2019

RELATING MARINE MAMMAL DISTRIBUTION TO PREY ABUNDANCE

Christopher D. Orphanides
University of Rhode Island, cdorphanides@gmail.com

Follow this and additional works at: https://digitalcommons.uri.edu/oa_diss

Recommended Citation

Orphanides, Christopher D., "RELATING MARINE MAMMAL DISTRIBUTION TO PREY ABUNDANCE" (2019).
Open Access Dissertations. Paper 895.
https://digitalcommons.uri.edu/oa_diss/895

This Dissertation is brought to you for free and open access by DigitalCommons@URI. It has been accepted for inclusion in Open Access Dissertations by an authorized administrator of DigitalCommons@URI. For more information, please contact digitalcommons-group@uri.edu.

RELATING MARINE MAMMAL DISTRIBUTION TO
PREY ABUNDANCE

BY

CHRISTOPHER D. ORPHANIDES

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

OCEANOGRAPHY

UNIVERSITY OF RHODE ISLAND

2019

DOCTOR OF PHILOSOPHY DISSERTATION
OF
CHRISTOPHER D. ORPHANIDES

APPROVED:

Dissertation Committee:

Major Professor Jeremy S. Collie

Melissa Omand

John Hoey

Nasser H. Zawia
DEAN OF THE GRADUATE SCHOOL

UNIVERSITY OF RHODE ISLAND
2019

ABSTRACT

Marine mammal foraging and diet in southern New England is not well known and has therefore been largely ignored as a component of habitat, distribution, and bycatch. Incorporating prey components into marine mammal management is key to improving management of these species, especially as fisheries management progresses towards ecosystem-based management, climate change results in shifting distributions of marine mammals, and we are faced with new management challenges stemming from offshore wind development. This dissertation aims to address data gaps for species highly impacted by human activities, specifically the North Atlantic right whale (*Eubalaena glacialis*) and the harbor porpoise (*Phocoena phocoena*), and a suite of species along the continental shelf break that may be subject to future offshore energy development.

The first chapter assesses harbor porpoise diet in southern New England, an area of recently increased bycatch where no diet information was previously available. The results of this study could be incorporated into ecosystem-based management, assess likely shifts in habitat due to climate changes, and inform future bycatch management regulations. For this study we examined stomach contents from 46 bycaught harbor porpoises collected over 24 years (1994-2017) between January and May on the continental shelf south of New England. Clupeids, true hakes (*Urophycis*), cephalopods, and silver hake (*Merluccius bilinearis*) constituted 85.5% of all estimated biomass, while cusk eels (*Ophidiidea*) and small flatfish (*Pleuronectiformes*) were frequently consumed (found in 29.8% and 27.7% of all stomach samples), but each made up less than 1% of estimated biomass due to their

small size. Porpoises were found to preferentially select their prey by size and species, overlapping little with gillnet catch, and average prey size was larger for larger porpoise, females, and during the first half of our study (1994-2006 compared to 2007-2017).

The second chapter investigated North Atlantic right whale prey choices on the continental shelf south of New England. Researchers recently found that these highly endangered whales inhabit the continental shelf south of Rhode Island and Massachusetts year round, and are present and feeding in higher numbers during the late winter and early spring. However, little is known about right whale foraging in this region and the factors driving distribution of their prey. During a short research cruise in April of 2018 we opportunistically investigated potential right whale prey choices in southern New England. After spotting two diving right whales in an area with numerous documented sightings in the previous two weeks, we sampled the water column for possible prey and physical oceanographic parameters using a variety of instruments. Our sampling revealed a consistent dense layer at about 35-40 m associated with a slight pycnocline that appeared to consist primarily of ctenophores and marine snow. However, net sampling throughout the water column showed a mix of *Pseudocalanus* and *Calanus finmarchicus* that were not visible in the echosounder or Video Plankton Recorder data. Our sampling suggest possible foraging on ctenophores and a zooplankton assemblage more diverse than most right whale feeding regions, but similar to Cape Cod Bay.

The third chapter demonstrates the use of echosounding to model marine mammal distribution and abundance with direct measurements of prey rather than proxies. The

study applies a published algorithm to classify echosounding data into four organism types on the shelf break south of New England, an area of potential offshore energy development rich with marine mammals. We built Generalized Additive Models (GAMs) for seven species using only these acoustically derived variables to explain marine mammal distribution. The resulting GAMs explained between 1% and 36% of model deviance, on par with other published studies that employed a suite of variables that served as proxies for water-column components driving marine mammal distribution.

The research in this dissertation aims to provide data and methods to improve management of marine mammals by considering how ecosystem components such as prey resources influence the distribution of marine mammals. Currently consideration of prey resources does not play a large role in most regional marine mammal management analyses, despite this consideration becoming more important with recent shifts in the ocean environment. This research lays the groundwork for considering prey distributions in ecosystem-based management.

ACKNOWLEDGMENTS

This has been quite a journey. This dissertation would not have been possible without help and support of numerous people. I would first like to thank my major advisor Jeremy Collie. Thank you for taking me on as an atypical older graduate student with the challenges that a full time job and a family entail. Thank you for your guidance and support along the way, as well as your patience as I found my way during a dissertation that shifted focus as it progressed. It has been a pleasure to be your student and I look forward to continued interactions in the future. I would next like to thank my other core committee members John Hoey and Melissa Omand. John, you gave me my start with National Oceanic and Atmospheric Administration (NOAA) and have always been supportive of my work. You have always understood and appreciated the direction I wanted to go with my research when others did not really get it. Thank you for taking the time out of your busy schedule to give me one last mentoring experience before you retire to better things. I really appreciate the role you have played in my career and will miss our chats and your input when you move on. Thank you Melissa for your guidance, support, and faith in what I was trying to accomplish. Your encouragement and collaboration led to our Endeavor cruises, for which I will always be extremely grateful. Not only did those cruises lead to a dissertation chapter, but they also were likely the most valuable (and enjoyable) learning experiences of my graduate career. I very much look forward to our future collaborations on the Endeavor and hopefully other future projects. Thank you also to my comprehensive exams professors, Gavino Puggioni and Jim Miller, who were both very helpful in laying a foundation in statistics and acoustics, respectively.

I would like to thank a number of people within NOAA for their support. Thank you to Debi Palka for your continued support of my professional growth, which sometimes occurred at the expense of other research projects that may have been more in line with my official job description. Thank you also for the program support for my Endeavor cruises, for your feedback, and for always being there to listen to my rambles as I verbally try to work through research challenges of one sort or another. Thank you to the NOAA Fisheries Advanced Study Program that supported some of this research. I am thankful for the support of that program and for Mike Simpkins and Debi Palka originally supporting my participation, and for Sean Hayes and Henry Milliken for continuing the support of previous supervisors. Thank you to the Northeast Fisheries Science Center Protected Species Branch bycatch group (particularly Marjorie Lyssikatos and Kimberly Murray) for their support and understanding as the pursuit of my PhD took time away from bycatch analyses. Also, a huge thank you to Mike Jech for taking me under his wing to teach me about acoustics and echosounding. Thank you for your continued availability, your patient manner, and all the time you spent helping me with these analyses. The last two chapters in this dissertation would not have been possible without you.

Thank you to the Graduate School of Oceanography for giving me a shot at this degree. Thank you to David Smith for always being available for helpful discussions, and for Bruce Corliss and the Rhode Island Endeavor Program for giving me a chance to be Chief Scientist on two Endeavor cruises. Also, thank you to my Collie lab mates for their continued support, particularly Conor McManus and Joe Langan. Conor was

always willing to talk through analyses or the doctoral process, and Joe provided many useful statistics insights. Hopefully our paths will continue to cross in future research. Also, thank you to Bob Kenney for several helpful conversations about right whales.

Most of all, thank you to my family, especially my wife Sheila, for patience and support as this degree took time and energy away from family considerations. Thank you for patience and support during early mornings and late nights away from family. Thank you for patience when my body was present but my mind was elsewhere. Thank you for when my mind just too full to hold much else, and for bearing with me as I managed day to day when you held weeks in your head. This would not have been possible without you, and I cannot wait to start our next phase of life.

PREFACE

The dissertation was formatted in accordance with the manuscript format guidelines established by the Graduate School of the University of Rhode Island. The first manuscript is formatted for the journal *Fishery Bulletin* with coauthors Frederick Wenzel and Jeremy Collie. The second manuscript is formatted for *Marine Ecology Progress Series*, with co-authors Elisabeth Broughton, J. Michael Jech, Melissa Omand, and Jeremy Collie. The third manuscript is formatted for *Endangered Species Research* with coauthors J. Michael Jech, Jeremy Collie, and Debi Palka.

TABLE OF CONTENTS

ABSTRACT	ii
ACKNOWLEDGMENTS	v
PREFACE.....	viii
TABLE OF CONTENTS.....	ix
LIST OF TABLES	xii
LIST OF FIGURES	1
MANUSCRIPT 1.....	1
ABSTRACT	2
INTRODUCTION	3
MATERIALS AND METHODS.....	5
Stomach Processing	5
Prey Frequency and Abundance	6
Net Catch and Prey Preference	7
Estimating Prey Lengths and Weights.....	9
RESULTS.....	12
Occurrence	12
Comparison to Gillnet Catch	12
Prey Preference	13
Consumption Estimates.....	15
DISCUSSION.....	15
CONCULSIONS	23
ACKNOWLEDGEMENTS.....	24
LITERATURE CITED	25
TABLES	31
FIGURES	36
MANUSCRIPT 2.....	43

ABSTRACT	44
MATERIALS & METHODS	47
Research Cruise Overview	47
Marine Mammal Observation	48
Video Plankton Recorder	49
Bongo Net Sampling	50
Oceanographic Data	51
Echosounder Data	53
RESULTS	58
Overview	58
Marine mammals	59
Physical Oceanography	59
Zooplankton	61
DISCUSSION	64
ACKNOWLEDGEMENTS	72
LITERATURE CITED	73
TABLES	80
FIGURES	82
MANUSCRIPT 3	91
ABSTRACT	92
INTRODUCTION	93
METHODS	96
Survey Design	96
Marine Mammal Observing	97
Echosounding Processing	98
Marine Mammal Modelling	101
RESULTS	103
DISCUSSION	104
ACKNOWLEDGEMENTS	112
LITERATURE CITED	113
TABLES	119

FIGURES	122
SUPPLEMENTAL FIGURES	127
CONCLUSIONS	132
LITERATURE CITED	137

LIST OF TABLES

TABLE	PAGE
Table 1-1. Equations used to estimate length and weight of harbor porpoise prey found with intact skulls or whole bodies in stomach samples.	31
Table 1-2. Summary of fish otoliths and squid beaks found in harbor porpoise stomachs. Number of Items, numerical abundance (%N), number of occurrences, frequency of occurrence (%FO) and number of individuals for each prey item and prey groupings.....	32
Table 1-3. Raw counts of grouped species by year period (1994-2006 and 2007-2017) and contributions of species groups to permutation analysis of variance (PERMANOVA) test	33
Table 1-4. Cross tabulation of porpoise sample sizes by sex, size, and year categories.	33
Table 1-5. Prey selection indices (Manley 2002). Confidence intervals for selected prey proportion are shown only for taxa used to test the null hypothesis that harbor porpoise selected prey randomly in proportion to their availability (Chi-squared test, $p < 0.001$)	34
Table 1-6. Porpoise prey measurements and biomass estimate	35
Table 2-1. Bongo net sample density and estimated energy contents by taxa and by stage for <i>Calanus finmarchicus</i>	80
Table 2-2. Bongo net sample density and estimated energy contents by taxa and by stage for <i>Calanus finmarchicus</i>	80
Table 2-3. Summary of acoustic characteristics on April 6 and 7, 2018. Data are subset	

by day and by the area where the Video Plankton Recorder (VPR) was set within an acoustically visible layer, the initial right whale sighting area (~1400 m of ship track in the northern corner of the bowtie shaped sampling area), and an area of the track defined by a school detection algorithm applied to 206 kHz frequency data. Acoustic analysis are presented for areas with a Distorted Wave Born Approximation (DWBA) <i>Mertensia ovum</i> Z-score of ≤ 1 and a minimum return of -80 dB re 1m^{-1} , an acoustic relative frequency pattern representing potential copepods, and a general characterization of the 206 kHz school detection subset. S_v refers volume backscattering strength (dB re 1m^{-1}).	81
Table 3-1. Summary of marine mammal sightings by species or genus.....	119
Table 3-2. . Correlation matrix among echosounding organism classifications at depths of 0-50 m, 50-100 m, and 0-200 m. Red font indicates correlation ≥ 0.6 . Abbreviations in the table include PHY = phytoplankton, ZOO = zooplankton, NSB = non-swim bladder fish, and SBF = swim bladder fish.....	120
Table 3-3. Generalized Additive Model (GAM) results showing variables included in each model, $p(0)$ estimate, model degrees of freedom, deviance explained, and Mean Absolute Percentage Error (MAPE) Mean Absolute Error (MAE), and Spearman's Rank Correlation Coefficient (RHO) results from k -fold cross validation. Qualitative classifications of MAPE, MAE, and RHO are color-coded and provided below following the example of Kinlan et al. and Chavez et al 2019	121

LIST OF FIGURES

FIGURE	PAGE
Figure 1-1. Study area, locations of harbor porpoise bycatch events from which stomach samples were retrieved, and degree to which gillnet catch data was available.	36
Figure 1-2. Distribution of porpoise stomach samples by year.	37
Figure 1-3. Porpoise stomach sample distribution by animal total length and sex. (Young of the year <125 cm; Juveniles 125-139 cm; Adults 140 cm and greater)	38
Figure 1-4. Costello diagram for major species groupings found in harbor porpoise stomachs. Prey importance is expressed from the bottom left to the upper right. Feeding strategy expressed along the axis from bottom right to upper left (Costello 1990)	39
Figure 1-5. Length distribution of porpoise stomach contents versus gillnet catch (A) from hauls that caught porpoise and had available catch length data, and (B) length distribution of NEFSC trawl catch and porpoise stomach contents.....	40
Figure 1-6. Forklength (A) and prey weight (B) distributions by sex, size, and year categories.....	41
Figure 1-7. Histogram of estimated biomass per porpoise stomach	42
Figure 2-1. Study area, right whale sightings, and oceanographic sampling locations. Focus of study is within the orange outline	82
Figure 2-2. Close up of primary study area with right whale sightings, and oceanographic sampling locations. Northeast Fisheries Science Center (NEFSC)	

sightings are from March 18- April 11	83
Figure 2-3. Temperature (C°) (dashed blue line) and density (σ_θ kg m ⁻³) (solid red line) profiles by depth (m) conducted near southeastern corner of "bowtie" (A), and (B) conducted on eastern end of the trackline adjacent to the right whale region	84
Figure 2-4. Simulated track of plankton on April 7 based on ADCP data at 21 m depth. Starting point is at point 0,0.	85
Figure 2-5. Right whale sightings, April 2018 chlorophyll a mean values from the MODIS Aqua satellite, and chlorophyll a measurements from a shipboard fluorometer (mg m ⁻³)	86
Figure 2-6. Bongo sample taxa density.....	87
Figure 2-7. Annual study area <i>Calanus finmarchicus</i> and <i>Pseudocalanus</i> densities (m-3) from NEFSC ECOMON surveys in March and April.....	88
Figure 2-8. Example echograms (dB re 1m ⁻¹) in the right whale region showing an acoustic layer at roughly 40 meters depth. Images are 38 kHz (top), 120 kHz (middle), and 206 kHz (bottom).The gridding represents 5 meter depth and 100 m length intervals, stretching about 1.3 nautical miles	89
Figure 2-9. Echograms of 120 kHz S _v limited to backscatter ≤ -80 dB re 1m ⁻¹) and a <i>Mertensia ovum</i> Z- score ≤ 1. (A) region of the initial right whale sighting on April 7, 2018, the area sampled by the VPR (black box) on April 7, 2018, and a section of an adjacent transect on April 6, 2018 just north of the location of the initial right whale sighting. The gridding represents 10 meter depth and 100 m length intervals	90
Figure 3-1. Marine mammal sightings and active echosounding locations along study area transects	122

Figure 3-2. Example of echosounding transect data processing. A) Original 38 kHz data, B) cleaned 38 kHz data with noise processing applied, below bottom removed, and off-transect areas removed, C) 38 kHz data classified as swim-bladder fish, D) 38 kHz data classified as swim bladder fish and binned to 50 m (vertical) by 1000 m (horizontal) bins (scale is distorted in the y direction). Note: Data displayed is S_v (volume backscattering coefficient) (dB re 1 m⁻¹), or the mean volume backscattering strength. Data used for analysis was ABC (area backscattering coefficient) (m²m⁻²), where $ABC = (10^{S_v/10}) \times T$, and where T is the mean thickness of the integrated cell

..... 123

Figure 3-3. Example shelf edge transect in the area of Georges Bank that crosses canyon mouths. Marine mammal sightings overlaid with 38 kHz data is S_v (volume backscattering coefficient) (dB re 1 m⁻¹). Grid intervals are 50 m in depth and 1000 m horizontally

..... 124

Figure 3-4. Generalized Additive Model (GAM) plots showing the relationship between common (A) and bottlenose (B) dolphins and Area Backscatter Coefficient (ABC) from swim-bladder fish in the first 50 m of the water column

..... 125

Figure 3-5. . Generalized Additive Model (GAM) plots for fin whale model truncated in the x-direction to exclude outliers and better display region with the vast majority of observations. Full plots can be seen in the supplemental appendix, Figure S6

..... 126

Figure 3-S1. Generalized Additive Model (GAM) plots for common dolphin model. The variables plotted are (from the top left going clockwise): the Area Backscatter Coefficient (ABC) for phytoplankton from 0-50 m, the ABC for swim bladder fish from 0-50 m, and the ABC for zooplankton from 0-50 m

..... 127

Figure 3-S2. Generalized Additive Model (GAM) plots for bottlenose dolphin model. The variables plotted are the Area Backscatter Coefficient (ABC) for swim bladder fish from 0-50 m (left), and the ABC for zooplankton from 0-50 m (right).....	128
Figure 3-S3. Generalized Additive Model (GAM) plots of Area Backscatter Coefficient (ABC) for swim bladder fish from 0-200 m for Risso’s dolphin (left) and striped dolphin (right) models	129
Figure 3-S4. Generalized Additive Model (GAM) plot for pilot whales of Area Backscatter Coefficient (ABC) for zooplankton from 0-50 m (left), and ABC for zooplankton from 50-100 m (right).....	130
Figure 3-S5. Generalized Additive Model (GAM) plot for fin whale model of Area Backscatter Coefficient (ABC) for phytoplankton from 0-200 m (left), and ABC for zooplankton from 0-200 m (right).....	131

MANUSCRIPT 1

Harbor porpoise (*Phocoena phocoena*) prey selection on the continental shelf off
southern New England

Christopher D. Orphanides^{1,3,*}, Frederick W. Wenzel², Jeremy S. Collie³

¹ NOAA Fisheries, 28 Tarzwell Drive, Narragansett, RI 02882

² NOAA Fisheries, 166 Water Street, Woods Hole, MA 02543

³ University of Rhode Island, Graduate School of Oceanography, 215 S Ferry Rd,
Narragansett, RI 02882

*corresponding author: phone: (401) 782-3283, fax: (401) 782-3201,

email: chris.orphanides@noaa.gov

Key words: harbor porpoise, prey, diet, bycatch

Publication status: in Northeast Fisheries Science Center review in preparation for
submission to *Fishery Bulletin*

ABSTRACT

Little is known about harbor porpoise (*Phocoena phocoena*) diet south of New England where bycatch has been a highly contentious issue since the late 1990s. To fill this data gap, stomach contents were examined from 46 bycaught harbor porpoises collected over 24 years (1994-2017) between January and May. Prey species were identified to the lowest possible taxonomic level through hard part analysis, primarily by identifying of otoliths and squid beaks. Porpoises were found to preferentially select their prey by size and species, overlapping little with gillnet catch. Average prey size was larger for larger porpoises, females, and during the first half of our study (1994-2006 compared to 2007-2017). Average total biomass consumed per stomach was estimated at 2.3 kg, which translates to approximately 12-24 hours of feeding; clupeids, true hakes (*Urophycis*), cephalopods, and silver hake (*Merluccius bilinearis*) constituted 85.5% of all estimated biomass. Cusk eels (*Ophidiidae*) and small flatfish (*Pleuronectiformes*) were frequently consumed (found in 29.8% and 27.7% of all stomach samples), but each made up less than 1% of estimated biomass due to their small size. These results could help improve harbor porpoise management by better defining prey preferences and predicting porpoise habitat shifts as climate changes.

INTRODUCTION

Marine mammals are threatened throughout their range by fisheries bycatch (Read et al. 2006, Lewison et al. 2014, Burgess et al. 2018, Gray & Kennelly 2018) and increasingly by climate change (Learmonth et al. 2006, Simmonds & Isaac 2007, Sydeman et al. 2015). In order to manage and mitigate these and other threats, we need to better understand the drivers behind marine mammal distributions. Regular abundance surveys and associated modelling have helped discern marine mammal distributions in some regions (e.g., Roberts et al. 2016), however, for many species, limited quantitative information exists to explain the reasons behind these distributions. Marine mammal distribution is primarily driven by prey resources for much of the year, with this reliance varying by species and reproductive life history strategies. For a small marine mammal such as the harbor porpoise (*Phocoena phocoena*), with high metabolic needs and no annual breeding migration, we expect prey distribution to be a primary driver of its distribution (Read et al. 1997).

The northwest Atlantic shelf waters that serve as the primary habitat for harbor porpoises are predicted to warm at nearly three times the global average (Saba et al. 2015). This area has already seen documented species shifts (Nye et al. 2009, Kleisner et al. 2016), which may impact harbor porpoise distribution and prey resources. The Gulf of Maine/Bay of Fundy stock occupies waters off the northeastern US and extends from North Carolina to the Bay of Fundy and the Scotian Shelf off Nova Scotia (Waring et al. 2014). Harbor porpoises are concentrated in the Gulf of Maine and southern Bay of Fundy during the summer months, and are more widely dispersed the rest of the year, extending as far south as North Carolina from January to April

(Polacheck et al. 1995, Orphanides 2010, Waring et al. 2014). Most harbor porpoises are thought to stay in continental shelf waters throughout the year, though they have occasionally been observed along and off the shelf edge (Read & Westgate 1997, Orphanides 2010, Waring et al. 2014).

Harbor porpoise bycatch has been one of the most contentious marine mammal management issues in the northeast US for years (Orphanides & Palka 2013). They are considered a strategic stock under the Marine Mammal Protection Act, meaning estimated bycatch exceeds prescribed limits. As a result, gillnet time-area closures were enacted in 2013 during a time when the groundfish fishery was already under immense stress due to reduced catch allowances and a transition to catch share management (Orphanides 2012, Murphy et al. 2015). Despite these management issues and the rapidly changing ocean in which harbor porpoises live, no published papers have assessed diet south of New England or from January to May, both the area and season where the majority of harbor porpoise bycatch now occurs off southern New England, USA (Orphanides & Palka 2013, Hatch & Orphanides 2015, Hatch & Orphanides 2016).

The last two published papers on harbor porpoise diets in the northwest Atlantic used data from 1985-87 during June to September in the Gulf of Maine (Gannon et al. 1998), and from 1989-94 during September into December in the Bay of Fundy, Canada (Recchia & Read 1989). This study aims to fill that data gap, assessing harbor porpoise diet on the continental shelf during the winter and early spring, quantifying prey preferences, examining prey relative to gillnet catch, and calculating biomass consumed. We hope that results from this study inform fisheries management for both

bycatch and target species, and contribute to modelling efforts of ecosystem and climate impacts.

MATERIALS AND METHODS

Stomach Processing

Stomach samples were collected by the Northeast Fisheries Observer Program (NEFOP), part of the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service. Fisheries observers retrieved animals incidentally caught in gillnet hauls on the continental shelf south of New England from 1994-2017 (Fig. 1 & 2). These observers recorded numerous aspects of fishing trips and hauls, including locations and dates of fishing events, gear characteristics such as mesh size, and details on both the kept and discarded catch (Branch 2016). Observers brought a small fraction of bycaught marine mammals to port for biological sampling. The majority of bycatch events, occurred from January to May, with 6, 7, 11, 16, and 6 stomach samples collected from each of the five months. Size and sex of most bycaught harbor porpoises were also recorded by observers or during a necropsy (Fig. 3).

Fifty harbor porpoises from 1994 to 2017 were collected by NEFOP in our study area and considered for analysis (Fig. 1). Most porpoises were necropsied for life history and biological information and all stomachs were retained and frozen for later examination. Of these 50 stomachs, four were either empty or only contained fragments of unidentified otoliths and were not included in this analysis. The remaining 46 comprised 17 females, 26 males, and 3 of unknown sex. Porpoise sizes

included 10 young of the year (<125 cm), 10 juveniles (125-139cm), 23 adults ($\geq$ 140 cm), and 3 of unknown maturity (Fig. 3) (Wenzel 2000). Given the relatively small samples sizes in each age class, any analysis examining prey differences by porpoise maturity or size was conducted by splitting the sizes at 140 cm, between adults and non-adults. Additional porpoise stomach samples were collected by NEFOP in the Hudson Canyon region east of New Jersey were examined in a separate research effort focused on the mid-Atlantic (Kroeger et al. in review).

We examined stomach contents to identify and enumerate prey and prey size through the presence of whole fish and squid, and by identification of prey by hard parts (otoliths, cephalopod beaks, fish jaws, etc.). These dissections generally followed the procedures outlined by Craddock et al. (2009) and Wenzel et al. (2013). We emptied the fore and main stomachs and whole, relatively intact prey were separated, identified, and measured. We removed otoliths from intact skulls to confirm identification. Next, we examined partially digested prey to retrieve identifiable hard parts (skulls, bones, otoliths, jaws, cephalopod beaks, etc.). We added water to well-digested prey and separated hard parts by elutriation, and by decanting them through a 0.5-mm mesh sieve. Prey were identified to the lowest taxonomic level possible by using Northeast Fisheries Science Center (NEFSC) reference collections, professional expertise (Hendrickson pers. comm.), and published guides (Brodeur 1979, Campana 2004).

Prey Frequency and Abundance

We summarized prey items by frequency of occurrence (%FO) and proportion of numerical abundance (%N), where %FO is the proportion of stomachs containing a

specific prey and %N is the percent occurrence of a specific prey type among all prey sampled (Wenzel et al. 2013). The occurrence and abundance of prey items were summarized by length and sex of the porpoises, and by two year groupings (1994-2006, 2007-2017).

We used the *vegan* package in R to run a permutation analysis of variance (PERMANOVA) to test whether porpoise prey species selection varied by sex, size, or year categories. For this analysis, species counts were square root transformed to minimize the influence of abundant species and species groups. The output of the PERMANOVA was checked for overdispersion. We also ran a similarity percentage analysis to examine the contribution of individual species and species groups to the overall Bray-Curtis dissimilarity.

Net Catch and Prey Preference

Fish and squid lengths from porpoise stomach samples were compared against those from the NEFSC bottom trawl survey, and against those from gillnet catch on hauls where porpoise stomach samples were collected. We used NEFOP data to quantify total net catch by species and length for hauls in which observers retrieved porpoise stomachs used in this study. Both kept and discarded net catch by species was available for 43 hauls containing 46 takes, while fish length was only available for 12 hauls from January, April, and May (Fig. 1). Mesh size for the hauls with bycatch was dominated by large mesh (12 or 12.5 in, 30.48 or 31.75 cm), with far fewer medium mesh hauls (6 or 6.5 in, 15.24 or 16.51 cm). Large mesh was employed on 11 out of 12 hauls with recorded fish lengths, and 32 out of 43 hauls with documented net catch were large mesh, 6 were medium mesh, and 5 were of an unrecorded mesh size.

Spring bottom trawl survey data from the NFESC during the period from 1994-2017 in the study area outlined in Fig. 1 were used as a measure of prey available for harbor porpoise consumption in order to assess prey preference. Samples were limited to fish and squid lengths less than 40 cm to correspond with the maximum prey sizes observed in this and other studies (Recchia & Read 1989). To ensure the most representative data, calibration factors were applied where available to adjust the time series for fishing vessels (Miller et al. 2010). Catchability quotients were also applied to estimate the true amount of fish in the swept area of the net, accounting for those fish that may successfully avoid being captured (Link et al. 2006, Link et al. 2008).

Survey samples were used in combination with porpoise stomach samples to develop prey selection indices as in Manly et al. (2002). Selection index values represent the amount consumed of a particular species compared to its availability in the population. The selection index is defined as:

$$\hat{w}_i = o_i / \pi_i$$

where $\hat{w}$ is the selection index, o is the proportion of a specific prey item consumed relative to all items of prey consumed, π is the proportion of prey available relative to all prey available, and i denotes a particular prey item. A value of one would mean that prey is being consumed in proportion to the amount of prey available. The standardized prey index assesses the predator's preference for one species over another and is defined as:

$$B_i = \hat{w}_i / \left(\sum_{j=1}^I \hat{w}_j \right)$$

Where w_i is again the selection index for a particular prey item, w_j are prey types consumed, and B_i is the standardized selection index. Since the standardized selection index sums to one, a value of one would indicate that the predator only eats one prey type. The standardized index allows comparison of the degree to which one species is preferred over another. For example, a value of one for a specific prey item would indicate that the predator only ate one type of prey, and hypothetical values for species a and b of 0.4 and 0.2 would indicate that species a was preferred twice as much as species b .

Estimating Prey Lengths and Weights

Fish otoliths and squid beaks found in stomachs were measured to determine lengths and weights of prey consumed. Individual otolith condition was rated on a scale of 0-5 following the example of Recchia and Read (1989) and Gannon et al. (1998). A rating of 0 applied to otoliths extracted from skulls, a rating of 1 applied to otoliths were found undamaged but loose in a stomach, and ratings 2-5 were for otoliths that were slightly, moderately, significantly, or severely damaged or eroded, respectively. We used ratings of 0-2 to estimate lengths or weights of prey. All unbroken squid beaks were measured because we observed little erosion or shrinkage of the lower rostral length used to estimate squid length. If more than 25 lower squid beaks or fish otoliths of a particular taxon were present within a stomach, and of appropriate quality for measuring, we counted all samples, but only measured a randomly chosen 25.

We used published equations to estimate fish and squid lengths from otoliths and squid beaks for most species (Table 1). For species with suitable regressions, we

assigned lengths from counted, but unmeasured, otoliths by resampling with replacement from measured otoliths within that same stomach sample and from that same taxon. This resampling assumed a similar size composition between measured and unmeasured otoliths and squid beaks. If no otoliths were measured for a specific species within a particular stomach, lengths were estimated by resampling with replacement from measured otoliths of that same taxon from all stomach samples.

We used fish and squid lengths to estimate biomass consumed per stomach by converting fish lengths to mass using length-weight formulas (Table 1). Most fish lengths described above were converted to mass with a standard length-weight formula ($\ln W = \ln a + b \ln L$) and coefficients from (Wigley et al. 2003). If available, coefficients were applied from regional spring surveys using both sexes of fish to best match fish found in harbor porpoise stomach samples. No length-weight regression was present in Wigley et al. (2003) for gulf stream flounder, so one was developed for this study from 2017 NEFSC spring bottom trawl data ($R^2 = 0.94$, $n=29$).

In the case of cusk eel (*Ophidiidea* family), Gulf Stream flounder (*Citharichthys arctifrons*), shortbeard codling (*Laemonema barbatulum*), and some taxa not identified to species (unidentified flatfish, small mouth flounder, unidentified/degraded gadidae, and other unidentified), no published otolith length-fish length equations were found in the literature. No lengths were calculated for these species, aside from cusk eel. For cusk eel, a regression was calculated using cusk eel samples from the NEFSC 2017 spring bottom trawl ($R^2 = 0.72$, $n=32$, $R^2 = 0.96$, $n=35$, respectively). A squid beak-mantle length regression for *long fin squid* (*Doryteuthis (Amerigo) pealeii*) was also developed using NESFC trawl samples to ensure that the regression represented prey

samples from the same region and season as the porpoise stomach samples ($R^2=0.78$, $n=39$) (Brodziak & Macy 1996). This regression was also applied to decapodiformes of unknown species.

For some species, we could not attain samples to develop otolith-length (or weight) regressions and none have been published to our knowledge. The otolith length-fish length and weight regressions for Atlantic herring (*Clupea harengus*) were applied to blueback herring (*Alosa aestivalis*) since they are in the same family. Similarly, Atlantic herring lengths were randomly selected with replacement and applied to two observations in the general *clupeida* category that did not have otolith length measurements. The Atlantic herring weight regression was also applied to these two samples. (Table 1). The Gulf Stream flounder lengths and weights were applied in the same manner to the unidentified flatfish and smallmouth flounder (*Etropus microstomus*), since they are also in the same family. We applied the same otolith length-fish length and weight regression to all *Urophycis* species and to the unidentified *gadiforme* category. An otolith length-fish length regression for Madeira lanternfish (*Ceratoscopelus madernisis*) yielded unreasonable size estimates (Wenzel et al. 2013). So, given the small size of Madeira lanternfish, we estimated lengths by sampling from a normal distribution centered at 5 cm with a standard deviation of one based on a size distribution between 3.8 and 6, with a maximum size of 8.1 cm for mature Madeira lanternfish (Froese & Pauly 2018). For Madeira lanternfish we estimated weights using a Bayesian length-weight regression (Froese & Pauly 2018).

No regressions were available for shortbeard codling and for otoliths categorized as unidentified or unidentifiable. For these taxa, which constitute 2% of all otoliths,

we estimated lengths and weights by randomly sampling from a truncated normal distribution defined by the mean weight and standard deviation from all prey samples. The resulting prey length distributions were compared across year categories and porpoise sex and length categories using Kolmogorov–Smirnov tests.

RESULTS

Occurrence

Frequency and numerical occurrence showed a diet concentrated on six species groups: squid (*cephalopoda*, %FO=51%, %N=19%), red, white, and spotted hakes (*Urophycis*, %FO=43%, %N=22%), clupeids comprising Atlantic herring, blueback herring, alewife (*Alosa pseudoharengus*), and unknown species of clupeid (*clupeidae*, %FO=34%, %N=8%), silver hake (*Merluccius bilinearis*, %FO=32%, %N=17%), small flatfish (*Citharichthys arctifrons*, *Etropus microstomus*, unknown Pleuronectiformes, %FO=28%, %N=18%), and cusk eels (*Ophidiidea*, %FO=30%, %N=6%) (Table 2). The combination of frequency and numerical occurrence (Costello 1990, Amundsen et al. 1996) suggests a generalist predator with *Urophycis* and cephalopods as the most dominant species groups (Fig. 4).

Comparison to Gillnet Catch

Harbor porpoise stomach contents had little overlap with gillnet catch. Among 25 fish species caught in gillnets that also caught porpoise used in this study, only 4 of the more rarely caught species were found in harbor porpoise stomachs. Among 36 unique observed hauls with porpoise bycatch, these fish made up 1.3% of all catch by number (both retained and discarded) and were caught in 10 hauls (haddock=2 hauls,

silver hake = 1 haul, white hake=1 haul, Atlantic mackerel = 6 hauls). Only one species (Atlantic mackerel, (*Scomber scombrus*) was found both in the harbor porpoises caught in that net and in the net catch, which occurred in 2 out of 6 hauls. Dominant net-caught species (winter skate *Raja ocellata* and monkfish *Lophius americanus*, 84% of catch by number) were not found in any harbor porpoise stomachs. In addition, there was no overlap in species lengths (Fig. 5) between recorded gillnet catch and porpoise prey lengths (max porpoise prey = 39 cm, min gillnet catch = 41 cm). The average length of 595 measured catch items was 73.6 cm (standard deviation=11.6), far larger than any harbor porpoise prey observed in stomach contents (mean= 11.7, standard deviation=7.7) These 595 lengths came from 12 hauls, all but one of which was fishing with 30.48 cm (12 in) mesh. Total fish caught in lbs was recorded for most hauls, but fish lengths were recorded on relatively few hauls.

Prey Preference

We examined preference using multiple methods. Permutation analysis of variance comparing diet of males and females, porpoises < 140 cm and >= 140 cm, and year categories (1994-2006, 2007-2017) did not show significant differences in prey in terms of taxa election based on harbor porpoise sex and size, but did show a difference in year categories ($Pr > F 0.025$) . Summaries of raw counts by year category and taxa contributions to the PERMANOVA show an apparent shift away from clupeids and towards true hakes (*Urophycis*), squids, and smaller prey (Table 3). Kolmogorov-Smirnov tests showed significant differences ($p < 0.001$) in fork length (FL) distributions and estimated biomass for the above mentioned, size, sex, and year

categories (weight by size: $D = 0.38828$; FL by size: $D = 0.24145$; weight by sex: $D = 0.54817$; FL by sex: $D = 0.43810$; weight by year: $D = 0.14763$; FL by year: $D = 0.11444$) (Fig. 6). Yet these statistical differences could be challenging to interpret because of imbalances between categories, particularly since 80% of the smaller porpoises (< 140 cm) were male (Table 4).

We also examined prey preference by comparing harbor porpoise stomach contents to the spring NEFSC trawl survey catch for both species lengths and composition. Fish length distributions (Fig. 5) were compared and found to be statistically different (Kolmogorov-Smirnov test, $p < 0.0001$, $D = 0.54292$). A Chi-squared test suggested that overall porpoise prey selection (Table 5) was not randomly selected in proportion to the prey caught in the NEFSC trawl survey ($p < 0.001$, $df = 7$, $X^2 = 99.483$). Nearly all harbor porpoise prey except some clupeids appeared to be preferentially selected because of selection index values greater than one, and because 95% confidence intervals do not overlap with the population proportion available (Neu et al. 1974, Byers et al. 1984). The species with the highest standardized selection indices were white hake (*Urophycis tenuis*), cusk eels (*Orphidiidae*), and small mouth flounder (*Etropus microstomus*). When species were grouped by taxa, clupeids as a whole appeared not to be preferentially selected, though alewives separately did. Clupeids were estimated to be 82.8% of adjusted trawl catch, when the trawl catch was limited to prey found in harbor porpoise stomachs, and when trawl catchability was taken into account, i.e., if the net caught all available fish in its swept area) (Link et al. 2006, Link et al. 2008). The standardized index suggests that relative to other species, cusk eel (*Ophidiidae* family) was preferred over 4 times more than hakes

(*Urophycis*), and about 3 times more than flatfish. Cephalopods, silver hake, and clupeids were preferred orders of magnitude less than cusk eel according to this standardized index.

Consumption Estimates

The mean biomass found in a harbor porpoise stomach as represented by otoliths and squid beaks was estimated to be 2.35 kg (Table 6), with a standard deviation on a per stomach basis of 2.38 kg, and a median value of 1.42 kg (Fig. 7). The distribution of total estimated live prey weight per stomach is quite variable and is skewed towards 1.0 kg and less, with some high weight outliers (Fig. 7). *Urophycis* constituted the most biomass per stomach on average (0.839 kg), and members of the Clupeids had the second most biomass (0.518 kg), together constituting more than half of the average estimated biomass per stomach. Cephalopods (0.382 kg) and silver hakes (0.271 kg) also contributed significantly, and together these four species groups (clupeids, *Urophycis*, cephalopods, and silver hake) constituted 85.7% of all estimated biomass. Frequently occurring but smaller prey items such as cusk eels and flatfish constituted less than 1% estimated biomass per stomach.

DISCUSSION

This is the first analysis of harbor porpoise diet on the continental shelf south of New England. It is also among the first papers examining harbor porpoise diet in 20 years in the northwest Atlantic, and among the first examining diet during winter and spring months (Gannon et al. 1998). These facts take on particular relevance given the increased harbor porpoise bycatch on the continental shelf south of New England

(Orphanides & Palka 2013, Hatch & Orphanides 2015, Hatch & Orphanides 2016), the recent fishing closures enacted due to harbor porpoise bycatch in this region (Orphanides & Palka 2013), potential redistribution of prey due to climate change in an area already rapidly changing (Nye et al. 2009, Saba et al. 2015, Kleisner et al. 2016, Kleisner et al. 2017), and a regional push toward ecosystem based fisheries management.

Harbor porpoises in this region were found to be generalist predators during the spring and winter months, primarily feeding on clupeids, *Urophycis*, squids, silver hake, cusk eels, and small flatfish. Prey consumption south of New England during the winter and spring appears to differ from previous studies in the Gulf of Maine during the remainder of the year (Smith & Gaskin 1974, Recchia & Read 1989, Smith & Read 1992, Gannon et al. 1998). One of the primary differences was that clupeids were the most important prey items in terms of biomass, though not to the magnitude found in other regions and studies. Previous studies in the Gulf of Maine and Bay of Fundy showed a heavy reliance on Atlantic herring, which made up 44% of ingested mass in the fall (Gannon et al. 1998) and 64% from June to September (Recchia & Read 1989). Herring accounted for 47.2% of all otoliths from May to September (Smith & Gaskin 1974), and occurred in 71.3% of all adult stomachs in a separate study from July to September (Smith & Read 1992). One possible reason for these differences is that the caloric value of Atlantic herring is known to increase seasonally with greater feeding and spawning in the spring and summer, which could contribute to their seasonal importance in the Gulf of Maine (Stevenson & Scott 2005).

Porpoise diet south of New England was more evenly distributed among species than in the Gulf of Maine. Average *Urophycis* biomass estimates per stomach were larger than clupeids (840 g vs 518 g, respectively) and *Urophycis* were the dominant prey item by number and frequency (22.3 %N and 42.6%FO for *Urophycis* versus 8.1 %N, 34.0%FO for clupeids). *Urophycis* was also a common prey during the fall in the Gulf of Maine, but not during the summer (Smith & Gaskin 1974, Recchia & Read 1989, Smith & Read 1992, Gannon et al. 1998).

Atlantic cod (*Gadus morhua*) were also found to be primary prey items during the summer in two studies (Smith & Gaskin 1974, Recchia & Read 1989), and to a lesser extent in a third (Smith & Read 1992), but no cod were present in any stomach samples in our study (Table 2). The lack of cod in stomach samples could be in part due to decline in the cod populations (Pershing et al. 2015), because much of the cod population is typically north of our study area (Fahay et al. 1999), or because most of the hauls from which these harbor porpoise stomach samples were taken were targeting monkfish or skate with 30.48 cm (12 in) mesh, whereas cod is typically caught with 16.51 cm (6.5 in) mesh.

Another primary difference was that squids were frequent prey (%FO=51.1%) that constituted a significant portion of the biomass (16.2% of biomass), whereas they were a negligible portion of the diet during the summer and fall in the Gulf of Maine (Smith & Gaskin 1974, Recchia & Read 1989, Smith & Read 1992, Gannon et al. 1998). Small flatfish and cusk eels were also a significant portion of harbor porpoise diet not seen in other studies. They were present in large numbers and frequency, although their caloric importance was limited due to their small sizes. In southern New

England, diet was more evenly apportioned across four species groups (clupeids, *Urophycis*, cephalopods, and silver hake) that constituted 85.7% of the biomass as compared to the diet being dominated by Atlantic herring in the Gulf of Maine, particularly in the summer (Table 6). One similarity between the regions was the importance of silver hake, which was common in both this and several previous studies (Smith & Gaskin 1974, Recchia & Read 1989, Smith & Read 1992, Gannon et al. 1998).

We found little direct overlap between porpoise prey and fish catch in the gillnets that incidentally caught harbor porpoises. The catch differed from porpoise prey in both size and composition. While there does not appear to be a direct connection between harbor porpoise prey and gillnet catch, there is likely an indirect connection. Monkfish, one of the primary gillnet target species, are known to prey on a variety of fish including clupeids and hakes (Bigelow & Schroeder 1953). Therefore, fish targeted with gillnets may be pursuing the same prey as harbor porpoises. The limited mouth gape of porpoises restrict their ability to prey on the large fish caught in gillnets, as does their feeding method (Kastelein et al. 1997b). Harbor porpoises catch their prey and then use suction to swallow it whole. The lack of chewing or tearing prey limits the ability to eat from the nets.

Harbor porpoises generally appear to preferentially select their prey species based on prey indices calculated using the NEFSC bottom trawl data. The NEFSC spring bottom trawl data used to calculate the prey index is the best available dataset that most closely reflects prey available for harbor porpoises. Its benefits are that it is a long time series and that it fishes in the bottom of the water column as a bottom-set

gillnet also does. However, it is not without its flaws for this application, particularly when attempting to estimate abundance of pelagic schooling species, which may either purposely avoid the trawl, or miss the trawl by the virtue of occupying a higher portion of the water column than the net.

Catchability quotients developed for a modelling exercise exploring the role of small pelagics in this ecosystem (Link et al. 2006, Link et al. 2008) were applied to adjust for these biases. These adjustments may indeed make the data more representative of the true species distribution available to porpoises, but they are estimates that can greatly expand the observed catch numbers and so include a degree of error. For example, Atlantic herring has a q of 0.02, resulting in an expansion of catch by a factor of 50. Error in catchability coefficients could play a role in our prey index values, decreasing apparent preference for Atlantic herring based on inflated abundance, and potentially boosting preference for other species.

That said, combined evidence from net catch, trawl survey data, and stomach samples suggest that harbor porpoises are at least selecting preferred prey based on size. The difference in prey species off southern New England as compared to the Gulf of Maine suggest seasonal foraging plasticity based on prey availability, while the consistency of some species between regions also suggests a degree of preference. Harbor porpoise high metabolic needs as a small cetacean living in a cold environment likely force them to be adaptable in their prey choices (Read & Hohn 1995).

Despite finding differences in biomass and fork length distributions between porpoise size, sex, and years (Fig. 6), we found no difference in their species selection by porpoise size or sex. Those findings match those of Gannon et al. (1998) who

found no difference in prey selection between sizes of porpoises except for calves. Similarly, Smith and Read (1992) found a different prey distribution for calves, which consumed large amounts of euphausiids. Porpoises in our study time and area would be past the calving stage (Smith & Read 1992, Read & Hohn 1995).

Some of the prey size differences we found could be expected as one would assume that larger porpoises would eat larger prey. Females also tend to be larger than males and have the added caloric burden of being pregnant for much of their mature lifetime (Read et al. 1997). Unfortunately, we did not have enough data to test the effect of pregnancy directly.

The PERMANOVA and Kolmogorov–Smirnov tests both found differences in prey between time periods (1994-2006 and 2007-2017). Porpoise prey in our samples shifted away from calorie rich clupeids and towards *Urophycis* species. Porpoise diet in recent years appears to have increased its reliance on squid, decreased its focus on silver hake, and generally diversified to include more smaller species (Table 3). The silver hake differences may be skewed by one sample with 314 small otoliths and another with 123. The overall differences between year periods are harder to explain but could reflect shifting species distributions due to climate change. For example, climate induced shifts have been documented in red, white, spotted, and silver hake as well as Atlantic herring and Atlantic mackerel (Nye et al. 2009, Nye et al. 2011), while cephalopods have been increasing globally (Doubleday et al. 2016).

One drawback of a diet study relying on hard parts is the possibility of over-counting prey due to secondary consumption. This concern may be elevated with regards to squid, *Urophycis*, and silver hake, which are all known to be cannibalistic

(Bigelow & Schroeder 1953, Cargnelli et al. 1999, Steimle et al. 1999). However, direct observation during this study of numerous partially intact small fish suggests that it would be erroneous to presume that all fish or otoliths below a particular size are secondary prey. Wisniewska et al. (2016) estimated that harbor porpoises in Danish waters have up to 200 prey encounters per hour during the daytime, with many of those prey measuring less than 5 cm, and as many as 550 encounters at night with a feeding success rate greater than a 90%. If a porpoise encounters a dense school of small prey, it may decide that it is worth the effort if the prey density is high enough (Benoit-Bird & McManus 2012, Benoit-Bird et al. 2013a).

Using hard parts for stomach content analysis also has potential consequences for prey length and biomass estimation. Otoliths and hard parts degraded due to digestion could yield negatively biased length and biomass estimates, may favor species with larger and less fragile otoliths, and has an unknown retention time due to otolith degradation during digestion. These issues have been thoroughly discussed in the literature (see Bowen & Iverson 2013). Correction factors have been proposed as a means to adjust for both erosion and residence time of otoliths and hard parts, but development of these factors has been focused primarily on hard parts found in seal scat. One study on small cetaceans suggested that otoliths degrade at a consistent rate that can be used to estimate residence time, although this was based on only three species found in European waters (Ross et al. 2016). It is not possible to definitively know the level of bias imparted by the use of eroded otoliths without doing a separate study subjecting prey to digestion or a simile of digestion. To minimize the influence of degraded otoliths we followed the example of Recchia and Read (1989) and

Gannon et al. (1998) and only used minimally eroded otoliths for length and biomass estimation.

Accurate estimation of consumed biomass depends on digestion and food passage rates. In captive a harbor porpoise, food took between 143 and 280 minutes (2.38-4.83 hr) to pass through the animal (Kastelein et al. 1997a). These authors also claimed that after 1-1.5 hours the harbor porpoise stomach was empty of “most solid fish remains” and that 30 minutes after eating herring only bones remained. This puts evacuation time at 30 minutes, while the upper limit may depend on the type of prey eaten and the size and fragility of its otoliths and squid beaks. In seals, passage rates of otoliths and squid beaks differed from each other and varied substantially by individual and activity level (Bigg & Fawcett 1985, Bowen & Iverson 2013).

We did not attempt to estimate the residence time of hard parts directly for this study, but we can back-calculate residence time using literature values of estimated daily consumption. Lockyer (2007) estimated 2.5-5 kg wet weight of herring daily, and Smith et al. (2015b) modeled daily consumption at 2.2 kg daily with an 80% CI of 0.94 and 3.3. Based on these values we estimate that our observed average of 2.35 kg of live weight per stomach equates to roughly 12-24 hours of feeding.

Estimates of daily consumption by species or taxa will be increasingly important as regional fisheries move towards ecosystem based management. Studies such as this one increase the spatial and temporal resolution of predator diet information such that seasonal and regional changes in predation can be included in future ecosystem models. This knowledge facilitates analysis of ecosystem function (Gaichas et al. 2015) and simulations to examine the role of top predators on the ecosystem (Smith et

al. 2015a, Smith et al. 2015b). Detailed diet information could be particularly important as the climate and harbor porpoise prey distribution shifts. Despite their plastic diet, harbor porpoises could be disproportionately threatened by changes in prey distribution because of their presumed high metabolism (Read & Hohn 1995, Wisniewska et al. 2016).

Diet information could also inform fisheries management. Most directly, this paper proves that harbor porpoises are not typically preying on the same species caught in gillnets in the study area. Fisheries managers could use these results to insure fish harvesting remains at a level that leaves an adequate food supply to sustain marine mammal populations. Eventually these data could be used in conjunction with models of prey distribution to better predict marine mammal presence such that bycatch can be avoided or reduced. Prey distribution is not currently known on a fine enough scale in this region to predict harbor porpoise distribution, although examining predicted spring distribution from the NEFSC bottom trawl survey could provide some insights. Yet, the apparent plasticity of harbor porpoise diet may make their distribution challenging to predict.

CONCLUSIONS

Gannon et al (1998) found that fall harbor porpoise diet in the Gulf of Maine was more diverse than during the summer in the Bay of Fundy and predicted that their diet would further diversify further as they move out of the Gulf of Maine for the winter and spring. Their prediction appears to have been correct. We found the diet less reliant on Atlantic herring, with an increased importance of *Urophycis* and squid,

Silver hake also played a primary role in porpoise diet. Cusk eel and small flatfish were important on a numerical basis but not in terms of biomass. Overall, there was a diversification of prey sources compared to previous studies in other regions. The shift towards *Urophycis*, squid, and smaller species appears to have occurred more in the recent past. We also found that larger animals consumed more biomass, but not different species. Lastly, porpoises appear select their prey preferentially, at least based on size, but these prey choices have little overlap with gillnet catch.

ACKNOWLEDGEMENTS

We would like to thank a number of people who contributed to the data collection and processing of the samples used in this study. We would like to specifically thank all the NEFOP observers who brought back samples, Henry Milliken for collecting samples on experimental trips, and various staff and volunteers at NOAA and WHOI who conducted necropsies. Thank you to Jackie Kroeger, Amanda Crandall, Marjorie Lyssikatos, and Gaelan Bergstrom for contributing to processing stomach samples. Thank you also for helpful discussions with Dave McElroy, Lisa Hendrickson, and Laurel Smith. This work was supported in part by the NOAA Advanced Study Program, and we appreciate Mike Simpkins, Sean Hayes, Debi Palka for supporting participation in this program. Lastly, thank you to Melissa Omand and John Hoey for helpful comments and suggestions.

LITERATURE CITED

- Amundsen, P. A., Gabler H. M., and Staldvik F. J. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990) method. *Journal of Fish Biology* 48:607-614.
- Benoit-Bird, K. J., Battaile B. C., Heppell S. A., Hoover B., Irons D., Jones N., Kuletz K. J., Nordstrom C. A., Paredes R., Suryan R. M., Waluk C. M., and Trites A. W. 2013. Prey Patch Patterns Predict Habitat Use by Top Marine Predators with Diverse Foraging Strategies. *PloS one* 8:e53348.
- Benoit-Bird, K. J., and McManus M. A. 2012. Bottom-up regulation of a pelagic community through spatial aggregations. *Biology letters* 8:813-816.
- Bigelow, H. B., and Schroeder W. C. 1953. *Fishes of the Gulf of Maine, United States* Government Printing Service, Washington DC.
- Bigg, M. A., and Fawcett I. F. 1985. Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). In *Maine mammals and fisheries* (J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne, eds.), p. 284–291. George Allen & Unwin, London, U.K, London, U.K.
- Bowen, W. D., and Harrison G. D. 1994. Offshore diet of grey seals *Halichoerus grypus* near Sable Island, Canada. *Marine Ecology Progress Series* 112:1-11.
- Bowen, W. D., and Iverson S. J. 2013. Methods of estimating marine mammal diets: A review of validation experiments and sources of bias and uncertainty. *Marine Mammal Science* 29:719-754.
- Brodeur, R. D. 1979. Guide to otoliths of some northwest atlantic fishes. US Dept Commer, Northeast Fish Sci Cent Ref Doc. 79-36; 70 p. Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026
- Brodziak, J. K. T., and Macy W. K. 1996. Growth of long-finned squid, *Loligo pealei*, in the Northwest Atlantic. *Oceanographic Literature Review* 43:1155.
- Burgess, M. G., McDermott G. R., Owashi B., Peavey Reeves L. E., Clavelle T., Ovando D., Wallace B. P., Lewison R. L., Gaines S. D., and Costello C. 2018. Protecting marine mammals, turtles, and birds by rebuilding global fisheries. *Science* 359:1255-1258.
- Byers, C. R., Steinhorst R. K., and Krausman P. R. 1984. Clarification of a Technique for Analysis of Utilization-Availability Data. *The Journal of Wildlife Management* 48:1050-1053.
- Campana, S. E. 2004. *Photographic Atlas of Fish Otoliths of the Northwest Atlantic Ocean* Canadian Special Publication of Fisheries and Aquatic Sciences No. 133, NRC Research Press.

- Cargnelli LM, Griesbach SJ, McBride C, Zetlin CA, Morse WW. 1999. Essential fish habitat source document: Longfin inshore squid, *Loligo pealeii*, life history and habitat characteristics. NOAA Tech Memo NMFS NE 146; 27 p.
- Clay, D., and Clay H. 1991. Determination of age and growth of white hake (*Urophycis tenuis* Mitchell) from the southern Gulf of St. Lawrence, Canada (including techniques for commercial sampling). Canadian Technical Report of Fisheries and Aquatic Sciences Report No. 1828. Dept of Fisheries and Oceans 35 p.
- Costello, M. J. 1990. Predator feeding strategy and prey importance: a new graphical analysis. *Journal of Fish Biology* 36:261-263.
- Craddock, J. E., Polloni P. T., Hayward B., and Wenzel F. 2009. Food habits of Atlantic white-sided dolphins (*Lagenorhynchus acutus*) off the coast of New England. *Fishery Bulletin* 107:384-394.
- Doubleday, Z. A., Prowse T. A. A., Arkhipkin A., Pierce G. J., Semmens J., Steer M., Leporati S. C., Lourenço S., Quetglas A., Sauer W., and Gillanders B. M. 2016. Global proliferation of cephalopods. *Current Biology* 26:R406-R407.
- Fahay MP, Berrien PL, Johnson DL, Morse WW. 1999. Essential fish habitat source document: Atlantic cod, *Gadus morhua*, life history and habitat characteristics. NOAA Tech Memo NMFS NE 124; 41 p.
- Froese, R. and D. Pauly. Editors. 2019. FishBase. World Wide Web electronic publication.
www.fishbase.org, version (02/2019) Gaichas, S., Aydin K., and Francis R. C. 2015. Wasp waist or beer belly? Modeling food web structure and energetic control in Alaskan marine ecosystems, with implications for fishing and environmental forcing. *Progress in Oceanography* 138:1-17.
- Gannon, D. P., Craddock J. E., and Read A. J. 1998. Autumn food habits of harbor porpoises, *Phocoena phocoena*, in the Gulf of Maine. *Fishery Bulletin* 96:428-437.
- Gray, C. A., and Kennelly S. J. 2018. Bycatches of endangered, threatened and protected species in marine fisheries. *Reviews in Fish Biology and Fisheries*.
- Hatch J, Orphanides C. 2015. Estimates of cetacean and pinniped bycatch in the 2013 New England sink and mid-Atlantic gillnet fisheries. *Northeast Fish Sci Cent Ref Doc.* 15-15; 26 p. doi: 10.7289/V5HD7SNK
- Hatch J, Orphanides C. 2016. Estimates of cetacean and pinniped bycatch in the 2014 New England sink and mid-Atlantic gillnet fisheries. US Dept Commer, Northeast Fish Sci Cent Ref Doc. 16-05; 22 p. Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026

- Hunt, J. J. 1992. Morphological Characteristics of Otoliths for Selected Fish in the Northwest Atlantic. *Journal of Northwest Atlantic Fishery Science* 13:63-75.
- Kastelein, R. A., Nieuwstraten S. H., and Verstegen M. W. A. 1997a. Passage time of carmine red dye through the digestive tract of harbour porpoises (*Phocoena phocoena*). *In* The biology of the harbour porpoise (A. J. Read, P. R. Wiepkema, and P. E. Nachtigall, eds.), p. 265-275. De Spil Publishers, Woerden, Netherlands.
- Kastelein, R. A., Staal C., Terlouw A., and Muller M. 1997b. Pressure changes in the mouth of a feeding harbor porpoise (*Phocoena phocoena*). *In* The Biology of the Harbor Porpoise (A. J. Read, P. R. Wiepkema, and P. E. Nachtigall, eds.), p. 279-291. De Spil Publishers, Woerden, Netherlands.
- Kleisner, K. M., Fogarty M. J., McGee S., Barnett A., Fratantoni P., Greene J., Hare J. A., Lucey S. M., McGuire C., Odell J., Saba V. S., Smith L., Weaver K. J., and Pinsky M. L. 2016. The Effects of Sub-Regional Climate Velocity on the Distribution and Spatial Extent of Marine Species Assemblages. *PloS one* 11:e0149220.
- Kleisner, K. M., Fogarty M. J., McGee S., Hare J. A., Moret S., Perretti C. T., and Saba V. S. 2017. Marine species distribution shifts on the U.S. Northeast Continental Shelf under continued ocean warming. *Progress in Oceanography* 153:24-36.
- Kroeger, J., Wenzel F. W., Craddock J. E., Gannon D. P., McAlarney R. J., and Pabst D. A. in review. Diet analysis of harbor porpoises (*Phocoena phocoena*) in the U.S. and mid-Atlantic.
- Learmonth, J., MacLeod C., Santos M. B., Pierce G., Crick H., and Robinson R. 2006. Potential effects of climate change on marine mammals. *Oceanography and Marine Biology* 44:431.
- Lewison, R. L., Crowder L. B., Wallace B. P., Moore J. E., Cox T., Zydelis R., McDonald S., DiMatteo A., Dunn D. C., Kot C. Y., Bjorkland R., Kelez S., Soykan C., Stewart K. R., Sims M., Boustany A., Read A. J., Halpin P., Nichols W. J., and Safina C. 2014. Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. *Proceedings of the National Academy of Sciences* 111:5271-5276.
- Link, J., Griswold C., ETMethratta, and GunnardEditors J. 2006. Documentation for the Energy Modeling and Analysis eXercise (EMAX). *In* Book Documentation for the Energy Modeling and Analysis eXercise (EMAX) (Editor, ed.)^eds.), p. 166. US Dep. Commer. Northeast Fish. Sci. Cent., City.
- Link, J., Overholtz W., O'Reilly J., Green J., Dow D., Palka D., Legault C., Vitaliano J., Guida V., Fogarty M., Brodziak J., Methratta L., Stockhausen W., Col L., and Griswold C. 2008. The Northeast U.S. continental shelf Energy Modeling and

- Analysis exercise (EMAX): Ecological network model development and basic ecosystem metrics. *Journal of Marine Systems* 74:453-474.
- Lockyer, C. 2007. All creatures great and smaller: a study in cetacean life history energetics. *Journal of the Marine Biological Association of the UK* 87:1035-1045.
- Manly, B., McDonald L., Thomas D., McDonald T., and Erickson W. 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*.
- Miller TJ, Das C, Politis PJ, Miller AS, Lucey SM, Legault CM, Brown RW, Rago PJ. 2010. Estimation of Albatross IV to Henry B. Bigelow calibration factors. *Northeast Fish Sci Cent Ref Doc.* 10-05; 233 p. Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026.
- Murphy T, Kitts A, Demarest C, Walden J. 2015. 2013 Final report on the performance of the northeast multispecies (groundfish) fishery (May 2013 -April 2014). *US Dept Commer, Northeast Fish Sci Cent Ref Doc.* 15-02; 106 p. doi: 10.7289/V5XS5SB9
- Neu, C. W., Byers C. R., and Peek J. M. 1974. A Technique for Analysis of Utilization-Availability Data. *The Journal of Wildlife Management* 38:541-545.
- NEFSC Fisheries Sampling Branch 2016. *Northeast Fisheries Science Center Fisheries Sampling Branch Observer Operations Manual 2016*. National Marine Fisheries Service. Woods Hole, MA.
- Nye, J. A., Joyce T. M., Kwon Y.-O., and Link J. S. 2011. Silver hake tracks changes in Northwest Atlantic circulation. *Nature communications* 2:412.
- Nye, J. A., Link J. S., Hare J. A., and Overholtz W. J. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Marine Ecology Progress Series* 393:111-129.
- Orphanides CD. 2012. New England harbor porpoise bycatch rates during 2010-2012 associated with Consequence Closure Areas. *US Dept Commer, Northeast Fish Sci Cent Ref Doc.* 12-19; 15 p. Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026.
- Orphanides, C. D. 2010. Protected Species Bycatch Estimating Approaches: Estimating Harbor Porpoise Bycatch in U.S. Northwestern Atlantic Gillnet Fisheries. *Journal of Northwest Atlantic Fishery Science* 42:55-76.
- Orphanides, C. D., and Palka D. L. 2013. Analysis of harbor porpoise gillnet bycatch, compliance, and enforcement trends in the US northwestern Atlantic, January 1999 to May 2010. *Endangered Species Research* 20:251-269.

- Pershing, A. J., Alexander M. A., Hernandez C. M., Kerr L. A., Le Bris A., Mills K. E., Nye J. A., Record N. R., Scannell H. A., Scott J. D., Sherwood G. D., and Thomas A. C. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 350:809-812.
- Polacheck, T., Wenzel F., W., and Early G. 1995. What do stranding data say about harbor porpoises (*Phocoena phocoena*). International Whaling Commission Science Document 12.
- Read, A. J., Drinker P., and Northridge S. 2006. Bycatch of Marine Mammals in U.S. and Global Fisheries. *Conservation Biology* 20:163-169.
- Read, A. J., and Hohn A. A. 1995. Life in the fast lane: the life history of harbor porpoises from the Gulf of Maine. *Marine Mammal Science* 11:423-440.
- Read, A. J., Wiepkema P. R., and Nachtigall P. E. 1997. *The Biology of the Harbour Porpoise*, De Spil Publishers.
- Read, J. A., and Westgate J. A. 1997. Monitoring the movements of harbour porpoises (*Phocoena phocoena*) with satellite telemetry. *Mar Biol* 130:315-322.
- Recchia, C. A., and Read A. J. 1989. Stomach contents of harbour porpoises, *Phocoena phocoena* (L.), from the Bay of Fundy. *Canadian Journal of Zoology* 67:2140-2146.
- Roberts, J. J., Best B. D., Mannocci L., Fujioka E., Halpin P. N., Palka D. L., Garrison L. P., Mullin K. D., Cole T. V. N., Khan C. B., McLellan W. A., Pabst D. A., and Lockhart G. G. 2016. Habitat-based cetacean density models for the U.S. Atlantic and Gulf of Mexico. *Scientific Reports* 6:22615.
- Ross, S. D., Andreasen H., and Andersen N. G. 2016. An important step towards accurate estimation of diet composition and consumption rates for the harbor porpoise (*Phocoena phocoena*). *Marine Mammal Science* n/a-n/a.
- Saba, V. S., Griffies S. M., Anderson W. G., Winton M., Alexander M. A., Delworth T. L., Hare J. A., Harrison M. J., Rosati A., Vecchi G. A., and Zhang R. 2015. Enhanced warming of the northwest Atlantic Ocean under climate change. *Journal of Geophysical Research: Oceans* n/a-n/a.
- Simmonds, M. P., and Isaac S. J. 2007. The impacts of climate change on marine mammals: early signs of significant problems. *Oryx* 41:19-26.
- Smith, G. J. D., and Gaskin D. E. 1974. The diet of harbor porpoises (*Phocoena phocoena* (L.)) in coastal waters of Eastern Canada, with special reference to the Bay of Fundy. *Canadian Journal of Zoology* 52:777-782.

- Smith, L., Gamble R., Gaichas S., and Link J. 2015a. Simulations to evaluate management trade-offs among marine mammal consumption needs, commercial fishing fleets and finfish biomass. *Marine Ecology Progress Series* 523:215-232.
- Smith, L. A., Link J. S., Cadrin S. X., and Palka D. L. 2015b. Consumption by marine mammals on the Northeast U.S. continental shelf. *Ecological Applications* 25:373-389.
- Smith, R. J., and Read A. J. 1992. Consumption of euphausiids by harbour porpoise (*Phocoena phocoena*) calves in the Bay of Fundy. *Canadian Journal of Zoology* 70:1629-1632.
- Steimle FW, Morse WW, Berrien PL, Johson DL. 1999. Essential fish habitat source document: Red Hake, *Urophycis chuss*, life history and habitat characteristics. NOAA Tech Memo NMFS NE 133; 34 p.
- Stevenson DK, Scott ML. 2005. Essential fish habitat source document: Atlantic herring, *Clupea harengus*, life history and habitat characteristics (2nd edition). NOAA Tech Memo NMFS NE 192; 84 p.
- Sydeman, W. J., Poloczanska E. S., Reed T. E., and Thompson S. A. 2015. Climate change and marine vertebrates. *Science* 350:772-777.
- Waring GT, Josephson E, Maze-Foley K, Rosel, PE, editors. 2014. U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments -- 2013. NOAA Tech Memo NMFS NE 228; 464 p. Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026.
- Wenzel, F. W. 2000. An examination of the distribution and causes of harbor porpoise (*Phocoena phocoena*) strandings in Massachusetts waters. Master of Science Northeastern University, Boston, MA, USA.
- Wenzel, F. W., Polloni P. T., Craddock J. E., Gannon D. P., Nicolas J. R., Read A. J., and Rosel P. E. 2013. Food habits of Sowerby's beaked whales (*Mesoplodon bidens*) taken in the pelagic drift gillnet fishery of the western North Atlantic. *Fishery Bulletin* 111:381-389.
- Wigley SE, McBride HM, McHugh NJ. 2003. Length-weight relationships for 74 fish species collected during NEFSC research vessel bottom trawl surveys, 1992-9. NOAA Tech Memo NMFS NE 171; 26 p.
- Wisniewska, Danuta M., Johnson M., Teilmann J., Rojano-Doñate L., Shearer J., Sveegaard S., Miller Lee A., Siebert U., and Madsen Peter T. 2016. Ultra-High Foraging Rates of Harbor Porpoises Make Them Vulnerable to Anthropogenic Disturbance. *Current Biology*.

TABLES

Table 1. Equations used to estimate length and weight of harbor porpoise prey found with intact skulls or whole bodies in stomach samples.

Scientific Name	Common Name	Length Equation (mm)	Length Equation Source	Weight Equation (cm & kg)	Weight Equation Source
<i>Alosa aestivalis</i>	blueback herring	FL = 69.23 OL - 27.48 ***	Recchia and Read, 1989	lnW = -12.2146 + 3.2428 lnL	Wigely et al 2004
<i>Alosa pseudoharengus</i>	alewife	FL = 69.23 OL - 27.48 ***	Recchia and Read, 1989	ln W = -13.3875 + 3.6716 ln L	Wigely et al 2003
<i>Ceratoscopelus maderensis</i>	madiera lanternfish	NA	NA	lnW = ln(0.00537) + 3.08 ln L	fishbase.org
<i>Citharichthys arctifrons</i>	gulf stream flounder	FL = (39.737 OL-14.141)	This study	lnW = -13.6310 + 3.3428 lnL	This study
<i>Clupea harengus</i>	Atlantic herring	FL = 69.23 OL - 27.48	Recchia and Read, 1989	ln W = -11.7972 + 3.0314 ln L	Wigely et al 2003
<i>Clupeidae</i>	Clupeidae	FL = 69.23 OL - 27.48 ***	Recchia and Read, 1989	ln W = -11.7972 + 3.0314 ln L	Wigely et al 2003***
<i>Doryteuthis (Amerigo) pealeii</i>	longfin inshore squid	ML = 3.277 LRL + 39.77	This study	M = 0.25662(ML/10) ^{2.1582}	Lange and Johnson 1981
<i>Etropus microstomus</i>	small mouth flounder	FL = (39.737 OL-14.141)/10 %	This study	lnW = -13.6310 + 3.3428lnL	This study%
<i>Gadidae</i>	Gadids	FL/10 = 1.525 OL ^{1.1457}	Clay and Clay, 1991	ln W = -12.4378 + 3.1568ln L	Wigely et al 2003* ^ξ
<i>Laemonema barbatulum</i>	shortbeard codling	NA	NA	lnW = ln(0.0019) + 3.355lnL/10	fishbase.org
<i>Peprilus triacanthus</i>	butterfish	FL = -13.1344 + 56.3944 OL	DuPaul and McEachran, 1973	lnw = -10.6315 + 2.9225*lnL	Wigely et al 2004
<i>Melanogrammus aeglefinus</i>	haddock	ln(FL/10) = 2.97753 + 1.58465 ln OL	Hunt, 1992	lnW = -11.8062 + 3.0766lnL	Wigely et al 2004
<i>Merluccius bilineari</i>	silver hake	ln(FL/10) = 3.01115 + 1.02758 ln OL	Hunt, 1992	ln W = -12.4934 + 3.1512 ln L	Wigely et al 2003
<i>Ophidiide</i>	cusk eel	FL = 35.264OL + 13.527	This study	ln W = -13.7333 + 3.2359ln L	Wigely et al 2005**
<i>Pleuronectiformes</i>	flatfish	FL = 39.737 OL-14.141 %	This study	lnW = -13.6310 + 3.3428lnL	This study%
<i>Scomber scombrus</i>	Atlantic mackerel	FL/10 = 7.33 OL + 0.37	Clay and Clay, 1991	ln W = -12.6713 + 3.3119ln L	Wigely et al 2004
Unidentified	unidentified	NA	NA	mean from all estimated weights	This study, Wigley et al 2003, and fishbase.org
<i>Unidentified Cephalopods</i>	squid	ML = 3.277 LRL + 39.77 [§]	This study	M = 0.25662(ML/10) ^{2.1582}	Lange and Johnson 1981
<i>Urophycis</i> (Genus)	hake	FL/10 = 1.525 OL ^{1.1457}	Clay and Clay, 1991	ln W = -12.4378 + 3.1568ln L	Wigely et al 2003*
<i>Urophycis chuss</i>	red hake	FL/10 = 1.525 OL ^{1.1456 ξ}	Clay and Clay, 1991	ln W = -12.3743 + 3.0979ln L	Wigely et al 2003
<i>Urophycis regia</i>	spotted hake	FL/10 = 1.525 OL ^{1.1456 ξ}	Clay and Clay, 1991	ln W = -11.9892 + 3.0823ln L	Wigely et al 2003
<i>Urophycis tenuis</i>	white hake	FL/10 = 1.525 OL ^{1.1456 ξ}	Clay and Clay, 1991	ln W = -12.9500 + 3.2903ln L	Wigely et al 2003

* Averaged *a* and *b* across *Urophycis chuss*, *tenuis*, and *regius* from spring combined sexes estimates

** *a* and *b* used from *Lepophidium profundorum* (fawn cusk eel)

*** Applied equation from *Clupea harengus*

% Applied equation for *Citharichthys arctifrons*

ξ Applied *Urophycis* equation

§ Applied *Doryteuthis (Amerigo) pealeii* equation

Table 2. Summary of fish otoliths and squid beaks found in harbor porpoise stomachs. Number of Items, numerical abundance (%N), number of occurrences, frequency of occurrence (%FO) and number of individuals for each prey item and prey groupings

Fishes & Cephalopods	Number of Items	%N	Number of Occurrences	%FO	Number of Individuals
longfin inshore squid	561	18.5	24	52.2	337
unidentified squids	21	0.7	2	4.3	11
squids	582	19.2	24	52.2	348
blueback herring	7	0.2	2	4.3	4
alewife	151	5.0	6	13.0	78
atlantic herring	84	2.8	10	21.7	37
unidentified <i>clupeidae</i>	2	0.1	1	2.2	1
herrings	244	8.1	16	34.8	120
gulf stream flounder	486	16.1	8	17.4	245
small mouth flounder	35	1.2	1	2.2	18
unidentified flat fish	23	0.8	5	10.9	16
flatfish	544	18.0	13	28.3	279
red hake	220	7.3	9	19.6	117
spotted hake	103	3.4	6	13.0	55
white hake	15	0.5	6	13.0	8
unidentified <i>Urophycis</i>	337	11.2	15	32.6	180
hakes	675	22.3	20	43.5	360
madeira lanternfish	108	3.6	1	2.2	54
krill	NA	NA	10	21.3	NA
unidentifiable/degraded gadidae	17	0.6	2	4.3	9
shortbeard codling	4	0.1	1	2.2	2
haddock	70	2.3	1	2.2	35
silver hake	527	17.4	15	32.6	266
cusk eel	172	5.7	14	30.4	94
butterfish	4	0.1	1	2.2	2
atlantic mackerel	30	1.0	6	13.0	17
unidentifiable/degraded	31	1.0	14	30.4	24
unidentified	17	0.6	6	13.0	8
Totals	3025	100.2			1618

Table 3. Raw counts of grouped species by year period (1994-2006 and 2007-2017) and contributions of species groups to permutation analysis of variance (PERMANOVA) test.

	Raw Counts 1994-2006	Raw Counts 2007-2017	Average Contribution	Standard Deviation of Contribution
True Hakes	56	619	0.169	0.166
Cephalopods	191	391	0.145	0.148
Clupeids	207	37	0.112	0.161
Other	29	252	0.104	0.100
Silver Hake	492	35	0.091	0.139
Flatfish	57	487	0.085	0.124
Cusk Eel	20	152	0.082	0.100

Table 4. Cross tabulation of porpoise sample sizes by sex, size, and year categories.

	Male	Female	Unknown Sex	Totals
1994-2006	14	9		23
< 140 cm	9	3	1	13
>= 140 cm	5	5		10
Unknown size		1	1	2
2007-2017	12	8		20
< 140 cm	7	1		8
>= 140 cm	5	7		12
Unknown size			1	1
All Years	26	17	3	46
< 140 cm	16	4	1	21
>= 140 cm	10	12		22
Unknown size		1	2	3

Table 5. Prey selection indices (Manley 2002). Confidence intervals for selected prey proportion are shown only for taxa used to test the null hypothesis that harbor porpoise selected prey randomly in proportion to their availability (Chi-squared test, $p < 0.001$)

Prey types	Population Proportion	Expected Count	Prey Count	Selected Prey Proportion	95% CI Selected Prey Proportion	Selection Index	Standardized Index
longfin inshore squid	0.051	116	561	0.24		4.82	0.006
unidentified squid			21	0.01			
squid	0.051	116	582	0.25	0.23-0.28	5.00	0.007
blueback herring	0.003	7	7	0.00		0.95	0.001
alewife	0.002	5	151	0.07		31.83	0.042
atlantic herring	0.823	1889	84	0.04		0.04	0.000
unidentified <i>clupeidae</i>			2	0.00			
herring	0.828	1901	244	0.11	0.09-0.12	0.13	0.000
gulf stream flounder	0.003	8	486	0.21		61.08	0.081
small mouth flounder	0.000	0	35	0.02		150.09	0.200
unidentified flat fish			23	0.01			
flatfish	0.004	8	544	0.24	0.21-0.26	66.42	0.088
red hake	0.004	9	220	0.10		23.76	0.032
spotted hake	0.003	6	103	0.04		16.80	0.022
white hake	0.000	0	15	0.01		287.21	0.382
unidentified <i>Urophycis</i>			337	0.15			
hake	0.007	15	675	0.29	0.26-0.31	43.71	0.058
silver hake	0.050	116	527	0.23	0.20-0.25	4.56	0.006
cusk eel	0.000	1	172	0.07	0.06-0.09	184.19	0.245
atlantic mackerel	0.009	20	30	0.01	0.006-0.019	1.54	0.002
madeira lanternfish	0.000	1	108	0.05		148.06	0.197
krill			NA				
unidentifiable/degraded gadidae			17	0.01			
shortbeard codling	0.000		4	0.00			
haddock	0.001	3	70	0.03		27.46	0.037
butterfish	0.050	115	4	0.00		0.03	0.000
unidentifiable/degraded			31	0.01			
unidentified			17	0.01			
lanternfish, krill, codling, haddock, butterfish, and unidentified	0.052	118	251	0.11	0.09-0.13	2.121	0.003
TOTALS	1.000	2296	2296	1.00		752.12	1.000

Table 6. Porpoise prey measurements and biomass estimate

	Otoliths or Beaks			Prey Length		Prey Weight		Stomach Contents	
	Number Measured	Average Length (mm)	Length Range (mm)	Average Length (mm)	Length Range (mm)	Average Weight (g)	Weight Range (g)	Average Total Weight (g)	Average Total Weight (%)
Fishes & Cephalopods									
longfin inshore squid	146	1.2	0.4 - 3.2	7.8	5.6 - 16.5	24.2	10.7 - 108.4	347.3	14.8%
unidentified squid	9	2.3	1.8 - 3.1	12.8	5.6 - 16.0	71.5	46.5 - 102.3	34.2	1.5%
squid	155	3.6	0.4 - 17.7	8.0	5.6 - 16.5	25.7	10.7 - 108.4	381.5	16.2%
blueback herring	4	4.6	4.4 - 4.7	22.7	27.6 - 30.1	183.5	176.4 - 227.6	31.9	1.4%
alewife	65	3.6	2.1 - 5.3	17.8	11.4 - 34.2	74.9	12.2 - 337.0	253.9	10.8%
atlantic herring	61	4.2	3.3 - 5.3	25.0	19.8 - 32.4	143.8	64.4 - 286.1	231.3	9.8%
unidentified <i>clupeidae</i>	0					26.7		1.2	0.1%
herring	130	3.9	2.1 - 5.3	24.8	11.4 - 34.2	144.8	12.2 - 337	518.3	22.1%
gulf stream flounder	77	1.7	0.8 - 3.5	5.0	1.6 - 12.4	0.6	0.006 - 5.5	6.3	0.3%
small mouth flounder	0					0.4		0.3	<0.1%
unidentified flat fish	0					0.6		0.4	<0.1%
flatfish	77	1.7	0.8 - 3.5	5.0	1.6 - 12.4	0.6	0.006 - 5.5	7.0	0.3%
red hake	73	10.5	5.2 - 12.4	22.7	10.0 - 27.2	74.3	5.3 - 117.4	378.1	16.1%
spotted hake	52	10.4	5.0 - 13.2	20.8	9.5 - 29.2	82.2	0.9 - 17.5	196.6	8.4%
white hake	10	13.1	11.4 - 14.8	28.4	24.9 - 33.4	144.2	93.1 - 246.3	50.2	2.1%
unidentified <i>Urophycis</i>	73	6.8	1.3 - 15.0	13.8	2.1 - 33.9	27.4	0.04 - 268.8	214.7	9.1%
hake	208	9.4	1.3 - 15.0	18.1	2.1 - 33.9	53.6	0.04 - 268.8	839.6	35.7%
madeira lanternfish	21	2.0	1.8 - 2.3			0.8		1.9	0.1%
krill	0							-	
unidentifiable/degraded gadidae	0					76.2		29.8	1.3%
shortbeard codling	0					44.0		3.8	0.2%
haddock	25	8.2	7.2 - 9.1	14.4	11.5 - 17.0	29.6	13.8 - 45.5	45.1	1.9%
silver hake	78	8.0	1.8 - 18.8	11.1	3.4 - 38.8	23.4	0.2 - 382.0	270.6	11.5%
cusk eel	111	2.9	1.0 - 5.4	10.3	4.8 - 20.3	4.1	0.2 - 18.3	16.6	0.7%
butterfish	3	2.3	2.1 - 2.6	10.7	10.6 - 13.1	10.2	8.5 - 15.4	0.8	<0.1%
atlantic mackerel	7	3.7	2.6 - 5.4	25.9	19.3 - 39.9	200.7	56.6 - 628.7	148.3	6.3%
unidentifiable/degraded	0					65.4		68.3	2.9%
unidentified	0					53.9		18.7	0.8%
TOTALS	815			11.7	1.6 - 39.9	33.6	0.1 - 628.7	2350.3	100.0%

FIGURES

Figure 1. Study area, locations of harbor porpoise bycatch events from which stomach samples were retrieved, and degree to which gillnet catch data were available

Figure 2. Distribution of porpoise stomach samples by year

Figure 3. Porpoise stomach sample distribution by animal total length and sex. (Young of the year <125 cm; Juveniles 125-139 cm; Adults 140 cm and greater).

Figure 4. Costello diagram for major species groupings found in harbor porpoise stomachs. Prey importance is expressed from the bottom left to the upper right. Feeding strategy expressed along the axis from bottom right to upper left (Costello 1990).

Figure 5. Length distribution of porpoise stomach contents versus gillnet catch from hauls that caught porpoise and had available catch length data and length distribution from Northeast Fisheries Science Center trawl catch. Plot was truncated not to include rare values greater than 100 cm.

Figure 6. Forklength (A) and prey weight (B) distributions by sex, size, and year categories

Figure 7. Histogram of estimated biomass per porpoise stomach

MANUSCRIPT 2

North Atlantic right whale (*Eubalaena glacialis*) potential prey sources in Southern
New England

Christopher D. Orphanides^{1,3,*}, Elisabeth Broughton², J. Michael Jech², Jeremy S.
Collie³, Karen Wishner³, Melissa Omand³

¹ NOAA Fisheries, 28 Tarzwell Drive, Narragansett, RI 02882

² NOAA Fisheries, 166 Water Street, Woods Hole, MA 02543

³ University of Rhode Island, Graduate School of Oceanography, 215 S Ferry Rd,
Narragansett, RI 02882

*corresponding author: phone: (401) 782-3283, fax: (401) 782-3201,

email: chris.orphanides@noaa.gov

Key words: right whales, prey, foraging, zooplankton, *Calanus*, ctenophores

Publication status: in preparation for submission to *Aquatic Mammals*

ABSTRACT

North Atlantic right whales (*Eubalaena glacialis*) are thought to feed primarily on copepods, especially *Calanus finmarchicus*. However, shifts in right whale distributions may have led to shifts in diet. In 2017 researchers reported that these whales inhabit the continental shelf south of Rhode Island and Massachusetts year round, and are present and feeding in higher numbers during the late winter and early spring. During a 6-day research cruise in April of 2018, we opportunistically investigated potential right whale prey choices in this understudied region. After spotting two diving right whales in an area with numerous documented sightings in the previous two weeks, we sampled the water column for possible prey and physical oceanographic parameters. Specifically, we deployed a video plankton recorder (VPR), a bongo net, conductivity temperature and depth (CTD) casts, an expendable bathythermograph (XBT), an acoustic Doppler current profiler (ADCP), a thermosalinograph (TSG), a fluorometer, and an active acoustic tow body equipped with 38, 120, and 206 kHz transducers. VPR sampling revealed a consistent dense layer at about 35-40 m associated with a slight pycnocline that appeared to consist primarily of ctenophores and marine snow. However, bongo net sampling throughout the water column revealed an additional population of *Pseudocalanus* and *Calanus finmarchicus* copepods that were not evident in the echosounder or VPR data. The density of copepods was low; *Calanus finmarchicus* density was 644 m^{-3} , below the typical densities found in other right whale foraging regions. These observations suggest that the right whales may have been foraging on ctenophores and a

zooplankton assemblage more diverse than most right whale feeding regions, but similar to Cape Cod Bay.

INTRODUCTION

The North Atlantic right whale is one of the most endangered whales in the world. As of 2015 there were an estimated 458 North Atlantic right whales (*Eubalaena glacialis*) remaining (Pace et al. 2017). Recent population trends are poor, with a decreasing population from 2010 to 2015, 17 documented right whale deaths during 2017, and no observed calves during the winter calving season in 2018 (Daoust et al. 2017, Pennisi 2017, Davies & Brillant 2019).

Accompanying this recent drop in abundance, there has been a shift in right whale distribution since 2011 (Davis et al. 2017). Traditional seasonal right whale distribution patterns have been well-documented (Winn et al. 1986, Kenney et al. 1986). Right whales occupied northern feeding grounds rich in their primary prey, *Calanus finmarchicus* copepods, hereafter referred to as *C. finmarchicus*, from late winter to early autumn. These areas included the Great South Channel, Cape Cod Bay, the Bay of Fundy, and Roseway Basin (Kenney et al 2001, Baumgartner & Mate 2005). Pregnant females and juveniles, and some males, would then migrate from northern feeding grounds south to calving grounds off Georgia and Florida for the majority of the winter, while much of the remaining population overwintered in the Gulf of Maine (Kraus et al. 1986, Winn et al. 1986, Mussoline 2012, Cole et al. 2013).

Right whales no longer visit their traditional feeding grounds at their usual times of the year (Pettis & Hamilton 2016, Hayes et al. 2018). In recent years, few have

been returning to the Bay of Fundy during the late summer, they are often in Cape Cod Bay a month earlier than usual, and in the summer of 2017 large numbers of animals were observed in the Gulf of Saint Lawrence (pers. comm. PSB). Recent research has also found an increased right whale presence in the mid-Atlantic, previously thought to be primarily a migratory corridor, and a decrease in the Gulf of Maine since 2010. Right whales have been detected year round with passive acoustics off the coast of Virginia and south of New England (Salisbury et al. 2016, Davis et al. 2017) , and aerial surveys south of New England have recorded right whales from December through April, with a peak presence in March, and documented feeding during March and April (Leiter et al 2017).

These shifts in habitat do not appear to align with shifts in right whale's primary prey associated with traditional feeding grounds. Right whales primarily consume calanoid copepods, particularly late stage *C. finmarchicus* (Kenney et al. 1986, Baumgartner and Mate 2003, Wishner et al. 1988, Wishner et al. 1995). *C. finmarchicus* is a sub-arctic species at the southern end of its range in the Gulf of Maine. Their distribution and abundance in the Gulf of Maine has been linked to right whale reproductive success and appears to be significantly impacted by the phases of the North Atlantic Oscillation and similar decadal-scale climate forcing (Greene et al. 2013, Meyer-Gutbrod et al. 2015, Meyer-Gutbrod & Greene 2018). The area *C. finmarchicus* has occupied on the northeast US shelf has decreased in recent years, particularly in the spring, as several copepod species off the northeast US have shifted northeast and towards deeper waters (Runge et al. 2014). Climate change is projected to further reduce *C. finmarchicus* density in the Gulf of Maine (Grieve et al 2017).

These changes in distribution and abundance could lead to a predator-prey spatial-temporal mismatch. Despite the predominant belief that right whales are *C. finmarchicus* specialists, they may be supplementing their diet with other prey items, particularly in secondary feeding grounds such as southern New England. The majority of right whale feeding studies have been conducted in the primary feeding grounds in the Gulf of Maine or on the Scotian Shelf (e.g., Baumgartner & Mate 2003, Baumgartner & Mate 2005, DeLorenzo Costa et al. 2006b, Davies et al. 2012, Davies et al. 2013, Baumgartner et al. 2017, Record et al. 2019). In this study we opportunistically investigate potential right whale prey resources south of New England during the spring. We used a 6-day research cruise in early April to visually search for right whales south of New England in a region where right whales have been observed feeding, and where numerous right whales were observed in the preceding weeks. After observing two right whales in this area that appeared to be feeding below the surface, we intensively sampled the water column and possible prey resources to assess potential right whale prey in the region and oceanographic mechanisms that may concentrate prey.

MATERIALS & METHODS

Research Cruise Overview

We conducted a short research cruise on the R/V Endeavor from April 3-8 2018 to collect data on marine mammal sightings in an attempt to relate these sightings to prey and oceanographic conditions in the water column. We ran transects for sighting marine mammals and deployed equipment to sample the oceanography and prey in the

region. Equipment deployed included a Video Plankton Recorder (VPR), echosounders, bongo nets, conductivity temperature and depth (CTD) sensors, expendable bathythermographs (XBTs), an acoustic Doppler current profiler (ADCP) and an underway thermosalinograph (TSG). Poor weather and sightings conditions plagued the cruise, resulting in few mammal sightings. At 3:10 pm on the final full day of the cruise (April 7), we observed our first of two right whales. The majority of the data collection presented here occurred in the hours following this sighting.

Marine Mammal Observation

We visually surveyed for marine mammals from the flying bridge of the R/V Endeavor using the naked eye, handheld binoculars, and two “Big Eye” (25x) binoculars mounted 10.2 m above the waterline, which were calibrated at the dock. Marine mammal observers rotated every half an hour between the two Big Eye stations and a recording station where observation took place using either naked eyes or handheld binoculars. Marine mammal observers recorded effort and sightings with a custom-built software program (VisSurvey, developed by Lance Garrison and Debra Palka) employed on National Oceanic and Atmospheric Administration (NOAA) marine mammal research cruises. Among the data recorded in this software were the species sighted, distance, latitude, longitude, time, date, behavior, and swim direction. The observer provided the remaining data, with the distance from the ship coming from the Big Eyes. Upon sighting a right whale, photographs were taken that were shared with the North Atlantic Right Whale Consortium (NARWC) and the NOAA Northeast Fisheries Science Center (NEFSC) for potential identification.

Additional right whale observations approximately two weeks before and one week after our Endeavor research cruise were documented in the sightings database maintained by the NEFSC (<https://www.nefsc.noaa.gov/psb/surveys/>) (Figs 1, 2). Sightings in this database included those observed by mariners, and those recorded during aerial surveys in March and April 2018 conducted by the NOAA Northeast Fisheries Science Center.

Video Plankton Recorder

A Video Plankton Recorder (VPR) was deployed off the starboard side and towed aft of the ship. The VPR captured black and white images of plankton and particulate matter from 50 μm to a few cm in size using a paired strobe and camera operating at 16 Hz with a 56 x 37 mm field of view. The resulting images represent 405.28 ml per frame. The Seascan VPR was mounted on a V-fin that also included a Seabird Fastcat CTD and a Wetlabs fluorometer/turbidity sensor. We towed the VPR behind the ship from the starboard side four times during our research cruise, paired each time with deployment of the active acoustic tow body (Fig. 1). It was towed at approximately 1.8 m/s (3.5 knots) in a tow-yo mode, oscillating in a sawtooth pattern throughout the water column, with tows ranging from 38 to 79 minutes. We deployed the tow associated with the right whale sightings for 38 minutes. We first operated this deployment in tow-yo mode, and then we set the instrument at depths (36-42 m) where high densities of organisms were observed in real time echosounding data.

Upon retrieving the VPR, we downloaded compressed video data and extracted regions of interest (ROI) from each image frame using Autodeck programming from Seascan. We hand processed each ROI to remove duplicate images and those with air

bubbles. We then classified the ROIs to general taxonomic groups and estimated density (counts and volume) per m^3 using a modified version of Visual Plankton software implemented in Matlab and developed at the Woods Hole Oceanographic Institution (Tang et al. 1998, Davis et al. 2004). The data were then further hand-processed for finer organism identification and measurement of *Mertensia ovum* ctenophores, hereafter referred to as *Mertensia*. We later used these measurements in calculations of density estimation and acoustic target strength (described below). Energy content of observed *Mertensia* was estimated by assuming a body density of $1.009 \text{ (g m}^{-3}\text{)}$ that of seawater (Warren & Smith 2007), volume based on a prolate ellipsoid ($4/3 * \pi * \text{length} * \text{width}^2$) parameterized by lengths and widths measured with from VPR images, and energy content of 0.21 kJ/g wet weight (Steimle & Terranova 1985).

Bongo Net Sampling

We towed Bongo nets in double oblique fashion to within 5 m of the bottom while the ship traveled between 1.5 and 2.0 knots. We deployed nets of 333 and $150 \mu\text{m}$ on the two 61-cm diameter bongo frames. A shipboard computer system (SCS) monitored bottom depth, GMT, the ship's position, and surface water temperature while a Seabird 19+ CTD deployed on the wire just above the bongo nets recorded oceanographic information along the cast. Samples were washed down into the cod end of the net with salt water and flushed into a sieve. We preserved samples from the $333 \mu\text{m}$ net in formalin, while we preserved the samples from the $150 \mu\text{m}$ net in ethanol, which we changed after 24-48 hours. Zooplankton samples from bongo nets were sent

to the Polish Sorting Center for processing species and quantities. These samples are still being processed.

The sample from the 333 μ net taken near the right whale observations was split in half and one half was sent to the Polish Sorting Center while the other half was processed at the University Rhode Island. The retained sample was split to 1/64 volume, zooplankton taxa were enumerated. We measured and identified *C.*

finmarchicus to stage, and we measured a sub-sample of 30 *Pseudocalanus*.

Pseudocalanus refers to a mixture *Pseudocalanus newmani* and *Pseudocalanus moultoni*, which are extremely difficult to tell apart without molecular techniques (Bucklin et al. 2001). Copepod caloric values were estimated using values from DeLorenzo Costa et al. (2006a) and converted from μg carbon per individual to calories (J) per individual using a relationship derived by Salonen et al. (1976). We used stage-specific caloric estimates for *C. finmarchicus* and a non-stage specific estimate for *Pseudocalanus*. We also examined regional historical zooplankton data from bongo samples on NOAA's ECOMON surveys to provide context to the observations recorded on this cruise. We subset data to include data from March and April from the study area (defined for these purposes between 40°30'00" and 41°17'00" latitude, and 70°00'00" and 71°29' 36" longitude). We then summarized and plotted. *C. finmarchicus* and *Pseudocalanus* densities per m^3 by year.

Oceanographic Data

A number of instruments were employed to characterize the oceanography during the cruise and in the right whale study area in particular. Instrumentation included CTDs, XBTs, a TSG, an ADCP, and chlorophyll satellite images. CTDs and XBTs

recorded physical oceanographic conditions at specific locations or on towed instrumentation. We attached Seabird 19+ CTD instrumentation to the cable for bongo net tows, attached to the VPR tow body, and a separate Seabird 911 CTD and rosette. We deployed one XBT in the region of the right whale sightings and two more in other regions. CTDs deployed in the area of right whales included one on the CTD rosette, a second attached to the bongo net cable, and a third on the VPR tow body.

Two instruments recorded along track oceanographic information throughout the cruise. The ADCP recorded currents at depth while the TSG recorded surface salinity and temperature from the ship's flow-through seawater system. We examined the ADCP current data at 21 meters depth, where the ADCP data were most complete. We summarized current velocity in the u and v directions into its component parts (mean, trend, inertial, diurnal, semidiurnal, residual) (Siegel & Deuser 1997, Siegel et al. 2008). We ran simulations in Matlab examining potential plankton transport over the course of the cruise and in the region of the right whale observations. Hypothetical particles were placed at the beginning of the right whale observation day and at the beginning of the cruise and then the recorded ADCP current data were allowed to act on these particles.

We examined fluorescence, water temperature, salinity, and density data from the TSG over the course of the cruise and in the primary right whale observation region. MODIS Aqua 1-km satellite imagery of chlorophyll a , primary production, sea surface temperature, and oceanographic fronts (Belkin & O'Reilly 2009) were examined relative to right whale sightings, our cruise track, and underway fluorescence data. Modeled ocean currents from the Unstructured Grid Finite Volume Community Ocean

Model (FVCOM) were also examined relative to cruise tracks, right whale sightings, and satellite data (fvcom.smast.umass.edu/necofs).

Echosounder Data

We mounted two Simrad EK60 echosounders (38 and 120 kHz) and one Biosonics DT-X echosounder (206 kHz) on a custom-made tow body crafted from a former Klein side-scan sonar towfish. The tow body was deployed from a boom on the port side that was located approximately 5 meters forward of the stern. When deployed, the tow body was stable and horizontal while towed 2-3 meters below the surface at 3-4 knots.

We calibrated the echosounders prior to deployment using standard techniques (Foote et al. 1987, Demer et al. 2015); however, we had difficulty placing the target sphere directly beneath the transducers in the center of the beams. Therefore, we did not use the Simrad EK60 beam model to calculate 38 and 120 EK60 transducer gain and S_a (area backscattering coefficient) correction. The calibration gains for the 38 kHz and 120 kHz echosounders were calculated using the beam estimation LOBE program in Echoview software (Echoview 2018). Target observations were limited to those within 1 degree on either side of the target for the 38 kHz transducer, and within a quarter degree for the 120 kHz transducer. Using these observations, we adjusted the 38 kHz gain such that the measured target strength matched the known target strength of the calibration sphere. The S_a (area backscattering coefficient) correction value for the 38 kHz echosounder was left as the default (0.0) due to few recorded target observations close to the center of the beam. Calibration values for the 120 kHz echosounder gain and S_a were calculated using methods outlined in the Simrad EK500

operation manual (Simrad 1996). Theoretical S_a and target strength were combined with measured target strength and a previous estimate of gain to calculate new gain and S_a values as shown below.

$$S_a (theory) = \frac{4\pi r_0^2 * \sigma_{bs} * (1852 \frac{m}{nm})^2}{\Psi * r^2}$$

$$G_{new} = G_{old} + \frac{TS_{measured} - TS_{theory}}{2}$$

$$S_a(new) = (G_{old} + S_a(old) - 10\log_{10}\left(\frac{S_a(theory)}{S_a(measured)}\right) - G_{new}$$

Where

TS = target strength of the sphere

$$\sigma_{bs} = 10^{TS_{sphere}/10}$$

r = distance between the transducer and the sphere

$$r_0 = 1 \text{ meter}$$

$$\Psi = 10^{dB\text{-value}/10}$$

G = transducer gain (G_{old} = previous gain estimate, G_{new} = new gain estimate)

S_a = area backscattering coefficient

Calibration offsets for the 206 kHz echosounder were calculated as suggested by Biosonics (<https://www.biosonicsinc.com/support/calibration-and-repair/>) resulting in an offset parameter of -0.36 dB, slightly greater than the precision of the instrument

(0.2 dB). However, given that target sphere detections that were not in the center of the beam and were skewed to one side, we used the default value (0.0) for an offset parameter. The instrument was last factory calibrated roughly a year prior to the cruise (March 1, 2017) and therefore should have needed limited correction. Sound speed and the absorption coefficient for all transducers were calculated using CTD data from the study region (Mackenzie 1981, Francois & Garrison 1982).

Echosounding data were processed using Echoview 8.0 software. Background noise removal was evaluated with established noise cleaning techniques (Ryan et al. 2015). The data were determined to be fairly free of noise, and a 3 x 3 convolution filter (Echoview 2018) with a value of 1 in the center and 0.5 around the perimeter was applied to the 38 and 120 kHz data for a measure of smoothing. The setting on the Biosonics echosounder differed from the Simrad EK60s so we ran an Echoview function to match the ping times of the Biosonics echosounder to the EK60s. Interference from the Simrad EK60s was evident on the data collected by the Biosonics DT-X. This interference was manually removed by drawing polygons around the affected area and replacing data from a 5 row by 21 column Gaussian blur function followed by a convolution 3x3 convolution filter (1s in the first and last column and the 2, 1, 2 on the center column) (Echoview 2018). We decided upon the application of these filters by visual inspection such that the output retained the character of the cells in the surrounding layer. The substituted values were retained for school detection calculations such that the interferences were not reasons for breaks in detected schools, but were later removed when estimating organism's density calculations.

Classification of acoustic data to potential prey types was explored through relative frequency response approaches. These methods use the fact that acoustic backscatter returned from one type of organism may vary by frequency from that returned from another type of organism. For example, the expected return from a copepod would increase with increasing frequencies from 38 to 120 to 200 kHz, whereas that from a fish with a swim bladder would be fairly steady across those same frequencies (Benoit-Bird & Lawson 2016). The ratios of these relative frequency responses depend on the properties of the animals rather than their abundance, so the relationship remains intact at varying levels of abundance (Korneliussen ICES 2018). Once classification has been established, abundance can be estimated using the magnitude of the backscatter at a particular frequency combined with the estimated target strength of the organism in question (Korneliussen Simmonds & MacLennan 2005, ICES 2018) .

A Z-score (normal deviate) method was applied to modeled frequency responses to classify acoustic backscatter to specific organisms observed on the cruise, specifically the ctenophore *Mertensia* and the copepod *C. finmarchicus* (De Robertis et al. 2010). To apply this method, we first needed to estimate the acoustic target strengths of each organisms. We estimated target strength of *Mertensia* and *C. finmarchicus* using Distorted Wave Born Approximation (DWBA) models (Chu et al. 2000, Lawson et al. 2004) as has been done in other studies employing the Z-score methodology (Jech et al. 2018).

We parameterized Distorted Wave Born Approximation (DWBA) models with length and width measurements of *Mertensia* from VPR images and measured lengths

of *C. finmarchicus* from bongo samples. Copepods were modeled as fluid-filled cylinders and ctenophores as ellipsoids. The density and sound speed ratios, g and h , play key roles in the DWBA models ($g = \rho_a / \rho_{sw}$ and $h = c_a / c_{sw}$, where ρ is density, c is the sound speed, a is the organism type and sw is seawater). For *Mertensia*, g was set at 1.009 and h at 1.007 based on measurements from the ctenophore *Mnemiopsis leidyi* in Warren and Smith (2007). For *C. finmarchicus*, values of g and h were set at 1.02 and 1.058 respectively based on (Lavery et al. 2007). Orientation of the targets can also have a significant impact on calculated target strength. For copepods, target strength was averaged over a range of angles from 0 to 30 degrees as done in other studies (Benfield et al. 2000). For ctenophores (ellipsoids) the DWBA calculations were limited to discrete angles, so target strength was averaged over angles of 0, 30, 60, and 90 degrees because we saw no reason for a ctenophore to favor one orientation over another. *Pseudocalanus* target strength based on DWBA models were not used because they could not be detected with the available frequencies employed on this cruise due to their small size limited target strength.

We classified acoustic backscatter to organism type through a DWBA-assisted Z-score approach (De Robertis et al. 2010, Jech et al. 2018). Z-score classification uses mean pairwise frequency differences of volume backscattering strength S_v (dB re 1m^{-1}), and the standard deviations of these pairwise frequency differences, to estimate a Z-score for each cell. Specifically, the Z-score (normal deviate) is calculated as, $Z_{k,l,m}$ for sample l as described below:

$$Z_{k,l,m} = \frac{\Delta S_{v,k,l} - \mu_{k,m}}{\sigma_{k,m}}$$

where $\mu_{k,m}$ and $\sigma_{k,m}$ are the sample mean and standard deviation of ΔS_v from frequency pair k and taxon m (De Robertis et al. 2010).

A more general relative frequency response was also applied to explore potential zooplankton frequency responses (Korneliussen ICES 2018). We relaxed the *C. finmarchicus* DWBA model output such that if the frequency response differences of the 120 kHz-38kHz S_v pair was ≥ 10 dB and the 206 kHz-38 kHz S_v pair was ≥ 5 dB, we classified this as potential zooplankton. No S_v threshold value was applied in this case because of the weak scattering of copepods at these frequencies.

The acoustic data analysis was organized into a few groups based on acoustic response and sampled regions. We analyzed the bowtie-shaped sampling that occurred on April 7, 2018 separately and will be referred to as the right whale region going forward (Fig. 2). Within that region, separate subsets were assessed for the area where the VPR was towed at set depths (Fig. 2), and for the initial right whale sighting region, which we described as the northern corner of the right whale bowtie-shaped sampling region, covering approximately 1400 m of ship track. An adjacent acoustic tow that occurred the morning prior to the right whale sightings (April 6) was also assessed (Fig. 2). We also ran the Echoview school detection algorithm on the *Mertensia* Z-score output and the 206 kHz echogram to further summarize data from regions within the water column.

RESULTS

Overview

At roughly 3:10 pm EST on the last full day of the cruise, we sighted the first of two right whales, and proceeded to sample the area for prey and oceanographic characteristics until approximately 10 pm (Fig. 2). The following Results section focuses on these right whale sightings and the prey and oceanographic sampling conducted in the region of the sightings.

Marine mammals

On April 7 we sighted two right whales (Fig. 2). After sighting the first right whale, we broke transect and monitored the location and dive pattern of this whale. Right whales were sighted 17 times and the average re-sighting time of right whales was 12 minutes, ranging from one to 31 minutes, and re-sighting locations did not suggest travel in a consistent direction, both of which are consistent with foraging. The whales were not observed surface feeding, were observed fluking, and presumed to be diving to depth. Preliminary identification by the NAWRC suggested one animal was a 9-year-old juvenile female that had been sighted in the southern New England region in previous years.

The North Atlantic Right Whale Consortium documented 28 additional right whale sightings in this area before and shortly after our cruise (Fig. 1, 2). From March 18 to April 11, 2018, 47 right whales were sighted among 28 groups that contained from one to six animals. Repeat sightings of the same animals on different days could be included in this count.

Physical Oceanography

We launched three XBTs for supplementary oceanographic information while 17 CTD deployments occurred on a variety of platforms (bongo nets, CTD rosette, and

the VPR) (Fig. 1). CTD data in the right whale region shows a slight pycnocline between 30 and 35 meters and the density (σ_θ) below 35 m just shy of 1026 kg m^{-3} , with warmer but saltier water below and colder fresher water above (Fig. 3A). In an adjacent area, there is also a slight pycnocline, but with a much more gradual transition to denser water with depth, very little change in salinity, less change in density, and density below the thermocline of about 25.75 kg m^{-3} (Fig. 3B). In this region the temperature change is again slight, but opposite of the first site, with colder water below and warmer on the surface.

Assessment of measured ADCP currents on the cruise (not shown), both over the whole course of the cruise and specifically in the right whale sighting region, suggested that currents were dominated by tidal and inertial currents, resulting in little mean flow over time. A simulation of Lagrangian trajectories based on ADCP measurements showed a circular movement over the course of the 24 hours, with a maximum displacement of only about 100 m, finishing roughly 85 m from the starting point (Fig. 4).

Satellite images of chlorophyll *a* and chlorophyll *a* fronts showed a bloom over Nantucket shoals during the cruise (Fig. 5). Right whale sightings were generally located adjacent to the front, on the northwest side with lower chlorophyll levels. The chlorophyll *a* pattern observed in the satellite data generally aligns with fluorescence observed in the TSG measurements where a transition in chlorophyll levels was in the region of the right whale sightings. The high chlorophyll area also generally coincides with high velocity currents shown in ocean models over the shallower Nantucket Shoals, with the chlorophyll levels dropping just outside of these shallow high current

areas (<http://fvcom.smast.umassd.edu/necofs/>), suggesting a transition area where zooplankton could aggregate.

Zooplankton

Bongo samples on the cruise, and in the right whale observation region, were fouled by the large phytoplankton bloom. Therefore, sampling using bongo nets could be used for qualitative assessment, but quantitative values should be interpreted with caution. In addition, fragile ctenophores were unlikely to endure the intensive rinsing process necessary to flush zooplankton samples to the cod end of the clogged nets. That said, the bongo sample in the region of the right whales (Fig. 6) was dominated by *Pseudocalanus* and *C. finmarchicus*, where *Pseudocalanus* per m^3 out-numbered *C. finmarchicus* by roughly 2 to 1, 1257 to 644 respectively (Fig. 6). Later stages of *C. finmarchicus* were the most prevalent and stage five was present in the highest numbers (Table 1). Despite being outnumbered, *C. finmarchicus* present in the sample represented roughly three times the caloric value of *Pseudocalanus*, with a total of $4,190 \text{ J m}^{-3}$ combined between the two taxa. Bongo samples collected by the NOAA's Northeast Fisheries Science Center during March and April in the study region show mean copepod densities lower than observed in our study ($251 \text{ C. finmarchicus m}^{-3}$, $548 \text{ Pseudocalanus m}^{-3}$), though in similar proportions (Fig. 7). Median values were lower, illustrating their patchy nature, and more skewed towards *Pseudocalanus* ($72 \text{ C. finmarchicus m}^{-3}$, $299 \text{ Pseudocalanus m}^{-3}$). The NOAA time series shows that densities are highly variable, particularly for *Pseudocalanus*, and the historical peaks correspond more closely to the densities observed in our study.

We deployed the VPR four times during the cruise. The VPR cast (Fig. 2) in the right whale region found almost no copepods ($0.29 \cdot \text{m}^{-3}$), large quantities of marine snow ($197.3 \text{ observations} \cdot \text{m}^{-3}$), and many gelatinous organisms ($30.2 \cdot \text{m}^{-3}$), particularly the ctenophore *Mertensia* $22.4 \cdot \text{m}^{-3}$). Counts of *Mertensia* between 36 and 42 m depth averaged 43 m^{-3} , with a maximum of 493 m^{-3} . The maximum density during the entire VPR tow was $1,233 \text{ m}^{-3}$. Individual *Mertensia* were also measured and found to have a median length of 3.88 mm (std=1.17, range=1.80-8.03) and a median width of 2.56 mm (std=1.17, range=1.52-4.57). Median weight per ctenophore was estimated at 0.11 g, which multiplied by 0.21 kJ/g, resulted in an energy density of 23.11 J per ctenophore. The total median ctenophore energy density in the portion of the VPR tow stationed at particular depths (36-42 m) was 955.10 J m^{-3} , and the maximum recorded in this range within 10 m distance intervals was $11,404 \text{ J m}^{-3}$. The maximum among the whole VPR tow (including tow-yo regions) was $28,511 \text{ J m}^{-3}$.

We deployed the echosounding tow body 5 times during the course of the cruise (Fig. 1). The tow body was deployed for approximately 4.75 hours in the region of the right whales on April 7 and for 2 hours in an adjacent area the previous day. The acoustic returns in the right whale observation region showed a distinct and consistent layer at roughly 35-40 m depth that was increasingly distinct with increasing echosounder frequencies (Fig. 8). Acoustic data in the adjacent region one day prior showed a similar layer slightly shallower (Table 3) that became narrower moving east to west.

Given that *Mertensia* and *C. finmarchicus* are both small relatively weak scatterers, the DWBA target strength calculations of both *Mertensia* and *C.*

finmarchicus resulted in mean dB values that would be difficult to distinguish from background noise, particularly at low densities and with the 38 kHz echosounder (Table 2). The estimated target strengths decreased in the 206 and 120 kHz frequencies with an increasing orientation angle, and in all frequencies, the number of outliers markedly increased at a 90° angle. These low target strengths combined with large standard deviations could bias classifications. Low concentrations of these organisms with low target strengths would likely not be detected, as the received backscatter would not be discernable from background noise. However, higher concentrations could theoretically be detected using the relative frequency responses (Table 2). The DWBA calculations resulted in relative target strengths that had very narrow standard deviations for *C. finmarchicus*, and much wider standard deviations for *Mertensia*.

Applying these target strengths to echosounding data collected in the right whale region resulted in very few classifications of *C. finmarchicus*, and many for *Mertensia*, particularly in the dense, consistent layer observed at ~40 m depth (Fig. 9). Using a restrictive maximum Z-score value of one, the estimated mean density of *Mertensia* in the bowtie right whale sampling region was 2233 individuals per m³, and 2635 per m³ when limited to the region where we held the VPR at depths associated with the layer observed acoustically (Table 3, Fig. 9). Classification of *C. finmarchicus* using the Z-score approach with the available frequencies yielded almost no detection of *C. finmarchicus* and therefore we do not provide those results here. We also applied a more lenient classification approach solely using the relative frequency differences (120-38 ≥ 10 dB, 206-38 ≥ 5 dB), although this also resulted in few detections of *C.*

finmarchicus (Table 3). Estimated detected density using the target strength at 206 kHz resulted in estimates of single digits per m³.

Data from the adjacent transect on the previous day yielded similar densities to those in the observed right whale region, with an estimate of 1957 *Mertensia* per m³ and very few *C. finmarchicus* detected acoustically. A general characterization of the regions, as defined by the school detection algorithm applied to the 206 kHz frequency, showed a similar backscatter response among frequencies. The mean depth of the layer was about 3 m shallower, and somewhat narrower, than the right whale region. The layer also thinned to the west, but both regions show consistent layers spreading more than 12 km along the ship tracks.

DISCUSSION

The continental shelf south of New England has recently been found to be a more important right whale habitat than previously thought, particularly in the late winter and early spring (Leiter et al. 2017). Our study investigated possible food resources in this region while near two right whales presumed to be foraging sub-surface. Echosounding data showed a dense layer of organisms at 35-40 m that aligned with a slight pycnocline at a density that has been associated with diapausing *C. finmarchicus* in other regions (Davies et al. 2014). Echosounding and VPR data suggest that this layer consisted primarily of ctenophores, although net sampling captured copepods that were not visible in echosounding or VPR data. Our results suggest that the right whales may be foraging on a more diverse food assemblage than typical of most traditional foraging regions, with a combination of *Pseudocalanus* and *C.*

finmarchicus copepods more similar to Cape Cod Bay (DeLorenzo Costa et al. 2006a), plus the possible consumption of ctenophores. Ancillary current, satellite, and ocean model data hint at tidally driven fronts that could concentrate zooplankton prey in this region.

The echosounding data provided insight into the water column structure, showing a consistent layer of backscatter centered at roughly 40 m during the right whale sightings. We observed this same pattern on the previous day just to the north, with a consistent layer at a similar depth that returned similar backscatter among the three available frequencies. Both layers stretched the majority of the ship track (>12 km) and thinned somewhat towards the west (Table 3, Fig. 9). The consistency in backscatter across time, area, and direction suggests a large and consistent feature.

Classification of the echosounding data based on DWBA models suggested that much of this layer could be filled with *Mertensia*, which would match with the VPR observations. However, modeled target strengths of an individual *Mertensia* were quite low, meaning that small concentrations would acoustically blend with background noise and not be detectable with the available frequencies. The standard deviations of the estimated target strengths were also quite broad, in part because we had no basis for choosing a particular orientation for the ctenophores. To compensate for these drawbacks, we took steps to limit potential misclassification. The Z-score was limited to a maximum value of 1 to partially limit the effect of this broad target strength, whereas a value of 2 was proposed when the methodology was developed (De Robertis et al. 2010), and values as high as 6 have been used in some cases (Jech et al. 2018). In addition, only areas with a backscatter of at least -80 dB in the 120 kHz

frequency were considered for the Z-score classification to further limit erroneous classification or potential contamination from background noise, and mean values in the Z-score defined *Mertensia* layers were well below -80 dB among all frequencies.

While acoustic methods were unable to effectively detect most copepods, dense aggregations of *C. finmarchicus* should have been discernable in the insonified area of the water column as strong backscatter in the 206 kHz, and little or none in the other frequencies, had they been there. Mutlu (2003) detected dense copepod aggregations with 120 and 200 kHz echosounders, and previous right whale studies have detected dense aggregations of *C.* with 200 kHz echosounders in (Wishner et al. 1988, Macaulay et al. 1995, Beardsley et al. 1996). David et al. (1999) argued that zooplankton (mysids) were detectable as small as 3 mm at 120 kHz, $\frac{1}{4}$ of the wavelength. *C. finmarchicus* measured from the bongo sample in the right whale region had a mean size of 2.1 mm and a maximum size of 3.0 mm, making them essentially undetectable at 120 kHz. At 206 kHz, a minimum size of 1.8 mm could be detected, placing most of the *C. finmarchicus* just within the detectability range, and all *Pseudocalanus* in our study would be undetectable (mean size = 0.9 mm, max = 1.19 mm). Detection of dense aggregations of *C. finmarchicus* copepods is theoretically possible, but smaller aggregations would likely be indistinguishable from background noise given their low target strength. Attempts at classifying the acoustic backscatter with the Z-score approach resulted in almost no areas classified as *C. finmarchicus*, and few areas were classified as *C. finmarchicus* even when relaxing the criteria to require less difference between frequencies.

The bongo net collected copepods in numbers that were not evident in either the acoustic data or the VPR. If there were dense aggregations of copepods present, they could have been missed at the near surface or at the bottom. Echosounding processing required removing the first few meters of data below the echosounder, and the tow body itself was deployed a few meters below the surface. In addition, bottom detection was done automatically in Echoview, and then was raised approximately one m to make sure there was no acoustic contamination from the ocean bottom structure. However, given that the whales appeared to be diving and not surface feeding, it seems unlikely that the surface was a source of dense copepods captured in the bongo nets and not detected in acoustics. The copepods may have been spread throughout the water column, and therefore invisible to the acoustics due to their sparsity, or they could have been concentrated near the bottom and the bongo net may have fished deeper than expected.

The *C. finmarchicus* and *Pseudocalanus* from the sole net sample were within the historical ranges of densities for that region. The average densities were on the high end of the historical range and the *C. finmarchicus*:*Pseudocalanus* ratio was similar to what has been recorded historically, even with a partially clogged net that could reduce the number of captured copepods. The estimated *C. finmarchicus* density was also similar to regional values found in the Great South Channel during a right whale study (585 m^{-3}), but less than areas more directly associated with a right whale observation (1136 m^{-3} , (Wishner et al. 1995) and 8700 m^{-3} , mean density, (Beardsley et al. 1996). Densities were much less than those found in the Bay of Fundy near feeding right whales ($6618 \pm 3481 \text{ m}^{-3}$) and Cape Cod Bay ($14778 \pm 18594 \text{ m}^{-3}$)

(Baumgartner & Mate 2003, Fortune et al. 2013). However, observed energy densities near feeding right whales were quite variable, particularly in Cape Cod Bay. The observed estimated copepod energy content in this study (4190 J m^{-3} , Table 1) did fall within the range of those found in Cape Cod Bay (1 to 87 kJ m^{-3}), where the mean energy density was $20 \pm 22 \text{ kJ m}^{-3}$ and the mean particle density was in the range of $\sim 6000 \text{ m}^{-3}$ (Fortune et al. 2013).

Dense aggregations of *C. finmarchicus* are known to have patchy and ephemeral distributions. *C. finmarchicus* patch sizes have been reported elsewhere as occurring on the scale of 0.3-0.5 km (Wishner et al. 1995). Given that similar densities have been found with net sampling in other areas known to be right whale feeding areas, it may be that the sampling was not directly in the dense patch where the whales were feeding. Net clogging by the phytoplankton bloom also could have significantly reduced estimated density, and integrating density throughout the water column may not be appropriate if *C. finmarchicus* are concentrated in discrete layers.

The VPR data did not align with expectations, but did align with prey classification from the acoustic data, at least in organism type, if not in number. The VPR-based *Mertensia* density estimation in the dominant acoustic layer was far lower than what was expected based on DWBA acoustic calculations. At these levels, the energetic content for a right whale would be paltry. However, there were instances in the tow-yo portion of the VPR tow where observed density reached values similar (1234 m^{-3}) to those estimated with the acoustics. Densities such as these would put caloric values within the estimated right whale metabolic needs ($28,512 \text{ J m}^{-3}$) (Kenney et al. 1986, Fortune et al. 2013). Similarly, echosounder estimated *Mertensia*

energy content was actually in line with estimated copepod energy densities in Cape Cod Bay ($20 \pm 22 \text{ kJ m}^{-3}$) (Fortune et al. 2013).

Right whales have previously been reported to consume gelatinous prey. Kenney (2008) reported observations of right whales feeding on salps in the Bay of Fundy, and Winn and Wishner (1987) found dense ctenophore layers mixed in with *C.*

finmarchicus, explaining observations of ctenophores found in right whale stomachs.

Recent research has shown that despite the low energy density of gelatinous prey, they are consumed by many more species on a regular basis than previously thought.

Predators include sea birds (McCanch & McCanch 1996), dogfish (Smith et al. 2016), salmon (Arai et al. 2003), tuna (Llopiz et al 2010), turtles (Smolowitz et al. 2015), penguins (Thiebot et al. 2016), and numerous other taxa (Hays et al. 2018). Hays et al. (2018) hypothesized that rapid digestion and availability are two components that may make consumption of gelatinous prey worthwhile, making it possible to consume large amounts over short durations. Consumption of ctenophores may also provide additional value in the form of ingesting newly captured copepods, boosting energy density, and undiscovered nutritional benefits aside from caloric needs. Whether consumption of gelatinous prey is incidental or purposeful, it is possible that it contributes to right whale diet.

Oceanographic data for the right whale region hints at a potential mechanism for the aggregation of zooplankton. In theory, the Coastal Current comes out of the Gulf of Maine and washes over Nantucket Shoals, bringing with it diapausing *C.*

finmarchicus and other plankton, which then aggregate at tidal fronts as the water comes off the shoals, aligning with the 1026 kg m^{-3} density layer. Satellite imagery

and TSG data show a chlorophyll bloom over the shallower areas of Nantucket Shoals and a chlorophyll frontal transition where the waters deepen, which also generally aligns with the 2018 March-April right whale observations (Fig. 5). This chlorophyll transition could be a proxy for subsurface density changes as well. Diapausing *C. finmarchicus* have been shown to aggregate at density layers of 1026 kg m^{-3} where they have a neutral buoyancy (Davies et al. 2013, Davies et al. 2014), which also defined the layer beneath the pycnocline in the right whale observation region. Furthermore, ADCP data suggests currents in this region are dominated by tidal and Coriolis forces, implying the possibility of tidally driven fronts that may aggregate zooplankton. This region of frontal transition and many of the March-April right whale sightings also align with a spring right whale hot spot documented via aerial surveys (Leiter et al. 2017).

Right whale prey resources and habitat use may be broader than the dominant view of right whales acquiring the vast majority of their calories from *C. finmarchicus*. Right whales have previously been found in areas without high densities of *C. finmarchicus* (Baumgartner & Mate 2005) and DeLorenzo Costa et al. (2006b) found right whales taking advantage of a seasonally shifting abundances of different zooplankton (*Centropages typicus*, *Pseudocalanus*, and *C. finmarchicus*) in Cape Cod Bay. As mentioned previously, gelatinous prey have been consumed at times, and krill, pteropods, and barnacle larvae have also been documented as occasional prey (Kenney 2008). Recent observations of right whales in the Gulf of St. Lawrence suggest spatial overlap with the copepod *Calanus glacialis*, also a likely prey item (Mayo et al. 2001, Brillant et al. 2017, Plourde et al. 2019). With shifts in right whale

distribution (Pace et al. 2017), and newly documented habitat use in southern New England and the mid-Atlantic (Davis et al. 2017), it is reasonable to assume that non-*C. finmarchicus* prey may constitute a larger portion of their diet than previously assumed. Foraging on non-*C. finmarchicus* prey may be more probable in areas south of the Gulf of Maine where *C. finmarchicus* presence is less likely. *Pseudocalanus* in particular may provide a less calorie dense but more stable food source given that it is unlikely to enter diapause in deeper waters during winter at lower latitudes (DeLorenzo Costa et al. 2006a). Dense patches of ctenophores or other gelatinous prey may also provide sustenance when whales are unable to find energy dense *C. finmarchicus*. It remains to be seen whether a more diverse diet is typical of right whales historically, or if it is due to the whales not being able to find their preferred prey in satisfactory densities due to a shifting ecosystem and climate.

The recovery of the North Atlantic right whale population has been constrained by entanglement and ship strike (Corkeron et al. 2018). A changing climate in which *C. finmarchicus* densities are predicted to decrease in their traditional feeding areas (Grieve et al. 2017) suggests that whales may have to seek out new foraging locations or different prey sources (and may already have) (Record et al. 2019). These distribution shifts may put whales in areas with increased risks of human interactions and reduced prey availability has been shown to be correlated with increased calving intervals (Meyer-Gutbrod et al. 2015, Meyer-Gutbrod & Greene 2018). In this shifting environment, it is important to understand the processes driving both whale and prey aggregation so that an understanding of these processes can inform future management measures (Meyer-Gutbrod et al. 2018).

This study examines an area that was recently found to be a more important right whale habitat than previously thought, with 30% of known calving females visiting this area, whales occupying the region throughout the year, and documented foraging during the late winter and early spring (Davis et al. 2017, Leiter et al. 2017). That said, little work had been done to quantify the potential prey field and the oceanographic factors driving aggregations of prey. We examined the relationships between physical oceanography, plankton distributions, and right whale observations and found a more diverse prey field than typically found in right whale foraging areas, with possible contributions from ctenophores, and a potential mechanism for plankton aggregation. While the cruise upon which this study is based is but a detailed snapshot of a specific area, the study draws from wider sources, making the findings relevant to the larger southern New England region and the late winter/early spring season. However, additional data are needed to ensure the future of this highly endangered whale, and we plan to further test the hypotheses presented in this paper with upcoming cruises.

ACKNOWLEDGEMENTS

This study was highly collaborative and we have several people and organizations to thank for their contributions. First, thank you to the Rhode Island Endeavor Program for funding ship time on the R/V Endeavor, and to the Endeavor crew for their flexibility and professionalism. Thank you to students of the URI Honors class, CSI:Oceans, who stood a lot of marine mammal watches in the cold: B. Bzdyra, E. Chille, G. Fall, L. Ilagan, G. Jennings, G. Jimenez, E. Koproski, and M. Ricker. The NOAA Advanced Study Program also helped fund some of this research as well as

NOAA's Atlantic Marine Assessment Program for Protected Species (AMAPPS). Thank you to Jerry Prezioso, Harvey Walsh, and Tamara Holzwarth Davis, and the NOAA NEFSC Climate and Oceans Division in general, for assistance setting up and running the CTD, bongo nets, and VPR recording. Thank you to Brennan Phillips for key assistance designing the acoustic tow body and Jennifer Johnson for help setting up the acoustics on the ship. Thank you to Kim Hyde for providing satellite data to help guide the cruise, the NOAA aerial survey the for advising on recent whale sightings, the North Atlantic Right Whale Consortium for sightings data, Debi Palka for assisting in the marine mammal observer set up, Beth Josephson for setting up the marine mammal observing software, Justin Stevens for the use of the EK60 equipment, Ryan Morse for discussions on *C. finmarchicus* and zooplankton, and anonymous reviewers for their helpful comments.

LITERATURE CITED

- Arai MN, Welch DW, Dunsmuir AL, Jacobs MC, Ladouceur AR (2003) Digestion of pelagic Ctenophora and Cnidaria by fish. *Canadian Journal of Fisheries and Aquatic Sciences* 60:825-829
- Baumgartner MF, Mate BR (2003) Summertime foraging ecology of North Atlantic right whales. *Marine Ecology Progress Series* 264:123-135
- Baumgartner MF, Mate BR (2005) Summer and fall habitat of North Atlantic right whales (*Eubalaena glacialis*) inferred from satellite telemetry. *Canadian Journal of Fisheries and Aquatic Sciences* 62:527-543
- Baumgartner MF, Wenzel FW, Lysiak NSJ, Patrician MR (2017) North Atlantic right whale foraging ecology and its role in human-caused mortality. *Marine Ecology Progress Series* 581:165-181
- Beardsley RC, Epstein AW, Chen C, Wishner KF, Macaulay MC, Kenney RD (1996) Spatial variability in zooplankton abundance near feeding right whales in the Great South Channel. *Deep Sea Research Part II: Topical Studies in Oceanography* 43:1601-1625

- Belkin IM, O'Reilly JE (2009) An algorithm for oceanic front detection in chlorophyll and SST satellite imagery. *Journal of Marine Systems* 78:319-326
- Benfield MC, Davis CS, Gallagher SM (2000) Estimating the in-situ orientation of *Calanus finmarchicus* on Georges Bank using the Video Plankton Recorder. *Plankton Biology & Ecology* 47:69-72
- Benoit-Bird KJ, Lawson GL (2016) Ecological Insights from Pelagic Habitats Acquired Using Active Acoustic Techniques. *Annual Review of Marine Science* 8:463-490
- Bucklin A, Guarnieri M, McGillicuddy DJ, Sean Hill R (2001) Spring evolution of *Pseudocalanus* spp. abundance on Georges Bank based on molecular discrimination of *P. moultoni* and *P. newmani*. *Deep Sea Research Part II: Topical Studies in Oceanography* 48:589-608
- Chu D, Wiebe P, Copley N (2000) Inference of material properties of zooplankton from acoustic and resistivity measurements. *ICES Journal of Marine Science* 57:1128-1142
- Corkeron P, Hamilton P, Bannister J, Best P, Charlton C, Groch KR, Findlay K, Rowntree V, Vermeulen E, Pace RM (2018) The recovery of North Atlantic right whales, *Eubalaena glacialis*, has been constrained by human-caused mortality. 5
- Daoust P-Y, Couture EL, Wimmer T, Bourque L (2017) Incident Report: North Atlantic Right Whale Mortality Event in the Gulf of St. Lawrence, 2017.
- David PM, Guerin-Ancey O, Van Cuyck JP (1999) Acoustic discrimination of two zooplankton species (mysid) at 38 and 120kHz. *Deep Sea Research Part I: Oceanographic Research Papers* 46:319-333
- Davies KTA, Brillant SW (2019) Mass human-caused mortality spurs federal action to protect endangered North Atlantic right whales in Canada. *Marine Policy* 104:157-162
- Davies KTA, Ross T, Taggart CT (2013) Tidal and subtidal currents affect deep aggregations of right whale prey, *Calanus* spp., along a shelf-basin margin. *Marine Ecology Progress Series* 479:263-282
- Davies KTA, Ryan A, Taggart CT (2012) Measured and inferred gross energy content in diapausing *Calanus* spp. in a Scotian shelf basin. *Journal of Plankton Research* 34:614-625
- Davies KTA, Taggart CT, Smedbol RK (2014) Water mass structure defines the diapausing copepod distribution in a right whale habitat on the Scotian Shelf. *Marine Ecology Progress Series* 497:69-85

- Davis CS, Hu Q, Gallager S, M., Tang X, Ashjian CJ (2004) Real-time observation of taxa-specific plankton distributions: an optical sampling method. *Marine Ecology Progress Series* 284:77-96
- Davis GE, Baumgartner MF, Bonnell JM, Bell J, Berchok C, Bort Thornton J, Brault S, Buchanan G, Charif RA, Cholewiak D, Clark CW, Corkeron P, Delarue J, Dudzinski K, Hatch L, Hildebrand J, Hodge L, Klinck H, Kraus S, Martin B, Mellinger DK, Moors-Murphy H, Nieukirk S, Nowacek DP, Parks S, Read AJ, Rice AN, Risch D, Širović A, Soldevilla M, Stafford K, Stanistreet JE, Summers E, Todd S, Warde A, Van Parijs SM (2017) Long-term passive acoustic recordings track the changing distribution of North Atlantic right whales (*Eubalaena glacialis*) from 2004 to 2014. *Scientific Reports* 7:13460
- De Robertis A, McKelvey DR, Ressler PH (2010) Development and application of an empirical multifrequency method for backscatter classification. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1459-1474
- DeLorenzo Costa A, Durbin EG, Mayo CA (2006a) Variability in the nutritional value of the major copepods in Cape Cod Bay (Massachusetts, USA) with implications for right whales. *27:109-123*
- DeLorenzo Costa A, Durbin EG, Mayo CA, Lyman EG (2006b) Environmental factors affecting zooplankton in Cape Cod Bay: implications for right whale dynamics. *Marine Ecology Progress Series* 323:281-298
- Demer DA, Berger L, Chabot D, Bernasconi M, Bethke E, Boswell K, Chu D, Domokos R, Dunford A, Fässler S, Stéphane G, Hufnagle LT, Jech JM, Bouffant N, Lebourges-Dhaussy A, Lurton X, Macaulay GJ, Perrot Y, Ryan T, Parker-Stetter S, Stienessen S, Weber T, Williamson N (2015) Calibration of acoustic instruments. International Council for the Exploration of the Sea, Copenhagen, Denmark
- Echoview SPL (2018) Echoview software. Echoview Software Pty Ltd, Hobart, Australia
- Foote KG, Knudsen HP, Vestnes G, MacLennan DN, Simmonds EJ (1987) Calibration of acoustic instruments for fish density estimation: A practical guide. International Council for the Exploration of the Sea, Copenhagen Denmark
- Fortune SME, Trites AW, Mayo CA, Rosen DAS, Hamilton PK (2013) Energetic requirements of North Atlantic right whales and the implications for species recovery. *Marine Ecology Progress Series* 478:253-272
- Francois RE, Garrison GR (1982) Sound absorption based on ocean measurements. Part II: Boric acid contribution and equation for total absorption. *The Journal of the Acoustical Society of America* 72:1879-1890

- Greene CH, Meyer-Gutbrod E, Monger BC, McGarry LP, Pershing AJ, Belkin IM, Fratantoni PS, Mountain DG, Pickart RS, Proshutinsky A, Ji R, Bisagni JJ, Hakkinen SMA, Haidvogel DB, Wang J, Head E, Smith P, Reid PC, Conversi A (2013) Remote climate forcing of decadal-scale regime shifts in Northwest Atlantic shelf ecosystems. *Limnology and Oceanography* 58:803-816
- Grieve BD, Hare JA, Saba VS (2017) Projecting the effects of climate change on *Calanus finmarchicus* distribution within the U.S. Northeast Continental Shelf. *Scientific Reports* 7:6264
- Hayes SA, Gardner S, Garrison L, Henry A, Leandro L (2018a) North Atlantic right whales - evaluating their recovery challenges. In: Fisheries N (ed). US Department of Commerce, Woods Hole, MA
- Hayes SA, Josephson E, Maze-Foley K, Rosel PE, Byrd B, Chavez-Rosales S, Cole T, Engleby L, Garrison L, Hatch J, Henry A, Horstman SC, Litz J, Lyssikatos MC, Mullin KD, Orphanides CD, Pace RM, Palka DL, Soldevilla M, Wenzel F (2018b) U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments -- 2017. NOAA National Marine Fisheries Service
- Hays GC, Doyle TK, Houghton JDR (2018) A Paradigm Shift in the Trophic Importance of Jellyfish? *Trends in Ecology & Evolution*
- ICES (2018) Acoustic target classification. In: Korneliussen RJ (ed) ICES Cooperative Research Report
- Jech JM, Lawson GL, Lowe MR (2018) Comparing acoustic classification methods to estimate krill biomass in the Georges Bank region from 1999 to 2012. 16:680-695
- Kenney RD (2008) Right Whales *Eubalaena glacialis*, *E. japonica*, *E. australis*. In: Perrin W, Würsig B, Thewissen JGM (eds) *Encyclopedia of Marine Mammals*. Academic Press
- Kenney RD, Hyman MAM, Owen RE, Scott GP, Winn HE (1986) Estimation of prey densities required by western north Atlantic right whales. *Marine Mammal Science* 2:1-13
- Lavery AC, Wiebe PH, Stanton TK, Lawson GL, Benfield MC, Copley N (2007) Determining dominant scatterers of sound in mixed zooplankton populations. *The Journal of the Acoustical Society of America* 122:3304-3326
- Lawson GL, Wiebe PH, Ashjian CJ, Gallagher SM, Davis CS, Warren JD (2004) Acoustically-inferred zooplankton distribution in relation to hydrography west of the Antarctic Peninsula. *Deep Sea Research Part II: Topical Studies in Oceanography* 51:2041-2072

- Leiter SM, Stone KM, Thompson JL, Accardo CM, Wikgren BC, Zani MA, Cole TVN, Kenney RD, Mayo CA, Kraus SD (2017) North Atlantic right whale *Eubalaena glacialis* occurrence in offshore wind energy areas near Massachusetts and Rhode Island, USA. *Endangered Species Research* 34:45-59
- Macaulay MC, Wishner KF, Daly KL (1995) Acoustic scattering from zooplankton and micronekton in relation to a whale feeding site near Georges Bank and Cape Cod. *Continental Shelf Research* 15:509-537
- Mackenzie KV (1981) Nine-term equation for sound speed in the oceans. 70:807-812
- McCanch NV, McCanch M (1996) Fulmars feeding on jellyfish. *British Birds* 89:569-570
- Meyer-Gutbrod EL, Greene CH (2018) Uncertain recovery of the North Atlantic right whale in a changing ocean. *Global Change Biology* 24:455-464
- Meyer-Gutbrod EL, Greene CH, Davies TA (2018) Marine Species Range Shifts Necessitate Advanced Policy Planning: The Case of the North Atlantic Right Whale. *Oceanography*
- Meyer-Gutbrod EL, Greene CH, Sullivan PJ, Pershing AJ (2015) Climate-associated changes in prey availability drive reproductive dynamics of the North Atlantic right whale population. *Marine Ecology Progress Series* 535:243-258
- Mutlu E (2003) Acoustical identification of the concentration layer of a copepod species, *Calanus euxinus*. *J Marine Biology* 142:517-523
- Pace RM, Corkeron PJ, Kraus SD (2017) State-space mark-recapture estimates reveal a recent decline in abundance of North Atlantic right whales. *Ecology and Evolution* 7:8730-8741
- Pennisi E (2017) North Atlantic right whale faces extinction. *Science* 358:703-704
- Pettis H, Hamilton P (2016) North Atlantic right whale consortium 2016 annual report card. Report to the North Atlantic Right Whale Consortium
- Record NR, Runge JA, Pendleton DE, Balch WM, Davies TA, Pershing AJ, Johnson CL, Stamieszkin K, Ji R, Feng Z, Kraus SD, Kenney RD, Hudak CA, Mayo CA, Chen C, Salisbury JE, Thompson CRS (2019) Rapid Climate-Driven Circulation Changes Threaten Conservation of Endangered North Atlantic Right Whales. *Oceanography*
- Runge JA, Ji R, Thompson CRS, Record NR, Chen C, Vandemark DC, Salisbury JE, Maps F (2014) Persistence of *Calanus finmarchicus* in the western Gulf of Maine during recent extreme warming. *Journal of Plankton Research*

- Ryan TE, Downie RA, Kloser RJ, Keith G (2015) Reducing bias due to noise and attenuation in open-ocean echo integration data. *ICES Journal of Marine Science* 72:2482-2493
- Salisbury DP, Clark CW, Rice AN (2016) Right whale occurrence in the coastal waters of Virginia, U.S.A.: Endangered species presence in a rapidly developing energy market. 32:508-519
- Salonen K, Sarvala J, Hakala I, Viljanen M-L (1976) The relation of energy and organic carbon in aquatic invertebrates. *Limnology and Oceanography* 21:724-730
- Siegel DA, Deuser WG (1997) Trajectories of sinking particles in the Sargasso Sea: modeling of statistical funnels above deep-ocean sediment traps. *Deep Sea Research Part I: Oceanographic Research Papers* 44:1519-1541
- Siegel DA, Fields E, Buesseler KO (2008) A bottom-up view of the biological pump: Modeling source funnels above ocean sediment traps. *Deep Sea Research Part I: Oceanographic Research Papers* 55:108-127
- Simmonds J, MacLennan D (2005) *Fisheries Acoustics, Theory and Practice*. Blackwell Publishing, Oxford, UK
- Simrad (1996) Operator manual, Simrad EK500, Fishery research echo sounder. Book Revision G, Horten, Norway
- Smith BE, Ford MD, Link JS (2016) Bloom or bust: synchrony in jellyfish abundance, fish consumption, benthic scavenger abundance, and environmental drivers across a continental shelf. *Fisheries Oceanography*:n/a-n/a
- Smolowitz RJ, Patel SH, Haas HL, Miller SA (2015) Using a remotely operated vehicle (ROV) to observe loggerhead sea turtle (*Caretta caretta*) behavior on foraging grounds off the mid-Atlantic United States. *J Exp Mar Biol Ecol* 471:84-91
- Steimle FW, Terranova RJ (1985) Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. *Journal of Northwest Atlantic Fishery Science* 6:117-124
- Tang X, Stewart WK, Huang H, Gallager SM, Davis CS, Vincent L, Marra M (1998) Automatic Plankton Image Recognition. *Artificial Intelligence Review* 12:177-199
- Thiebot J-B, Ito K, Raclot T, Poupart T, Kato A, Ropert-Coudert Y, Takahashi AJMB (2016) On the significance of Antarctic jellyfish as food for Adélie penguins, as revealed by video loggers. 163:108

- Warren JD, Smith JN (2007) Density and sound speed of two gelatinous zooplankton: Ctenophore (*Mnemiopsis leidyi*) and lion's mane jellyfish (*Cyanea capillata*). 122:574-580
- Winn HE, Wishner KF (1987) Why whales eat ctenophores. Tenth Biennial Conference on the Biology of Marine Mammals, Miami, FL
- Wishner KF, Durbin E, Durbin A, Macaulay M, Winn H, Kenney R (1988) Copepod patches and right whales in the great south channel off new england. Bulletin of Marine Science 43:825-844
- Wishner KF, Schoenherr JR, Beardsley R, Chen C (1995) Abundance, distribution and population structure of the copepod *Calanus finmarchicus* in a springtime right whale feeding area in the southwestern Gulf of Maine. Continental Shelf Research 15:475-507

TABLES

Table 1. Bongo net sample density and estimated energy contents by taxa and by stage for *Calanus finmarchicus*

Sample	Taxa	Stage	Density (count/m3)	J/individual (mean)	J/individual (std)	J/m3 (total)	J/m3 (+/- std)
Bongo	<i>Psuedocalanus</i>	Unknown	1256.70	0.84	0.01	1052.05	17.34
Bongo	<i>C. Finmarchicus</i>	Female	79.69	6.84	1.64	544.72	11.22
		Male	24.52	8.77	0.98	215.09	8.59
		V	18.39	7.79	1.98	1909.54	15.40
		IV	128.74	2.51	0.78	354.11	1.96
		III	141.00	0.63	0.23	80.53	0.14
		II	245.21	0.18	0.01	3.30	0.00
		Unknown	6.13	5.06	0.17	30.99	0.84
		Total	643.68			3138.28	21.02
<i>Psuedocalanus</i> &							
Bongo	<i>C. Finmarchicus</i>	Total	1900.38			4190.32	27.25

Table 2. Distorted Wave Born Approximations (DWBA) of acoustic target strength from *Mertensia ovum* and *Calanus finmarchicus* and the relative frequency difference among 38, 120, and 206 kHz frequencies.

Taxa	Target Strength	38 kHz	120 kHz	206 kHz
<i>Pleurobrachia</i>	Mean	-110.73	-96.16	-99.27
	Standard Deviation	7.36	4.86	7.44
<i>Calanus finmarchicus</i>	Mean	-118.25	-99.10	-91.60
	Standard Deviation	7.71	7.33	6.46
Relative Frequency Difference		38-120 kHz	206-120 kHz	206-38 kHz
<i>Pleurobrachia</i>	Mean Difference	-14.57	-3.11	11.46
	Standard Deviation of Difference	4.83	9.06	10.74
<i>Calanus finmarchicus</i>	Mean Difference (model)	-19.15	7.51	26.65
	Standard Deviation of Difference	0.39	0.93	1.32

Table 3. Summary of acoustic characteristics on April 6 and 7, 2018. Data are subset by day and by the area where the Video Plankton Recorder (VPR) was set within an acoustically visible layer, the initial right whale sighting area (~1400 m of ship track in the northern corner of the bowtie shaped sampling area), and an area of the track defined by a school detection algorithm applied to 206 kHz frequency data. Acoustic analysis are presented for areas with a Distorted Wave Born Approximation (DWBA) *Mertensia ovum* Z-score of ≤ 1 and a minimum return of $-80 \text{ dB re } 1\text{m}^{-1}$, an acoustic relative frequency pattern representing potential copepods, and a general characterization of the 206 kHz school detection subset. S_v refers volume backscattering strength ($\text{dB re } 1\text{m}^{-1}$).

Region	Subset	Analysis	Frequency			School Size, Density, and Energy Content				
			38 kHz Mean	120 kHz Mean	206 kHz Mean	Mean Depth	Mean Thickness	Estimated Length	Density	Energy Content
			S_v (Std)	S_v (Std)	S_v (Std)	(m)	(m)	(m)	(m^3)	(J/m^3)
Right Whale (4/7/18)	VPR	<i>Mertensia ovum</i> Z-score ≤ 1	-70.9 (-1.4)	-62 (-1.6)	-62.6 (-1.6)	40.5	3	1,222.1	2,634.7	60,887.9
Right Whale (4/7/18)	Initial Sighting	<i>Mertensia ovum</i> Z-score ≤ 1	-75.6 (-1.4)	-65.6 (-1.7)	-65.9 (-1.9)	38.1	16.9	1,410.5	1,146.4	26,493.3
Right Whale (4/7/18)	All	<i>Mertensia ovum</i> Z-score ≤ 2	-71.4 (-1.1)	-62.7 (-1.5)	-63.4 (-1.9)	41.8	11.9	14,317.4	2,233.0	51,604.6
Adjacent Track (4/6/18)	All	<i>Mertensia ovum</i> Z-score ≤ 3	-71.5 (-1.3)	-63.2 (-1.4)	-64.3 (-1.6)	37.6	4.8	6,020.2	1,957.1	45,228.6
Right Whale (4/7/18)	VPR	Copepod pattern*	-102 (-31.0)	-90.3 (-34.9)	-84.2 (-32.2)	40.5	3	1,222.1	5.5**	27.8**
Right Whale (4/7/18)	Initial Sighting	Copepod pattern*	-103 (-21.9)	-91.3 (-24.7)	-85.1 (-26)	38.1	16.9	1,410.5	4.5**	22.6**
Right Whale (4/7/18)	206 kHz School Detection	Copepod pattern*	-100.7 (-22.9)	-89.3 (-25.5)	-83 (-36.1)	NA	NA	NA	7.3**	36.9**
Right Whale (4/7/18)	All	Copepod pattern*	-105.8 (-38.2)	-94.4 (-41.8)	-88 (-60.8)	NA	NA	NA	2.3**	11.5**
Adjacent Track (4/6/18)	All	Copepod pattern*	-112.7 (-74)	-101.5 (-78.6)	-95.2 (-82.8)	29.9	43.7	13,671.8	0.4**	2.0**
Right Whale (4/7/18)	206 School Detection	General characterization	-71.2 (-0.8)	-61.8 (-1.7)	-63.5 (-1.9)	39.3	13.6	13,436.7	NA	NA
Adjacent Track (4/6/18)	206 School Detection	General characterization	-69.3 (-1.3)	-63.5 (-1.6)	-64.1 (-1.8)	36.1	8.2	12,449.3	NA	NA

* Increasing S_v with increasing frequencies with a minimum of 10 dB difference between the 38 kHz and 120 kHz frequencies, and minimum 15 dB difference between 38 kHz and 206 kHz frequencies

** Assuming *Calanus* energy content and target strength at 206 kHz

FIGURES

Figure 1. Study area, right whale sightings, and oceanographic sampling locations. Focus of study is within the orange outline.

Figure 2. Close up of primary study area with right whale sightings, and oceanographic sampling locations. Northeast Fisheries Science Center (NEFSC) sightings are from March 18- April 11.

Figure 3. Temperature (C°) (dashed blue line) and density (σ_θ kg m⁻³) (solid red line) profiles by depth (m) conducted near southeastern corner of "bowtie" (A), and (B) conducted on eastern end of the trackline adjacent to the right whale region

Figure 4. Simulated track of plankton on April 7 based on ADCP data at 21 m depth. Starting point is at point 0, 0.

Figure 5. Right whale sightings, April 2018 chlorophyll *a* mean values from the MODIS Aqua satellite, and chlorophyll *a* measurements from a shipboard fluorometer (mg m⁻³).

Figure 6. Bongo sample taxa density. Note logarithmic scale on x-axis

Figure 7. Annual study area *Calanus finmarchicus* and *Pseudocalanus* densities (m⁻³) from NEFSC ECOMON surveys in March and April. Taxa mean and median values are depicted with dashed red and solid blue lines respectively.

Figure 8. Example echograms (dB re 1m^{-1}) in the right whale region showing an acoustic layer at roughly 40 meters depth. Images are 38 kHz (top), 120 kHz (middle), and 206 kHz (bottom). The gridding represents 5 meter depth and 100 m length intervals, stretching about 1.3 nautical miles.

Figure 9. Echograms of 120 kHz S_v limited to backscatter ≤ -80 dB re 1m^{-1} and a *Mertensia ovum* Z-score ≤ 1 . (A) region of the initial right whale sighting on April 7, 2018, (B) the area sampled by the VPR (black box) on April 7, 2018, and (C) a section of an adjacent transect on April 6, 2018 just north of the location of the initial right whale sighting. The gridding represents 10 meter depth and 100 m length intervals.

MANUSCRIPT 3

Relating marine mammal distribution to prey fields derived from echosounding

Christopher D. Orphanides^{1, 3, *}, J. Michael Jech², Jeremy S. Collie³, Debra Palka.²,

¹ NOAA Fisheries, 28 Tarzwell Drive, Narragansett, RI 02882

² NOAA Fisheries, 166 Water Street, Woods Hole, MA 02543

³ University of Rhode Island, Graduate School of Oceanography, 215 S Ferry Rd,
Narragansett, RI 02882

*corresponding author: phone: (401) 782-3283, fax: (401) 782-3201,

email: chris.orphanides@noaa.gov

Key words: marine mammals, habitat, distribution, prey, echosounding

Publication status: in preparation for submission to *Endangered Species Research*

ABSTRACT

Managing human impacts on marine mammal populations depends on understanding their distributions in space and time. Knowledge of these distributions is becoming increasingly important due to offshore energy development and climate induced shifts in oceanic habitat. Most models assessing pelagic marine mammal abundance and distribution primarily use ocean surface or bottom variables as proxies for water-column components driving habitat. Here we use a ship-based marine mammal sighting survey to test the utility of echosounder-based predictive variables for modelling marine mammal distribution and abundance. We assessed the distribution of seven marine mammal species along the shelf break south of New England relative to the spatial structure of organism groups derived from acoustic data with an established algorithm. We used this algorithm to classify detected prey into four categories: 1) fish with swim bladders, 2) larval fish and zooplankton, 3) fluid-like zooplankton, and 4) fish with no swim bladder. Acoustic backscatter was quantified using the area backscattering coefficient along the survey track line within bins 1000 m in length and either 50 or 200 m in depth. We then built Generalized Additive Models (GAMs) using only these acoustically derived variables to explain marine mammal distribution. The resulting GAMs explained between 1% and 37% of deviance, with model fit reflecting feeding depth and prey preference. This work demonstrates the potential of echosounding to model marine mammal distribution and abundance using direct measurements of prey rather than proxies.

INTRODUCTION

Human endeavors are increasingly encroaching on marine pelagic habitat. Fishing and shipping have long occurred in pelagic waters, and now energy development is expanding further into offshore environments (US Executive Order No. 13795). Constraining the impacts of these activities on marine life requires a thorough understanding of the distribution, abundance, and habitat use of the animals that occupy these waters. Marine mammals in these waters are of particular concern, whether due to their protected status under the US Marine Mammal Protection Act, specific concerns for small and endangered populations (e.g. US Endangered Species Act), or high sensitivity to sonar (DeRuiter et al. 2013) or construction impacts such as pile driving (Brandt et al. 2011).

Recent studies modelling marine mammal coast-wide distributions in both the Atlantic and the Pacific linked data from marine mammal surveys to environmental covariates, nearly all of which represented either ocean surface or ocean floor characteristics (Forney et al. 2012, Roberts et al. 2016, Becker et al. 2019, Chavez-Rosales et al. 2019). These environmental covariates, while proven useful, act as proxies for water-column characteristics such as prey concentrations that define pelagic habitat but are not directly sampled. A few studies have examined spatial organism structure within the water column as it relates marine mammal distribution (e.g. Benoit-Bird & McManus 2012, Benoit-Bird et al. 2013). However, until now, this approach has not been applied to large-scale abundance surveys involving numerous species.

The portion of the northwest Atlantic that is south of New England along the shelf break (Figure 1) has regionally high densities of marine mammals during the summer, yet we know little about the distribution of prey resources in this region. Typical fish sampling for management purposes focuses on continental shelf bottom fish, and limited effort has focused on pelagic habitat and the area off the continental shelf. Yet, to pursue offshore energy development in the US, companies must comply with the Marine Mammal Protection Act (MMPA). The MMPA requires an assessment of factors that could cause a decline or impede recovery of strategic stocks, including the effects on marine mammal habitat and prey. In our study region strategic stocks include right (*Eubalaena glacialis*), fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis*), blue (*Balaenoptera musculus*), sperm (*Physeter microcephalus*), long-finned pilot (*Globicephala melas*), and short-finned pilot whales (*Globicephala macrorhynchus*)

In order to assess available prey during an abundance survey, two likely options are to conduct net sampling or echosounding. Net-based pelagic prey sampling relevant to marine mammal observations is difficult to accomplish on a marine mammal abundance survey where the primary objective is to count cetaceans along a constantly moving track line. Net sampling during the day limits marine mammal observing, and sampling at night results in a temporal mismatch between sightings of highly mobile animals and prey resources in the water column. An alternative is to examine organism spatial structure in the water column with echosounding while simultaneously observing for marine mammals at regular survey speeds.

Biological acousticians have done extensive research on distinguishing marine organisms from their acoustic backscatter (Benoit-Bird & Lawson 2016). The principles are founded in mathematical acoustic scattering models (Stanton et al. 1998, Stanton & Chu 2000) and validated in both controlled (Wiebe et al. 1990, Stanton et al. 2004) and field testing (Wiebe et al. 1996, Lawson et al. 2001, Lawson et al. 2004). An organism's characteristic backscatter depends on the acoustic frequency encountering the organism, as well as its shape, orientation, and body structures. Organisms can be categorized acoustically by using something called a relative frequency response. This approach uses the fact that organisms have a characteristic backscattering response to particular echosounding frequencies, allowing researchers to distinguish unique patterns particular to a certain class of organism. Multi-frequency classification approaches using this technique have been employed successfully numerous times in the field (Korneliussen & Ona 2002, Jech & Michaels 2006, Benoit-Bird 2009, De Robertis et al. 2010, Trenkel & Berger 2013, Jech et al. 2018).

In this study we employ the multi-frequency organism classification algorithm develop by Trenkel and Berger (2013) to quantify the acoustic response into four organism types (fish with swim bladders, larval fish and phytoplankton, fluid-like zooplankton, and fish with no swim bladder). We then used the categorized backscatter to model marine mammal distribution along the track lines. We hope the results of this study could spur incorporation of prey and water column structure in future marine mammal abundance and distribution estimates. These models could

then contribute to improved management of marine mammals through more accurate modelling of species distribution.

METHODS

Survey Design

The National Oceanic and Atmospheric Administration (NOAA) collected marine mammal observations and echosounding data during the summer of 2013 as part of the Atlantic Marine Assessment Program for Protected Species (AMAPPS). AMAPPS is a comprehensive multi-agency research program to assess the abundance, distribution, ecology, and behavior of marine mammals, sea turtles, and seabirds throughout the US Atlantic Outer Continental Shelf, from Maine to the Florida Keys. The AMAPPS program has conducted research that spans taxonomic groups and trophic levels and provides an integrative view of protected species, placing them in an ecosystem context that can help inform marine federal protected species management decisions (NOAA 2013).

NOAA collected marine mammal sightings and echosounding data used in this study on two shipboard surveys conducted on the R/V Bigelow from July 2 through August 18, 2013. The ship ran established transects that are repeated each abundance survey. The transects considered for this study include 22 transects that traverse the continental shelf break, where each transect is a straight line intersecting the shelf break at diagonal angles (Figures 1-3). Echosounding equipment was set to passive mode (listening, not actively pinging) for portions of the survey because of multiple

cruise objectives, and we did not consider these portions for our analysis. Among these 22 transects, 18 were used in this study, although several transects were repeated, resulting in 24 total (Figure 1). Occasionally, only portions of a transect were sampled due to weather or time considerations, where the remainder of a transect was sampled the following day when the echosounding equipment was recording in passive mode. In all, we analyzed survey data from approximately 1200 km of track line in this study.

Marine Mammal Observing

While traversing these transects, two independent observing teams visually scanned for cetaceans, seals, turtles, and some fish species. We only analyzed data from the upper team, as they are typically the more accurate team with the best sighting vantage point. Each team consisted of two people surveying with high-powered “Big Eye” binoculars (magnification power of 25 with a 150 mm lens), and at least one person recording sightings and observing with the naked eye. The data were recorded in VizSurvey, a custom NOAA software program created by Lance Garrison and Debra Palka. Data recorded included numerous aspects of each sighting, including species, a best estimate of group size, behavior, location, distance and angle from the ship, and sea state, among other variables. If observers could not discern a sighting’s species, the sighting was classified into a more general species groups.

We adjusted sighting locations along the transect so that they aligned with the proper echosounding data. For example, if observers recorded a sighting at a distance of 1700 m along the track line from the ship’s current position, we assigned that

sighting a time stamp associated with the approximate position of the ship in 1700 m, given its mean speed. This way, the echosounding data match that of the animal's location.

Echosounding Processing

Echosounding data were collected using a Simrad EK60 system consisting of 18, 38, 70, 120, and 200 kHz transducers. The system was mounted in the keel of the R/V Bigelow and calibrated prior to the cruise with standard calibration techniques (Foote et al. 1987, Demer et al. 2015). We undertook several steps to clean the data. The data from each frequency were evaluated for noise contamination and attenuation and cleaned following the methods proposed by Ryan et al. (2015) and implemented in Echoview version 9.0 (Echoview 2018). Impulse noise removal, attenuated signal correction, transient noise removal, and background noise removal were evaluated for each frequency and parameters tuned accordingly. We only applied the transient noise filter to the 18 and 38 kHz frequencies, as its effect was not apparent in the higher frequencies.

We removed the first 10 meters of water column and the areas below the sea floor from consideration for this analysis. We removed the initial 10 meters due to the echosounder near field effect where detected values close to the echosounders are not accurate, and because of potential bubble interference in the surface waters. Since we were primarily concerned with pelagic structure, we ensured that echosounding values from the sea floor were not interpreted as pelagic marine organisms. The

bottom line was first drawn automatically by Echoview's best bottom candidate algorithm, and then buffered 3-5 m upwards and manually adjusted.

After the primary data cleaning, we applied the Echoview school detection function for each frequency. The purpose of this step was to further reduce the impact of noise on the analysis and to focus analysis on sizeable aggregations of organisms. We applied the default parameters for the school detection algorithm except for the maximum horizontal linking distance, which was set to 100 m after comparing different linking distances. Acoustic backscatter not assigned to a school was removed from the analysis. The final data retained for analysis only included those data collected on the track line and those data collected when marine mammal survey effort was underway.

The remaining data were processed with a multi-frequency indicator (MFI) algorithm published by Trenkel and Berger (2013). This MFI classifies acoustic backscatter into four categories: 1) fish swim with bladders and large gas bubbles, 2) larval fish, zooplankton, and small resonant bubbles, 3) fluid like zooplankton (copepods & euphausiids), and 4) fish with no swim bladder (e.g., mackerel). The approach operates on the idea that different organisms have unique acoustic responses to a suite of acoustic frequencies. By comparing the relative responses of different frequencies, the dominant organism types in a particular parcel of water can be distinguished. Based on this principle, Trenkel and Berger (2013) created an index that classifies acoustic backscatter to particular organism classes. These authors employed modeled data for plankton and empirical data for fish to develop the

relative frequency responses applied in this index. They validated their approach through simulations and via application to the Bay of Biscay, where the results aligned with the expected spatial structure of species groups. This algorithm was also recently used to estimate biomass of euphausiids in the northwest Atlantic where it compared favorably to other classification approaches (Jech et al. 2018).

After classifying the backscatter to species groups, we extracted the volume backscatter strength (S_v) (dB re 1 m^{-1}) associated with the assignment of a specific species group from the frequency most associated with that particular species group. For example, we extracted the S_v from 38 kHz for the areas classified as phytoplankton and fish larvae because in the design of the classification index, the small bubbles associated with these organisms had their peak resonance at 38 kHz. We also applied the 38 kHz frequency to swim bladder fish since this frequency has often represented swim bladder fish in other studies, particularly when paired with 120 kHz (Logerwell & Wilson 2004, Simmonds & MacLennan 2005, Jech & Michaels 2006). The 120 kHz was used for fluid-like zooplankton as this frequency is often used for distinguishing euphausiids (Jech et al. 2018). We applied the 200 kHz for non-swim bladder fish because they are weak scatterers, their modeled frequency response was highest at 200 kHz, and this frequency was recommend for mackerel assessments (Trenkel & Berger 2013, Scoulding et al. 2016).

The resulting Area Backscattering Coefficient (ABC) values (m^2m^{-2}) associated with each MFI classification were then summarized by bins 1000 m in length and either 50 or 200 m in depth (Figure 2). The total ABC in a bin represents the

backscatter area that an organism class occupies within that particular bin. We created acoustic variables representing phytoplankton and fish larvae, zooplankton, swim-bladder fish, and non-swim bladder fish to be employed as potential predictor variables at three depths: 0-50 m, 50-100m, and 0-200m. We did not use variables representing acoustic depth bins of 100-150 m and 150-200 m in this analysis because of too many missing values (transect locations shallower than 100 m). Each transect was processed separately using an identical template and the acoustic output representing the ABC of the four species groups were merged with sightings data along each track line. We then exported and analyzed the data in R (R Core Team 2018).

Marine Mammal Modelling

Generalized Additive Models (GAMs) (Hastie 1990, Wood 2017) were built to explain the density of marine mammals observed along the transects using the “mgcv” package (Wood 2011) implemented in the R statistical language (v. 3.5.2) (R Core Team 2018) . We built density models for seven species (common dolphin *Delphinus delphis*, bottlenose dolphin *Tursiops truncatus*, Risso’s dolphin (*Grampus griseus*), striped dolphin (*Stenella coeruleoalba*), pilot whale, sperm whale, and fin whale). We did not model beaked whales and many baleen whales due to small sample sizes (Table 1). We did not model marine mammals not identified to species modeled.

We converted counts of sighted marine mammals per cell to model species density with the following formula:

$$D = \left(\frac{S * G}{L} \right)$$

where D is the density of a particular marine mammal in a specified cell, S is the number of sightings per cell, G is the mean group size per cell, and L is the length of the cell (1000 m).

Density models were fit using the restricted maximum likelihood (REML) criterion with the Tweedie family, allowing for flexibility among candidate distributions and the ability to deal with excess zeros and overdispersed data. Smooth functions for individual variables were fit with thin plate regression splines with an additional null space penalization that allowed the smooth term to shrink to a linear fit and provided additional restraint against overfitting (Wood 2003).

Model building was guided by the “mgcv” automatic term selection functionality. We removed non-significant terms ($p > 0.10$) selected by the automatic term selection in stages to ensure stability of the model and a lack of dependence on removed terms. We examined correlation in the final candidate models to assess whether strongly related terms should be included in the same model. We did not allow a model to include both a 50 m and 200 m category for the same organism classification. We assessed selection of final candidate variables based on the amount of deviance explained, REML score, and fit of the predictors. These models were further evaluated using k -fold cross validation with 10 random data subsets and assessed with a suite of diagnostic indicators evaluating error in the model following

the example of Chavez-Rosales et al. (2019). These diagnostic indicators included Spearman's rank correlation coefficient (RHO), mean absolute error (MAE), and mean absolute percentage error (MAPE).

RESULTS

GAMs were built for seven species with 12 candidate acoustic variables, whereby each variable was calculated for 1242 one-km horizontal bins. Species models were built for common dolphins, bottlenose dolphins, Risso's dolphins, striped dolphins, pilot whales, sperm whales, and fin whales. Correlations between variables in the final models were kept low, except for one instance in the common dolphin model that included 0-50 m swim-bladder fish and phytoplankton with a correlation of 0.774 (Tables 2 and 3). The highest correlation in any of the other model was 0.333 between zooplankton at 0-50 m and swim bladder fish at 0-50 m. The correlation matrix did show two surprisingly consistent patterns in which swim-bladder fish was commonly correlated with phytoplankton/fish larvae, and non-swim bladder fish was often correlated with zooplankton.

Model fits varied by species, from strong fits for common dolphin and fin whales, to no viable model for sperm whale (no significant predictors) (Table 3). The common dolphin model had the highest deviance explained, but also the highest effective degrees of freedom, a poor RHO value, and one of the lower numbers of group sightings, and therefore could be over-fit. Fin whales, which had the second most group sightings (39) (Table 1), had a respectable amount of deviance explained

(25.4%) and among the best error fits, particularly for the RHO value (0.122) derived from the k -fold cross validation. The striped dolphin model explained 11.0% of deviance, and fair to excellent k -fold cross validation test statistics, but had the smallest group sightings size (10). The Risso's dolphin model, which had the most frequently sighted groups (51), was fit with only one variable (swim bladder fish at 0-200 m), had fair to excellent and qualitative valuation metrics, but only explained 3.6% of deviance. Pilot whale and bottlenose dolphin models both explained near 6% of deviance, and their MAPE and MAE values evaluated in the fair to good range, however, the pilot whale RHO fell just within the poor classification range. In general, MAE values suggested much better fits than the other metrics across all species.

Common dolphin, bottlenose dolphin, and fin whale all appeared to have positive relationships with potential prey in their final models. Common and bottlenose dolphins showed positive and increasing relationships with increasing swim bladder fish (Figure 4), and fin whales showed a similar relationship with zooplankton (Figure 5). Additional GAM plots for each model are provided in the Supplemental Appendix (Figures S1-S5).

DISCUSSION

This study provides the first validation relating marine mammal abundance to a measure of prey density within the water column from a dedicated abundance survey. Recent attempts to model similar data relied almost entirely on parameters measuring

surface or bottom characteristics, most of which were physical rather than biotic variables (Forney et al. 2012, Roberts et al. 2016, Becker et al. 2019, Chavez-Rosales et al. 2019). Our study demonstrates that acoustic-based measures of organism structure alone can explain a large amount of variance when describing marine mammal abundance. The top two models explained 37% and 25% of model deviance, with an average of 15% deviance explained across all models except sperm whale. These fits are similar to previous studies modelling marine mammal distribution in this same region and off the west coast of the US.

Many marine mammal distribution models typically explain less than 50% of variability, and often are below 25% (Palacios et al. 2013). Becker et al. (2019) recently produced marine mammal models of encounter rates and single responses in the California Current Ecosystem with explained deviances ranging from 2.8% to 50.1%. Similar models of encounter rates and group size models in the Eastern Tropical Pacific produced explained deviances ranging from 3.8% -58.6% (Forney et al. 2012).

Marine mammal abundance models prepared Chavez-Rosales et al. (2019) for the east coast of the US and part of Canada explained between 16% to 69% of deviance, based on data from 2010 to 2013 that overlapped with this study. Their study developed models from 17 potential predictor variables, though most final models contained five predictor variables. Models often included aerial survey data from other seasons and areas other than the shelf break region, so evaluations between the Chavez-Rosales et al. (2019) models and those presented here are not

directly comparable. That said, they are useful for a general validation of modelling with acoustic variables. The explained deviance was similar in this study for common dolphin (36.8% vs 42.1%) and fin whale (25.4% vs 34.7%) (Table 1). Models from our study did not compare as well when the species was known to feed more deeply, or more concentrated on squid. Models of Risso's dolphins, pilot whales, and sperm whales explained much less deviance than the Chavez-Rosales et al. (2019) study (3.6% vs 49.6% for Risso's dolphins, 5.7% vs 56.2% for pilot whales, and no deviance explained vs 33.5% for sperm whales).

One would expect that models based on organism structure of the first 200 m of the water column would not perform well when representing the abundance of marine mammals that feed below 200 m depth. Sperm whales have recorded mean foraging depths in the Atlantic ocean deeper than 600 m (Watwood et al. 2006). Both pilot whales and Risso's dolphins can feed deep in the water column, with pilot whales averaging 738 m for feeding dives (Aguilar Soto et al. 2008) and Risso's dolphins foraging anywhere from tens of meters to about 500 m on mesopelagic, epipelagic, and sometimes benthic organisms (Arranz et al. 2018, Arranz et al. 2019). However, in our study region pilot whales have been suggested to feed between 70 and 165 m based on known prey species (Baird et al. 2002).

Prey choice also appears to play a role in weaker acoustic species model fits in addition to foraging depth. Sperm whales, pilot whales, and Risso's dolphins feed primarily on cephalopods such as squid, although pilot whale diet may be more varied and may at times include mackerel as a primary prey item (Overholtz & Waring

1991, Gannon et al. 1997a, Gannon et al. 1997b, Smith et al. 2015). The Trenkel and Berger (2013) multi-frequency algorithm does not have a classification category specifically for cephalopods, and therefore squid concentrations may be underrepresented. Given the lack of a cephalopod category, the GAM model fits generally scale with prey and depth preferences, whereby most models with poorer fits are for species that feed deeper and rely more heavily on squid.

The algorithm does contain a classification for non-swim bladder fish, which may pick up some squid, as both are weak scatters (Jones et al. 2009, Scoulding et al. 2016). However, some studies show squid having a stronger relative frequency response at 38 kHz than mackerel, as modeled by Trenkel and Berger (2013), and therefore squid concentrations could be reflected in the swim-bladder fish category. These results illustrate that further studies are needed to potentially apply acoustic squid models (e.g., Jones et al. 2009) to marine mammal survey data. It would also be beneficial to examine relative frequency responses in areas and at depths where squid-specialist marine mammals are present.

The swim bladder fish classification proved a useful predictor for bottlenose and common dolphins. Both species' models had positive and increasing relationships with swim bladder fish in the first 50 m of the water column (Figure 4). Both species consume fish and squid, although they are thought to be more generalists and less squid specialists than Risso's dolphins, pilot whales, and sperm whales. (Kenney 1990, Santos et al. 2001, Wells & Scott 2009). Common dolphins feed on both epipelagic and mesopelagic schooling fish and squid, with most dives less than 100 m

(Waring et al. 1990, Overholtz & Waring 1991, Lahaye et al. 2005, Pusineri et al. 2007). Feeding is thought to primarily occur at dusk or at night as myctophids migrate upwards in the water column to feed (Waring et al. 1990, Pusineri et al. 2007), although some feeding may occur during the daylight hours on concentrations of other fish and squid at shallower depths.

Striped dolphins have a much more offshore distribution on the continental slope than the other dolphins in this study and, have been associated with the north wall of the Gulf Stream and warm-core ring features (Waring 1992), which matches their suspected foraging depth of 200-700 m (Ringelstein et al. 2006). Diet information on this species is limited, with no studies directly in our study region. However, a study in the Eastern Tropical Pacific suggests foraging primarily on myctophids migrating from the deep scattering layer in the evening (Perrin et al. 2008), while a study in the eastern Atlantic shows a more varied diet of myctophids, squid, and pelagic shrimp (Ringelstein et al. 2006). The only significant predictor in our model for striped dolphin showed a negatively sloping swim-bladder fish relationship from 0-200 m (Figure S3). It is not clear what this association signifies, but may be an indicator of an unknown aspect of their deep habitat reflected in the photic zone.

The non-swim bladder fish classification did not show up in any final marine mammal models in this study. The lack of non-swim bladder fish in these models could be due to the correlation between zooplankton and non-swim bladder fish (Table 2) such that zooplankton explained similar variability more effectively. It could also be partly due to the use of the 200 kHz frequency to represent this

category. Higher frequencies do not penetrate as deeply as lower frequencies. At increasing depths, the 200 kHz signal dissipates and begins to fade into the acoustic background noise. A strong scatterer will show up at depth in the 200 kHz frequency, but a weak scatterer such as non-swim bladder fish may be indistinguishable from background noise if not present at a high density. This issue could be compounded by our use of the Echoview fish school algorithm to help clean the echograms and limit the classified data to true aggregations of organisms, reducing backscatter from deeper regions. However, recent recommendations for estimating mackerel biomass suggested using the 200 kHz frequency because of relatively stable echoes compared with the 38 kHz and 120 kHz, which tend to be more variable. This same study also suggested use up to 300 m depth (Scoulding et al. 2016).

Fin whales were the only large whale species abundant enough to model with this dataset. The GAM plots showed positive and increasing relationships with zooplankton. This fits the fin whale's profile of primarily feeding on zooplankton, although at times they can have a diverse prey profile that includes a mix of schooling squid and fish (Pauly et al. 1998, Smith et al. 2015). Of the final GAM models that included phytoplankton/fish larvae as predictors (common dolphin and fin whale), both had linear negatively sloping relationships whereby the relationship is positive at low concentrations and quickly slopes to negative as the phytoplankton/fish larvae concentrations increase. While one would expect productive areas with high phytoplankton levels, it could take several days before high primary productivity results in a congregation of higher trophic levels (Olson et al. 1994). Alternatively,

zooplankton could graze down phytoplankton in productive areas, resulting in a positive relationship at low phytoplankton levels. Modelling acoustic variables together with other parameters may illuminate the reason behind this relationship.

The models presented in this study validate the application of acoustic classifications from echosounding data for use in modelling marine mammal abundance. The fit of most models as measured both in deviance explained and via error estimation from k -fold cross validation, is similar to previous models using proxies for water column characteristics, despite being limited by small sample sizes (Forney et al. 2012, Palacios et al. 2013, Roberts et al. 2016, Becker et al. 2019, Chavez-Rosales et al. 2019). The MAE values from the k -fold cross validation were particularly strong, although they may have been unduly influenced by a large number of zeros, effectively doing very well at predicting where the marine mammals are not as compared to where they are.

The models in this study used the area of the backscatter from organisms of interest to model the fit between prey availability and marine mammal abundance. These models fit best for cetaceans that feed in the photic zone. They fit less well for species that forage heavily on cephalopods, and worse for animals that both forage heavily on cephalopods and feed deeper than 200 m. Future research should aim to include direct classification of cephalopods and of deep foraging layers. Identification of portions of the deep scattering layer that migrate upwards in the evening could also improve species models for many dolphin species that appear to take advantage of this resource at night (Benoit-Bird 2009).

Future research should include additional years of data to ensure robust models, and areas off the shelf break should be included to allow for abundance estimations over a wider region. Future research should also confirm proper bin sizes for best model fit, particularly in the horizontal direction. We chose a horizontal distance of 1000 m in this study in an attempt to retain the potential fine-scale relationships that drive predator-prey interactions. Recent research into marine patchiness examining the scales shaping zooplankton, fish, and seabird distribution via acoustics found that sub-mesoscale processes from 100 m to 1 km play a significant role in shaping the pelagic seascape (Bertrand et al. 2014). Use of an overly small horizontal scale could result in autocorrelation and artificially inflate explanatory power; however, GAMs limit that possibility since they are considered robust to autocorrelation. Furthermore, recent analysis of acoustic observations near seamounts have found that autocorrelation was not present at scales greater than 1 km (Cascão et al. 2017), suggesting that a comparable relationship may apply in a similarly high relief area such as the continental shelf break.

Future abundance estimation models should combine acoustically sensed prey layers with more traditional variables like sea surface temperature and latitude that could provide structure within which acoustic variables may become more informative, improving accuracy and possibly informing the reasons behind some acoustic relationships. In order to achieve prediction in areas not on the ship track, a two or three-dimensional surface of water column prey characteristics would need to be applied across the full study area. Currently, acoustic sampling in the study region,

particularly in areas along and off the shelf break, are not well sampled outside of the repeated AMAPPS ship tracks. Interpolating only using the AMAPPS ship tracks would result in large areas with high uncertainty. A more accurate surface could be created by modeling prey layers relative to existing bathymetry, satellite-derived oceanographic variables, and ocean models currently used for abundance modelling.

Application of acoustically-sensed prey layers could improve abundance models so that they are more responsive to changing ocean conditions and result in higher accuracy by directly modelling prey abundance, thought to be the single most desirable predictor variable for modelling marine mammal distributions (Palacios et al. 2013). This approach would get closer to a mechanistic prediction of distribution; the next step would be to include physical processes that drive much of the lower trophic level prey aggregations. Improved abundance models should assist in managing human impacts on marine mammals as climate shifts preferred habitats and human use of the ocean for energy resources increases.

ACKNOWLEDGEMENTS

NOAA survey data used in this study were collected as part of the Atlantic Marine Assessment of Protected Species project, which was supported by the US Bureau of Ocean and Energy Management to assess protected species populations in areas of potential energy development. A portion of this work was also supported by the NOAA Fisheries Advanced Study Program; thank you to Mike Simpkins, Debi Palka, and Sean Hayes for supporting the senior author's involvement in this

program. Thank you to Melissa Omand and John Hoey for very helpful reviews, suggestions, and support of this research. Thank you to Sam Chavez for helpful discussions about model building. Additional thanks to anonymous reviewers for their valuable edits, comments, and time that greatly improved this manuscript.

LITERATURE CITED

- Aguilar Soto N, Johnson MP, Madsen PT, Díaz F, Domínguez I, Brito A, Tyack P (2008) Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). *Journal of Animal Ecology* 77:936-947
- Arranz P, Benoit-Bird KJ, Friedlaender AS, Hazen EL, Goldbogen JA, Stimpert AK, DeRuiter SL, Calambokidis J, Southall BL, Fahlman A, Tyack PL (2019) Diving Behavior and Fine-Scale Kinematics of Free-Ranging Risso's Dolphins Foraging in Shallow and Deep-Water Habitats. *Frontiers in Ecology and Evolution* 7
- Arranz P, Benoit-Bird KJ, Southall BL, Calambokidis J, Friedlaender AS, Tyack PL (2018) Risso's dolphins plan foraging dives. *The Journal of Experimental Biology* 221:jeb165209
- Baird RW, Borsani JF, Hanson MB, Tyack PL (2002) Diving and night-time behavior of long-finned pilot whales in the Ligurian Sea. *Marine Ecology Progress Series* 237:301-305
- Becker EA, Forney KA, Redfern JV, Barlow J, Jacox MG, Roberts JJ, Palacios DM (2019) Predicting cetacean abundance and distribution in a changing climate. *Diversity and Distributions* 25:626-643
- Benoit-Bird KJ (2009) The effects of scattering-layer composition, animal size, and numerical density on the frequency response of volume backscatter. *ICES Journal of Marine Science* 66:582-593
- Benoit-Bird KJ, Battaile BC, Heppell SA, Hoover B, Irons D, Jones N, Kuletz KJ, Nordstrom CA, Paredes R, Suryan RM, Waluk CM, Trites AW (2013) Prey Patch Patterns Predict Habitat Use by Top Marine Predators with Diverse Foraging Strategies. *PloS one* 8:e53348
- Benoit-Bird KJ, Lawson GL (2016) Ecological Insights from Pelagic Habitats Acquired Using Active Acoustic Techniques. *Annual Review of Marine Science* 8:463-490

- Benoit-Bird KJ, McManus MA (2012) Bottom-up regulation of a pelagic community through spatial aggregations. *Biology letters* 8:813-816
- Bertrand A, Grados D, Colas F, Bertrand S, Capet X, Chaigneau A, Vargas G, Mousseigne A, Fablet R (2014) Broad impacts of fine-scale dynamics on seascape structure from zooplankton to seabirds. *Nature communications* 5
- Brandt MJ, Diederichs A, Betke K, Nehls G (2011) Responses of harbour porpoises to pile driving at the Horns Rev II offshore wind farm in the Danish North Sea. *Marine Ecology Progress Series* 421:205-216
- Cascão I, Domokos R, Lammers MO, Marques V, Domínguez R, Santos RS, Silva MA (2017) Persistent Enhancement of Micronekton Backscatter at the Summits of Seamounts in the Azores. *Frontiers in Marine Science* 4
- Chavez-Rosales S, Palka DL, Garrison LP, Josephson EA (2019) Environmental predictors of habitat suitability and occurrence of cetaceans in the western North Atlantic Ocean. *Scientific Reports* 9:5833
- De Robertis A, McKelvey DR, Ressler PH (2010) Development and application of an empirical multifrequency method for backscatter classification. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1459-1474
- Demer DA, Berger L, Chabot D, Bernasconi M, Bethke E, Boswell K, Chu D, Domokos R, Dunford A, Fässler S, Stéphane G, Hufnagle LT, Jech JM, Bouffant N, Lebourges-Dhaussy A, Lurton X, Macaulay GJ, Perrot Y, Ryan T, Parker-Stetter S, Stienessen S, Weber T, Williamson N (2015) Calibration of acoustic instruments. International Council for the Exploration of the Sea, Copenhagen, Denmark
- DeRuiter SL, Southall BL, Calambokidis J, Zimmer WMX, Sadykova D, Falcone EA, Friedlaender AS, Joseph JE, Moretti D, Schorr GS, Thomas L, Tyack PL (2013) First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. *Biology letters* 9
- Echoview SPL (2018) Echoview software. Echoview Software Pty Ltd, Hobart, Australia
- Foote KG, Knudsen HP, Vestnes G, MacLennan DN, Simmonds EJ (1987) Calibration of acoustic instruments for fish density estimation: A practical guide. International Council for the Exploration of the Sea, Copenhagen Denmark
- Forney KA, Ferguson MC, Becker EA, Fiedler PC, Redfern JV, Barlow J, Vilchis IL, Ballance LT (2012) Habitat-based spatial models of cetacean density in the eastern Pacific Ocean. *Endangered Species Research* 16:113-133

- Gannon DP, Andrew JR, Craddock JE, Fristrup KM, Nicolas JR (1997a) Feeding Ecology of long-finned pilot whales *Blainvillea melanocephala* in the western North Atlantic. *Marine Ecology Progress Series* 148:1-10
- Gannon DP, Andrew JR, Craddock JE, Mead JG (1997b) Stomach contents of long-finned pilot whales (*Blainvillea melanocephala*) stranded on the U.S. mid-Atlantic coast. *Marine Mammal Science* 13:405-418
- Hastie T, Tibshirani, R. (1990) *Generalized Additive Models*. Chapman & Hall, London.
- Jech JM, Lawson GL, Lowe MR (2018) Comparing acoustic classification methods to estimate krill biomass in the Georges Bank region from 1999 to 2012. *ICES Journal of Marine Science* 16:680-695
- Jech JM, Michaels WL (2006) A multifrequency method to classify and evaluate fisheries acoustics data. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2225-2235
- Jones BA, Lavery AC, Stanton TK (2009) Use of the distorted wave Born approximation to predict scattering by inhomogeneous objects: Application to squid. *The Journal of the Acoustical Society of America* 125:73-88
- Kenney RD (1990) Bottlenose Dolphins off the Northeastern United States. In: Leathwood S, Reeves RR (eds) *The Bottlenose Dolphin*. Academic Press, Inc., San Diego, California
- Korneliussen RJ, Ona E (2002) An operational system for processing and visualizing multi-frequency acoustic data. *ICES Journal of Marine Science* 59:293-313
- Lahaye V, Bustamante P, Spitz J, Dabin W, Das K, Pierce GJ, Caurant F (2005) Long-term dietary segregation of common dolphins *Delphinus delphis* in the Bay of Biscay, determined using cadmium as an ecological tracer. *Marine Ecology Progress Series* 305:275-285
- Lawson GL, Barange M, Fréon P (2001) Species identification of pelagic fish schools on the South African continental shelf using acoustic descriptors and ancillary information *ICES Journal of Marine Science* 58:275-287
- Lawson GL, Wiebe PH, Ashjian CJ, Gallagher SM, Davis CS, Warren JD (2004) Acoustically-inferred zooplankton distribution in relation to hydrography west of the Antarctic Peninsula. *Deep Sea Research Part II: Topical Studies in Oceanography* 51:2041-2072
- Logerwell EA, Wilson CD (2004) Species discrimination of fish using frequency-dependent acoustic backscatter. *ICES Journal of Marine Science* 61:1004-1013

- NOAA Fisheries (2013) Annual Report of a Comprehensive Assessment of Marine Mammal, Marine Turtle, and Seabird Abundance and Spatial Distribution in US Waters of the Western North Atlantic Ocean. In: Center NFS, Center SFS (eds), Woods Hole, MA, USA
- Olson DB, Hitchcock GL, Mariano AJ, Ashjian CJ, Peng G, Nero RW, Podestá GP (1994) Life on the Edge: Marine Life and Fronts. *Oceanography* 7:52-60
- Overholtz WJ, Waring GT (1991) Diet Composition of Pilot Whales *Globicephala* sp. and Common Dolphins *Delphinus delphis* in the Mid-Atlantic Bight during Spring 1989. *Fishery Bulletin* 89:723-728
- Palacios DM, Baumgartner MF, Laidre KL, Gregr EJ (2013) Beyond correlation: integrating environmentally and behaviourally mediated processes in models of marine mammal distributions. *Endangered Species Research* 22:191-203
- Pauly D, Trites AW, Capuli E, Christensen V (1998) Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science* 55:467-481
- Perrin W, Roberston KM, Walker WA (2008) Diet of the Striped Dolphin *Stenella coeruleoalba* in the Eastern Tropical Pacific. In: NOAA Fisheries SFSC (ed), La Jolla, CA, USA
- Pusineri C, Magnin V, Meynier L, Spitz J, Hassani S, Ridoux V (2007) Food and feeding ecology of the common dolphin (*Delphinus delphis*) in the oceanic northeast Atlantic and comparison with its diet in neritic areas. *Marine Mammal Science* 23:30-47
- R Core Team (2018) R: A language and environment for statistical computing. Vienna, Austria
- Ringelstein J, Pusineri C, Hassani S, Meynier L, Nicolas R, Ridoux V (2006) Food and feeding ecology of the striped dolphin, *Stenella coeruleoalba*, in the oceanic waters of the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 86:909-918
- Roberts JJ, Best BD, Mannocci L, Fujioka E, Halpin PN, Palka DL, Garrison LP, Mullin KD, Cole TVN, Khan CB, McLellan WA, Pabst DA, Lockhart GG (2016) Habitat-based cetacean density models for the U.S. Atlantic and Gulf of Mexico. *Scientific Reports* 6:22615
- R Core Team (2018) R: A language and environment for statistical computing. Vienna, Austria
- Ryan TE, Downie RA, Kloser RJ, Keith G (2015) Reducing bias due to noise and attenuation in open-ocean echo integration data. *ICES Journal of Marine Science* 72:2482-2493

- Santos MB, Pierce GJ, Reid RJ, Patterson IAP, Ross HM, Mente E (2001) