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Incorporating prey fields into North Atlantic right whale density surface models

Camille H. Ross[1,2,3,*], Jason J. Roberts[4], Daniel E. Pendleton[5], Damian C. Brady[2], Karen Stamieszkin[1], Nicholas R. Record[1]

[1]Tandy Center for Ocean Forecasting, Bigelow Laboratory for Ocean Sciences, East Boothbay, ME 04544 USA
[2]Darling Marine Center, School of Marine Sciences, University of Maine, Walpole, ME 04573, USA
[3]Anderson Cabot Center for Ocean Life, New England Aquarium, Boston, MA 02110, USA
[4]Marine Geospatial Ecology Lab, Duke University, Durham, NC 27708, USA
[5]Northeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Woods Hole, MA 02543, USA

ABSTRACT: Predictions of North Atlantic right whale *Eubalaena glacialis* distributions are an increasingly important tool used in conservation efforts for this Critically Endangered species. Right whales feed upon calanoid copepods, primarily *Calanus finmarchicus*. Incorporating prey distributions and characteristics into right whale density surface models (DSMs) has the potential to improve predicted whale distribution and provide a more mechanistic basis for interpretation. To explore this possibility, we tested different prey and prey proxy covariates to represent prey within a right whale DSM. We then assessed the relationship fitted to each prey or prey proxy covariate and determined which covariates added the most predictive power. The top-performing model included a combination of covariates representing high-density *C. finmarchicus*, *Centropages typicus*, and *Pseudocalanus* spp. aggregations and resulted in density predictions consistent with the observed distribution patterns of right whales. Predicted density was most prominent in the deep basins of the Gulf of Maine and the Great South Channel. Density generally increased in the summer and decreased in the winter, consistent with the current understanding of right whale foraging phenology. Continued monitoring of prey resources and development of prey fields for use in models are imperative to successful conservation of endangered marine predators.

KEY WORDS: North Atlantic right whale · *Eubalaena glacialis* · *Calanus finmarchicus* · Density surface model · Endangered species · Prey

1. INTRODUCTION

The North Atlantic right whale *Eubalaena glacialis*, a large baleen whale species, is listed as Critically Endangered on the IUCN Red List (Cooke 2020), with an estimated 372 (+11/−12) individuals remaining as of 2023 (Linden 2024). Key right whale foraging and calving grounds overlap with regions of high anthropogenic activity — including fishing and shipping — stunting post-whaling recovery. Entanglement in trap-pot fishing gear is the leading cause of death for right whales, followed closely by vessel strikes (Henry et al. 2023). Right whales primarily consume the lipid-rich late-stages of the calanoid copepod *Calanus finmarchicus*, and secondarily smaller copepods including *Centropages typicus* and *Pseudocalanus* spp. (Watkins & Schevill 1976, Kenney et al. 1986, Wishner et al. 1988, 1995, Murison & Gaskin 1989, Mayo & Marx 1990, Baumgartner et al. 2003). *C. finmarchicus* are available throughout the northern portion of known right whale habitat in the USA (Fig. 1). *C. typicus* and *Pseudocalanus* spp. are important secondary prey resources, particularly in Cape Cod Bay in the winter and spring (Hudak et al. 2023).

*Corresponding author: cross@neaq.org

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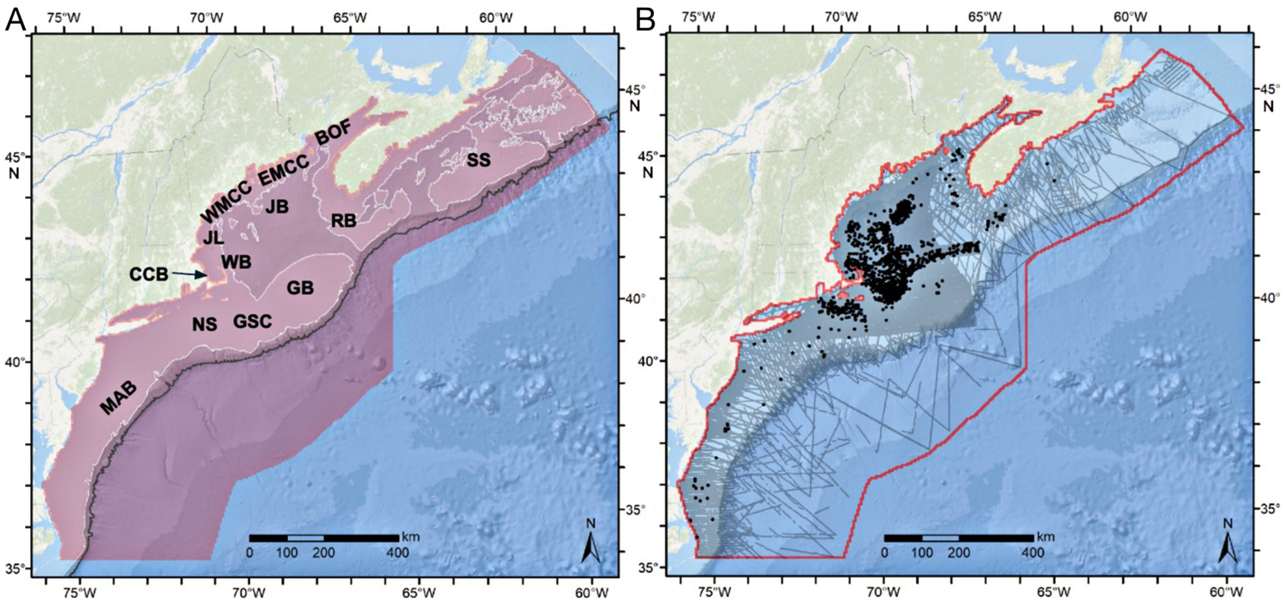


Fig. 1. Map of the study area extending from Cape Hatteras, NC, USA, northward to the Laurentian Channel, Canada, with (A) 125 and 1500 m isobaths and important regions labeled and (B) North Atlantic right whale sightings (black dots) and survey segments from 2003 through 2017 produced by Roberts et al. (2020). MAB: Mid-Atlantic Bight; NS: Nantucket Shoals; GSC: Great South Channel; GB: Georges Bank; CCB: Cape Cod Bay; WB: Wilkinson Basin; JL: Jeffreys Ledge; JB: Jordan Basin; WMCC: Western Maine Coastal Current; EMCC: Eastern Maine Coastal Current; BOF: Bay of Fundy; RB: Roseway Basin; SS: Scotian Shelf

Right whales have been monitored through extensive aerial and shipboard visual surveys in US waters for decades and since the mid-2010s in Canadian waters (CETAP 1982, Cole et al. 2007, Lawson & Gosselin 2009, Khan et al. 2018, DFO 2020, Crowe et al. 2021, St. Pierre et al. 2024). However, survey effort is inherently patchy, with large gaps in spatial and temporal coverage. Whale detection probability varies by survey platform, protocol, ocean conditions, and whale behaviors. Due to these limitations, species distribution models are one of several important tools available for effective management of right whales and other threatened and endangered species (e.g. Pendleton 2010, Gilles et al. 2011, Becker et al. 2012, 2016, Forney et al. 2012, Goetz et al. 2012, Keller et al. 2012, Pendleton et al. 2012, 2020, Hammond et al. 2013, Redfern et al. 2013, Roberts et al. 2024). These techniques are particularly useful for informing the management of cryptic species with low population numbers, such as right whales. The US and Canadian governments are continuing to work together towards conservation solutions, including producing realistic, informative species distribution models.

Temporally dynamic species distribution models are now ubiquitous, and there is a large range of environmental data products available from which to produce environmental variables for modeling. Despite these advances, direct biological drivers of whale distributions, such as prey abundance, are not commonly available covariates. This is for a multitude of reasons, including sampling limitations. Proxies for phytoplankton biomass, including satellite-derived chlorophyll *a*, have been used in numerous studies to represent marine mammal prey (e.g. Forney et al. 2012, Pendleton et al. 2012, 2022, Becker et al. 2016, Roberts et al. 2016, 2024, Ross et al. 2021). Right whales target only a few key zooplankton species due to baleen morphology (Mayo et al. 2001, Lehoux et al. 2020) and energetic requirements (Kenney et al. 1986, Goodyear 1996, Michaud & Taggart 2007, Swaim et al. 2009, Fortune et al. 2013). The trophic ambiguity that emerges when using products such as satellite-derived chlorophyll *a* leads to a loss of valuable information that could otherwise improve model performance and predictive power. In consideration with the assumption that right whale distributions are in part prey-driven (Wishner et al. 1988, Murison & Gaskin 1989, Mayo & Marx 1990, Baumgartner & Mate 2003), replacing prey proxies with direct prey covariates tailored to foraging requirements has great potential to improve model performance. Developing and including these covariates in decision-making tools is an imperative management goal and has been recommended by the NOAA Atlantic Large Whale Take Reduction Team.

