill, OSU matched concurrent whale sighting (see step 1) and acoustic krill data (see step 11) collected onboard the R/V *Bell M. Shimada* (2018-2022) by day and location (Figure 7). These data were used in Generalized Additive Mixed Models predicting humpback whale occurrence at a series of nested spatial scales: 1 km, 2 km, 5 km, and 20 km. Krill relative abundance at a spatial scale of 5 km had the greatest correlation with humpback whale occurrence (Figure 8). Whale predator and krill prey relationships at this 5 km scale may be both energetically profitable to whales attempting to optimize foraging efficiency, and evident via traditional methodological approaches (paired observer and echosounder surveys). This work led to the recommendation that prey data at the 5 km scale be incorporated into the next steps of this project and considered for management applications in this region. This work is currently in review in the journal *Marine Ecology Progress Series* and the full manuscript is attached to this report (Kaplan et al. In review; appendix 1).

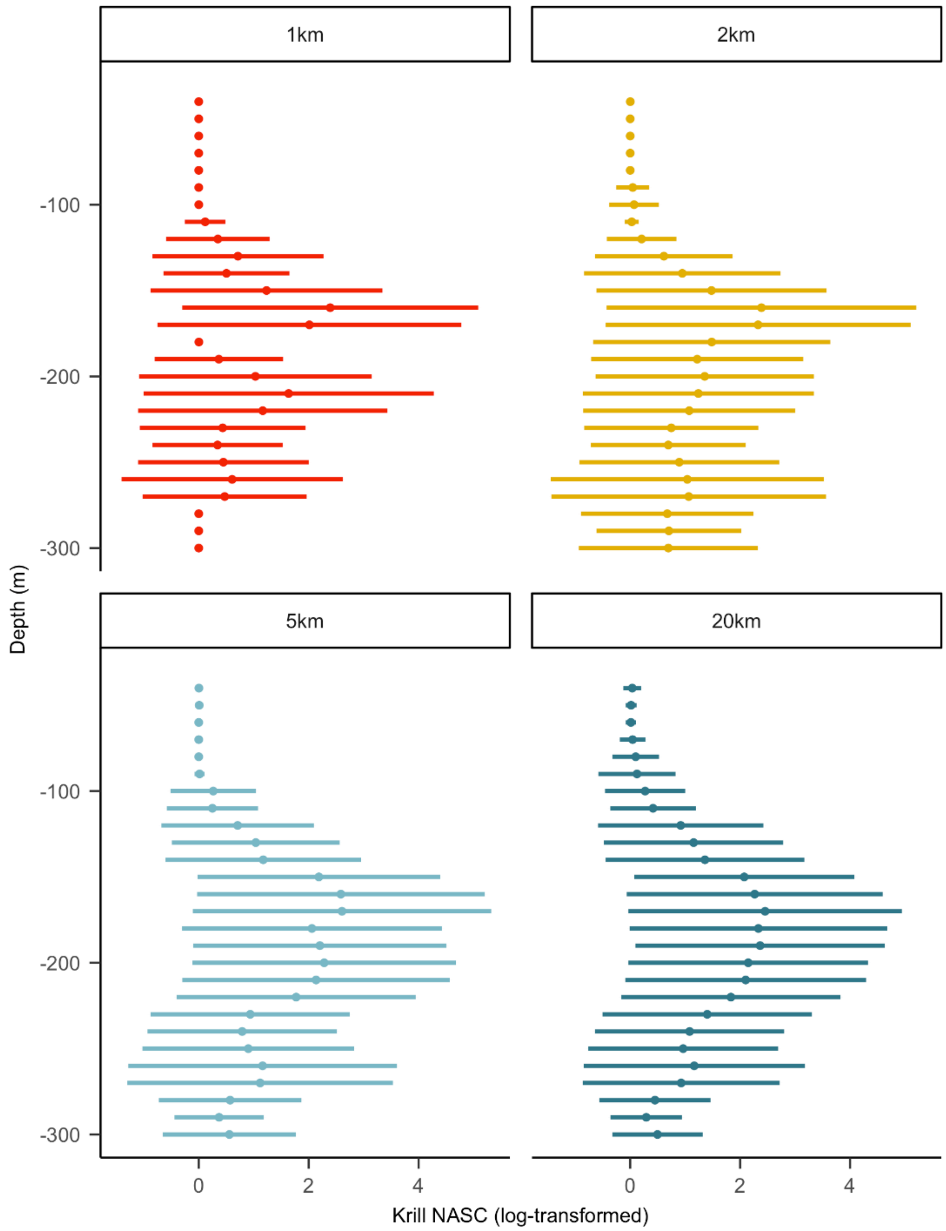


Figure 7: Average depth distribution of krill relative abundance (NASC) at each buffer radius scale surrounding the sighted humpback whales. Standard deviations are shown as horizontal bars across each point. Source: Kaplan et al. In review

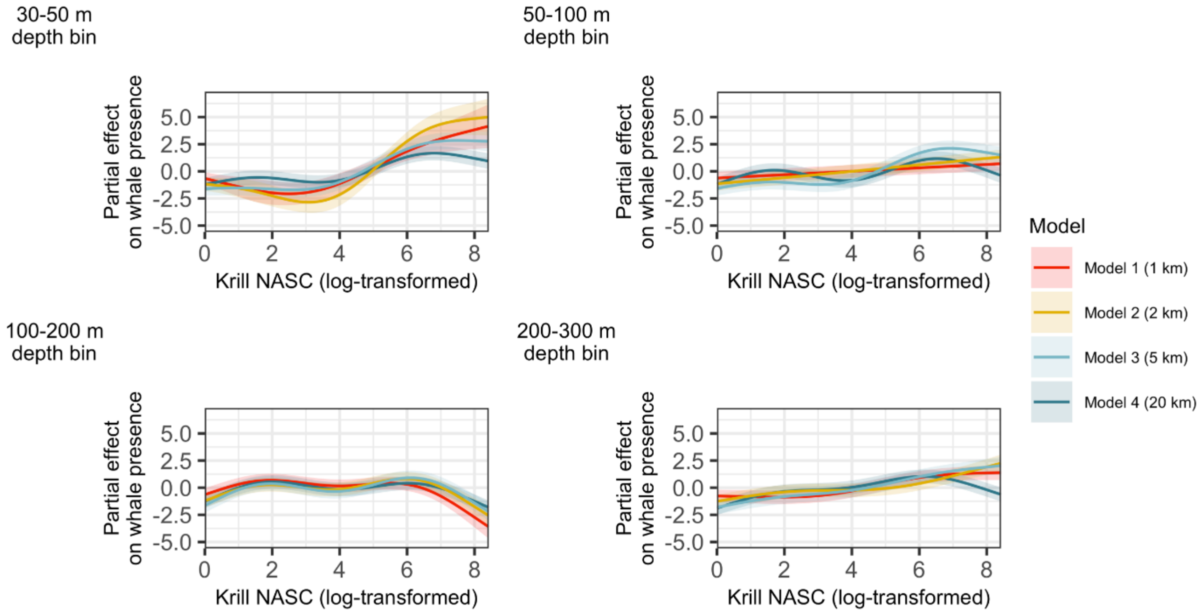


Figure 8: Humpback whale-krill relationships modeled across multiple depth bins and spatial scales. Response curves represent the effect of the smooth function upon the trend in humpback whale presence, with higher values indicating higher predicted probability of occurrence. Shaded ribbons represent the 95% confidence intervals colored per fitted trend. All variables have significant p-values <0.0001. Source: Kaplan et al. In review

## <u>Humpback whale genetic and photo-ID analysis</u>

### Step 17-18: genetic DPS assignment and site fidelity analysis by individual and DPS

As part of NOAA award NA22NMF4690373, OSU worked with John Calambokidis from Cascadia Research Collective to retrieve sighting data of humpback whales in Oregon waters. A table of resights of photo-identified individuals was generated to investigate resighting rates of individuals through time (1990-2022) and space (north, central, south regions of Oregon waters as defined in Derville et al., 2023). Overall, the dataset includes 4,609 sightings in the Pacific Ocean (including breeding, foraging and migratory areas) of 601 unique individuals observed at least once in Oregon waters.

Sightings recorded within Oregon waters were selected to be analyzed under this award. The majority of sightings in Oregon were made between 2017 and 2020 in central Oregon. A lack of photo-identification data was identified in the north (Figure 9). However, more photo-identification data collected as part of this award and through other collaborations are expected to be incorporated in this analysis (see Step 1: 2022-2023 MOSAIC cruises and May 2023 NCC cruise).

Distinct Population Segment assignment information for each individual derived from either genetics or sighting information from breeding grounds (if available) will be incorporated into this dataset to assess site fidelity in Oregon relative to DPS.

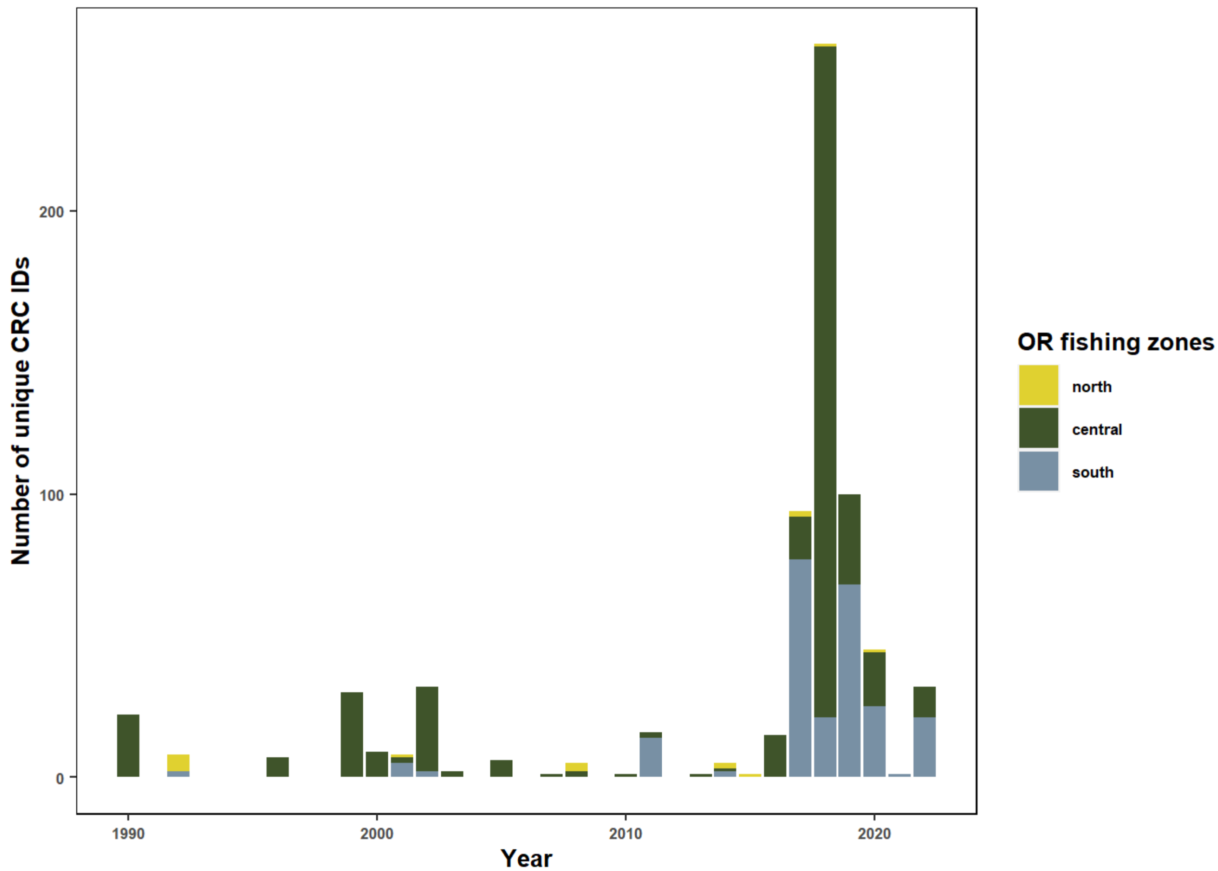


Figure 9: Number of uniquely photo-identified humpback whales observed every year in Oregon waters as part of the Cascadia Research Collective surveys and the GEMM Lab (OSU) surveys. Zones correspond to crab harvest areas: south, from Bandon to the southern Oregon border; central, between Bandon and Cascade Head; and north, from Cascade Head to the northern Oregon border. Data source: Cascadia Research Collective.

## <u>Explanation of any problems or delays in accomplishing planned activities</u>:

Helicopter surveys may be missed for a combination of reasons that are out of OSU's control and are often unpredictable. Scheduling opportunities with USCG for flights are limited (typically 4-5 days per month), do not always align with good weather for survey effort, and cannot be planned more than 1 week in advance in the case of the North Bend sector. Bad weather conditions (fog, rain, strong winds) cannot always be anticipated, as well as search and rescue operation (SAR) that may cancel a flight unexpectedly. Helicopter maintenance and availability of trained personnel may also limit survey schedules.

The California Current Regional Ocean Modeling System (ROMS) variables could not be updated due to a crash of the ROMS THREDDS server in the winter 2023, which has not been resolved as of today. OSU is in touch with the University of California Santa Cruz Ocean Sciences Department to resolve this issue or find an alternate solution to acquire this data as soon as possible. This technical issue affected steps 5 (compilation of environmental variables), 8 (R shiny app), 11 (krill analysis), and 13 (whale models). In the meantime, OSU worked on step 12 (whale ~ fish models) although it was not initially planned to be conducted during this reporting period.

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# Too Big, Too Small, and Just Right: Humpback-Krill Relationships Investigated Across Four Spatial Scales

Rachel L. Kaplan[1, 2], Solène Derville[2], Kim S. Bernard[1], Elizabeth M. Phillips[3], Leigh G. Torres[2]

[1] College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, 104 Ocean Admin Bldg, Corvallis, OR

[2] GEMM Lab, Marine Mammal Institute, Department of Fisheries, Wildlife and Conservation Sciences, Oregon State University, 2030 SE Marine Science Drive, Newport, OR 97365, United State

[3] Fishery Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Blvd E., Seattle, WA, 98112, United States



***Abstract (200 word maximum)***

Understanding scale-dependent variability in predator-prey relationships is essential to ecosystem management. The Northern California Current (NCC) ecosystem provides important foraging grounds for humpback and other rorqual whales, where these animals also face diverse anthropogenic threats. Clarifying the most meaningful spatial scale to analyze relationships between humpback whales and krill, a key prey item, is important to understanding ecosystem function and informing research and management efforts. To examine spatially-explicit relationships between humpback whales and krill, we matched concurrent whale sighting and acoustic krill data collected in the NCC (2018-2022) by day and location. These data were used in Generalized Additive Mixed Models predicting humpback whale occurrence at a series of

nested spatial scales: 1 km, 2 km, 5 km, and 20 km. We found that krill relative abundance at a spatial scale of 5 km had the greatest correlation with humpback whale occurrence. Whale predator and krill prey relationships at this 5 km scale may be both energetically profitable to whales attempting to optimize foraging efficiency, and evident via our traditional methodological approaches (paired observer and echosounder surveys). We recommend that prey data at the 5 km scale be incorporated into future models and considered for management applications in this region.

## *Introduction*

Trophic relationships drive the function of communities, flow of energy through ecosystems, and biogeochemical cycles integral to the earth system (Lindeman, 1942). Predator-prey relationships both result from and control the distribution of species, causing feedback loops on species' behavior, genetics, and evolution (Barbosa & Castellanos, 2005). Across diverse environments, ecological studies have revealed how distributions of prey structure those of predators, from the inverse and cyclical population dynamics of lynx and snowshoe hare across Canada (Elton & Nicholson, 1942), to multiscale distributions of murres and capelin in the Barents Sea (Fauchald et al., 2000), to penguins foraging for fish in shallow eastern Australia waters (Carroll et al., 2017).

Prey patches in many ecosystems exist within a hierarchical framework that contains nested spatiotemporal scales (Kotliar & Wiens, 1990). However, ecological relationships between predators and prey differ depending on the scale of observation; thus, identifying the most relevant scales at which to observe, understand, and manage these relationships is complex. Ecosystems are characterized by variability across a range of spatial and temporal scales, and the act of observation intrinsically biases the relationships perceived (Levin, 1992). The issue of scale is particularly pertinent in marine environments, which are highly dynamic and characterized by resource patchiness. This inherent complexity is evident in the divergent results of studies that seek to link predator and prey distributions in the marine environment. For example, incorporating prey data into fine-scale species distribution models did not improve predictions of bottlenose dolphin (*Tursiops truncatus*) occurrence in Florida Bay, in the southeastern United States (Torres et al., 2008). In contrast, metrics of a krill prey species (*Nyctiphanes australis*) helped predict the fine-scale distribution of blue whales (*Balaenoptera musculus brevicauda*) in New Zealand's South Taranaki Bight (Barlow et al., 2020). The spatial scale at which prey is sampled relative to predators is important for drawing ecological conclusions, and using proxy environmental data sampled with higher resolution yields better predictions when prey data are unavailable at appropriate scales (Torres et al., 2008). Other studies have used satellite tracking and multiple descriptors of prey quantity and quality to document positive relationships between fine-scale prey patches and individual whales, seals, and seabirds (e.g. Benoit-Bird et al., 2013; Ryan et al., 2022).

Understanding scale-dependent variability in ecological relationships is essential to developing a sound understanding of ecosystems, and to managing them (Levin, 1992). Such efforts may be particularly crucial to animals based on their life history traits. Humpback whales (*Megaptera novaeangliae*) are cosmopolitan feeders and capital breeders, relying on stored energy reserves to complete their migrations between foraging and breeding grounds and reproduce (Dawbin, 1966). Exploiting prey resources efficiently during the limited time spent on the foraging grounds is key for humpback migration timing, survivorship, and reproductive success. Every spring, several populations of humpback whales (Central American, Mexican, and Hawaiian Distinct Population Segments; NOAA Fisheries, 2016) migrate from low-latitude calving grounds to important foraging grounds in the Northern California Current (NCC) region off the U.S. west coast. One of the globe's four eastern boundary current systems, the California Current extends from the transition zone separating the North Pacific and Alaska gyres in the north to Baja California, Mexico, in the south (Checkley & Barth, 2009). Wind-driven upwelling drives seasonal nutrient input and high biological productivity both along the continental shelf and offshore, supporting euphausiids and other zooplankton, as well as predatory fish, seabirds, cetaceans, and pinnipeds (Checkley & Barth, 2009). Two species of krill, *Euphausia pacifica* and *Thysanoessa spinifera,* are abundant in this region and are targeted by foraging rorqual whales, including humpbacks (Brinton, 1962).

Krill are patchily distributed and undergo diel vertical migration, taking refuge from predators at depth during the day and moving to the surface to feed at night (Brinton, 1967). Humpback whales are generalist feeders capable of prey-switching in response to prey availability driven by oceanographic and environmental conditions, such as targeting krill during positive phases of the North Pacific Decadal Oscillation, and schooling fish during negative phases (Fleming et al., 2016). Anomalously low krill abundance in the central California Current region during the 2014-2015 marine heatwave event caused humpback whales to target inshore anchovy schools rather than offshore krill patches, and this resulting habitat compression led to an increase in fisheries entanglement events (Santora et al., 2020). Humpback whales also change the depth at which they forage based on vertical prey availability. In particular, they may target shallower prey when available to reduce the additional energetic costs of feeding at depth, which requires longer dives and extended breath holding (Goldbogen et al., 2012).

Recent work has examined humpback-prey relationships at multiple scales in the broader California Current Large Marine Ecosystem (CCLME), with the aim to enhance understanding of ecosystem function and inform ecosystem-based management (e.g. Fleming et al., 2016; Rockwood et al., 2020; Santora et al., 2020). A multiscale study utilized telescoping spatial scales (25 km, 50 km, and 100 km) and incorporated multiple prey types (herring, anchovy, krill) to describe relationships between humpback whales and prey across the CCLME (Szesciorka et al., 2023). While whale abundances were not strongly correlated with prey biomass, models based on the number of proximate prey hotspots had stronger predictive capacity (Szesciorka et al., 2023). Clarifying the most meaningful spatial scale at which to analyze humpback-prey relationships in this region is important to understanding ecosystem function, anticipating humpback whale response to climate change, and informing research and management.

Whales throughout the CCLME are threatened by diverse anthropogenic impacts, including entanglement, ship strikes, noise, water quality, and marine debris (Oldach et al., 2022). Hence, there is a direct need to understand the impactful scales of relationships between whales and prey in the NCC (Derville et al., 2023). Krill is abundant relative to other prey types in the NCC region (Szesciorka et al., 2023), and *E. pacifica* and *T. spinifera* (hereafter "krill") are considered the main component of the preyscape for humpback whales. In this study, we explore humpback-krill relationships and clarify the meaningful spatial scales at which these relationships operate in the NCC region. We use a concurrent dataset of humpback whale visual observations and an acoustically-derived krill abundance proxy collected over four years (2018-2022) to model relationships across multiple spatial scales, with the objective to identify the most relevant scale of prey drivers of humpback whale distributions. We hypothesized that associations between whales and krill are strongest at finest spatial scales and decline at increasing scales (1 km > 2 km > 5 km > 20 km). As no common definition of scale resolution from fine to coarse exists across the fields of oceanography and spatial ecology (e.g. Stommel, 1963; Mannocci et al., 2017; Torres, 2017), we refer to 1 km and 2 km as very fine-scale, 5 km as fine-scale, and 20 km as mesoscale.

## *Methods*

### *Whale data collection and processing*

From 2018 to 2022, marine mammal observers collected cetacean distribution data during cruises aboard the NOAA Ship *Bell M. Shimada*. These cruises occur in February, May, and September annually, and they transit between La Push, WA to Crescent City, Trinidad, or San Francisco, CA, USA, sampling oceanographic stations up to 200 nautical miles offshore. Observers collected data during transits between oceanographic stations, following a distance sampling protocol (Buckland et al., 2015). A handheld GPS was used to record the trackline of the ship, which was subsequently interpolated to 1 position every 30 seconds to ensure consistency across surveys. Survey speed averaged 10 kts, with occasional periods of 5 kt travel due to other research needs. Observers (typically two) were positioned on either side of the vessel's flying bridge, 13 m above the waterline, and during poor survey conditions would transition to the bridge, 10.5 m above the waterline. During on-effort survey periods, observers constantly scanned from the ship to the horizon for animals, using binoculars at least 30% of the time. Individuals were identified to species if a positive visual ID was possible and recorded as unidentified whales if not, and group sizes were estimated conservatively based on the number of simultaneous observations of nearby whales. In addition, the angle of the animal to the trackline at the point of first observation was estimated and recorded. Radial distance was estimated visually for nearby animals within 1000 m, and using binocular reticles for those farther away (Fujinon 7x50's). These data were used to trigonometrically derive geographic coordinates of the sighted whales using the *geosphere* R package (version 1.5-14). Whale groups that included either humpback whales or unidentified rorqual whales were considered for further analysis (Table 1, Figure 1).

*Acoustic data collection and processing*

Acoustic backscatter data were collected via hull-mounted downward-looking Simrad EK60 (2018) and EK80 (2019-2022) narrow-band split-beam echosounders operating at multiple frequencies (18, 38, 70, 120, and 200 kHz). Data were recorded continually from the surface to a depth of 750-1000 m using a 1.024-ms narrow-band pulse at rates ranging between 1 ping/sec to 1 ping/8 sec, depending on bottom depth.

Acoustic data were processed using Echoview version 13.1 (Echoview Pty Ltd, Hobart, Australia) following the workflow described in Phillips et al. (Phillips et al., 2022). Background noise was estimated based on the mean volume backscattering strength (MVBS or $S_v$, dB re 1 $m^{-1}$) in 40 ping x 10 m cells, and removed by subtracting estimated background noise from the original signal using a maximum noise threshold of -125 dB and a 10 dB signal-to-noise ratio threshold (De Robertis & Higginbottom, 2007). Impulse noise spikes were removed using a dedicated Echoview operator. The bottom was detected acoustically and corrected manually as needed to omit seafloor echoes and bottom intrusion, which was minimized by a 2 m offset. In addition, data within 30 m of the water surface were omitted to remove surface noise and bubbles, and to account for the near-field range of the 38 kHz echosounder. Though this exclusion may omit small amounts of krill near the surface and seafloor, we consider the losses to likely be negligible. Data from below a depth of 300 m were excluded to account for decreased signal-noise ratio with depth, especially for the 120 kHz frequency. Acoustic data were also omitted when vessel speeds dropped below 5 kts. Data are reported in relative units of abundance using Nautical Area Scattering Coefficient (NASC, $m^2nmi^{-2}$), which is a proxy for biomass. Because the data were collected using uncalibrated echosounders, we did not attempt to compare overall abundances of krill between years, but instead focused on relationships between relative krill abundance and whales within each survey.

*Krill identification and quantification*

We used frequency differing to identify the acoustic signal of krill, based on published frequency difference ranges for krill in the North Pacific (De Robertis et al., 2010) and previous efforts in the region (Phillips et al., 2022). We first aligned our data in Echoview by matching 120 kHz cells to 38 kHz cells in space and time using ping times and sample geometry, and used a $\Delta MVBS_{120\text{-}38}$ range of 10.0-16.3 dB to classify krill from other backscatter. We then used an integration threshold of MVBS values less than -70 dB at 120 kHz to export georeferenced 120 kHz volumetric Sv and NASC, integrated in 10 x 10 m bins.

These data were scrutinized for possible contamination by noise spikes or inclusion of targets like small fish with swim bladders by visually examining cells with mean Sv values between -35 and -45 dB and removing noise manually if needed. Cells with an Sv value of -80 dB or below were then set to 0 to omit weak signals that represented less than 3-4 krill $m^{-3}$ (Phillips et al. 2022).

*Whale-krill analysis*

To examine *in situ* relationships, georeferenced whale and krill data were matched by day and location. Krill data were restricted to periods of daytime (one hour after sunrise to sunset) on-effort whale observation to remove the effects of diel vertical migration and align with them temporally with whale data. All analyses were conducted using the program R (R Core Team, 2021). The data were projected in the Universal Transverse Mercator system (UTM) and concentric circles (hereafter referred to as “buffers”) with radii of 1 km, 2 km, 5 km, and 20 km were drawn around all rorqual whale observations (Figure 2; R *sf* R package, version 1.0-8). Given that only humpback whales were included in this analysis, krill data in the vicinity of non-humpback whales were removed to ensure a more realistic sampling. Krill data were assigned as being within or outside the area of each buffer, and the average log-transformed NASC vertical profiles were assessed within the four different buffer sizes. Based on these profiles, NASC was vertically averaged into 30-50 m, 50-100 m, 100-200 m, and 200-300 m depth bins for further comparisons to humpback whale observations. Across depth bins, a check for autocorrelation between these log-transformed mean NASC yielded a maximum Pearson's pairwise correlation of 0.36, and therefore all were maintained for modeling purposes (*corrplot* R package, version 0.92).

To compare and quantify the relationships between krill and whales at a range of spatial scales, these data were used in a series of models run across the four buffers described above. We used Generalized Additive Mixed Models (GAMMs, *mgcv* R package, version 1.8-42, Wood, 2011) to quantify the relationships between humpback whale presence versus absence and krill NASC. GAMMs use data-defined smoothing elements to model non-linear responses to a set of predictors (Elith & Leathwick, 2009). We selected GAMMs for their capacity to adeptly represent realistic ecological relationships and accommodate complex interactions between species distributions and environmental variability (Torres et al., 2008), which makes them useful for modeling  marine mammals distributions (e.g. Derville et al., 2018; Orphanides et al., 2023; Szesciorka et al., 2023). Cruise ID was included as a random effect in the models to account for variability in effort and environmental conditions between surveys, and interaction effects were quantified by including an interaction between krill NASC and depth bin. Whale group size was accounted for through weights equal to the number of individuals comprising a whale group within a given buffer, so that differences in habitat use by one foraging whale versus a group of foraging whales could be quantified. GAMMs were fitted with a binomial response distribution using a logarithmic link function and a Restricted Maximum Likelihood method (bam and fREML, *mgcv* R package, version 1.8-42). The effect of krill relative abundance on humpback whale occurrence was modeled with penalized thin-plate regression splines with basis size limited to 5 to prevent overfitting (Wood, 2017). Variable selection was conducted with a shrinkage approach implemented in the *mgcv* R package, which adds an extra penalty to each smoother and penalizes non-significant variables to zero (Marra & Wood, 2011). Model fit was evaluated based on the percent deviance explained, as calculated and reported by *mgcv* for a binomial error distribution (Wood, 2011).

Across all whale survey transects, acoustic data were analyzed within 1 km of a total of 29 humpback whale groups containing 37 individuals. We ran a series of humpback whale-krill association models using this subset of humpback whale groups to investigate the strength of these predator-prey relationships across spatial scales (Table 1). We also conducted this analysis using all rorqual whale observations, which included fin whales, humpback whales, and unidentified rorqual whales (n = 235 individuals in 178 groups). For our final model, we ran another version of the 5 km spatial scale model using the full subset of humpback whales observed within 5 km of the trackline (n = 79 groups).

***Results***

A total of 670 rorqual whales (1-10 individuals per group) were sighted during 19,288 km of survey effort during eight cruises between 2018 and 2022 (Table 1). Krill were detected throughout our study area during each summer and fall survey, and krill relative abundance in the vicinity of whales increased with the spatial scale of observation (i.e., with buffer size; one-way ANOVA: df = 3, F = 3.8, p = 0.011; Figure 3). Relative to concurrently observed whales, less krill (log NASC $m^2nmi^{-2}$) were detected at a 1 km very fine scale (mean 13.83 ± SD 0.66), compared to the 20 km mesoscale (mean 28.80 ± SD 0.86; post-hoc Tukey test: p-adjusted = 0.018), and there was not a significant difference between krill relative abundance detected at the 20 km mesoscale and the 5 km fine scale (post-hoc Tukey test: p-adjusted = 0.541).

The subset of humpback whale observations (n = 29 groups of 37 individuals) associated with krill data collected within 1 km of the sightings was used in model 1 (1 km scale), model 2 (2 km scale), model 3 (5 km scale) and model 4 (20 km scale). Model deviance explained increased with buffer size, from 14.1 % at 1 km, to 18.7% at 2 km, to 25.2% at 5 km, to a maximum of 36.0% at the 20 km scale (Table 2). However, marginal deviance explained, which describes the contribution of krill NASC to the explanatory power of the model, increased with scale to a maximum at the 5 km scale (3.8%; model 3), and then declined at the 20 km mesoscale (2.5%; model 4). Overall, krill positively influenced whale occurrence at all spatial scales and depth bins, and relationships were generally stronger at smaller scales and shallower depth bins (Figure 4). In the shallowest layer (30-50 m), the relationship was strongest at very fine scales (1 km and 2 km) as identified from the magnitude of the smooth effect variations in the partial response plots (Figure 4). In the 100-200 m bin, the response curves at all scales exhibited the same slight bimodal shape. In the 50-100 m and 200-300 m depth bins, the influence of krill on whale presence was strongest at 2 km and 5 km. Across all depth layers and all spatial scales, the effect of krill on whales became positive at a mean log-transformed NASC value of 4 (54.60 unlogged). At the 20 km scale, this relationship consistently became negative in each depth bin at relatively large values of mean log-transformed NASC (~ 6.5).

Given that relationships between whales and krill appeared strongest at the 5 km scale, an additional model was run at this scale using all humpback whale observations that had associated krill data within 5 km (model 5, n = 79 whale groups containing 105 individuals). We found that model 5 had 26.7% conditional deviance explained and 3.4% marginal deviance explained, hence showing relatively similar performance to model 3. In the 100-200 m and 200-300 m depth bins, partial response to krill NASC was similar to model 3, while the response was stronger in the 30-50 m and 50-100 m depth bins than in model 3 (Figure 5). In models run across a larger set of all rorqual whales (see Supplementary Material), deviance explained increased from 15.6% at 1 km to 33.9% at 20 km, with a marginal deviance explained of 2.6 % at 5 km.

***Discussion***

Our study illuminates the scale-dependent relationships that exist between humpback whales and krill, one of their key prey items. We found that krill relative abundance at a spatial scale of 5 km has the greatest correlation with humpback whale occurrence in the NCC region. This result speaks to both meaningful scales of observation and ecological relationships between humpback whales and their euphausiid prey, and this scale has proven effective in other modeling efforts in this region (Derville et al., 2022). Observations made at the 5 km scale appear the most useful for understanding and anticipating humpback-krill relationships in the NCC ecosystem, and we suggest this scale of observation will be the most helpful to inform efforts to conserve the marine predators and protect this critical prey resource.

Contrary to our hypothesis, the models at very fine scales (1 km and 2 km) did not perform as well as those at fine and meso scales (5 km and 20 km). This result may indicate that acoustic prey data at very fine scales do not fully contextualize the foraging environment of a humpback whale. While the 20 km scale model (model 4) had higher explanatory capacity than the 5 km scale model (model 3), krill was less descriptive of whale presence, indicating that this scale may describe a prey environment that is less relevant or immediately perceptible to foraging whales. Mean krill NASC per unit area was not significantly greater at the 20 km scale than the 5 km scale, and the patchiness of the marine environment and tendency of krill to form discrete swarms (Brinton, 1962) makes it likely that areas of high NASC within a 20 km area are separated by more waters devoid of krill. Prey patches up to 20 km away may not be perceivable to a whale, or they may simply not be worth the energy expenditure of increased travel and searching – particularly if the near environment remains favorable. This may drive the negative relationship between high krill relative abundance and whale presence at the 20 km spatial scale, and in the 50-100 and 100-200 depth bins at the 5 km scale (Figure 4). From an observational standpoint, the 5 km scale is coarse enough to average out fine-scale variation in prey density and describe the prey environment the whale can "observe" (Levin, 1992), while also being narrow enough that it is perceptible to a whale sensing the environment to locate patchy food resources, perhaps acoustically (Torres, 2017). We hypothesize that a 5 km area containing numerous and profitable prey patches offers whales an opportunity to minimize interpatch travel time and spend more time foraging to maximize energetic gain.

Ecologically speaking, these scale-explicit relationships between humpbacks and krill contextualize the landscape of choice that a humpback whale must navigate on the feeding grounds. Prey density must reach a certain threshold to elicit whale foraging effort and aggregation, activities which become unprofitable below this threshold (Piatt & Methven, 1992). Optimal foraging theory predicts that an animal will choose to either maximize gained energy or minimize the time spent pursuing a given amount of energy (MacArthur & Pianka, 1966). This “time saving” approach is assumed to be adopted in favor of risk mitigation or the pursuit of other behaviors like reproduction (MacArthur & Pianka, 1966). As humpback whales in our study area are on their foraging grounds, we assume individuals are attempting to maximize their gained energy by targeting the most advantageous krill patches. In our models, the steep functional response at intermediate krill relative abundances observed across spatial scales (i.e., log 4 NASC) may represent a threshold of profitability for foraging humpbacks. At some point during foraging, any individual prey patch will drop below the threshold of profitability, whether from exploitation or predator-avoidance behaviors by the prey, and the predator will move on to find a new patch (Charnov, 1976). Marginal value theorem predicts that a predator acting to maximize its energetic gain will depart a prey patch when the marginal capture rate in the patch drops to the average for the broader environment (Charnov, 1976). Areas that are profitable at the 5 km scale may offer the right balance between effort and reward, sustaining a whale above the threshold of foraging profitability.

In addition, the depth of krill patches may drive foraging habitat selection. At very fine spatial scales, the 30-50 m depth bin stands out as a strong predictor of whale presence (Figure 4, Figure 5). Foraging on near-surface krill may allow a whale to maximize its energetic gain by minimizing the need to dive and use “acrobatic” feeding strategies (Goldbogen et al., 2013). Throughout the period of study, the depth of maximum krill relative abundance was centered around 170 m (Figure 3), which aligns with the findings from previous studies in the region (Brinton, 1962; Phillips et al., 2022). Interestingly, whale presence as predicted by the 100-200 m depth bin exhibits a slight bimodal distribution across all models, likely reflecting the patchy distribution of krill. Humpback whale foraging dives have been recorded deeper than 400 m (Derville et al., 2020), and they may dive more shallowly during the night and based on season

(Nichols et al., 2022). While krill undergo a diel vertical migration that takes them from depth during the day to the surface at night, our observational approach based on visual surveys prevented us from assessing nightime whale distribution when krill is most shallow and accessible. Therefore, the depth-based relationships we identified may vary diurnally.

Overall, these findings echo previous research illustrating the scale dependency of predator-prey spatiotemporal co-occurrence. Model outcomes depend upon the scales at which data are collected and analyzed (Wiens, 1989), highlighting the role of methodology in ecological interpretation. A positive predictive relationship between blue whales and acoustically-detected krill was found in New Zealand at a 4 km scale (Barlow et al., 2020), similar to our study. Findings from both studies contrast with Torres et al. (2008), who found that environmental predictors far outperformed prey metrics derived from net tows when modeling bottlenose dolphin distributions in Florida. Though these studies focused on different ecosystems and species, part of this discrepancy is likely driven by the difference in methods for quantifying prey: discrete net tows versus continuous hydroacoustic surveys that are more spatially comprehensive and enable essentially *in situ* observation of the prey field in the vicinity of predators. Moreover, while several tracking studies at the scale of discrete prey patches have shown strong relationships with pinnipeds, seabirds, and rorqual whales (e.g. Benoit-Bird et al., 2013; Kirchner et al., 2018; Cade et al., 2022), it is difficult to describe such fine-scale relationships based on visual survey data, which constitute a snapshot of predator distributions. The marginal deviance explained values characterizing our models are in line with other studies that use a visual detection approach (e.g. Lambert et al., 2019; Receveur et al., 2022; Szesciorka et al., 2023). Despite the lack of behavioural resolution in our data compared to that obtained by satellite tracking (e.g., travel versus foraging states), our approach revealed relevant scales of predator-prey relationships.

Prey quality is also crucial to energetic gain, and humpback whales may target larger and reproductive krill with higher energetic value, if available (Cade et al., 2022). For the purposes of this study, all krill were considered of equal quality, and we applied NASC as a proxy for krill relative abundance as the sole krill metric. However, krill quality, aggregation structures, and biomass density have been shown to shape whale foraging behaviors and patch selection (Cade et al., 2021; Miller et al., 2019). Differences between the nutritional value of krill species and developmental stages can have significant consequences for the foraging success and distributions of humpback whales, which may preferentially target the larger, more lipid-rich *T. spinifera* krill, like other whale species (Fiedler et al., 1998). Krill nutritional quality, swarm structure, and the impact of changing ocean conditions on these foraging characteristics warrant further investigation. In addition to humpback whales, blue (*Balaenoptera musculus*) and fin (*Balaenoptera physalus*) whales also forage on krill in the region (Fiedler et al., 1998). While our sample size of blue and fin whales was too small to perform the same hierarchical scale analysis for these species individually, analysis of all rorquals at the 5 km scale echoed the relationships seen for humpback whales (see Supplementary Material), and future work could determine whether these species show similar spatial relationships. Fin and blue whales are larger, and increased body size both facilitates and requires increased prey capture (Goldbogen et al., 2019). Thus, blue and fin whales foraging in the NCC may require larger-scale prey patches than humpbacks, and higher prey densities within them to meet their energetic needs.

These findings are salient to ecological relationships in the NCC ecosystem, and to management efforts across the CCLME. Just as prey distributions are dynamic, so are the responses of their predators and the needs of adaptive ecosystem management. Increased awareness of humpback-krill relationships can support tools and resources that benefit marine resource management (Rockwood et al., 2020; Santora et al., 2020). Incorporating prey data may improve modeling efforts and predictions of how these animals and ecosystems will respond to ongoing and future ocean changes (Derville et al., 2022). As the 5 km model yielded the strongest relationship between humpback whales and krill relative abundance, we recommend that prey data at that scale be incorporated into future models and considered for management applications in the NCC, such as entanglement mitigation efforts and fisheries planning. Considering relationships at this scale can allow us as ecosystem observers to find a compromise on the problem of scale, bridging the distance between what the whale experiences in the environment and what we can accurately describe and manage.

***Supplementary Material***

A table and figure describing the supplementary models are available at *ICESJMS* online.

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***Author Contributions***

LT, KB, and SD acquired funding, conceived, and designed the project; EP provided guidance and oversight on acoustic analysis protocols; SD provided guidance on data analysis and visualization; RK collected and processed the data, developed acoustic analysis protocols, conducted data analysis, and wrote the manuscript; all authors critically reviewed the manuscript. All authors contributed to the article and approved the submitted version.

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## *Figures and Tables*

***Table 1.*** *Concurrent active acoustics and whale observation data collection (km and days) per cruise, and all rorqual whale and humpback whale groups observed and included in models.*

| Year | Season | Effort (km) | Effort (days) | Humpback whale groups used in this study (Model 1-4 / 5) | All rorqual whale groups / average group size used in rorqual-krill models (see Supplementary Material) |
|---|---|---|---|---|---|
| 2018 | Summer | 3,516.9 | 9 | 6 / 10 | 21 / 1.9 |
| | Fall | 2,561.2 | 9 | 1 / 3 | 9 / 1.1 |
| 2019 | Summer | 3,015.0 | 10 | 0 | 0 |
| | Fall | 1,952.5 | 9 | 3 / 9 | 22 / 2.4 |
| 2020 | Fall | 3,030.3 | 11 | 8 / 34 | 73 / 1.2 |
| 2021 | Summer | 257.6 | 10 | 0 | 5 / 1.7 |
| 2022 | Summer | 3,562.1 | 12 | 18 / 47 | 102 / 1.2 |
| | Fall | 1,392.4 | 5 | 1 / 2 | 3 / 1 |

***Table 2.*** *Summary of humpback whale-krill association models at each spatial scale (buffer radius). For each model, we report: conditional and marginal deviance explained, the number of humpback whale groups included ($N_{wh}$), and the absence, presence, and total number of data points in each model (N). For each smooth term (e.g., NASC 30-50 m, NASC 50-100 m, etc.) and the random effect (survey), we report: estimated degrees of freedom (edf) and F-statistics. All approximate significance of smooth terms showed p-values <0.0001.*

| **Scale** | **Model** | **Buffer radius** | **$N_{wh}$** | **N *(absence, presence)*** | **Conditional deviance explained** | **Marginal deviance explained** | **NASC 30-50 m** | **NASC 50-100 m** | **NASC 100-200 m** | **NASC 200-300 m** | **Survey (re)** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Very fine | 1 | 1 km | 29 | 604849 *(594477, 10372)* | 14.1% | 1.34% | edf = 2.264, F = 236 | edf = 1.002, F = 265 | edf = 3.918, F = 782 | edf = 2.652, F = 330 | edf = 6.711, F = 1573 |
| Very fine | 2 | 2 km | 29 | 593845 *(569424, 24421)* | 18.7% | 2.22% | edf = 2.787, F = 2625 | edf = 1.230, F = 2767 | edf = 3.955, F = 4225 | edf = 3.686, F = 1649 | edf = 6.743, F = 3501 |
| Fine | 3 | 5 km | 29 | 565945 *(508332, 57613)* | 25.2% | 3.82% | edf = 2.894, F = 3077 | edf = 2.948, F = 3007 | edf = 3.891, F = 8926 | edf = 3.708, F = 6964 | edf = 6.769, F = 7541 |
| Meso | 4 | 20 km | 29 | 580710 *(386409, 194301)* | 36.0% | 2.50% | edf = 2.961, F = 2399 | edf = 2.980, F = 2350 | edf = 2.995, F = 3606 | edf = 2.983, F = 20990 | edf = 6.790, F = 20986 |
| Fine (final model) | 5 | 5 km | 79 | 649376 *(508332, 141044)* | 26.7% | 3.36% | edf = 3.908, F = 2838 | edf = 3.577, F = 2761 | edf = 3.882, F = 9401 | edf = 3.680, F = 9063 | edf = 6.787, F = 14624 |

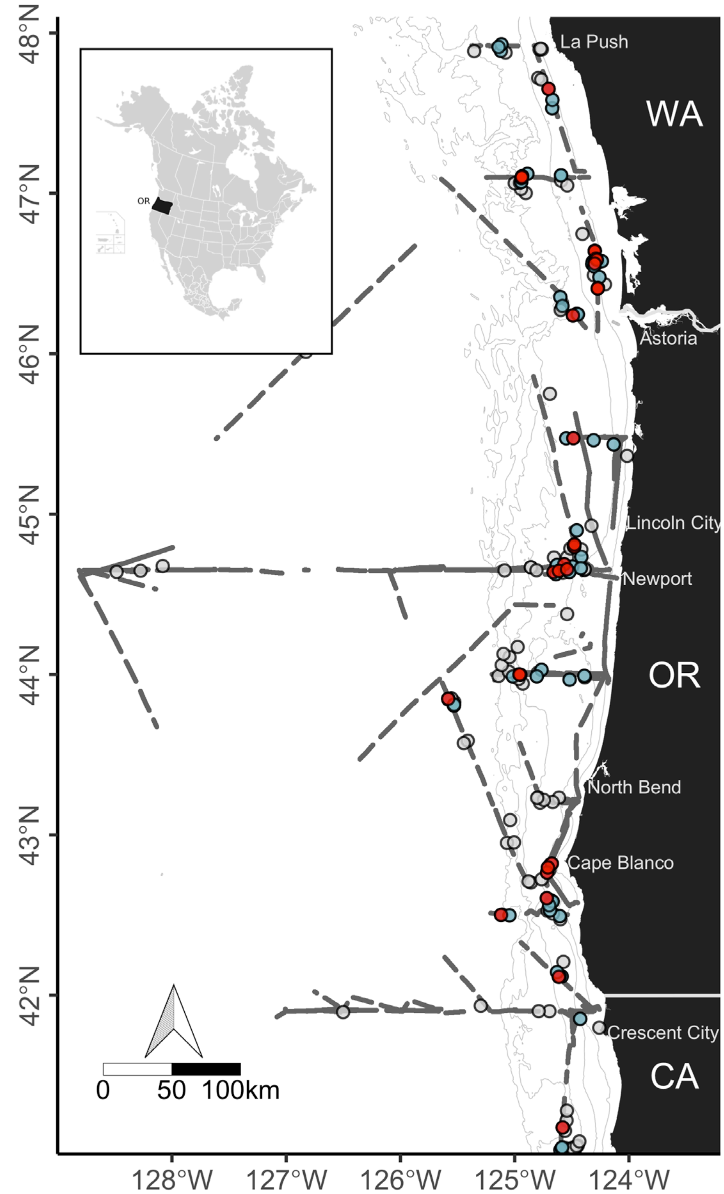


***Figure 1.*** *Concurrent echosounder data and whale surveys in the NCC region off the northern California, Oregon, and Washington coasts (U.S. west coast; gray lines). Humpback whale groups included in models 1-4 are shown as red dots, additional humpback whale groups included in the final model (model 5) are shown as pale blue dots, and other rorqual whale observations are shown as gray dots (see Supplementary Material for results of rorqual-krill models). Land is shown in black and isobaths (50, 100, 500, 1,000 and 1,500 m deep) are represented with light gray line.*

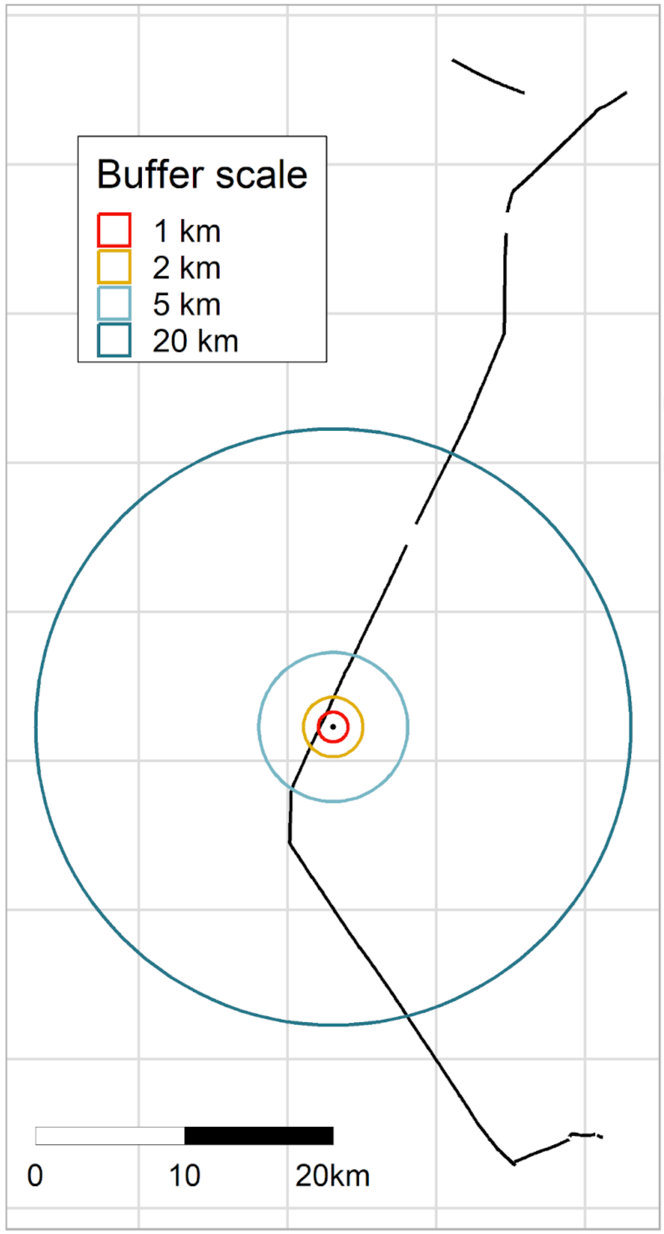


***Figure 2.*** *An example of ship survey effort where concurrent echosounder and whale survey data were collected (black lines), a humpback whale observation (black point) and buffer radii drawn at increasing spatial scales around the whale sighting (circles color coded from 1 km to 20 km).*

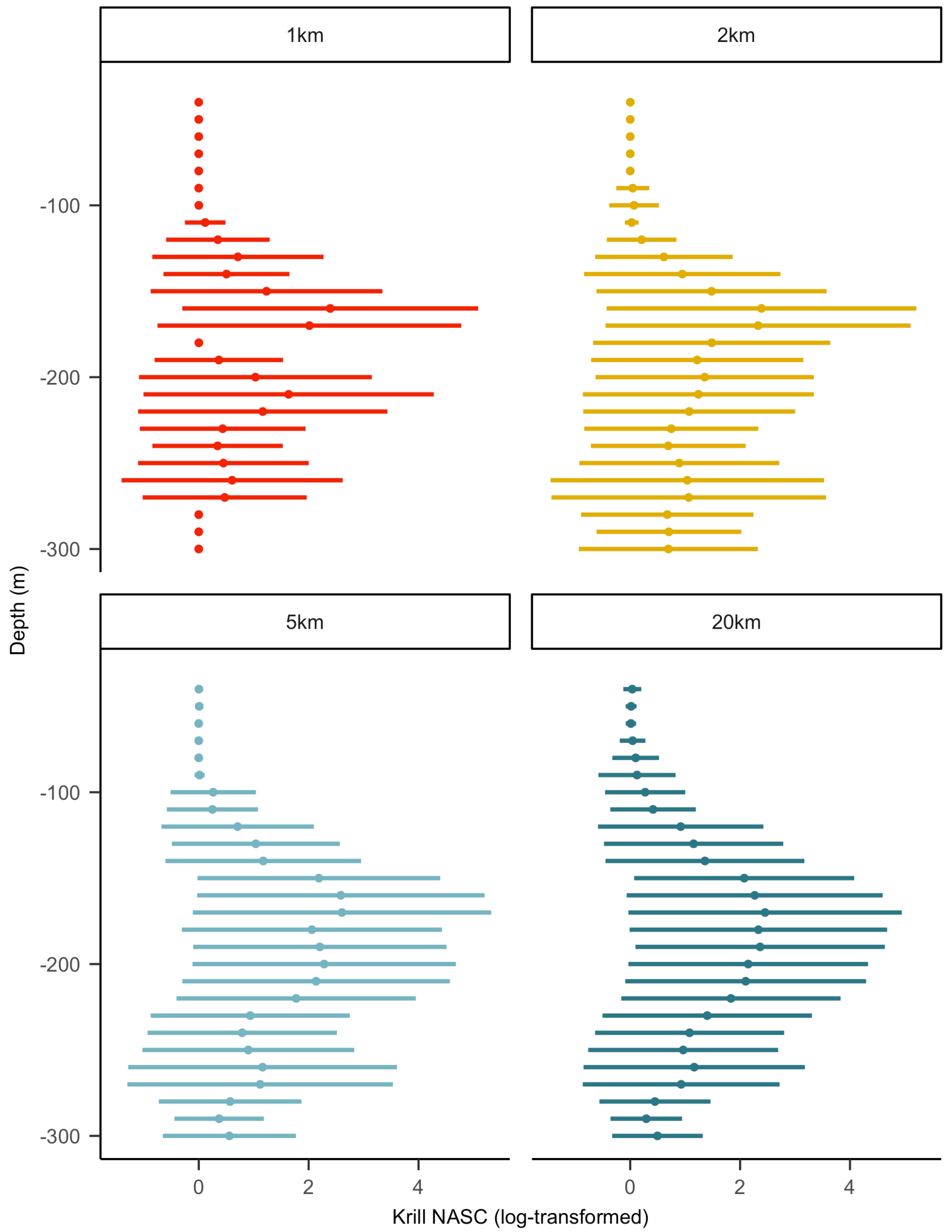


***Figure 3.*** *Average depth distribution of krill relative abundance (NASC) at each buffer radius scale surrounding the sighted humpback whales. Standard deviations are shown as horizontal bars across each point.*

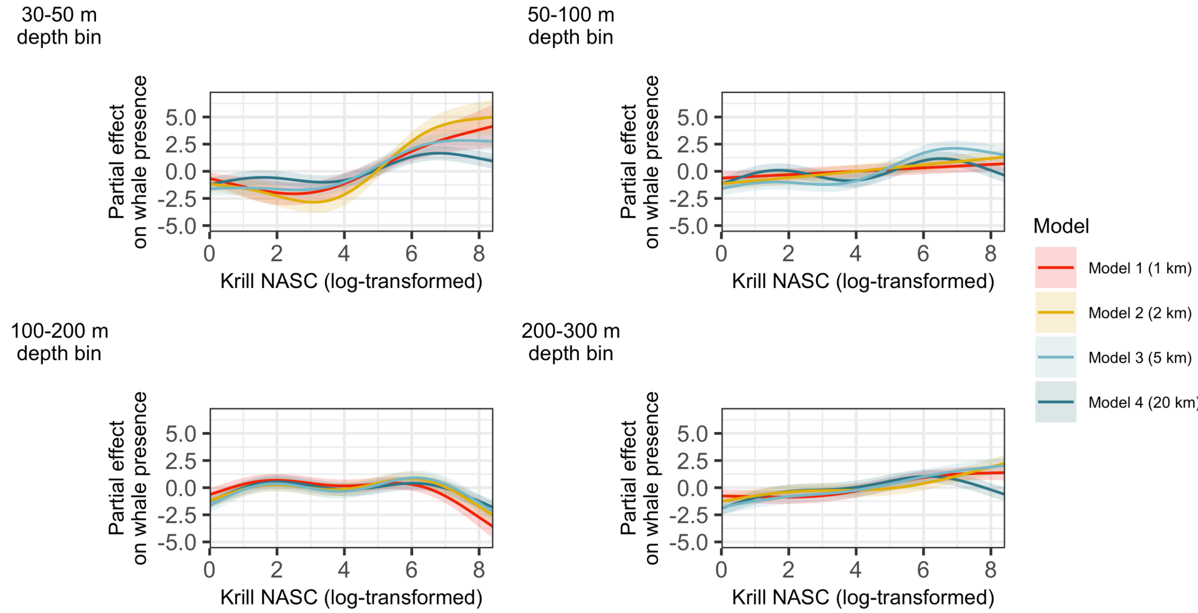


***Figure 4.*** *Humpback whale-krill relationships modeled across multiple depth bins and spatial scales. Response curves represent the effect of the smooth function upon the trend in humpback whale presence, with higher values indicating higher predicted probability of occurrence. Shaded ribbons represent the 95% confidence intervals colored per fitted trend. All variables have significant p-values <0.0001.*

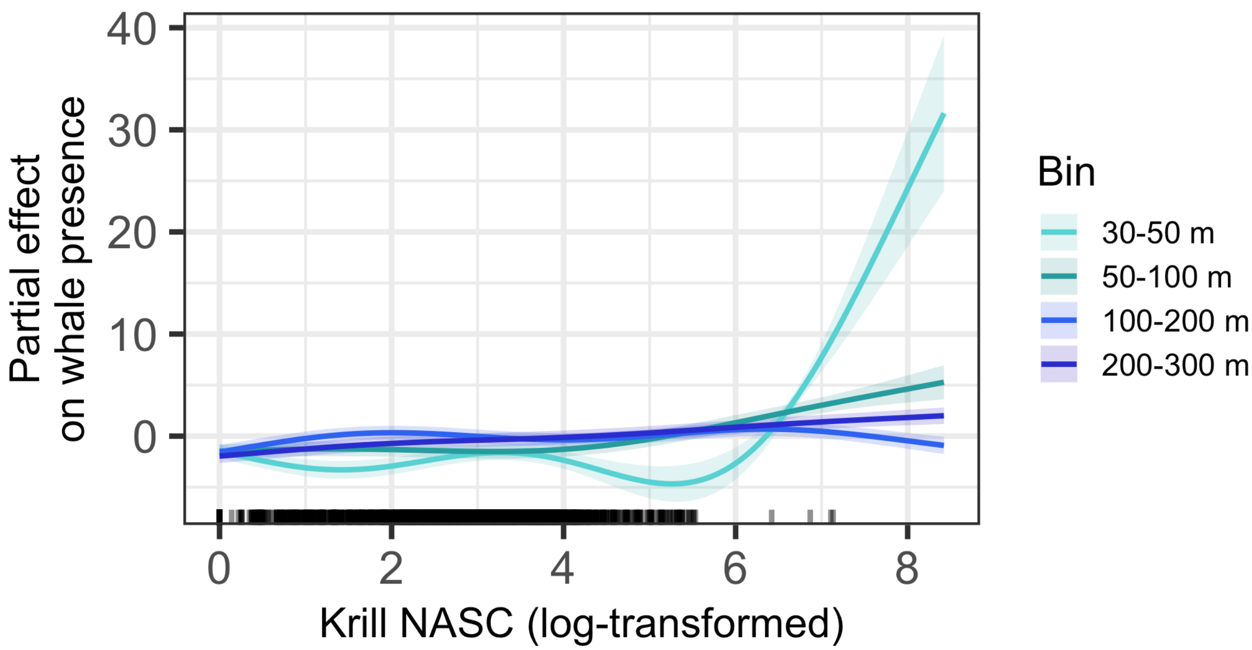


***Figure 5.*** *Humpback whale-krill relationships modeled across depth bins at the 5 km scale in model 5. Response curves represent the effect of the smooth function upon the trend in humpback whale presence, with higher values indicating higher predicted probability of occurrence. Shaded ribbons represent the 95% confidence intervals colored per fitted trend. All variables have significant p-values <0.0001. The rug plot along the x-axis represents the distribution of the krill NASC data across all depth bins.*

***Supplementary Material***

***Table S1.*** *Summary of rorqual whale-krill association models at each spatial scale (buffer radius). For each model, we report: conditional and marginal deviance explained, the number of whale groups included ($N_{wh}$), and the absence, presence, and total number of data points in each model (N). For each smooth term (e.g., NASC 30-50 m, NASC 50-100 m, etc.), and the random effect (survey), we report: estimated degrees of freedom (edf) and F-statistics. All approximate significance of smooth terms showed p-values <0.0001.*

| **Scale** | **Model** | **Buffer radius** | $N_{WH}$ | **N *(absence, presence)*** | **Conditional deviance explained** | **Marginal deviance explained** | **NASC 30-50 m** | **NASC 50-100 m** | **NASC 100-200 m** | **NASC 200-300 m** | **Survey (re)** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Very fine | S1 | 1 km | 46 | 609261 *(594477, 14784)* | 15.6% | 1.05% | edf= 2.277, F = 232 | edf = 1.851, F = 343 | edf = 3.909, F = 568.3 | edf = 3.137, F = 277 | edf = 6.884, F = 1951 |
| Very fine | S2 | 2 km | 80 | 620041 *(569424, 50617)* | 21.2% | 1.80% | edf = 2.872, F = 5118 | edf = 1.967, F = 7943 | edf = 2.998, F = 5284 | edf = 3.914, F = 5304 | edf = 6.903, F = 6972 |
| Fine | S3 | 5 km | 134 | 723978 *(508332, 215646)* | 27.9% | 2.59% | edf= 3.923, F = 3414 | edf = 2.975, F = 5323 | edf = 3.612, F = 12799 | edf = 3.541, F = 14544 | edf = 6.917, F = 18117 |
| Meso | S4 | 20 km | 178 | 1302550 *(386409, 916141)* | 33.9% | 1.60% | edf = 3.829, F = 1897 | edf= 3.944, F = 21315 | edf = 2.997, F = 2462 | edf = 2.985, F = 18754 | edf = 6.927, F = 47413 |

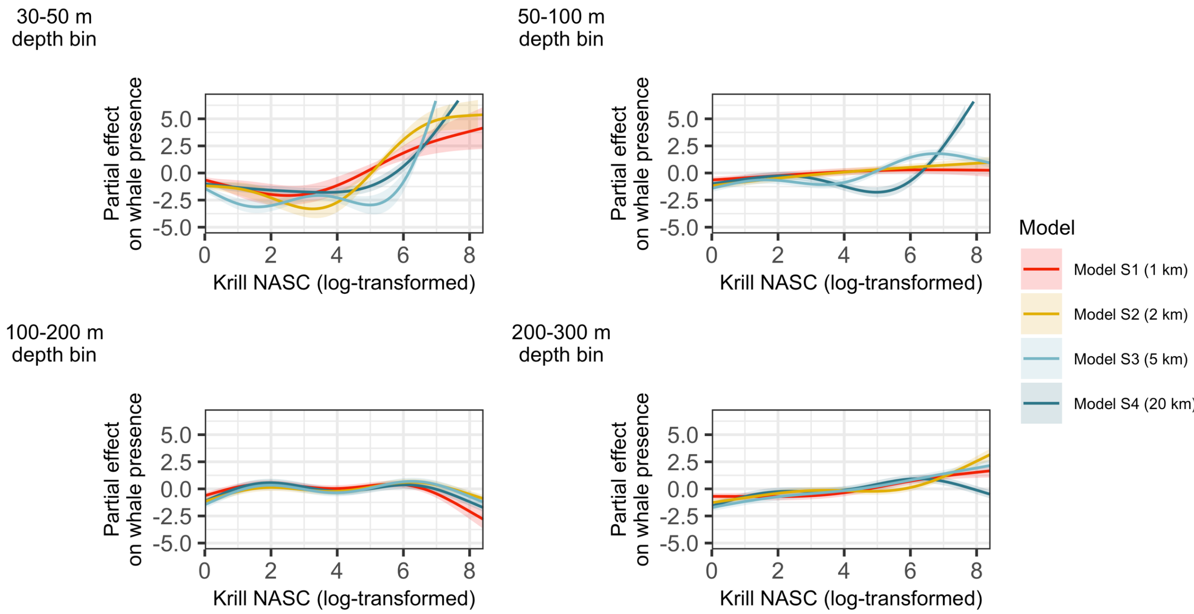


***Figure S1.*** *All rorqual whale-krill relationships modeled across multiple depth bins and spatial scales. Response curves represent the effect of the smooth function upon the trend in rorqual whale presence, with higher values indicating higher predicted probability of occurrence. Shaded ribbons represent the 95% confidence intervals colored per fitted trend. All variables have significant p-values <0.0001.*