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Adaptive approaches are needed to effectively manage dynamic marine systems, and ecological forecasts can help managers anticipate when and where conservation issues are likely to arise in the future. The recent development of subseasonal global environmental forecasts provides an opportunity to inform management by forecasting species distributions in advance over operational timeframes. We demonstrate the utility of environmental forecasts for managing marine mammals by integrating species distribution models with subseasonal forecasts to predict the arrival of migratory humpback whales (Megaptera novaeangliae) at foraging grounds in the Northeast US. Environmental forecasts showed high model skill at lead times of up to 2 weeks and resulting humpback whale models performed well in predicting humpback arrival. Forecasts of whale distribution can shape management efforts to minimize both impacts on whales and economic costs. Applying subseasonal forecasts to anticipate future risk presents a powerful tool for the dynamic management of marine mammals.

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ffective management of populations threatened by anthropogenic impacts is particularly challenging in marine environments, which are highly dynamic and difficult to observe (Maxwell et al. 2015; Hobday et al. 2016). In both marine and terrestrial systems, spatial management targets regions of high risk for anthropogenic impacts (Maxwell et al. 2015). Static management approaches have proven problematic or ineffective in marine environments, particularly for highly migratory species (Lascelles et al. 2014; Dunn et al. 2016) or for species undergoing distributional shifts due to climate change (Lascelles et al. 2014). Dynamic management can improve management outcomes by adjusting the spatial and/ or temporal extent of an area of concern (Dunn et al. 2016). However, implementation of dynamic management where managers make decisions about the future requires anticipating when and where conservation risks are likely to arise (Clark et al. 2001; Lascelles et al. 2014; Dietze et al. 2018). Ecological forecasting tools that use environmental data are one way to anticipate future conservation risks.

Environmental data have been previously used to inform dynamic management by integrating recent environmental conditions into distributional models of marine species (Becker et al. 2016; Dunn et al. 2016; Hazen et al. 2016). In

these applications, the most recent available satellite-derived measurements of environmental conditions, also known as "near real-time data", are used to predict distributions of species of concern in the immediate future (Hazen et al. 2016). Although this approach is useful for making predictions over would allow managers to better anticipate conservation risks. However, an alternative approach, commonly referred to as "ecological forecasting", can inform future risk by incorporating species distribution models into forecasts that predict future environmental variables (Clark et al. 2001; Dietze et al. 2018).

To date, ecological forecasts using environmental data have primarily focused on seasonal time scales (Kaplan et al. 2016). While this work is key to understanding trends on the order of weeks to months, subseasonal forecasts - those that generate predictions over one to several weeks - may be needed to inform certain management decisions (Hobday et al. 2016; Dietze et al. 2018; Jacox et al. 2020). Accurate subseasonal forecasts have been historically difficult to produce, but recent developments have bridged the gap between short-term weather forecasts and monthly (or longer) climate projections (Mariotti et al. 2020). The Subseasonal Experiment (SubX) is a National Oceanic and Atmospheric Administration (NOAA) Climate Test Bed project that provides novel subseasonal global forecasting products for multiple global models by forecasting atmospheric and ocean variables at weekly-to-monthly time scales, which are typically difficult to resolve. SubX is unique compared to traditional weather forecasting models because it combines (1) more frequent model initialization, defined as how often a new model is generated; and (2) longer forecast lead times, which describes the amount of time forecasted into the future from the model initialization date

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(Pegion *et al.* 2019). SubX models are publicly available and the forecast is provided in near real-time, which allows for immediate integration with ecological models, and could yield a powerful forecasting tool for dynamic management by anticipating times and places of conservation concern over a weekly timeframe.

Here, we assess the potential for subseasonal forecasts to inform and improve the management of marine mammal populations. Marine mammals are highly mobile and many are impacted by anthropogenic activities such as fisheries bycatch, vessel strikes, and entanglement in fishing gear (Avila *et al.* 2018). Dynamic factors such as temperature and variability in prey distribution can drive changes in the distribution of marine mammal species (Davies *et al.* 2019), which can render static management approaches ineffective (Lascelles *et al.* 2014). Using ecological forecasting to predict future spatial distributions of marine mammals over subseasonal time-frames could improve management efforts.

We use humpback whales (Megaptera novaeangliae) in the Northeast US (NEUS) as a case study to assess the utility of subseasonal forecasts for dynamic management of marine mammal populations. The NEUS is heavily impacted by commercial and recreational fishing, major shipping ports, and recent offshore wind developments. Humpback whales typically undergo seasonal migrations between low-latitude winter breeding grounds and high-latitude foraging grounds including the NEUS (Stevick et al. 2006). Currently, management concerns are focused on anthropogenic mortality of multiple populations of large whales that forage in the NEUS, such as minke whales (Balaenoptera acutorostrata), North Atlantic right whales (Eubalaena glacialis), and humpback whales (Avila et al. 2018). Current mitigation efforts include fishing gear modifications or restrictions and vessel slowdown zones: large vessels are required to reduce speed in seasonal static management areas (SMAs) or are recommended to reduce speed in triggered-closure dynamic management areas (DMAs) when North Atlantic right whales are present (NOAA 2014). We assess the potential for forecasting humpback whale arrival into NEUS foraging grounds by (1) modeling historical variability in the timing of arrival in the NEUS and SMAs using a distribution model; (2) forecasting arrival by integrating the distribution model with SubX forecasts; and (3) assessing the performance of humpback whale density forecasts relative to the performance of density predicted using traditional satellite-derived sea-surface temperature (SST) measurements to assess if forecasts can maintain a high level of model performance.

Methods

Creation of the humpback whale density model

To create a humpback whale density model that could be integrated with the SubX forecast data, we first prepared estimated abundances of humpback whales from line transect survey data following distance sampling protocols (Hedley and Buckland 2004). Line transect surveys were conducted in the NEUS from aerial and shipboard platforms by the University of North Carolina Wilmington, the Northeast Fisheries Science Center, the New Jersey Department of Environmental Protection, and the Virginia Aquarium and Marine Science Center from 1995 to 2016, under appropriate federal permits. The data were prepared for density surface modeling by Roberts *et al.* (2016) by splitting vessel and aerial survey tracklines into approximately 10 km segments, fitting detection functions, and correcting availability and perception bias to estimate per-segment abundances of humpback whales (see Roberts *et al.* [2016] for details).

To build density models, we fit generalized additive models (GAM) to the segment abundances using relevant environmental covariates with a log-link and the segment area as an offset (WebTable 1; Figure 1). We assessed collinearity using the variance inflation factor (VIF), with covariates removed from the analysis if their VIF was below 3.0 (Zuur et al. 2009). In addition, any paired covariates that displayed a detectable nonlinear relationship or a Pearson correlation coefficient ≥ 0.6 or ≤ -0.6 were not included in the same model (Mannocci et al. 2017). To eventually integrate the humpback density model with SubX data, we were restricted to using environmental covariates in the model that were either static (for example, distance to the coastline) or dynamic covariates that can be predicted by SubX (SST and variables derived from SST; WebTable 1). We fit models using the mgcv package in R (R Core Team 2019) using thin plate regression splines with shrinkage (Marra and Wood 2011), a maximum of 5 knots (Hazen et al. 2016), a Tweedie distribution (Shono 2008), and restricted maximum likelihood (REML). To capture species-environment relationships that were indicative of the northward migration into foraging grounds, we used data from weeks 10 (starting on March 4) to weeks 34 (starting on August 25) of each year when humpback whales are migrating into the NEUS (875,116 km of survey effort, 2964 sightings of humpbacks, and 4870 individual whales during years 1995-2016; WebFigure 1). We conducted backward model selection, and assessed GAM outputs by selecting the GAM with the lowest Akaike's information criterion (AIC; Hazen et al. 2016; Palka 2020). All candidate covariates are defined in WebTable 1. The final model included satellite SST, spring onset (6°C threshold), the natural log of depth, and distance to shore (Figure 1; WebPanel 1). To evaluate whether model performance varied seasonally, we used 6-fold cross-validation, where each month of the study period was a fold. Each fold was assessed using deviance explained (Becker et al. 2010, 2016).

This density model of humpback whales was then integrated with either satellite SST or SubX forecasted SST. We first predicted weekly mean humpback density (abundance per 100 km²) in the US and Canadian Exclusive Economic Zones using grids of satellite SST as well as the static variables that were used to initially build the model (Becker *et al.* 2010; Roberts



Figure 1. Workflow of the distribution model and sea-surface temperature (SST) forecast integration. (a) Daily SST forecasts from one of the seven SubX global models (namely, the NCEP-GEFS [National Centers for Environmental Prediction–Global Ensemble Forecast System] global model) are selected for the Northeast US. (b) Species–environment relationships for humpback whales (*Megaptera novaeangliae*): the natural log of depth, distance to shore, satellite SST, and spring onset (6°C threshold). (c) The SST forecast is then integrated with the species–environment relationships to forecast species density. Here we demonstrate a forecast of humpback whale density with a 2-week lead time and highlight the location of five static seasonal management areas (Massachusetts, Block Island Sound, New York Harbor, Delaware Bay, and Chesapeake), where vessel speed reductions are implemented in migratory months of North Atlantic right whales (*Eubalaena glacialis*).

et al. 2016). We then examined the spatial and temporal variability of this prediction, which we termed the "standard humpback prediction", to assess whether our model could detect humpback whale arrival on the foraging grounds at a weekly scale from March to August of each year from 1995 to 2016 in the Massachusetts SMA, and in each of the five SMAs in the NEUS. We then created a "humpback forecast" for the same time period by integrating the density model with weekly SubX SST forecasts that were developed 1- to 2- weeks in advance (described below), rather than satellite SST, to create weekly spatial forecasts of humpback whale density.

Assessment of SubX models in the NEUS

The SubX project (Pegion *et al.* 2019) produces subseasonal forecasts of environmental and atmospheric variables from seven global models with a minimum lead time of 32 days and a minimum of weekly initialization (WebPanel 2; Pegion *et al.* 2019). The global SubX models have been initialized in historical conditions (1999–2015) to create a hindcast that can be used for model validation and bias correction, as well as in recent years (since 2017) to create a forecast that is updated in real time, where the model used in the hindcasts and forecasts is the same. Before integrating the SubX SST data and the humpback whale density model to

create a humpback forecast, we evaluated SubX forecast skill (ie accuracy) using a temporal anomaly correlation coefficient between SubX hindcasts and corresponding satellite SST observations over the 17-year hindcast period (1999–2015) to identify the most accurate SubX SST product for our study region. We assessed skill for three SubX models: NCEP-GEFS, NASA-GEOS5, and NCAR-CESM1 (WebPanel 2). We then downscaled the model with the highest skill from 1.0 to 0.2 decimal degrees using the delta method (Hare *et al.* 2012) to match the satellite SST resolution used to build the initial density model. Finally, we averaged daily forecasts by week, resulting in 5 weeks of forecast lead days (eg week 1 representing the average of 1- to 7-day forecast leads and week 2 representing 8- to 14-day leads).

Humpback forecast creation and assessment

We integrated our humpback whale density model with the downscaled SubX SST data to create ecological forecasts of humpback whale distributions at 1- and 2-week lead times, hereafter referred to as the "humpback forecast". We assessed the performance of both the humpback forecast and the standard humpback prediction for the same time period using ratios of observed-to-modeled density (Becker *et al.* 2010, 2016). We first built humpback forecasts using hindcasted SST data (where the SubX product is initiated on a historical date) from 1999 to 2015 to permit comparison between the line transect data, the standard humpback model, and the humpback forecast. To do this, we calculated ratios of observed monthly densities from line transect data between 1999 and 2015 (the majority of years covered by the line transect surveys) and the monthly densities from both the standard humpback prediction and the humpback forecast for this same time period. We examined whether ratios deviated more from 1 when humpback whale density surfaces were developed with SubX forecasts (the humpback forecast) rather than satellite-derived SST measurements (the standard humpback prediction) for each month forecasted.

Results

SubX surface temperature models in the NEUS

The SubX SST model skill decreased substantially after week 2 in the NEUS for the three SubX models we analyzed, especially in the highly dynamic Gulf Stream region (WebPanel 2). Because the NCEP-GEFS model showed the highest forecast skill on the continental shelf (WebPanel 2), we integrated the NCEP-GEFS SST product with the humpback whale distribution model to create the ecological forecast.

Performance of humpback whale models

The standard humpback whale predictions (Figure 2, a and b) reflected migration into the NEUS, with density progressively increasing from south to north between April and June (Figure 2, a and b), consistent with previous studies and models (Stevick et al. 2006; Roberts et al. 2016). Model validation indicated that both the humpback standard prediction and the humpback forecast performed better in April and May than in later months (June through mid-August), which suggests a strong ability to predict arrival at foraging grounds (Table 1). The ecological forecast performed relatively well when compared to the standprediction (Table however, ard 1); ratios of observed-to-predicted density overpredicted in March for both the standard prediction and ecological forecast, which could be due to the relatively low number of humpback whale sightings (Table 1). Overall, ratios were slightly closer to 1 for the standard prediction, reflecting a better fit with the data when the humpback whale density model was applied to SST observations rather than forecasts of future SST conditions (Table 1). However, ratios for the ecological forecast were generally close to 1 (1.11 and 1.07 for the forecasts with lead times of 1- and 2-weeks, respectively), suggesting that humpback whale forecasts produced using the SubX product maintained an overall high level of model performance.

The weekly standard humpback prediction highlighted considerable interannual variability in the timing of arrival (Figure 2, a and b). For example, the predicted peak humpback density in the Massachusetts SMA varied by 5 weeks between years, from the week starting on May 28 (observed in 2010 and 2012) to June 25 (in 2005), indicating that interannual variability is detectable at a weekly temporal scale (Figure 2a). The week of peak density shifted earlier throughout the study period, although this relationship was not statistically significant (Pearson's correlation -0.416; P = 0.068). The predicted peak humpback whale density in the five NEUS SMAs varied in both timing and density, suggesting that weekly forecasts built using this model could discern timing of potential risks to whales between SMAs in the NEUS at a weekly scale (Figure 2b).

A spatial output of the 2-week humpback forecast for a 3-week period of 2019 and 2020 demonstrated both inter- and intra-annual variation in forecasted humpback whale distribution. The density of humpback whales in 2019 was forecasted to be higher than in 2020 in the southern Gulf of Maine, but both years showed an increase in forecasted density between weeks (Figure 2c), demonstrating that model output could be used to inform timing of arrival.

Discussion

We developed habitat models that effectively captured the spatial and temporal variability in humpback whale distributions in NEUS foraging grounds and demonstrated that SubX forecast products could skillfully predict arrival time of humpbacks 1-2 weeks in advance. To our knowledge, this is the first application of subseasonal forecast products to predictive modeling efforts for marine mammals. Forecasts of future species density could allow managers to anticipate future risks and pursue dynamic management strategies. The within- and between-year variability observed in humpback whale spatial predictions combined with the high model skill of SubX SST forecasts indicate that developing subseasonal forecasts of marine mammal distributions presents a powerful tool for dynamic management. In the future, the humpback forecasts can be iteratively verified against real-time data in an adaptively managed approach to improve predictions and forecasting skill (Dietze et al. 2018).

Our humpback whale density forecast directly integrates species distribution models with environmental covariate forecasts to predict future density over time scales relevant to managers. We developed GAMs to elucidate species–environment relationships, but our forecasting methodology can also be applied to other statistical frameworks used to develop ecological models. This approach is advantageous because it could provide managers with predictions about the risk of threats to marine mammals (such as fisheries bycatch, vessel strikes, or entanglement) in the future, rather than relying on current environmental conditions to anticipate future distributions. Creating spatial predictions of future risk to marine mammal populations provides the opportunity to address threats before they occur (Dietze *et al.* 2018; Jacox *et al.* 2020). Presently, closures,



Figure 2. Spatial and temporal variability in weekly mean humpback whale densities in the Northeast US within and between years using (a, b) satellite SST and (c) SubX temperature forecasts. Panels (a) and (b) display modeled density outputs based on data collected in 1995 and from 1998 through 2016. (a) Between-year variability in the Massachusetts SMA. Peak abundance, depicted by vertical black lines, varied from May 28 to June 25. (b) Spatial variability averaged for all years was consistently lower and peaked earlier in three SMAs (namely, New York Harbor, Delaware Bay, and Chesapeake) located farther south than the Massachusetts SMA. (c) Example of humpback whale density forecast in the Gulf of Maine and southern New England at a 2-week lead time. Earlier warming in 2019 leads to earlier predictions of humpback arrival in comparison to 2020.

management, and threats are typically determined through monitoring, and management changes are triggered by previous detections of concerning events. For example, triggered closures rely on reaching a threshold of acoustic, aerial, or visual detections (NOAA 2014; Dunn *et al.* 2016). By integrating ecological forecasts into this framework, managers could determine when to begin survey efforts to detect marine mammals, or whether dynamic closures need to be enacted, triggered early, or extended. In addition, the adoption of ecological forecasts into the dynamic management framework could allow for management flexibility under climate-change scenarios. For instance, if humpback whales arrive earlier in the NEUS in conjunction with changes in SST, this could be detected with the ecological forecast and could be integrated into a dynamic management framework. Ultimately, forecasts provide time for stakeholders to adapt and plan for closures and avoid harmful interactions with marine mammals.

In the future, forecasts of marine mammal distributions could be used to inform management decisions, plan management interventions, or improve currently existing dynamic management efforts to minimize impacts on marine mammals as well as fishers or managers. For example, SMAs are implemented between November 1 and April 1 and DMAs are triggered by acoustic or visual detections of North Atlantic right whales, but the timing of migration has shifted over the past decade (Davies et al. 2019). For humpback whales, the historical peak densities in the Massachusetts, Block Island Sound, and New York Harbor SMAs are substantially later than the last day of the current SMA period and the timing of peak density is highly variable between years. The timing of SMA or DMA implementation could be tailored based on forecasted migration to ensure vessel speed reductions are in place during migratory periods, ensuring protection for the at-risk species while preventing unnecessary slowdowns and financial burdens on the shipping industry during non-migratory times. Furthermore, considerable offshore wind development is underway or planned throughout the NEUS, and risks to marine mammals stemming from construction and operation of these facilities include increased vessel traffic and acoustic impacts. Forecasts could inform high-risk times and locations for wind farms to avoid construction and reduce vessel traffic, which would minimize risk to marine mammals while preventing costly shutdowns. Finally, the location and timing of fishing effort could be shifted slightly to avoid areas of high forecasted overlap with high marine mammal

density. For example, the Maine American lobster (*Homarus americanus*) fishery is highly seasonal, with low landings in offshore waters in winter months and high landings inshore in the summer, which can be forecasted (Mills *et al.* 2017). A forecasting system to adjust the timing of gear shifts to inshore waters based on forecasted large whale migration into offshore waters could minimize gear–whale overlap and reduce entanglement risks and costs to fishers (Hobday *et al.* 2019).

Due to recent advances in forecasting weather, climate, and associated socioeconomic impacts, effort is now being directed to improve skill in the intermediate range between short-term weather forecasts and long-range seasonal

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Table 1. Input and performance of the density model, the standard humpback prediction (satellite-derived SST), and the humpback forecast (SubX surface temperature) at lead times of 1 and 2 weeks

Predictions of humnhack whale density

						(animals per 100 km ²)					
Segment information					Model output	Standard predi (satellite SST)		Forecast wk 1 (SubX temp)		Forecast wk 2 (SubX temp)	
Month	# seg	Area (km²)	# sight	Obs dens	Dev exp	Pred	Ratio	Pred	Ratio	Pred	Ratio
Mar	10,020	472,843	53	5.94	19.3%	23.17	0.25	21.83	0.27	22.23	0.27
Apr	14,219	747,312	391	36.81	22.0%	35.63	1.03	39.48	0.93	39.21	0.94
May	13,624	717,243	572	59.18	20.0%	59.98	0.99	61.86	0.96	61.93	0.95
Jun	14,623	798,654	835	78.68	23.3%	63.92	1.23	55.89	1.41	55.29	1.42
Jul	10,149	532,471	474	38.85	19.6%	24.95	1.56	12.02	3.23	12.66	3.07
Aug	9120	334,990	185	24.67	20.2%	26.74	0.92	19.10	1.29	19.22	1.28
All months	71,755	3,603,513	2510	4.36	20.6%	4.25	1.03	3.94	1.11	3.95	1.07

Notes: Each month represents one fold of the 6-fold cross-validation. Observed and predicted values were calculated across the test dataset for each month by comparing the sum of total humpback whale density from line transect sightings (assumed observed value) to the predicted humpback whale density estimated by the model for each cross-validation and each month. The standard humpback prediction model, run for all months combined, is described in the bottom row. Ratios refer to the ratio of observed to predicted values of humpback whale density (animals per 100 km²). Wk = week; # seg = number of segments; # sight = number of sightings; Obs dens = observed density; Dev exp = deviance explained; Pred = predicted density.

forecasts. The forecast products used in our analysis will therefore likely improve further over time (Pegion *et al.* 2019; Mariotti *et al.* 2020). Moreover, the SubX product that we used is a global product, and we evaluated forecast skill within the NEUS, which is strongly influenced by Gulf Stream dynamics. The skill of the SubX product may be higher over longer lead times in more oceanographically stable regions such as gyre systems. As reliable forecasting products become available, aspirations for ecological forecasting discussed in the past two decades (Clark *et al.* 2001; Dietze *et al.* 2018) now become a reality.

Future improvements to forecasting products could help to address several of the limitations of the integrated modeling framework presented here. For example, our humpback model is constrained by available forecastable covariates, and as a result the explanatory power of the model was lower than that described for similar humpback whale models in studies that used multiple dynamic covariates (Roberts et al. 2016; Palka 2020). This could explain the overprediction of humpback whales in cooler months when abundance is low, as SST was the sole dynamic covariate in our model. Improvements to forecasts that include additional dynamic variables that can be calculated or derived could enhance the predictive capacity of forecasts of marine mammal distributions, while combining multi-models of forecasts could increase the overall skill both spatially and temporally (Pegion *et al.* 2019).

Conclusion

Dynamic management is critical to effective conservation in marine systems, particularly for long-lived marine mammals with slow population growth whose recovery is threatened by anthropogenic impacts. Here, we demonstrate the utility of integrating a species distribution model with a subseasonal forecast to predict migratory arrival and density. Using environmental forecasts rather than near real-time conditions is advantageous, as future impacts can be anticipated and used to guide management efforts and allow stakeholder adaptation, such as timearea closures, fishery gear shifts, and vessel speed regulations.

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Data Availability Statement

Raw sightings of humpback whales and associated survey effort are available from the Ocean Biodiversity Information System– Spatial Ecological Analysis of Megavertebrate Populations (OBIS-SEAMAP) repository, which includes contact information and data-sharing permissions for data used in this study: https://seamap.env.duke.edu. Derived estimated abundance and detection functions were fitted according to the methods detailed in Roberts *et al.* (2016). Additional information is available at https://seamap.env.duke.edu/model s/Duke/EC. SubX forecast and hindcast data are publicly available at http://cola.gmu.edu/subx. Sources for static and dynamic environmental covariates are provided in WebTable 1. Novel code for covariate extraction, forecast download, forecast and ecological model integration, and figure and table creation is available at https://doi.org/10.5281/zenodo.5587211.

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