Previous *C. finmarchicus* modeling studies provide interesting insight into species distributions and dynamics across varying spatial and temporal scales. *C. finmarchicus* models have been produced using different underlying approaches ranging from statistical modeling methods (e.g. Reygondeau & Beaugrand 2011, Chust et al. 2014, Grieve et al. 2017) to numerical and individual-based modeling methods (e.g. Pershing et al. 2009a, Ji 2011, Ji et al. 2017). Previous studies have also attempted to explicitly represent prey in right whale models. Pershing et al. (2009a) produced a biophysics-driven life-history *C. finmarchicus* model that improved predictions of the arrival of right whales to the Great South Channel region (Pershing et al. 2009b), an area of historical ecological importance to the species. Pendleton et al. (2012) used a similar *C. finmarchicus* model in species distribution models that predicted interannual, weekly right whale habitat in 2 key right whale foraging grounds: Cape Cod Bay and the Great South Channel. Models that included the *C. finmarchicus* covariate performed significantly better than models using only abiotic covariates and helped successfully identify the Nantucket Shoals as suitable right whale feeding habitat before whales were observed in the region (Pendleton et al. 2012). Pendleton (2010) found that incorporating 3 right whale prey taxa — *C. finmarchicus*, *C. typicus*, and *Pseudocalanus* spp. — into a fine-scale model of right whale habitat in Cape Cod Bay improved model performance. These studies demonstrated that modeled prey is an important predictor of right whale habitat use and emphasized the need for improved prey fields for species distribution models of zooplanktivorous whales.

To fill this knowledge gap more broadly, Ross et al. (2023) produced right whale prey fields by modeling the probability of the presence of high-density *C. finmarchicus* aggregations across US right whale foraging grounds (Fig. 1). Specifically, Ross et al. (2023) interpolated *C. finmarchicus* data by computing the probability that abundances will exceed a threshold of 40 000 ind. m^{-2} in each spatial grid cell, as informed by a literature review of right whale foraging requirements. This method resulted in prey fields tailored to right whale feeding requirements, attempting to address the shortcomings of prey proxies. In the present study, we extended the methods of Ross et al. (2023) to produce 2 additional prey fields representing the copepods *C. typicus* and *Pseudocalanus* spp. These taxa are important secondary prey resources for right whales in Cape Cod Bay and surrounding waters in the winter and spring (Watkins & Schevill 1976, Mayo & Marx 1990, Mayo & Goldman 1992, Hudak et al. 2023). The objective of this study was to determine whether the prey fields developed in Ross et al. (2023), when used as covariates in right whale density surface models (DSMs), provide better predictive power than lower trophic level prey proxies such as chlorophyll concentration or the rate of primary productivity. To test this, we fitted and evaluated a series of simplified DSMs using the training data from Version 9 of the 'North Atlantic right whale density model' (Roberts et al. 2020), which is used to develop management measures to reduce fishing gear entanglements (NMFS 2021) and vessel strikes (Garrison et al. 2022). We tested a suite of prey and prey proxy covariates, assessing the resulting changes in model performance relative to a baseline model that lacked them and qualitatively describing the spatial and temporal differences in density predictions. Improving model performance and predictive power provides decision-makers and stakeholders with the best possible information, with the potential to improve conservation outcomes.

2. MATERIALS AND METHODS

2.1. Study area

The study area extended from 35.01° N to 46.36° N and from −57.16° E to −76.02° E, covering right whale foraging habitat north of Cape Hatteras, NC, USA, northward to the Laurentian Channel, Canada (Fig. 1). This includes the northern portion of US right whale management areas, excluding calving grounds in the southeast. We highlight important right whale habitats and oceanographic features of key regions relevant to copepod phenology, including the Nantucket Shoals, Great South Channel, Georges Bank, Wilkinson Basin, Jeffreys Ledge, Jordan Basin, Western Maine Coastal Current, Eastern Maine Coastal Current, Bay of Fundy, Roseway Basin, and the Scotian Shelf (Fig. 1A).

2.2. Right whale data

The right whale survey data consisted of 187 146 segments (mean length = 4.99 km, SD = 0.30 km, sum = 934 346 km; Fig. 1B) from visual aerial and shipboard line-transect cetacean surveys conducted between Cape Hatteras and the Laurentian Channel by 7 institutions between 2003 and 2017 (see Table 1 in Roberts et al. 2020, exclusive of FWRI, HDR, and WLT/SSA/CMARI). Collectively, these surveys re-

Table 1. Descriptions, units, resolutions, and sources for the model covariates

Covariate	Description	Type	Unit	Source
Depth	Depth of the seafloor derived from the SRTM30_PLUS bathymetry	Abiotic	m	Becker et al. (2009)
Sea surface temperature (SST)	Mean monthly L4 SST from multiple satellites, from the GHRSST Level 4 MUR Global Foundation Sea Surface Temperature Analysis (v4.1)	Abiotic	°C	Chin et al. (2017)
Calanus finmarchicus prey patch	Probability of *C. finmarchicus* patch exceeding 40 000 individuals m^{-2}	Prey	Unitless probability	Ross et al. (2023)
Centropages typicus prey patch	Probability of *C. typicus* patch exceeding 57 000 individuals m^{-2}	Prey	Unitless probability	Extended Ross et al. (2023) methods; Fig. S1A
Pseudocalanus spp. prey patch	Probability of *Pseudocalanus* spp. patch exceeding 28 000 individuals m^{-2}	Prey	Unitless probability	Extended Ross et al. (2023) methods; Fig. S1B
ZOO_SEAPODYM	Generalized zooplankton biomass model	Prey	g C m^{-2}	Senina et al. (2008), Lehodey et al. (2008, 2010, 2015)
GlobColour_Chl	Mean monthly L4 multi-satellite chlorophyll-a concentration from the Copernicus-GlobColour processor	Prey proxy	mg m^{-3}	https://resources.marine.copernicus.eu/?option=com_csw&task=results?option=com_csw&view=details&product_id=OCEANCOLOUR_GLO_CHL_L4_REP_OBSERVATIONS_009_082
CAFE	Carbon, Absorption, and Fluorescence Euphotic-resolving net primary productivity model	Prey proxy	mg C m^{-2} d^{-1}	Silsbe et al. (2016); model output produced and maintained by Oregon State University
CbPM	Carbon-based Productivity Model	Prey proxy	mg C m^{-2} d^{-1}	Westberry et al. (2008); model output produced and maintained by Oregon State University
EVGPM	'Eppley' Vertically Generalized Production Model	Prey proxy	mg C m^{-2} d^{-1}	Eppley (1972), Morel (1991); model output produced and maintained by Oregon State University
VGPM	Vertically Generalized Production Model	Prey proxy	mg C m^{-2} d^{-1}	Behrenfeld & Falkowski (1997); model output produced and maintained by Oregon State University

ported right whale sightings on 1323 of the segments, comprising 1563 right whale groups totaling 5196 individual whales (Fig. 1B). We focused on this region because it represented plausible right whale feeding habitat. Although survey data south of Cape Hatteras were available, we excluded that region under the assumption that whales there were likely to be fasting and focused on reproduction. Sightings in Cape Cod Bay were included in the model, but this region was not part of the interpretation due to the small spatial area and unique features of this habitat. Future efforts should focus on resolving this region independently.

2.3. Model covariates

2.3.1. Abiotic covariates

We used bathymetry and sea surface temperature (SST) in all DSMs. Bathymetry was derived from the SRTM30_PLUS bathymetry product (Becker et al. 2009). SST was derived at a mean monthly scale from the GHRSST Level 4 MUR Global Foundation Sea Surface Temperature Analysis satellite product (v4.1; Chin et al. 2017; Table 1). Bathymetry and SST were obtained on a 5 × 5 km grid at monthly temporal resolution.

2.3.2. Prey covariates

The prey covariate representing *Calanus finmarchicus* was produced using the modeling approach described in Ross et al. (2023) with a right whale prey aggregation threshold of 40 000 ind. m^{-2}. We extended the methods of Ross et al. (2023) to produce prey covariates representing 2 smaller copepod taxa — *Centropages typicus* and *Pseudocalanus* spp. — using random forests (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n058p067_supp.pdf). Ross et al. (2023) established that a random forest algorithm resulted in the highest model performance in comparison to the other algorithms tested (i.e. boosted regression trees and generalized additive models [GAMs]). Oblique tow data for *C. finmarchicus*, *C. typicus*, and *Pseudocalanus* spp. were obtained from the Ecosystem Monitoring Program (EcoMon) for 2003 through 2017 (NEFSC 2019). Samples were collected using a 333-µm mesh bongo net and a randomly stratified survey design. Due to data limitations and insufficient knowledge of potential right whale feeding thresholds when foraging on secondary prey taxa, we implemented a sensitivity analysis testing different percentiles of the sampled abundances in the EcoMon data: the 75th, 85th, 90th, and 95th percentiles were rounded to the nearest 1000 ind. m^{-2} to avoid high precision in the thresholds. We used the same covariates as the *C. finmarchicus* prey patch model: wind, time-integrated chlorophyll *a* (log transformed), SST, SST gradient, day of year, current velocity gradient, bathymetry (log transformed), bathymetric slope, bottom salinity, and bottom temperature (see Table 1 in Ross et al. 2023). We recognize that the true right whale feeding threshold for these smaller species could be higher due to their smaller size and reduced individual caloric value relative to *C. finmarchicus*, or lower due to potential selective feeding dynamics when more than one prey species is present. Additionally, the feeding thresholds for all 3 copepod species are likely dynamic and contingent upon factors including season and right whale demographics, which were not explicitly captured in the present methodology.

We also tested a generalized zooplankton biomass covariate derived from the Spatial Ecosystem and Populations Dynamics Model (SEAPODYM; Lehodey et al. 2010, 2015) as an additional prey covariate. SEAPODYM accounts for biophysical interactions between lower trophic level populations and the pelagic ocean ecosystem, simulating the distributions from the surface to the bottom or roughly 1000 m of zooplankton and 6 functional micronekton groups. A general schematic of SEAPODYM's modeling framework, including optimization approaches, can be found in Senina et al. (2008). This generalized covariate captures the broader zooplankton community rather than the species that right whales are targeting. Thus, it represents a more indirect prey covariate in comparison to the tailored *C. finmarchicus*, *C. typicus*, and *Pseudocalanus* spp. covariates. We tested SEAPODYM as a readily available alternative to tailored prey fields that, while more general, might serve as a more effective proxy for right whale prey than those related to primary productivity discussed below.

2.3.3. Prey proxy covariates

We tested 5 prey proxies (Table 1) associated with primary productivity. L4 multi-satellite mean monthly chlorophyll *a* concentrations were obtained from the Copernicus-GlobColour processor. Net primary productivity (NPP) models were obtained from Oregon State University (for additional details, see http://orca.science.oregonstate.edu/index.php). These models relied upon the same general underlying calculations and represent primary productivity rates (mg C m^{-2} d^{-1}). We tested 4 NPP models: the vertically generalized production model (VGPM; Behrenfeld & Falkowski 1997); the Eppley vertically generalized production model (EVGPM; Eppley 1972, Morel 1991); the carbon, absorption, and fluorescence euphotic resolving model (CAFE; Silsbe et al. 2016); and the carbon-based productivity model (CbPM; Behrenfeld et al. 2005, Westberry et al. 2008).

2.4. Density surface models

We modeled right whale density (individuals 25 km^{-2}) using the 2-stage DSM approach described in Roberts et al. (2016, 2020) (see Miller et al. 2013 for the overall method). The first DSM stage developed detection functions to estimate the detectability of right whales based on distance from the survey transect line and additional covariates (see Buckland et al. 2001). Because detectability modeling was not the focus of this analysis, we used the detection function developed by Roberts et al. (2020).

The focus of this study was the second DSM stage, which utilized log-link GAMs (Hastie & Tibshirani 1990) to estimate right whale density using a range of covariate combinations. We followed the methods described in Roberts et al. (2016, 2020), mimicking the right whale DSM that currently informs decision-making in the USA. GAMs were fitted using the *mgcv* package (version 1.9-0; Wood 2011, 2017) in R 4.3.2 (R Core Team 2023) using the restricted maximum likelihood (REML) smoothness selection method (Wood 2011) and the Tweedie distribution to account for zero-inflation and overdispersion (Wood et al. 2016, Roberts et al. 2020). Smooth functions were constructed for each covariate using the *mgcv* default set of thin spline basis functions with shrinkage (i.e. bs = 'ts'; Wood 2003). The response variable was right whale abundance per segment, corrected by the detectability model, with the natural log of the segment area surveyed as an offset.

To test the relative influence of prey covariates versus prey proxies, we first produced a baseline DSM using all training data with bathymetry and SST as smooth terms. The bathymetry covariate was included to correct for unrealistic extrapolation off the continental shelf (i.e. >1500 m), where prey may be present but is theoretically too deep to be accessible by right whales. The SST covariate was included to help constrain the model to the preferred thermal envelope of right whales. Then, after fitting this baseline DSM, we added each of the 9 prey and prey proxy covariates in turn to assess their relative influences. We also built a combined model that included all 3 prey covariates, yielding a total of 11 candidate models (Table 2). Model formulas are presented in Table 2; hereafter, models will be referred to by the naming scheme defined in the 'Model name' column. As our study sought to assess whether we can directly represent feeding habitat with prey fields, we excluded the other covariates used in Roberts et al. (2020) under the assumption that these represented proxies for feeding habitat.

All covariates were obtained at a monthly temporal resolution. We predicted DSMs across the corresponding time series of monthly covariate surfaces from 2003 to 2017. Predicted right whale density surfaces were averaged across years into monthly climatologies for ease of interpretation.

2.5. Model assessment

Models were evaluated and compared using 3 independent goodness-of-fit statistics: deviance explained (%), Akaike's information criterion (AIC; Akaike 1974), and REML score. We computed the variance-to-mean ratio (VMR) of the fitted models to assess the degree to which spatial clustering in model outputs impacted the ability of the model to predict right whale distributions. We examined concurvity between the covariates of each model to confirm independence between covariates and the resulting smooth functions. To qualitatively explore how including prey covariates influenced spatiotemporal patterns in right whale density predictions in critical habitats (Fig. 1), we subtracted the *m_base* model predictions from each of the other models' predictions. Because the focus of the present study is the influence of prey covariates specifically, we present these density anomaly maps for the *m_cfin*, *m_ctyp*, *m_pcal*, and *m_combined* models. To isolate the combined effect of *C. typicus* and *Pseudocalanus* spp. on density predictions, we also subtracted *m_cfin* from *m_combined*.

3. RESULTS

We tested 4 potential thresholds for each of the secondary prey taxa. Higher thresholds resulted in higher right whale model performance and those modeled relationships exhibited similar patterns across thresholds. Based on these results, we selected the 95th percentile for both species as the thresholds to inform right whale density surface models (*Centropages typicus* threshold = 57 000 ind. m^{-2}, *Pseudocalanus* spp. threshold = 28 000 ind. m^{-2}).

Table 2. Model names, smooth terms, and performance metrics: deviance explained (%), Akaike's information criterion (AIC), restricted maximum likelihood (REML) score, root mean squared error (RMSE), and mean absolute error (MAE). Models are sorted by deviance explained and AIC. AIC and REML score are reported relative to the base model; a lower AIC or REML score indicates better model performance

Model name	Smooth terms	Deviance explained (%)	AIC	REML	RMSE	MAE
m_combined	$\log_{10}$(Depth) + SST + *Calanus finmarchicus* + *Centropages typicus* + *Pseudocalanus* spp.	18.08	−405.0	−184.6	1.396	1.387
m_cfin	$\log_{10}$(Depth) + SST + *Calanus finmarchicus*	16.80	−311.4	−150.3	1.402	1.393
m_pcal	$\log_{10}$(Depth) + SST + *Pseudocalanus* spp.	15.97	−237.6	−108.4	1.402	1.392
m_seapodym	$\log_{10}$(Depth) + SST + SEAPODYM	15.75	−219.8	−100.8	1.403	1.394
m_evgpm	$\log_{10}$(Depth) + SST + EVGPM	14.87	−145.6	−32.84	1.405	1.395
m_vgpm	$\log_{10}$(Depth) + SST + VGPM	14.87	−143.6	−61.32	1.407	1.398
m_cbpm	$\log_{10}$(Depth) + SST + CbPM	14.63	−134.4	−79.25	1.406	1.397
m_ctyp	$\log_{10}$(Depth) + SST + *Centropages typicus*	14.66	−125.9	−49.48	1.406	1.397
m_cafe	$\log_{10}$(Depth) + SST + CAFE	14.37	−111.5	−53.29	1.409	1.400
m_chl	$\log_{10}$(Depth) + SST + $\log_{10}$(Chlorophyll)	13.49	−32.22	−6.243	1.411	1.402
m_base	$\log_{10}$(Depth) + SST	12.95	0	0	1.413	1.404

Considering AIC relative to *m_base* (AIC = 0), *m_combined* was the highest performing model (AIC = −405.0; Table 2). The second highest performing model was *m_cfin* (AIC = −311.4; Table 2). The third highest performing model was *m_pcal* (AIC = −237.6), followed by *m_seapodym*. *M_ctyp* had the fourth lowest performance, ranking higher than only *m_cafe*, *m_chl*, and *m_base* (AIC = −125.9; Table 2). All DSMs that included a prey or prey proxy covariate performed better than *m_base*.

We calculated the VMR to measure the variability of the fitted model values relative to the mean. We used VMR to determine whether model performance as measured by deviance explained and AIC was improved by increasing the spatial variability of the model output (Fig. 2). The benefit of this approach was that we could diagnose at least one of the factors that leads to model improvement from the inclusion of prey fields.

The partial effects analysis showed similar responses to bathymetry and SST across models (Figs. 3 & 4, Figs. S2 & S3 in the Supplement). For interpretation, the *x*-axis represents the range of a given covariate, and the *y*-axis represents the log-scale partial effect of that covariate on estimated right whale density; the number included in the smooth function on the *y*-axis label is estimated degrees of freedom, which indicates the complexity of the spline. The bathymetry covariate functioned to filter out waters where prey may be present but at depths unreachable by right whales. The SST covariate helped represent the thermal envelope of right whales, exhibiting a strong negative relationship with whale density (i.e. *y*-axis), reflecting the species' preference for colder waters. The *Calanus finmarchicus* prey patch covariate partial effect in *m_cfin* showed a positive relationship between the probability of the presence of a prey patch and whale density, with a strong increase between patch probabilities of 0.2 and 0.6 (Fig. 3). This suggests that a higher probability of a patch of *C. finmarchicus* generally predicts higher right whale density.

The *C. typicus* prey patch covariate partial effects in *m_ctyp* showed a slightly negative bimodal relationship between the probability of the presence of a prey patch and the partial density of right whales (Fig. S2C). Partial density increased slightly between a prey patch probability of 0.0 and 0.15, peaked at 0.15, then decreased slightly, approaching a smaller local maximum at roughly 0.35, and decreased again as the prey patch probability approached 0.6.

Similarly, the *Pseudocalanus* spp. prey patch covariate in *m_pcal* exhibited a weakly unimodal, but mostly negative, relationship between the probability of a prey patch and partial density (Fig. S3C).

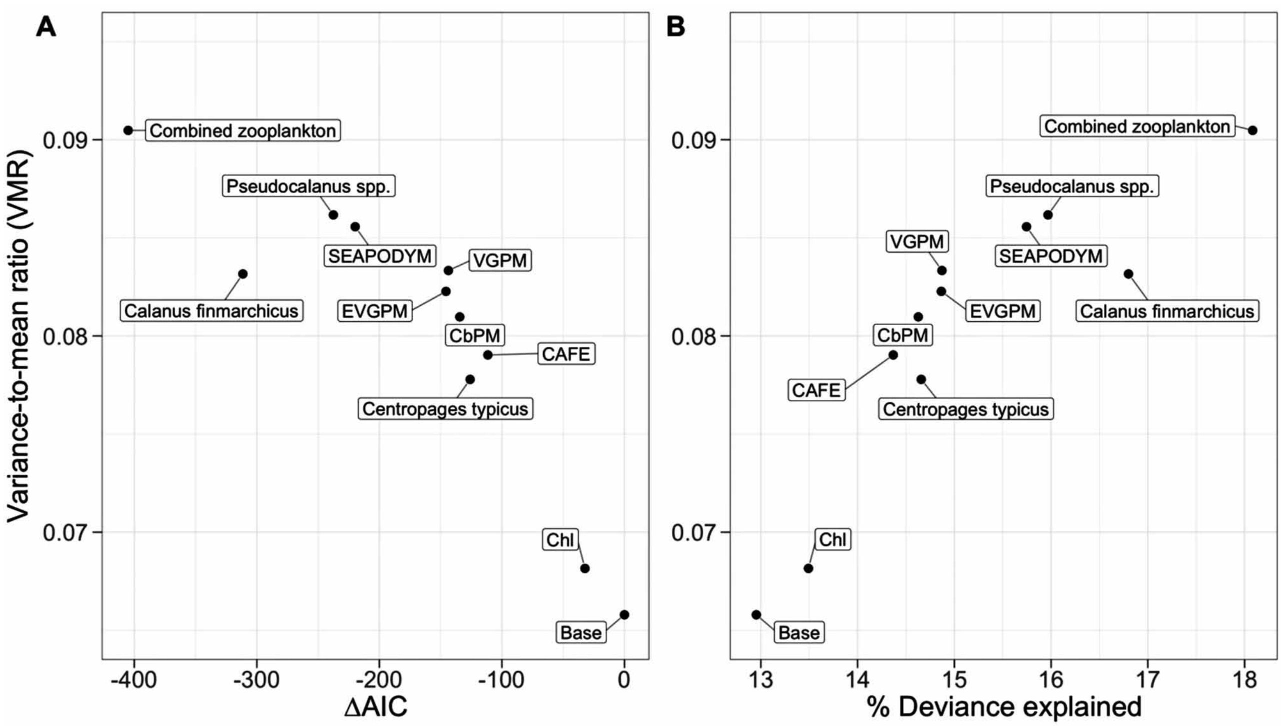
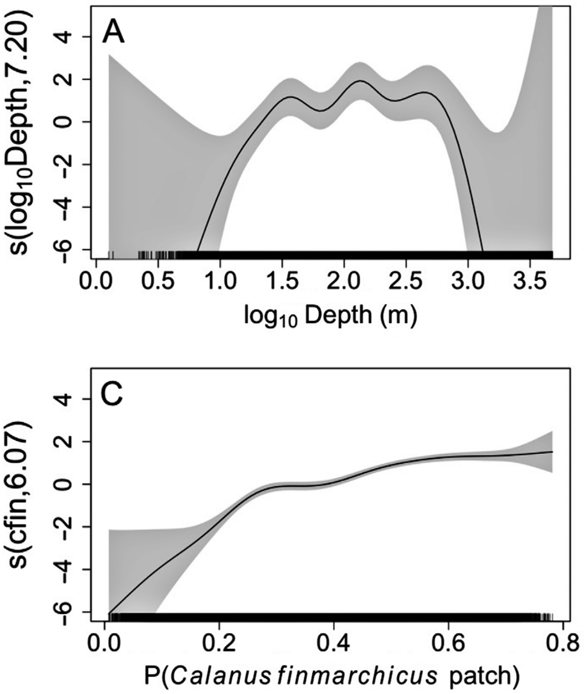


Fig. 2. Variance-to-mean ratio (VMR) as a function of (A) Akaike's information criterion relative to the baseline model (ΔAIC) and (B) deviance explained (%) for all model runs. A higher VMR suggests a higher degree of clustering; a lower ΔAIC indicates higher model performance



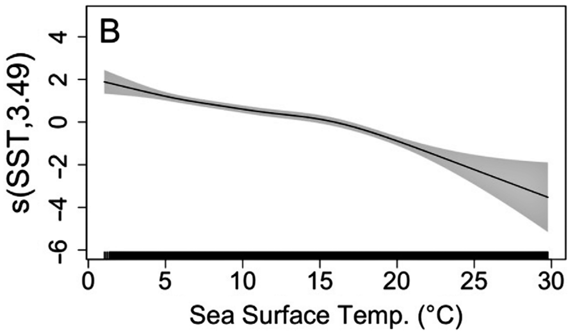
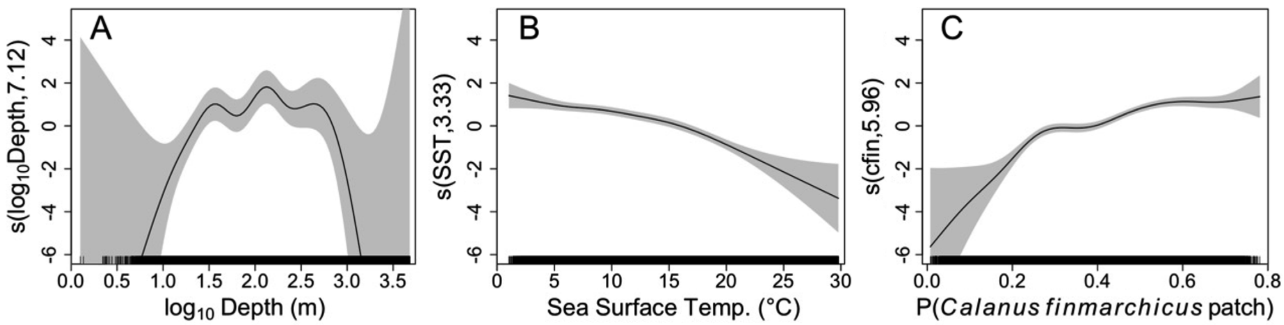


Fig. 3. Partial effects on North Atlantic right whale density for *m_cfin* for covariates (A) bathymetry (estimated degrees of freedom [EDF] = 7.20), (B) sea surface temperature (EDF = 3.49), and C) the probability of a *Calanus finmarchicus* prey patch (EDF = 6.07). The *x*-axis represents the covariate value, and the *y*-axis represents the log-scale partial effect on density. EDF indicates spline complexity



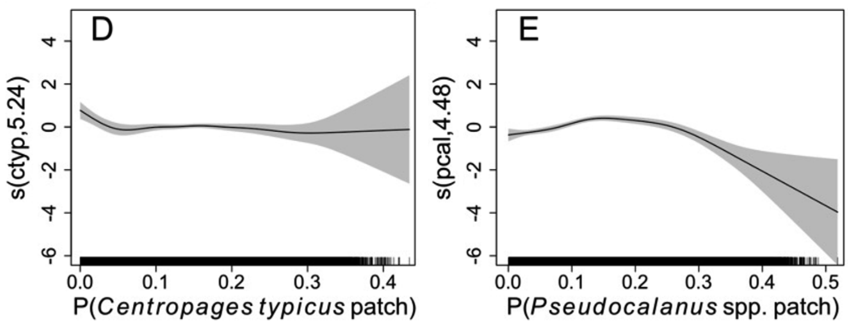


Fig. 4. Partial effects on North Atlantic right whale density for *m_combined* for covariates (A) bathymetry (EDF = 7.12), (B) sea surface temperature (EDF = 3.33), (C) the probability of a *Calanus finmarchicus* prey patch (EDF = 5.96), (D) the probability of a *Centropages typicus* prey patch (EDF = 5.24), and (E) the probability of a *Pseudocalanus* spp. prey patch (EDF = 4.48). The *x*-axis represents the covariate value, and the *y*-axis represents the log-scale partial effect on density. EDF indicates spline complexity

The smooth function increased slightly between a prey patch probability of 0.0 and 0.3, peaked, and then decreased as the prey patch probability approached 0.7.

The partial effects plots for bathymetry and SST in *m_combined* exhibited similar functional patterns to those in the individual prey models (i.e. *m_cfin*, *m_ctyp*, and *m_pcal*; Fig. 4A,B). The *C. finmarchicus* prey patch partial effect in *m_combined* confirmed the importance of this covariate in representing right whale prey, exhibiting a positive relationship (Fig. 4C). The *C. typicus* prey patch covariate partial effect exhibited a weakly negative relationship with partial density (Fig. 4D), diverging slightly from the functional relationship in *m_ctyp* (Fig. S2). The *Pseudocalanus* spp. prey patch covariate partial effect was unimodal, similar to the functional response in *m_pcal*, with a more pronounced decrease at higher patch probabilities (Fig. 4E).

Anomaly maps showing the change in whale density predictions relative to the baseline model demonstrated the impact of including prey covariates. The *C. finmarchicus* prey patch covariate increased whale density predictions in Grand Manan Basin, Bay of Fundy, especially in April and May (Fig. 5). This covariate also reduced predicted right whale density in the central Gulf of Maine and the Mid-Atlantic Bight in autumn (October and November) and winter (January through March; Fig. 5). Density increased in the central Gulf of Maine in May through August, with the strongest increases in May and the weakest in August. In December, density decreased in the central Gulf of Maine except in the deep basins, where density increased (Fig. 5). The Scotian Shelf exhibited pronounced increases in density during April, May, and December. Density predictions decreased in the adjacent Roseway Basin in December. Limited survey effort and few sightings on the Scotian Shelf necessitate cautious interpretation of predictions in this region (see Fig. 1).

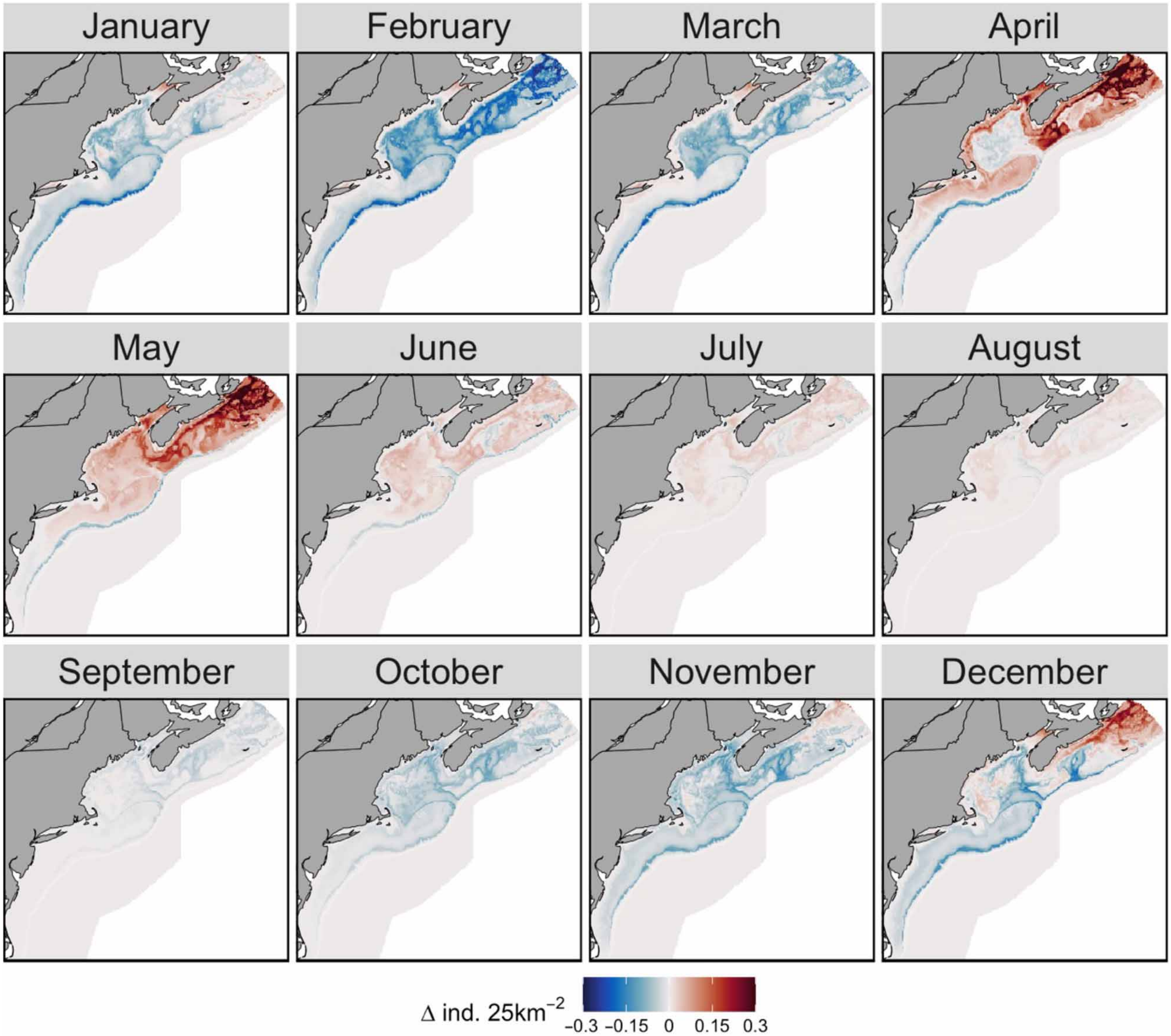


Fig. 5. Change in North Atlantic right whale density (Δ ind. 25 km^{-2}) between the model with the *Calanus finmarchicus* prey patch covariate (*m_cfin*) and the baseline model (*m_base*) from 2003 to 2017. Blue indicates the model with the zooplankton covariate predicted lower density than the baseline model; red indicates higher predicted density. These are anomaly maps; do not interpret as absolute right whale density

The changes in predicted whale density due to the addition of the *C. typicus* prey patch covariate (Fig. S4 in the Supplement) were overall smaller in magnitude compared to the differences from the addition of the *C. finmarchicus* covariate (Fig. 5). Some notable features include the more pronounced increases inshore on the Scotian Shelf in January through May and the increase in modeled density in the central Gulf of Maine in November. Similar to the *C. finmarchicus* covariate, the *C. typicus* covariate generally resulted in lower magnitude density increases in the Maine Coastal Current from April through August. Density generally increased north of the Mid-Atlantic Bight in April and May (Fig. S4). Density changes were trivial from July through September (Fig. S4).

Density predictions with the *Pseudocalanus* spp. covariate followed a similar spatial pattern to predictions with the *C. finmarchicus* covariate, but at a smaller magnitude overall. The *Pseudocalanus* spp. prey covariate increased predicted right whale density in May and June and decreased density throughout the domain from October to December, apart from the Bay of Fundy and northeastern Scotian Shelf (Fig. S5 in the Supplement).

The combined model, which included all 3 copepod covariates, resulted in the highest magnitude density anomaly relative to the baseline model (Fig. 6). The spatial distribution of the density changes across the domain was similar to densities with the *C. finmarchicus* covariate alone. Overall, the combination of all 3 zooplankton prey patch covariates resulted in more right whale density increases relative to the addition of prey patch covariates individually. Notable density changes include the slight increase in Wilkinson Basin in January, despite an overall decrease in predicted density in the rest of the Gulf of Maine; increases across the Gulf of Maine in May; increases in the Nantucket Shoals in April and May; increases on Georges Bank, the Great South Channel, the Maine Coastal Current, and Roseway Basin in April; increases in the Western Maine Coastal Current in October; and increases following the Maine Coastal Current in December (Fig. 6).

To isolate the combined effect of *C. typicus* and *Pseudocalanus* spp. on density predictions, we plotted the difference in density predictions between the combined model and the *C. finmarchicus* model (Fig. 7). Overall, the density changes were of a smaller magnitude than in Figs. 5 and 6, and are reported on a narrower color scale to emphasize differences, ranging from −0.1 to 0.1 right whales per 25 km^2 instead of −0.3 to 0.3 right whales per 25 km^2. The most pronounced density changes were in December, with the predictions exhibiting density decreases in the Maine Coastal Current, the central Gulf of Maine, and the Scotian Shelf. Density predictions increased in January in the central Gulf of Maine, including Wilkinson and Jordan Basins. Predictions decreased in Jordan Basin in April and May and increased in June through August. Predictions decreased in the Maine Coastal Current and the Great South Channel in June. Density predictions increased along the Maine Coastal Current, Jeffreys Ledge, and the Bay of Fundy in September.

4. DISCUSSION

North Atlantic right whales are Critically Endangered (Cooke 2020). The combined pressures of anthropogenic threats (especially entanglement in fishing gear and vessel strikes) and climate change necessitate the rapid, dynamic development and implementation of management strategies. DSMs are a powerful tool for characterizing the spatiotemporal distribution of marine species and have the potential to illuminate distribution patterns to aid in management planning. Under the assumption that right whale distribution patterns are primarily food-driven at the mesoscale (e.g. Wishner et al. 1988, Murison & Gaskin 1989, Mayo & Marx 1990, Baumgartner & Mate 2003), prey should be an important component of these models, but current right whale management DSMs do not include prey (Roberts et al. 2024). Spatially contiguous, time-varying modeled prey fields are relatively unavailable, necessitating the use of prey proxy covariates representing a lower trophic level (e.g. chlorophyll *a* concentration). Ross et al. (2023) aimed to fill this data gap by producing *Calanus finmarchicus* prey fields tailored to observed right whale foraging requirements (see Ross et al. 2023 Table 2). We extended this method to produce prey fields for *Centropages typicus* and *Pseudocalanus* spp. (Fig. S1), 2 smaller right whale prey resources that are important primarily in the winter and spring in Cape Cod Bay (Mayo & Marx 1990, DeLorenzo-Costa et al. 2006a,b, Pendleton et al. 2009, Hudak et al. 2023). We tested 9 prey and prey proxy covariates to examine the relative effects of these copepod prey fields versus lower-trophic proxies in a simplified right whale DSM (Table 2). We also produced a combined model that included *C. finmarchicus*, *C. typicus*, and *Pseudocalanus* spp. simultaneously (i.e. *m_combined*). Combining the 3 copepod species produced the best model, even after incorporating penalties for added complexity through AIC. The second

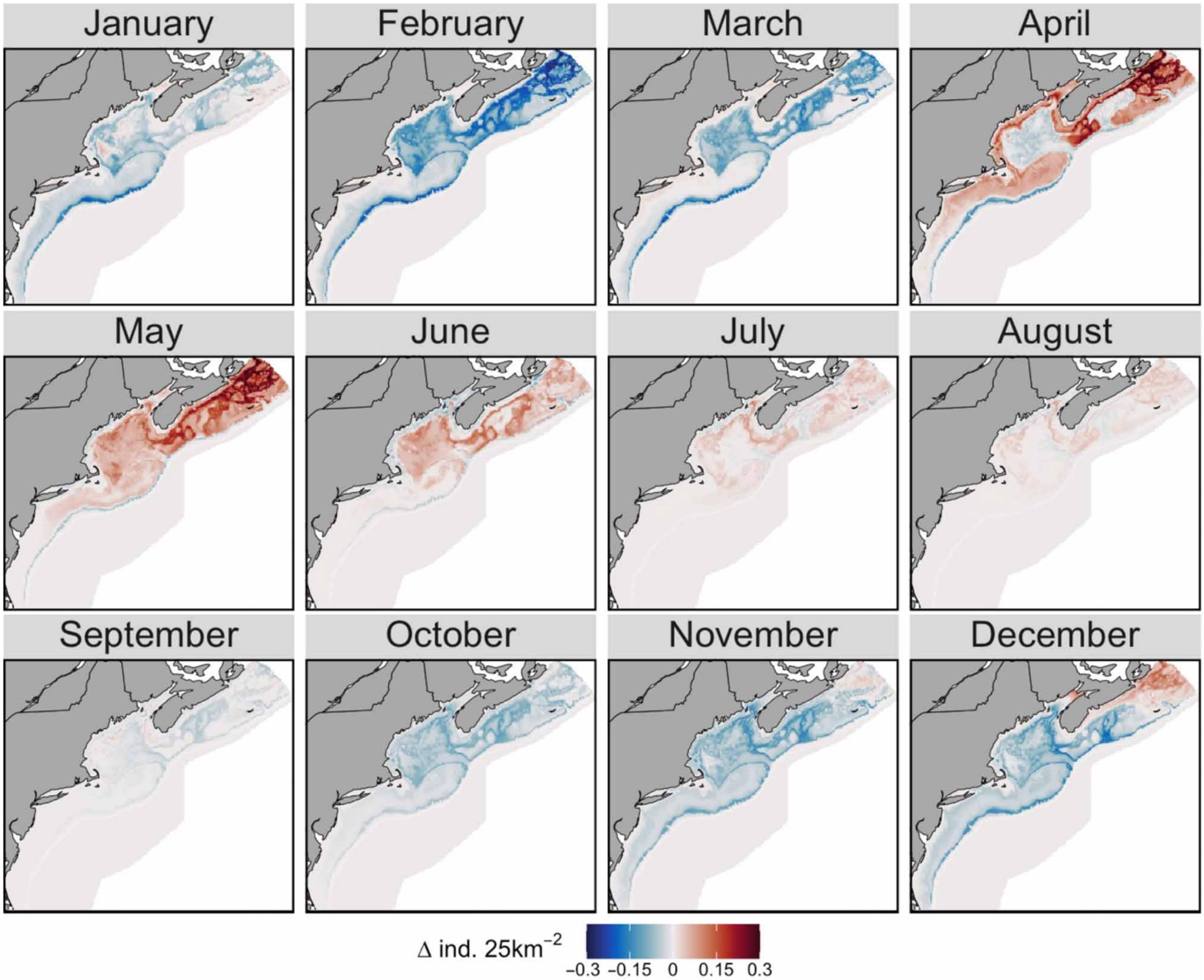


Fig. 6. Change in North Atlantic right whale density (Δ ind. 25 km^{-2}) between the model with prey patch covariates representing all 3 zooplankton species — *Calanus finmarchicus*, *Centropages typicus*, and *Pseudocalanus* spp. (*m_combined*) — and the baseline model (*m_base*) from 2003 to 2017. Blue indicates the model with the zooplankton covariate predicted lower density than the baseline model; red indicates higher predicted density. These are anomaly maps; do not interpret as absolute right whale density

highest performing model was that which included only *C. finmarchicus* (i.e. *m_cfin*). These results showcase the value of including prey covariates in right whale DSMs, especially *C. finmarchicus*.

Model comparison suggests that including prey in simplified right whale DSMs improves predictive power by explaining more deviance. Additionally, it appears that including prey results in density distribution changes in key right whale foraging grounds and regions where *C. finmarchicus* often aggregates (e.g. western portion of the Gulf of Maine; Runge et al. 2015). The inclusion of prey covariates also better replicates the high spatial dispersion that is expected when modeling a rare species, as assessed using VMR (Fig. 2). Generally, models that included prey fields performed better than models that included proxies related to primary production, such as chlorophyll *a* concentration. The DSMs that only included the *C. typicus* prey layer did not perform as well, with *m_ctyp* ranking fourth to last (AIC = −125.9; Table 2), and exhibited lower dispersion according to VMR (Fig. 2). It is possible that the lower performance of *m_ctyp* relative to *m_combined*, *m_cfin*, and *m_pcal* is the result of right whales' documented preference for *C. finmarchicus* throughout most of their foraging range (e.g. Wishner et al. 1988, Murison & Gaskin 1989, Mayo & Marx 1990, Baumgartner & Mate 2003, Hudak et al. 2023). The higher performance of

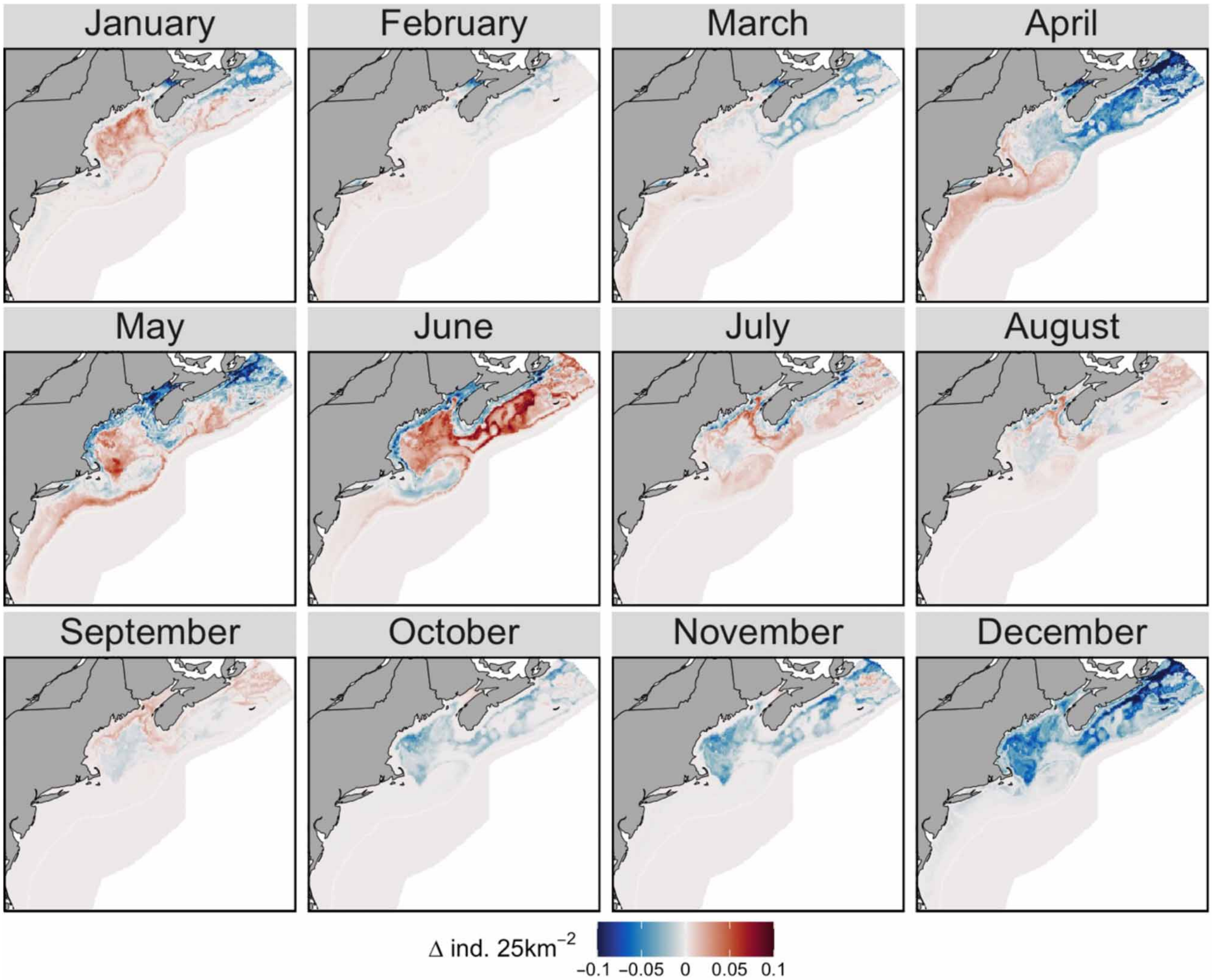


Fig. 7. Change in North Atlantic right whale density (Δ ind. 25 km^{-2}) between the model with prey patch covariates representing all 3 zooplankton species — *Calanus finmarchicus*, *Centropages typicus*, and *Pseudocalanus* spp. (*m_combined*) — and the model with the *C. finmarchicus* prey patch covariate (*m_cfin*) from 2003 to 2017. Blue indicates the model with the zooplankton covariate predicted lower density than the baseline model; red indicates higher predicted density. These are anomaly maps; do not interpret as absolute right whale density. Note that the range of the color scale is narrower than that of Figs. 5 & 6 in order to facilitate interpretation

m_pcal relative to *m_ctyp* and the models containing primary productivity covariates suggests the importance of considering *Pseudocalanus* spp. as a potential counter-indicator of right whale density in modeling efforts and emphasizes the need for continued zooplankton sampling and covariate improvements.

M_cfin and *m_combined* exhibited a positive relationship between the *C. finmarchicus* prey patch covariate and right whale density (Figs. 4C & 5C). This makes sense ecologically; right whale distributions are likely prey driven, so increased abundance of *C. finmarchicus* in a region should theoretically lead to higher right whale density, assuming whales are able to detect the high-density prey patches. Pendleton et al. (2009) found a similar relationship between the abundance of *C. finmarchicus* and right whale sightings per unit effort in the Great South Channel, which, in combination with the results of this study, supports the assumption that distributions are prey driven and whales are able to find high-density prey aggregations. Because the right whale diet is primarily composed of *C. finmarchicus*, the high performance of *m_cfin* and the positive partial effect relationship previously described suggest that the prey layer produced in Ross et al. (2023) captures at least some of the real-world dynamics at play in the ecosystem and accounts for some of the variance in right whale density.

The partial effects plots for *m_ctyp* and *m_pcal* did not show a strong positive relationship between prey patch probability and partial right whale density. This could be a result of the regional and seasonal variation in the importance of these smaller copepods to the right whale diet; current knowledge suggests they are important species primarily in the winter and spring in Cape Cod Bay (Mayo & Marx 1990, DeLorenzo Costa et al. 2006a,b, Hudak et al. 2023), a region too geographically small to be appropriately resolved on the 5 × 5 km model grid. Results from a modeling study suggest that concentrations of smaller copepod species, specifically *Pseudocalanus* spp., could act as a counter-indicator for right whale abundances in the western Gulf of Maine (Pendleton et al. 2009), indicating that some sort of prey selection between the different copepod species could be at play based on availability. If this is true ecologically, it could explain the relatively high performance of *m_pcal*. Similarly, *m_combined* indicates lower right whale abundance at relatively high *Pseudocalanus* spp. availability (Fig. 4). Further zooplankton sampling targeting smaller copepod species and additional studies on the prey preferences of right whales, including the role of potential counter-indicator species, are necessary to further explore this hypothesis.

To qualitatively assess the effects of including prey covariates on right whale density predictions, we mapped the differences in predicted density by subtracting *m_base* from the predictions for each model that included a prey covariate. The results showed the prey covariates better identified key right whale foraging grounds and increased seasonal dynamics. For example, the *C. finmarchicus* covariate decreased right whale density predictions in the central Gulf of Maine from October through April, except for Jordan and Wilkinson Basins in November through April (Fig. 5). The exception of Wilkinson and Jordan Basins is consistent with the positive *C. finmarchicus* abundance anomalies observed in the deep basins in the Gulf of Maine (Runge et al. 2015, Record et al. 2019, Ji et al. 2022), and with the results of Meyer-Gutbrod et al. (2023) that showed sustained right whale use of those regions of the Gulf of Maine. Pendleton et al. (2009) found a significant positive correlation between the mean concentration of *C. finmarchicus* in the western Gulf of Maine with right whale sightings in the Great South Channel, further corroborating the importance of this covariate as a predictor of right whale density. The density anomaly maps for *m_cfin* also showed an increase in right whale density predictions on the Nantucket Shoals in April through June, which has emerged as an important right whale feeding ground since around 2010 (e.g. Quintana-Rizzo et al. 2021, O'Brien et al. 2022, Grech et al. 2023). The general decrease in predicted right whale density in the central Gulf of Maine in the winter months is consistent with times of year at which we would not expect right whales to be foraging in the Gulf of Maine. Density decreases in the central Gulf of Maine in September through December (excluding the deep basins in December) are consistent with the 2010 regime shift of right whales out of the northern Gulf of Maine into Canadian waters resulting from an oceanographic regime shift in the Gulf of Maine (Davis et al. 2017, Record et al. 2019, Friedland et al. 2020, Gonçalves Neto et al. 2021). Our models did not distinguish between pre-2010 and post-2010 oceanographic regimes, and instead spanned the years 2003 through 2017; patterns consistent with expected right whale distributions post-2010 are mentioned anecdotally. Rigorously analyzing the impact of the copepod prey fields on right whale density predictions with respect to the regime shift is an important future direction.

While *m_ctyp* and *m_pcal* (Figs. S2 & S3) were not top-performing models, *C. typicus* and *Pseudocalanus* spp. are known to be important secondary prey resources to right whales, especially in Cape Cod Bay in the winter and spring (e.g. Mayo & Marx 1990, Pendleton et al. 2009, Hudak et al. 2023). Despite lower model performance, some patterns in these density anomaly maps for *m_ctyp* and *m_pcal* are relevant to the interpretation of *m_combined*, suggesting their importance as right whale prey may be habitat wide. Because there was no clear positive relationship between the probability of a patch of *C. typicus* or *Pseudocalanus* spp. and whale density (Figs. S2 & S3), it is possible that a mid-range probability of a smaller copepod patch indicates that more *C. finmarchicus* are available. At higher patch probabilities, it appears these smaller copepods, specifically *Pseudocalanus* spp., may be counter-indicators of right whale density (e.g. Pendleton et al. 2009). Assessing the combined effect of including *C. typicus* and *Pseudocalanus* spp. by subtracting *m_cfin* density predictions from *m_combined* density predictions (Fig. 7) helps illuminate possible interactions between the copepod prey fields and helps more comprehensively explain the patterns exhibited in *m_combined* without the added complexity of a tensor interaction (Fig. 6). One interesting feature that does not appear to be strongly present in the density anomaly maps for *m_cfin*, *m_ctyp*, *m_pcal*, or *m_combined*, but does appear in the anomaly map isolating the combined effects of *C. typicus* and *Pseudocalanus* spp. (Fig. 7), is the slight increase in predicted density on Jeffreys Ledge in September. This feature is consistent with a seasonal peak in right whale sightings observed on Jeffreys Ledge in October through December by Weinrich et al. (2000), with individuals often exhibiting surface feeding behaviors. This is a time of high overturn in the Western Maine Coastal Current, leading to a seasonal ecosystem-wide increase in primary production and food availability (e.g. Townsend & Spinrad 1986, Townsend 1992, Townsend et al. 1994, Durbin et al. 2003). Considering Fig. 7 in this context emphasizes the importance of considering right whale prey species beyond *C. finmarchicus*. Taking this analysis a step further and assessing potential interactions between the *C. finmarchicus*, *C. typicus*, and *Pseudocalanus* spp. covariates will be a crucial next step in understanding the influence of primary (i.e. *C. finmarchicus*) and secondary prey (e.g. *C. typicus* and *Pseudocalanus* spp.) resources on right whale density predictions. The better we can predict whale density and foraging patterns in the context of a rapidly changing ocean, the more useful models will be in facilitating the discovery of unknown or potential future foraging grounds (e.g. Mellinger et al. 2011, Pendleton et al. 2012, Silva et al. 2012) and informing management.

The *C. finmarchicus* prey fields produced by Ross et al. (2023) were a first attempt at modeling right whale prey through the lens of right whale foraging requirements. It is imperative that we continue to develop and improve these prey fields. Because Ross et al. (2023) took a depth-integrated approach to modeling prey (i.e. one value for the entire water column at each grid cell), potential improvements include considering the tendency of *C. finmarchicus* to concentrate vertically in the water column into dense layers (e.g. Baumgartner & Mate 2003, Krumhansl et al. 2018). Additionally, Ross et al. (2023) produced prey layers based on abundance data (ind. m^{-2}). Extending the approach of Ross et al. (2023) to account for energetics or biomass would likely provide a better representation of right whale prey (e.g. Michaud & Taggart 2007, Swaim et al. 2009, Fortune et al. 2013). It is important to note that we did not propagate the variance from the estimation of the prey fields through to the final density estimates.

There is also a need for continued data collection and research on the energetic requirements of right whales generally and in the context of climate change (e.g. Helenius et al. 2024). For example, estimating the quantities of smaller copepod species required to sustain a right whale would be an important next step (e.g. Kenney et al. 1986, Goodyear 1996). Another plausible explanation for the lower performance of *m_ctyp* and *m_pcal* relative to *m_cfin* is this knowledge gap surrounding how smaller copepods supplement the right whale diet, thus necessitating a theoretical approach to determining the prey patch threshold (i.e. using percentiles instead of thresholds derived from literature review). Additionally, the EcoMon sampling protocol utilizes a 333-µm mesh net; this filtering efficiency is ideal for capturing late-stage *C. finmarchicus* (Lehoux et al. 2020) and is roughly equivalent to the estimated filtering efficiency of right whale baleen (Mayo et al. 2001), likely capturing roughly what is available to right whales in that environment. However, this mesh size is not ideal for measuring abundance of smaller species such as *C. typicus* and *Pseudocalanus* spp., likely resulting in artificially low abundances in the dataset. It is possible that smaller stages of *C. typicus* and *Pseudocalanus* spp. play a role in right whale foraging success, whether though potentially representing a proxy for the quality of *C. finmarchicus* prey or by helping sustain whales directly.

Another important caveat to note is that the right whale survey data used in our models had few records from the Bay of Fundy and few sightings from the Scotian Shelf; predictions in those regions must be interpreted cautiously. Our models highlight the need for continued survey effort in order to more rigorously analyze the impact of adding prey covariates in key right whale foraging habitats, such as Grand Manan Basin in the Bay of Fundy (Baumgartner et al. 2003). Ongoing collaborations between the USA and Canada would benefit from combining modeling efforts to elucidate cross-boundary right whale distribution patterns. Additionally, there are ongoing efforts to improve upon Ross et al. (2023) and additional efforts to produce more comprehensive right whale prey layers (e.g. Plourde et al. 2024).

Management of right whales and other Critically Endangered species requires the highest quality data to inform modeling and management efforts. Members of NOAA's Atlantic Large Whale Take Reduction Team (see https://www.fisheries.noaa.gov/new-england-mid-atlantic/marine-mammal-protection/atlantic-large-whale-take-reduction-plan) have emphasized the need to include a realistic prey representation in right whale DSMs. Successful management also depends, in part, on habitat models because monitoring whales is costly, time intensive, and feasibility limited. The novel method of producing prey fields presented in Ross et al. (2023) represents an important advancement in efforts to include a representation of right whale prey in management models. The *C. finmarchicus* prey field shows great potential to improve right whale DSMs, especially when used in conjunction with the *C. typicus* and *Pseudocalanus* spp. covariates produced using the same method. One example of the potential of modeling efforts to aid in endangered species conservation are the results from Pendleton et al. (2012), which used a *C. finmarchicus* covariate to successfully highlight the potential importance of the Nantucket Shoals habitat in advance of right whales being observed in the region, serving as a key example of the power of models to increase the proactivity of management efforts. Conservation outcomes depend upon a combination of techniques to approach the problem from multiple angles. Accurate, high-performing models are key to informing survey effort, better understanding suitable habitat, and simulating potential management strategies to assess the outcomes. With fewer than 380 right whales remaining (Linden 2024), every single whale is important to the future of the species; it is imperative that scientists, managers, and policymakers continue to develop and use the best tools available to prevent as many anthropogenic mortalities as possible.

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