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Effects of changing temperature phenology on the abundance of a critically endangered baleen whale

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ABSTRACT

Incorporating the effects of climate change in species management strategies is one of today's greatest conservation challenges. Mechanistic models can be used to address these challenges because they explain how climate change effects cascade through ecosystems and influence species distributions. We used structural equation models to test hypotheses about the cascading effects of climate change and basin-scale variables on the local abundance of North Atlantic right whales, a critically endangered species, in a historically important feeding habitat. We found that effects of the North Atlantic Oscillation, a basin-scale variable, on local right whale abundance occurred through a cascade of effects on other ecosystem variables, including chlorophyll *a* concentration, *Calanus finmarchicus* abundance, and zooplankton patchiness. These effects varied by month. We also found that the western Gulf of Maine spring thermal transition date (a proxy for climate change) is a major direct and indirect driver of variations in local right whale abundance. The indirect effect of earlier spring transition dates, through a pathway of prey abundance, suggested a decrease in local right whale abundance. However, right whale abundance increased because of the direct effect of regional spring transition date. The direct effect suggests that right whales may be using regional temperatures as a movement cue. The counteracting direct and indirect effects of spring transition date suggest that right whales could face a mismatch with their prey, which could ultimately result in another large-scale distribution shift. Our causal modeling approach demonstrates that the influence of climate change on local right whale abundance in the Gulf of Maine cascades through a network of variables. These cascading effects make predicting local right whale abundance challenging and suggest that successful endangered species conservation requires identifying the mechanisms underlying species distributions.

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1. Introduction

Incorporating climate change effects in species management strategies are necessary for marine species globally and is one of today's greatest conservation challenges. Species responses to climate change can include reductions in the survivorship of vulnerable age classes, pole-ward shifts in distribution, decreased reproductive success, shifts to deeper waters, changes in migration timing (e.g., arrival and departure dates), and longer residency times in higher latitudes (Friedland et al., 2020; Hazen et al., 2013; Johnston et al., 2005; Learmonth et al., 2006; Nye et al., 2009; Pendleton et al., 2022; Ramp et al., 2015). For example, Hazen et al. (2013) found that changes in core habitat size in response to climate change for top predators varied by species. These authors predicted that by 2100 most marine mammals will experience a decline in potential habitat, while more seabirds will experience an increase. Fin (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*) migrating to the Gulf of St. Lawrence, Canada, have shifted their arrival time earlier by one month. This change in arrival time is related to earlier sea ice break-up and rising sea surface temperatures (Ramp et al., 2015). Many fish stocks in the Northeast United States continental shelf ecosystem have shifted their center of biomass poleward, increased their depth, and expanded their northern range (Nye et al., 2009).

Species responses to climate change are often associated with species management challenges. In the Gulf of Maine, which is one of the fastest-warming ecosystems in the world (Pershing et al., 2015), these management issues impact economically valuable fisheries and critically endangered species. For example, surface warming caused reductions in recruitment and increased mortality of Atlantic cod (*Gadus morhua*). Failure to include these climate-driven demographic changes in management strategies contributed to overfishing (Pershing et al., 2015). In contrast, increased bottom water temperature has been associated with an increase in suitable lobster habitat and, concomitantly, the rapid expansion of the American lobster (*Homarus americanus*) fishery (Friedland et al., 2020; Goode et al., 2019; Le Bris et al., 2018). This expansion exacerbated an existing management challenge because entanglements in lobster and other fixed fishing gear have decreased survival rates for both humpback whales and the critically endangered North Atlantic right whale (*Eubalaena glacialis;* hereafter, right whale) (Robbins et al., 2015).

Right whales are predicted to go extinct in less than 30 years (Meyer-Gutbrod and Greene, 2018). In addition to the issues caused by entanglements, shifts in right whale distributions, caused by climate change (e.g., changes in bottom water temperature, changes in prey abundance distribution, changes in temperature phenology, etc.), are causing management challenges. Specifically, right whales have abandoned some historically important habitats (e.g., the Bay of Fundy, Davies et al., 2019) and recolonized areas that have not had large numbers of right whales since the whaling era (e.g., Gulf of St. Lawrence, Simard et al., 2019; Nantucket shoals, O'Brien et al., 2022). In contrast to the declines in other historically important habitats, right whale abundance has increased in Cape Cod Bay in recent decades (Ganley et al., 2019). Right whale management strategies are well established in historically important habitats and have included the designation of critical habitats, management of fishing activities, and changes to ship traffic patterns and speeds (Massachusetts Division of Marine Fisheries, 2021; NOAA, 2013, 2008a, 2008b). Similar protections did not exist in areas newly occupied by right whales, resulting in high levels of human-caused mortalities and a subsequent uplisting, in 2020, of the right whale by the International Union for Conservation of Nature from Endangered to Critically Endangered (Cooke, 2020; Davies and Brillant, 2019).

To avoid management challenges caused by future shifts in right whale distributions, we need to predict where right whale abundance might increase. Correlative statistical habitat models have been successfully used to develop short time-scale management strategies (Becker et al., 2012). However, the correlative relationships inferred from these models may not be appropriate for multi-decadal projections and predictions in novel environments (Elith et al., 2010; Silber et al., 2017). Additionally, randomized controlled studies, in which experimental manipulations are used to infer causality, are not possible for large migratory animals, such as right whales.

Certain mechanistic models have the potential to successfully predict climate-induced changes in species distributions because they can be used to explain the cascading effects of ocean warming through ecosystems and the ultimate influence of these effects on species distributions. Structural equation models (SEMs) are a causal modeling technique that can be used to evaluate hypotheses about the mechanistic drivers of habitat use because they allow for testing variables within a network; they are depicted using diagrams with arrows that represent a hypothesized relationship between variables (Wilson et al., 2021). The hypothesized relationships are then modeled using equations, such as generalized linear mixed-effects models. Within the network diagram, variables that only have outgoing arrows are predictors. Variables that have an incoming and outgoing arrow are considered both a predictor and a response, making it possible to assess the influence of variables that indirectly affect species distributions. The ability to have predictor variables that are more than one step removed from the response variable makes SEMs an ideal method for testing influences within ecosystems (i.e., testing for indirect effects), which is not possible with other statistical approaches (e.g., multiple regression analyses).

We used SEMs to test hypotheses about the cascading effects of climate change and basin-scale variables on right whale abundance in Cape Cod Bay, Massachusetts (hereafter, local right whale abundance). The importance of Cape Cod Bay as a right whale habitat has been recognized for decades. Cape Cod Bay is considered a winter and spring right whale foraging habitat (Mayo et al., 2018) and hunting for right whales occurred here as early as the first half of the 17th century (Reeves et al., 1999). A substantial amount of research has occurred in Cape Cod Bay, including over twenty years of right whale aerial surveys and zooplankton sampling (DeLorenzo Costa et al., 2006; Ganley et al., 2019; Mayo et al., 2018). The unique increase in right whale abundance observed in Cape Cod Bay (Ganley et al., 2019) and the long time series of prey data make this habitat an ideal case study system. Understanding the mechanistic drivers of variability in right whale abundance in Cape Cod Bay (local right whale abundance in our SEM) could aid in right whale protection by increasing our ability to predict other areas where right whale populations may increase.

We hypothesized that local right whale abundance will be affected by changes in basin-scale variables (e.g., the North Atlantic Oscillation (NAO)) and climate change impacts (represented by the western Gulf of Maine spring thermal transition date) that cascade through biotic and abiotic variables measured across the Gulf of Maine (i.e., regional scale) and in Cape Cod Bay (i.e., local scale). For example, the NAO is a major cause of basin-scale climate fluctuations (Hurrell, 1995) and affects regional physical conditions, such as wind stress (Visbeck et al., 2003; Xu et al., 2015). *Calanus finmarchicus*, the primary prey of right whales, is expatriate to Cape Cod Bay and must be advected into the Bay. Consequently, the NAO may affect local-scale *C. finmarchicus* abundance and, ultimately, local right whale abundance through its influence on advection processes. Additional information about our hypothesized connections between the NAO and local right abundance is provided in the methods.

The trend towards earlier spring thermal transition dates (hereafter, regional spring transition date) is an indicator of climate change in the western Gulf of Maine. The spring thermal transition date is the date that smoothed, daily sea surface temperature first exceeds the annual average of the region (Friedland et al., 2015). Since 2006, the regional spring transition date has shifted earlier by two weeks (Friedland et al., 2015). Friedland et al. (2015) found that the earlier occurrence of the regional spring transition date results in earlier and larger magnitude phytoplankton blooms (Friedland et al., 2015). These phytoplankton blooms ultimately impact right whales because their primary prey, *C. finmarchicus*, relies on these phytoplankton blooms as a food source (Drinkwater et al., 2003). Additional information about our hypothesized connections between the regional spring transition date and local right abundance is provided in the methods.

2. Material and methods

2.1. A priori structural equation model

We developed an *a priori* SEM (Supplemental Fig. S.1) to explore the cascading effects of basin-, regional-, and local-scale variables on local right whale abundance (i.e., right whale abundance in Cape Cod Bay). This *a priori* SEM also captures hypotheses about how climate change, as represented by variations in the western Gulf of Maine spring thermal transition date (i.e., regional spring transition date), cascades through a chain of variables and ultimately impacts local right whale abundance.

Ganley et al. (2019) used distance sampling techniques to estimate monthly local right whale abundance using aerial survey data.

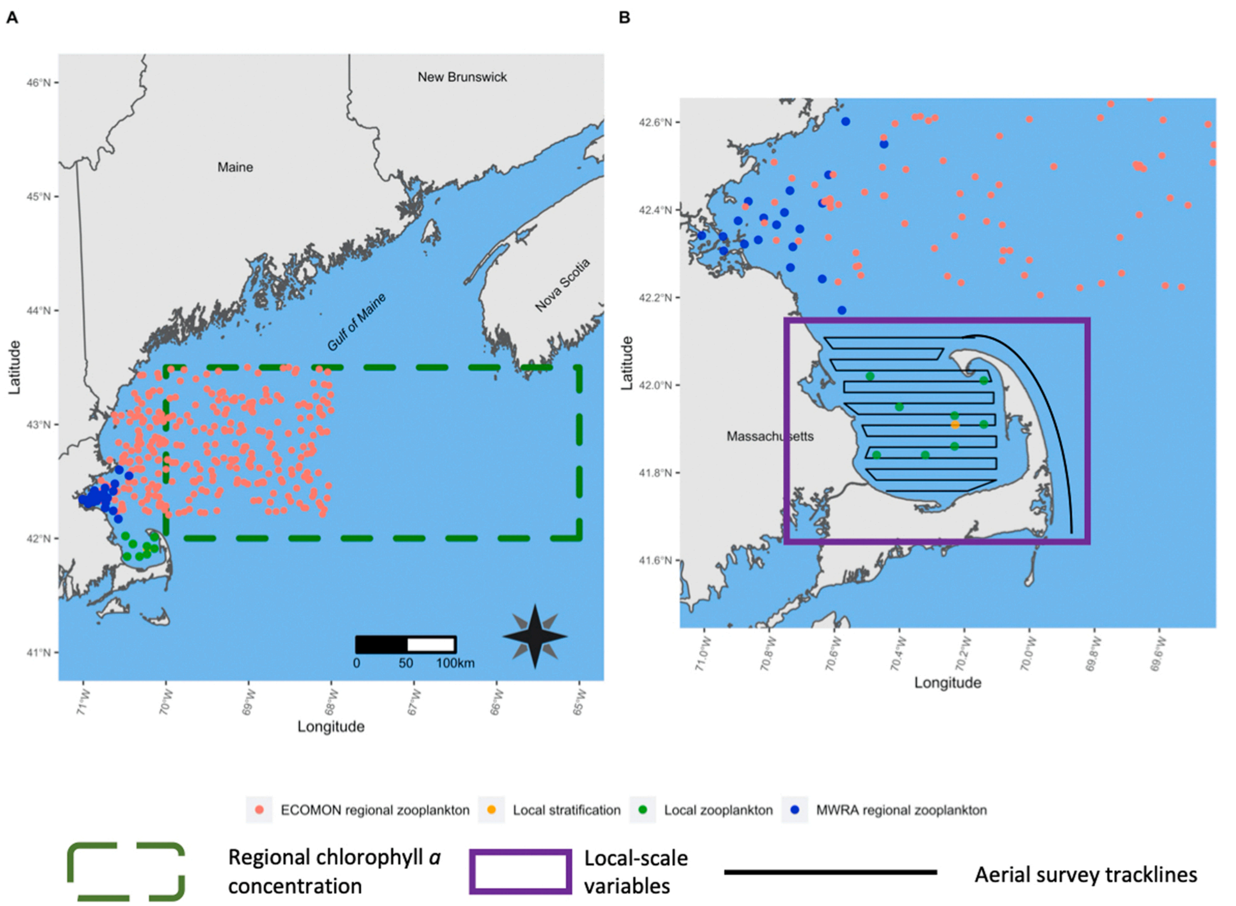

Fig. 1. Locations of regional and local data stations used in our structural equation model. A.) Regional-scale variables are derived from data collected in the Gulf of Maine; B.) Local variables are derived from data collected in Cape Cod Bay, which is shown in a purple box.

Aerial surveys were conducted in Cape Cod Bay (Fig. 1B) on good weather days from 1998 to 2017 in a Cessna Skymaster at a groundspeed of 185 km/h. Two observers, seated behind two pilots, scanned either side of the plane, recording marine mammal sightings. When a right whale was spotted the plane diverted from the trackline to record an exact location, obtain information about group size, photographs, and behavioral observations.

2.1.1. *Basin-scale influences on local right whale abundance*

We tested the influence of three basin-scale variables on local right whale abundance: the size of the entire right whale population, the NAO, and the Gulf Stream North Wall (GSNW) Index. The size of the entire right whale population, which predominantly occurs in waters from Florida, USA, to the Gulf of St. Lawrence, Canada, has been estimated using mark-recapture analyses (Pace et al., 2017) (Table 1). We hypothesized that the size of the entire right whale population will directly affect local right whale abundance. Specifically, we expected higher population sizes to result in higher local abundances.

We also hypothesize that basin-scale changes in ecosystem conditions, as represented by two basin-scale indices, will indirectly affect local right whale abundance. A number of studies have described possible connections between the NAO, our first basin-scale index, and right whales. We hypothesized that the NAO could indirectly influence local right whale abundance through its direct effect on two regional-scale variables: *C. finmarchicus* abundance and chlorophyll *a* (Greene et al., 2003, 2013; Greene and Pershing, 2004;

Table 1
Data sources for variables used in our structural equation model. Sampling stations are shown in Fig. 1. NOAA: National Oceanic and Atmospheric Administration, MWRA: Massachusetts Water Resources Authority, CCS: Center for Coastal Studies.

Variable	Data source	Methods	Data source for prior distribution for the intercept
Basin-scale influences			
Hurrell North Atlantic Oscillation Index	Climate Analysis Section, National Center for Atmospheric Research Staff (Eds), Boulder, USA, Hurrell (2003). Accessed 30 January 2018	Yearly boreal winter (December–March) station-based NAO index	
Gulf Stream North Wall Index	Taylor and Stephens (1998)	Yearly mean of monthly Gulf Stream North Wall Index values	
North Atlantic right whale population estimate	Pace et al. (2017)	Mark-recapture analysis	
Regional influences			
Chlorophyll *a* concentration (mg/m^3chlor – *a*)	GlobColour data from SeaWiFS (1998–2002) and MODIS-Aqua (2003 – 2017) sensors	Monthly data at 4 km resolution averaged for the area in Fig. 1A	Song et al., 2010
Western Gulf of Maine Spring Transition Date	Friedland et al. (2015)	Annually, the date that smoothed, daily sea surface temperature first exceeds the annual average of the region.	
***Calanus finmarchicus* (CI – CVI) (org/100 m^3)**	Northeast Fisheries Science Center ECOMON zooplankton data and MWRA	ECOMON zooplankton data. When ECOMON data were unavailable MWRA zooplankton data were used (see the section on missing data for more details). MWRA protocols in Libby et al. (2014). ECOMON protocols in Kane (2007).	ECOMON 1977–1997
Local influences			
Stratification (kg/m^3)	Right Whale Ecology Program, Water Quality Monitoring Program, CCS; MWRA	Sigma-t, the difference between the min and max values of water column density (DeLorenzo Costa et al., 2006), averaged monthly in Cape Cod Bay (Fig. 1B).	Right Whale Ecology Program, CCS 1995 and 1996
Mean Total Zooplankton density (including *Centropages typicus, Pseudocalanus spp., and Calanus finmarchicus* (org/10 m^3))	Right Whale Ecology Program, CCS	Surface tow zooplankton samples at the stations in Fig. 1B (Jaquet et al., 2005). Data are the mean monthly abundance from all stations combined.	Right Whale Ecology Program, CCS 1988–1997 surface tows
Zooplankton patchiness	Right Whale Ecology Program, CCS	Adapted from Kraus and Rolland (2009). Zooplankton patchiness measures the ratio of peak to background zooplankton concentration. Peak concentration is the highest zooplankton density measured monthly. Background concentration is the mean zooplankton density from all surface tow stations monthly.	
Right whale abundance	Right Whale Ecology Program, CCS	Distance sampling analysis of aerial survey data (Ganley et al., 2019)	Oedekoven et al. (2015) estimated distributions of relative right whale abundance for the mid-Atlantic coastal U.S. region for January and April. Priors are based on the inverse of these distributions.

Thomas et al., 2017). Hydrographic changes in the Gulf of Maine caused by the NAO could drive fluctuations in the advected supply of *C. finmarchicus* into the Gulf of Maine (MERCINA, 2001). Furthermore, increases in regional chlorophyll *a* caused by a positive NAO index would be expected to increase regional *C. finmarchicus* abundance. Increases in *C. finmarchicus* abundance through advection or increased chlorophyll *a* would be expected to increase local right whale abundance in response to improved foraging conditions. However, the influence of the NAO varies by time lag, region, and the magnitude of the NAO phase change (MERCINA, 2004, 2001; Turner et al., 2006). We obtained basin-scale data (NAO 2-yr lag and GSNW Index) from yearly data sources (Table 1).

We hypothesized that the GSNW Index, our second basin-scale index, could indirectly influence local right whale abundance through its effect on local-scale stratification. The Gulf Stream is composed of warm and salty waters. Therefore, changes in the proximity of the GSNW to the Gulf of Maine could impact stratification. Stratification causes vertical boundaries which could increase zooplankton patchiness (Gregr and Coyle, 2009). Right whales require concentrated patches of zooplankton to elicit feeding behaviors. Therefore, we hypothesized that changes in stratification caused by the GSNW influence local-scale right whale abundance. We calculated local stratification, sigma-t, using the average of monthly water column density values derived from CTD sampling at fixed stations in Cape Cod Bay (Fig. 1B, Table 1).

2.1.2. Regional-scale influences on local right whale abundance

We tested the influence of three regional-scale variables on local right whale abundance: spring transition date, chlorophyll *a* concentration, and *C. finmarchicus* abundance. The regional spring transition date could indirectly influence local right whale abundance through a number of pathways. Friedland et al. (2015) found earlier spring transition dates were correlated with earlier, and higher magnitude, spring phytoplankton blooms. Copepods benefit from early spring phytoplankton blooms; high chlorophyll concentrations in February lead to higher egg production rates (Durbin et al., 2003), and copepods emerging from diapause in December benefit from early phytoplankton blooms (Johnson et al., 2006; Friedland et al., 2015). Additionally, the regional spring transition date could indirectly influence local right whale abundance through its influence on local-scale stratification. The establishment of a stratified water column coincides with warming waters, therefore earlier spring warming could result in earlier stratification. Methods for determining the regional spring transition date were defined by Friedland et al. (2015).

Higher chlorophyll *a* concentrations are expected to increase the regional abundance of *C. finmarchicus*. Consequently, we hypothesized an indirect effect of chlorophyll *a* on local right whale abundance through the influence of chlorophyll *a* on the regional abundance of *C. finmarchicus*. We used the mean of gridded, monthly, remotely sensed, regional-scale, chlorophyll *a* data (Fig. 1A, Table 1). We also tested hypotheses about the direct influence of regional abundance of *C. finmarchicus* (i.e., abundance in the Gulf of Maine) on local right whale abundance. In particular, there are two opposing hypotheses that explain the influence of regional *C. finmarchicus* on local right whale abundance. First, the competing habitat hypothesis suggests that neighboring habitats with high *C. finmarchicus* abundance attract right whales and decrease local right whale abundance. Second, the habitat linkage hypothesis suggests that high regional *C. finmarchicus* abundance in neighboring habitats acts as a source of local *C. finmarchicus* and increases local right whale abundance by creating good feeding conditions. Regional *C. finmarchicus* abundance was compiled from field sampling conducted by the Northeast Fisheries Science Center ECOMON cruises and the Massachusetts Water Resources Authority (Fig. 1A, Table 1). We also tested whether the direct influence of regional *C. finmarchicus* abundance on local right whale abundance varied by month.

2.1.3. Local-scale influences on local right whale abundance

We tested the influence of three local-scale variables on local right whale abundance: zooplankton abundance, zooplankton patchiness, and stratification. Our measure of local zooplankton is comprised of three species *C. finmarchicus, Pseudocalanus spp.*, and *Centropages typicus*, which are known prey species for right whales (Mayo and Marx, 1990; Pendleton et al., 2009). Local-scale zooplankton densities are monthly averages of zooplankton samples collected at fixed stations in Cape Cod Bay (Fig. 1B, Table 1). Local-scale zooplankton samples were taken at the surface using a 30 cm diameter conical plankton net with 333 μm mesh. Local-scale zooplankton abundance was represented by the mean of *C. finmarchicus, Pseudocalanus spp.*, and *Centropages typicus* abundances. High abundances of these species do not necessarily correspond to high right whale abundances because right whales feed in areas where prey is highly concentrated (i.e., in areas of local patchiness) (Baumgartner et al., 2003). Therefore, rather than hypothesizing a direct effect of local zooplankton on local right whale abundance, we hypothesized that the influence of local zooplankton abundance on local right whale abundance was mediated by local zooplankton patchiness. Local-scale zooplankton patchiness was represented by the ratio of peak zooplankton density to the monthly averaged zooplankton density (Table 1). We also tested whether stronger stratification would cause increased zooplankton patchiness.

2.2. Missing data

If a variable was missing a monthly value, we explored other sources of data to complete the time series (e.g., other sensors or sampling programs). First, we used linear regressions between pairwise sets of data. If the regressions showed a 1:1 relationship between data sets, missing monthly values were extracted from the second data set. Otherwise, we estimated the missing monthly values using regression imputation. If a relationship was not found in the regressions, or there were no additional potential data sources, we used a Kalman filter to interpolate the missing monthly values (Cowpertwait and Metcalfe, 2009). To obtain missing monthly regional chlorophyll *a* values, data from two sensors were required. The bias between the sensors varied by month; to calculate a bias correction specific to each month we used an interaction effect in the linear regression.

2.3. Modeling

We used a mixed-model SEM, with a random intercept for each year, to test for direct and indirect effects on monthly local right whale abundance. We tested goodness-of-fit using Fisher's C tests (Shipley, 2009) in the *piecewiseSEM* package (Lefcheck, 2016) in R (R Core Team, 2021). We used d-separation (Shipley, 2009) to test for conditional independence and updated the a priori model (Fig. 2) when the model did not fit adequately (i.e., $p < 0.05$).

Historically, SEMs used global estimation to solve all equations in the model simultaneously. Global estimation assumes normality for all variables used in the model (Grace and Keeley, 2006). Alternatively, fitting piecewise SEMs allows the assumption of normality to be relaxed. Piecewise SEMs are composed of many generalized linear mixed-effects models or "pieces" with a single response variable predicted by one or more explanatory variables. For example, in our final model, the piece that directly explained local right whale abundance included the basin-scale population size, regional spring transition date, local-scale zooplankton patchiness, and the interaction between month and regional *C. finmarchicus* (Fig. 2). When using piecewise SEM, each piece is modeled with a family that is appropriate for the distribution of the response variable (Table S.1) (Lefcheck, 2016). While the model structure was initially fit using likelihood methods, we refit the final model using a Bayesian hierarchical framework to incorporate prior knowledge about the system, obtain probabilistic estimates of parameters based on posterior distributions, and incorporate variables at multiple temporal scales (i.e., yearly vs. monthly covariates).

We used published studies to inform prior distributions for model slopes (Table S.1) and we based prior distributions for the intercepts on relevant data from sources that were not used for model fitting (Table 1; Table S.1 and S.2). We gave positive (negative)

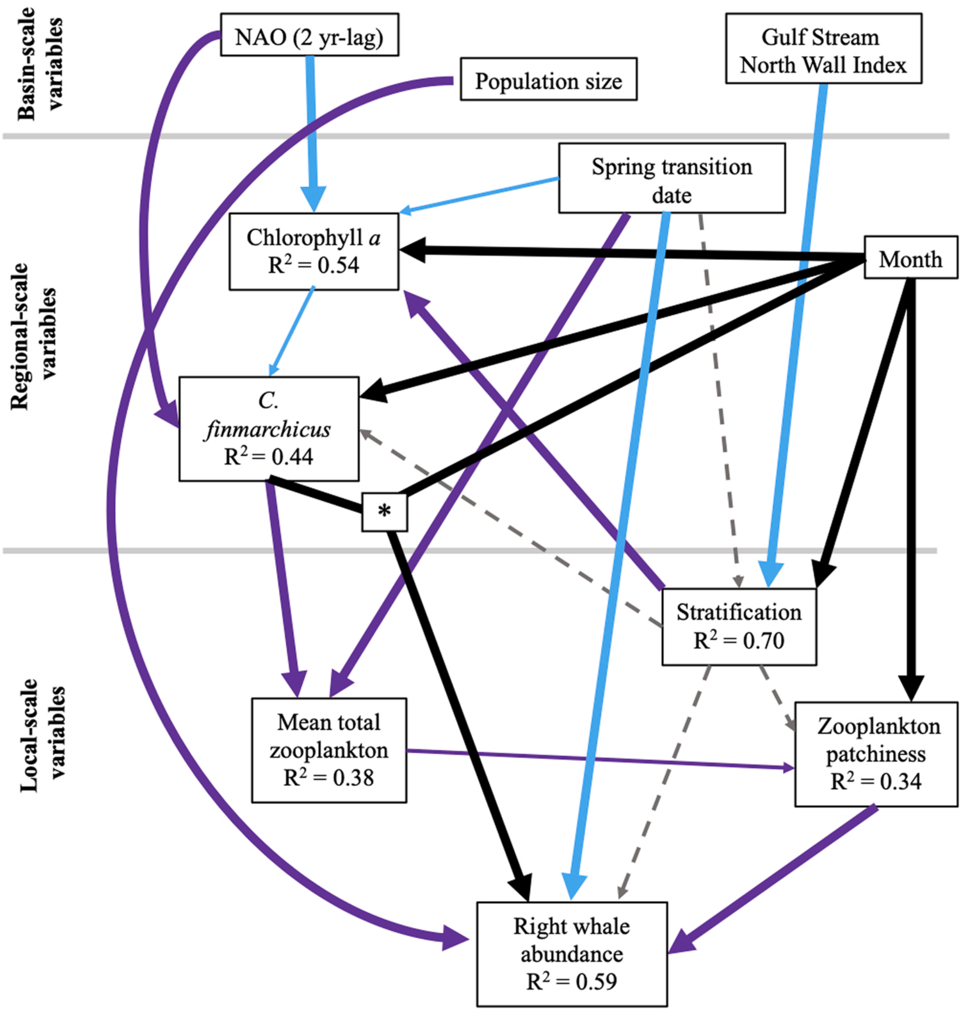

Fig. 2. Fit structural equation model (Fisher's C p = 0.919). Coefficients from thick, solid arrows have an effect at the 90 % credible interval, coefficients from thin arrows have an effect at the 80 % credible interval, and coefficients from thin dashed arrows indicate no effect at the 80 % credible interval. Blue arrows indicate a negative effect on the response, purple arrows indicate a positive effect, and black arrows indicate an effect that varies monthly. Solid, gray horizontal lines are used to separate the spatial scales. Bayesian R^2 values are included for each piece of the model. The white square with an asterisk indicates an interaction effect.

prior distributions for slopes when the relationships reported in the literature were positive (negative) over the range of the current data with the tail of the normal distribution including zero. The prior distribution included zero when we found conflicting relationships in the literature.

We fit the Bayesian model using the R package *brms* (Bürkner, 2017). We visually inspected trace plots and used Gelman-Rubin statistics to look for convergence. We used the Intergovernmental Panel on Climate Change (IPCC) likelihood terminology to describe the probability that the predictor variable had an effect on the response (Reay et al., 2007). We considered predictors that did not include 0 in the 90 % credible intervals (CIs) to have a very likely effect on the response. Coefficients represent the change in the response variable caused by a unit change in the predictor variables. Therefore, a coefficient greater than one indicated an increase in the response variable, a coefficient less than one indicated a decline, and a coefficient equal to one indicated no change.

We used the minimum and maximum values of the basin-scale NAO 2 yr-lag index, basin-scale GSNW index, and the regional-scale spring transition date to test for the cascading effects of these variables on local right whale abundance. We ran the fit SEM with the minimum and maximum values of the basin-scale NAO 2 yr-lag index, basin-scale GSNW index, and the regional-scale spring transition date to generate monthly predictions for the regional and local variables in the path between local right whale abundance and the NAO 2 yr-lag, the GSNW, and the regional spring transition date. We held variables that were not impacted by changing these variables at their means. For example, to measure the cascading effect of the regional spring transition date on local right whale abundance, we used the minimum and maximum regional spring transition date to generate two distributions of fitted predictions of regional chlorophyll *a* concentration values. We then used these regional chlorophyll *a* distributions to generate two distributions of fitted regional *C. finmarchicus* abundance values. We repeated this process until we generated two fitted distributions of local right whale abundance. These two distributions illustrate the difference in local right whale abundance caused by variations in the regional spring transition date.

We used the IPCC likelihood terminology to describe the probability that the difference between the predicted response distributions was greater than zero when using the maximum versus the minimum value of the predictor variable (Reay et al., 2007). An effect was described as virtually certain if there was a greater than 99 % probability that the difference between the predicted response distributions was greater than zero when using the maximum versus the minimum distribution of the predictor variable. An effect was

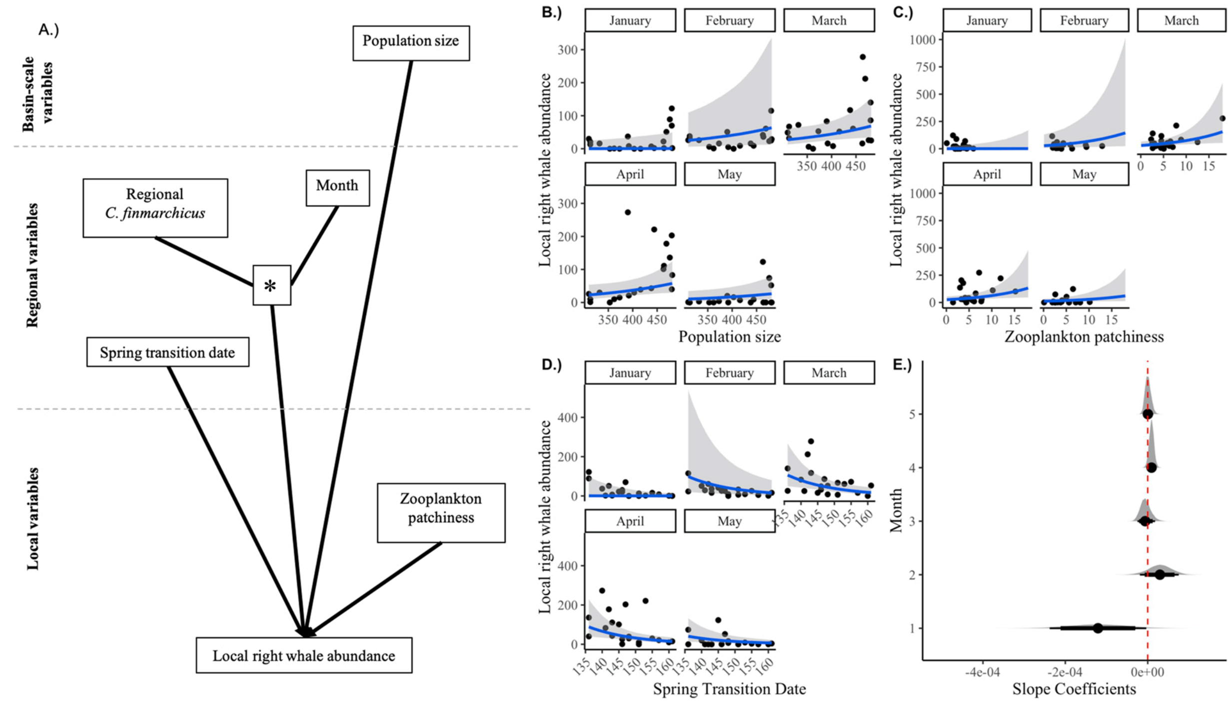

Fig. 3. A) Variables in the structural equation model that had a direct effect on local right whale abundance. Marginal effects, conditioned on the mean of the other predictors, of (B) basin-scale right whale population size ($\beta = 1.005$, 90 % credible intervals (CI) = 1.00–1.01), (C) local zooplankton patchiness ($\beta = 1.09$, 90 % CI = 1.02–1.18), and (D) regional spring transition date ($\beta = 0.929$, 90 % CI = 0.88–0.97). β coefficients are back transformed. Dots are raw data points; gray shading represents the 2.5 and 97.5 CIs. E) Posterior distribution of the interaction coefficients between month and regional *C. finmarchicus* density (shown as a white square with an asterisk) before back transformation. Thick black lines are 80 % posterior intervals, thin black lines are 90 % posterior intervals, and black dots are the medians of the posterior distributions. The red dashed line indicates a slope coefficient of 0; monthly distributions to the right of the red vertical line indicate a positive effect on the response variable, while distributions to the left indicate a negative effect. Back transformed 90 % CIs: January = 0.9997–0.9999, February = 0.99–1.00, March = 0.99–1.00, April = 0.99–1.00, May = 0.99–1.00. Coefficients for the interaction between regional *C. finmarchicus* and month are estimated with regional *C. finmarchicus* held at its mean. Variables that had no direct effect are not included.

described as extremely likely if there was a 95–99 % probability that the difference was greater than zero. An effect was described as very likely if there was a 90–95 % probability that the difference was greater than zero. An effect was described as likely if there was a greater than 66 % probability that the difference was greater than zero and an effect that was about as likely as not if there was a probability between 33 % and 66 % that the difference was greater than zero.

3. Results

Our *a priori* model (Supplemental Fig. S.1) required several modifications to achieve adequate goodness-of-fit. Specifically, we changed the 4 yr NAO lag to a 2 yr-lag, removed regional sea surface temperature anomalies due to collinearity with the regional spring transition date, and added a direct relationship between regional spring transition date and local right whale abundance. Most of the existing right whale literature indicates that any correlation between the NAO and right whales exists at a 2 or 4 yr-lag (Conversi et al., 2001; Greene et al., 2008; MERCINA, 2004, 2001; Pickart et al., 1999; Turner et al., 2006). Therefore, we fit the *a priori* model with the NAO 4 yr-lag. Our assessments of model fit suggested that the NAO 2 yr-lag had more explanatory power and this variable was used in the final model. The fit model is shown in Fig. 2. From this point forward, we only refer to the fit model.

3.1. Direct effects on local right whale abundance

As the size of the entire right whale population (a basin-scale variable) increased, local right whale abundance increased (Fig. 3B). Local right whale abundance also increased with increasing local zooplankton patchiness (Fig. 3C) and earlier regional spring transition dates (Fig. 3D). In January, regional *C. finmarchicus* density had a negative effect on local right whale abundance, while in April it had a positive effect (Fig. 3E). Local-scale water column stratification had no direct effect on local right whale abundance (90 % CIs of coefficient = 0.42–1.30).

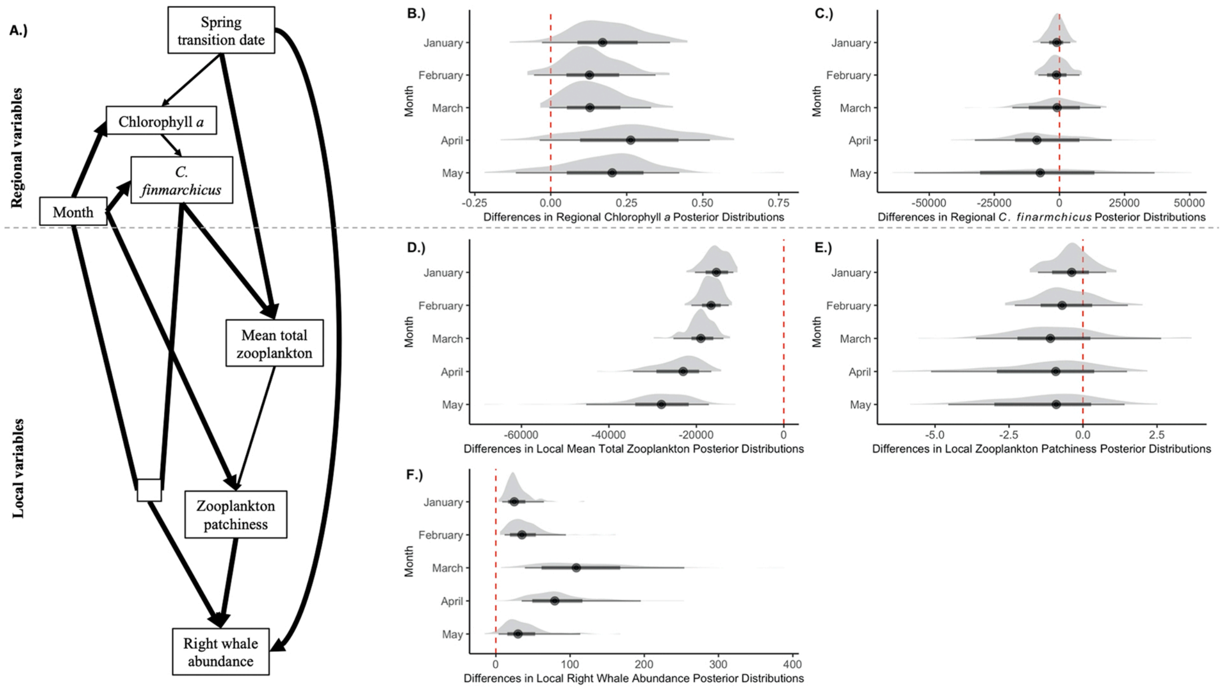

Fig. 4. Cascading effect of regional spring transition date on local right whale abundance. A) The pathways showing the cascading relationships among variables. Distributions of the difference between the marginal distribution of fitted predictions for the minimum and maximum regression lines explaining (B) the direct effect of the regional spring transition date on regional chlorophyll *a* concentration, (C) the indirect effect of the regional spring transition date on regional *C. finmarchicus* density, using regional chlorophyll *a* predictions, (D) the direct and indirect effect of the regional spring transition date on local-scale mean total zooplankton density, using regional *C. finmarchicus* density predictions, (E) the indirect effect of the regional spring transition date on local-scale zooplankton patchiness, using local zooplankton density predictions, (F) the direct and indirect effect of the regional spring transition date on local right whale abundance, using local zooplankton patchiness predictions and an interaction (shown as a white square with an asterisk) between month and regional *C. finmarchicus* density. Thick black lines are 66 % posterior intervals, thin black lines are 95 % posterior intervals, and black dots are the medians of the posterior distributions. Red dashed lines indicate the slope coefficient of 0; monthly distributions to the right of the red dashed lines indicate a positive effect on the response variable while distributions to the left indicate a negative effect. The probability that the difference in the posterior distributions between the maximum and minimum regional spring transition date was greater than zero for each variable in the chain can be found in Table S.3.

3.2. Cascading effects on local right whale abundance

3.2.1. Regional spring transition date

To test the cascading effect of the regional spring transition date on local right whale abundance, we calculated the probability that the difference in the posterior distributions was greater than zero between the maximum and minimum regional spring transition date for each variable in the chain (Table S.3). It is likely to extremely likely that years with the earliest regional spring transition dates had higher regional chlorophyll *a* concentrations (Fig. 4B, Table S.3). It was likely or about as likely as not that regional *C. finmarchicus* density was lower in years with the earliest regional spring transition dates (Fig. 4C). It is virtually certain that years with the earliest regional spring transition dates had lower local total zooplankton density (Fig. 4D), and it is likely that they had weaker local zooplankton patchiness (i.e., the local peak zooplankton concentration was similar to the local background concentration of zooplankton) (Fig. 4E). It was extremely likely to virtually certain that years with the earliest regional spring transition dates had higher local right whale abundances (Fig. 4F).

3.2.2. NAO 2 yr-lag

To test the cascading effect of the NAO 2 yr-lag on local right whale abundance we calculated the probability that the difference in the posterior distributions between the maximum and minimum NAO 2 yr-lag was greater than zero for each variable in the chain (Table S.4). In years with the highest NAO 2 yr-lag indices, it is very to extremely likely that regional chlorophyll *a* concentrations were lower (Fig. 5B, Table S.4), it is extremely likely that regional *C. finmarchicus* density was higher (Fig. 5C), and likely that local zooplankton density was higher (Fig. 5D). Higher local zooplankton patchiness was about as likely as not to be associated with years with the highest NAO 2 yr-lag indices (Fig. 5E). The influence of the NAO 2 yr-lag index on local right whale abundance depended on month. In years with the highest NAO 2 yr-lag indices it is very likely in January and likely in March that local abundance was lower, while it is likely that local abundance was higher in February and April (Fig. 5F). Years with the highest NAO 2 yr-lag indices were about as likely as not to have higher local abundance in May.

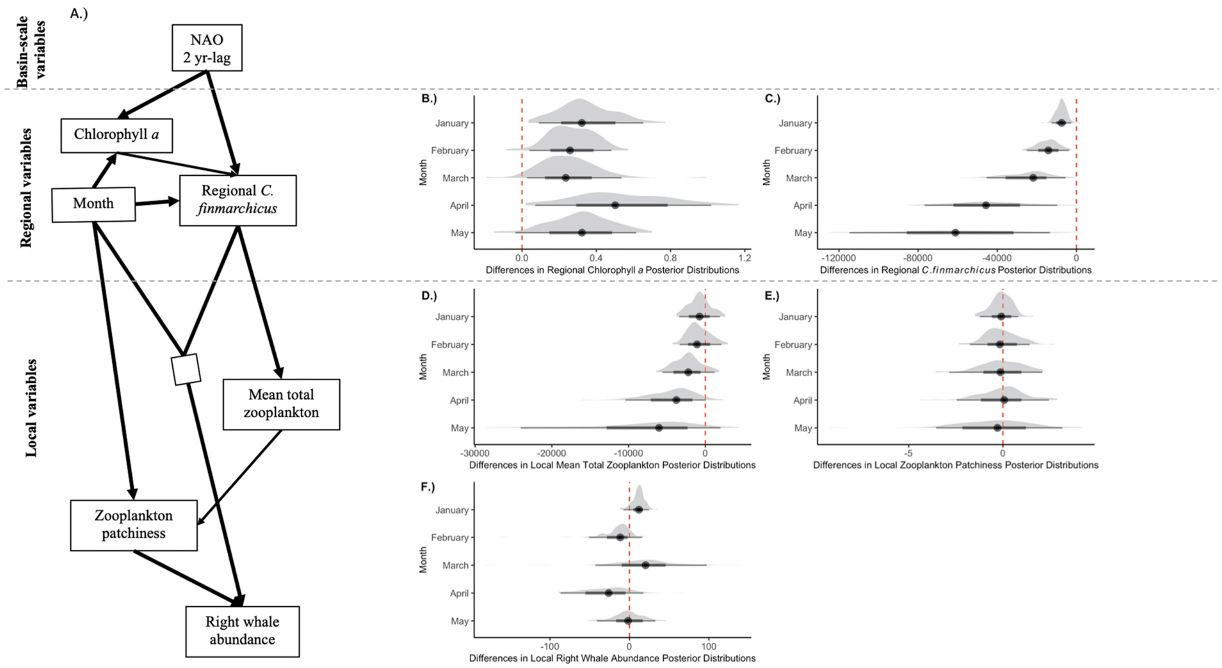

Fig. 5. Cascading effect of NAO 2 yr-lag on local right whale abundance. A) The pathways showing the cascading relationships among variables. Distributions of the difference between the marginal distribution of fitted predictions for the minimum and maximum regression lines explaining (B) the direct effect of the NAO 2 yr-lag on regional chlorophyll *a* concentration, (C) the direct and indirect effect of the NAO 2 yr-lag on regional *C. finmarchicus* density, using regional chlorophyll *a* concentration predictions, (D) the indirect effect of the NAO 2 yr-lag on local zooplankton density, using regional *C. finmarchicus* density predictions, (E) the indirect effect of the NAO 2 yr-lag on local zooplankton patchiness, using local zooplankton density predictions, (F) the indirect effect of the NAO 2 yr-lag on local right whale abundance, predictions from the interaction (shown as a white square with an asterisk) between month and regional *C. finmarchicus* density and local zooplankton patchiness. In each figure, all of the variables in the model are held at their mean. Thick black lines are 66 % posterior intervals, thin black lines are 95 % posterior intervals, and black dots are the medians of the posterior distributions. Red dashed lines indicate the slope coefficient of 0; monthly distributions to the right of the red dashed lines indicate a positive effect on the response variable while distributions to the left indicate a negative effect. The probability that the difference in the posterior distributions between the maximum and minimum NAO 2 yr-lag was greater than zero for each variable in the chain can be found in Table S.4.

3.2.3. Gulf Stream North Wall Index

To test the cascading effect of the GSNW on local right whale abundance we calculated the probability that the difference in the posterior distributions between the maximum and the minimum GSNW index was greater than zero for each variable in the chain (Table S.5). It is extremely likely to virtually certain that years with the lowest GSNW latitudes, compared to years with the highest GSNW latitudes, had stronger local stratification in all months (Fig. 6B, Table S.5). It is also likely that they had higher regional chlorophyll *a* concentrations in January, April and May, and were about as likely as not to have higher concentrations in February and March (Fig. 6C). Variations in GSNW latitudes did not affect regional *C. finmarchicus* density, local-scale zooplankton density, local zooplankton patchiness, and local right whale abundance (Fig. 6D–G).

3.3. Intermediary model pieces

Higher local zooplankton density led to an increase in the degree of local zooplankton patchiness (Fig. S.3B). Local patchiness increased over the season until May, when it decreased (Fig. S.3C). Regional-scale *C. finmarchicus* density was lower when regional chlorophyll *a* concentration was higher (Fig. S.4B) and was higher when the NAO 2 yr-lag was higher (Fig. S.4C). Regional-scale *C. finmarchicus* density also varied by month, with increasing density as the season progressed (Fig. S.4D). Local stratification was affected by month with January – April having low levels and May having high levels (Fig. S.5C). Regional chlorophyll *a* concentration was lower when the NAO 2 yr-lag index was higher (Figs. S.6A and S4B), and when the regional spring transition date was later (Fig. S.6C). Regional chlorophyll *a* concentration was higher when the local water column was more strongly stratified (Fig. S.6D), and was higher in April, relative to other months (Fig. S.6E).

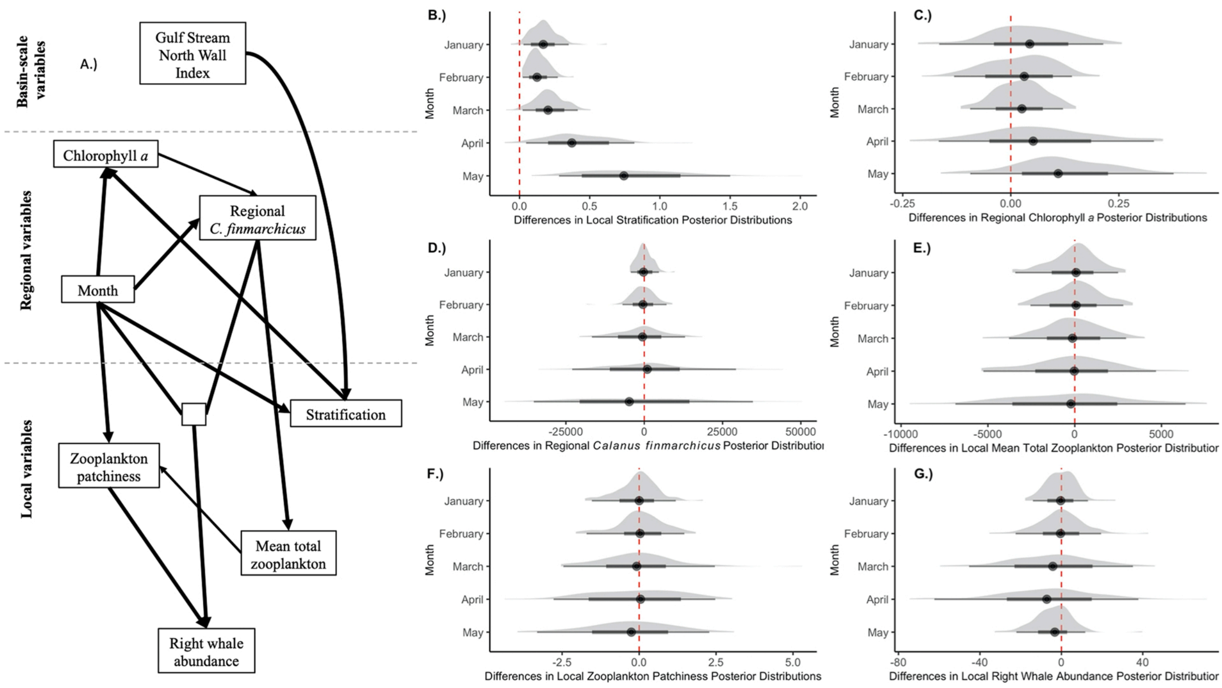

Fig. 6. Cascading effect of the Gulf Stream North Wall Index on local right whale abundance. A) The pathways showing the cascading relationships among variables. Distributions of the difference between the marginal distribution of fitted predictions for the regression lines explaining (B) the direct effect of the Gulf Stream North Wall Index on local stratification, (C) the indirect effect of the Gulf Stream North Wall Index on regional chlorophyll *a* concentration, using local stratification level predictions, (D) the indirect effect of Gulf Stream North Wall Index on regional *C. finmarchicus* density, using regional chlorophyll *a* concentration predictions, (E) the indirect effect of the Gulf Stream North Wall Index on local mean total zooplankton density, using regional *C. finmarchicus* density predictions, (F) the indirect effect of the Gulf Stream North Wall Index on local zooplankton patchiness, using local mean total zooplankton density predictions, (G) the indirect effect of the Gulf Stream North Wall Index on local right whale abundance, using predictions from an interaction (shown as a white square with an asterisk) between month and regional *C. finmarchicus* density and local zooplankton patchiness predictions. In each figure, all of the variables in the model are held at their mean. Thick black lines are 66 % posterior intervals, thin black lines are 95 % posterior intervals, and black dots are the medians of the posterior distributions. Red dashed lines indicate the slope coefficient of 0; monthly distributions to the right of the red dashed lines indicate a positive effect on the response variable while distributions to the left indicate a negative effect. The probability that the difference in the posterior distributions between the maximum and minimum Gulf Stream North Wall Indices was greater than zero for each variable in the chain can be found in Table S.5.

4. Discussion

We used twenty years of prey and oceanographic data to explore the effects of basin-scale variables (NAO and GSNW indices) and climate change (regional spring transition date) on right whale abundance in Cape Cod Bay (local right whale abundance). This exploration was conducted using a SEM because SEMs can be used to evaluate hypotheses about the mechanistic drivers of habitat use. In particular, SEMs represent networks of variables and can be used to test the cascading effects of variables through ecosystems and the ultimate influence of these effects on species distributions. Identifying the environmental variables associated with the increased use of Cape Cod Bay by right whales may help to identify other areas of novel or increased right whale habitat use.

Our SEM identified the regional spring transition date as a major driver of variations in local right whale abundance. In particular, we found a direct and indirect effect of regional spring transition date on local right whale abundance. The direct effect of regional spring transition date resulted in years with earlier regional spring transition dates having higher local right whale abundance. The indirect effect of spring transition date on local right whale abundance occurred through the cascading effect of chlorophyll *a*, prey density, and prey patchiness on local right whale abundance. Years with earlier spring transition dates had lower prey densities (i.e., local-scale total zooplankton density) and weaker local zooplankton patchiness, which would be expected to result in lower local right whale abundances. The direct and indirect effects of regional spring transition date were antagonistic on local right whale abundance, but because of the stronger direct effect local right whale abundance was higher.

Identifying and understanding the competing direct and indirect effects of spring transition date on local right whale abundance was possible because we tested our hypotheses using a network of variables, rather than assuming a univariate relationship between local right whale abundance and spring transition date. However, we did not initially expect a direct effect of regional spring transition date on local right whale abundance, and our *a priori* causal structure only included an indirect effect. We added the direct effect after the test of d-separation revealed that this relationship was not conditionally independent. Therefore, our regional spring transition date results could indicate a direct causal relationship, meaning right whales are responding to changes in temperature (discussed below). Alternatively, right whales might be responding to an unobserved variable that changes with temperature (indirect cause). Or the relationship could be spurious, if we have omitted a confounding variable.

The strong, direct effect of the regional spring transition date on local right whale abundance could indicate that right whales are using regional temperature as a cue for migratory movements and movements between habitats, as hypothesized by Kenney et al. (2001). When the spring transition date occurs earlier, the temperature cue directing right whales to Cape Cod Bay occurs earlier, which extends the period of high habitat suitability in Cape Cod Bay. This process may help explain the phenological shift found by Pendleton et al. (2022) indicating that the day of peak habitat use of Cape Cod Bay by right whales has shifted almost three weeks later since 1998. Numerous studies have connected changes in cetacean distribution and migratory timing to changes in sea surface temperature and sea ice cover (Hauser et al., 2017; Heide-Jørgensen et al., 2010; Ramp et al., 2015). For example, humpback and fin whale migrations to and from their summer feeding grounds in the Gulf of St. Lawrence are occurring earlier. Fin whale arrival dates, correlated with ice break up and sea surface temperature, are shifting faster than departure dates leading to longer fin whale residencies in this region (Ramp et al., 2015). In the Gulf of Maine, several studies have documented earlier diadromous fish migrations that are associated with warming water temperatures (Ellis and Vokoun, 2009; Juanes et al., 2004; Otero et al., 2014; Staudinger et al., 2019). If the direct relationship between right whales and regional spring transition date occurs in future years and spring onset continues to occur earlier, we would expect a further increase in local abundance, conditional on the size of the entire population.

There are two hypotheses that can explain the relationship between regional *C. finmarchicus* density and local right whale abundance. The first hypothesis assumes that high regional *C. finmarchicus* densities attract right whales to other good feeding habitats, which lowers local right whale abundance (i.e., the abundance in any particular habitat). The second hypothesis, which we call the habitat linkage hypothesis, suggests that high regional *C. finmarchicus* leads to high local-scale zooplankton density and, subsequently, high local right whale abundance. Based on our current model structure and available data, we were unable to distinguish between the two hypotheses. If the competition between Cape Cod Bay and neighboring habitats was the sole driver of local right whale abundance, we would expect high regional-scale *C. finmarchicus* to lead to low local right whale abundance and higher right whale abundance in the surrounding, good feeding habitats. Instead, depending on the month, we found elevated local right whale abundance when regional-scale *C. finmarchicus* density was high. The habitat linkage hypothesis proposes that high regional *C. finmarchicus* leads to high local-scale zooplankton density, and therefore high local right whale abundance. We found that high regional *C. finmarchicus* abundance causes high local zooplankton abundance but we found that months with low local zooplankton abundance can still have high local right whale abundance. Our SEM suggests that this result was likely an outcome of the direct effect of the regional spring transition date on local right whale abundance. This influence of the direct effect of regional spring transition date on local right whale abundance is an important potentially negative effect of climate change. If lower local zooplankton abundance causes right whales to reduce their use of Cape Cod Bay, it could lead to further large-scale distribution changes. Alternatively, the potential for earlier regional spring transition dates to cause lower local zooplankton abundance and higher local right whale abundance could lead to a mismatch between predator and prey. Declines in the health of individual right whales have been observed in recent years (Stewart et al., 2021) and could be an earlier warning of mismatch with their prey. In particular, it is possible that these declines are a result of the increased use of Cape Cod Bay by right whales during years of early regional spring transition dates and lower local zooplankton concentrations.

The NAO 2 yr-lag is linked to Gulf of Maine *C. finmarchicus* density (i.e. regional *C. finmarchicus* density) through the control that the NAO exerts on ocean circulation patterns (Greene et al., 2008; MERCINA, 2004, 2001; Pickart et al., 1999). Similar to Greene et al. (2003), who found a positive correlation between the NAO and *C. finmarchicus* density, we found a positive effect of the NAO 2 yr-lag on regional *C. finmarchicus* density (Fig. S.4C). But by quantifying the cascading effects, we found that the NAO 2 yr-lag has both a negative indirect effect on regional *C. finmarchicus* (through the influence of the NAO on regional chlorophyll *a*) and a positive direct effect. The complicated ecological interpretation of the NAO 2 yr-lag on local right whale abundance indicates that this driver needs further study prior to drawing causal conclusions. Many studies have described opposing, often regionally dependent, relationships between the NAO and regional-scale *C. finmarchicus,* but synthesizing the conclusions of these studies is difficult due to varying time lags, the magnitude of phase change in the NAO, and different *C. finmarchicus* sampling protocols (MERCINA, 2004, 2001; Turner et al., 2006).

Our results indicate that an interaction between regional-scale *C. finmarchicus* density and month mediates the relationship between basin-scale forces (the NAO 2-yr lag) and local right whale abundance. While month had an important effect on local right whale abundance, it is likely acting as a proxy for one or more variables that were not included in our SEM. Depending on the variables that month represents, the relationship between a specific month and local right whale abundance may be dynamic as the climate continues to change. For example, the progression of water temperatures throughout the winter and spring will continue to change. Consequently, conditions that were previously typical of April may be more typical of March in the future. Future studies should consider the impact of summarizing data over large spatial (Fig. 1A) and temporal scales (i.e. month). The large spatio-temporal scales used in our study may have removed smaller-scale environmental cues that right whales use for habitat selection. For example, representing local zooplankton patchiness by a monthly average may not provide an adequate reflection of the prevalence of small ephemeral patches, which are likely an important cue for right whale habitat selection.

We used a causal modeling approach (SEM) to explore the direct and indirect influence of ecosystem variables on local right whale abundance. The SEM demonstrated the potential for hierarchical mechanistic models to detect 1) drivers of prey aggregations; 2) causal relationships between focal species and prey distributions; and 3) causal relationships between focal species and environmental variables. In particular, we found that climate change, represented by an earlier onset of the spring thermal transition date in the Gulf of Maine, cascades through an inter-connected network of variables. However, this cascading effect is overwhelmed by the direct effect of regional spring transition date on local right whale abundance. The SEM also suggests that right whales could face a mismatch with their prey. Specifically, our SEM suggests that earlier regional spring transition dates were associated with a decrease in right whale prey and an increase in local right whale abundance, possibly by influencing right whale thermal migration cues. Alternatively, right whales could detect the decline in zooplankton in Cape Cod Bay and abandon this habitat for another, more suitable habitat. A similar chain of events likely occurred when right whales abandoned the traditional Gulf of Maine summer and fall habitats for the Gulf of St. Lawrence. Ultimately, these cascading changes resulting from earlier regional spring transition dates could result in another large-scale shift in right whale habitat use.

Our SEM suggests we need to identify the mechanisms underlying species habitat use patterns to understand and forecast potential impacts of climate change on species distributions (e.g., Silber et al., 2017). Traditionally, a randomized control trial is required to draw causal inference. However, randomized control trials are impossible for large migratory animals, such as right whales. Instead, correlative habitat models have been used to predict species distributions (Becker et al., 2019; Pendleton et al., 2012, 2020; Roberts et al., 2016). These correlative habitat models have also been used to successfully forecast novel conditions at scales of a single day, several months, or a year (e.g., Becker et al., 2012, 2019). This success may occur because the correlative relationships have remained constant over the forecasted periods. However, it is possible that these relationships will change over longer time scales, particularly if the correlative relationships do not capture the mechanisms underlying species habitat use patterns (Cribb et al., 2015). To understand longer-term, climate-driven changes in species distributions we need to combine causal models, such as the SEM we developed for right whales, with species distribution models. Combining species distribution models with structural equation modeling has successfully been used in other habitats to understand food web dynamics over large spatial and temporal scales (Sivy et al., 2017). A combined modeling approach for right whales could allow the expansion of our model to other seasons and parts of the right whale range. Successful endangered species conservation in a changing climate requires identifying the mechanisms causing species distribution patterns (Silber et al., 2017; Wilson et al., 2021).

Data accessibility

North Atlantic right whale sightings data are available from the North Atlantic Right Whale Consortium upon request and review. All of the data sources and information about how to obtain the data used in these analyses are described in Table 1.

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CRediT authorship contribution statement

Laura Ganley: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration. **Jarrett Byrnes:** Methodology, Writing – review & editing. **Daniel Pendleton:** Conceptualization, Writing – review & editing. **Charles A. Mayo:** Data curation, Investigation, Writing – review & editing. **Kevin Friedland:** Data curation, Investigation, Writing – review & editing. **Jessica Redfern:** Writing – review & editing, Funding acquisition. **Jefferson Turner:** Data curation, Investigation, Writing – review & editing. **Solange Brault:** Conceptualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02193.

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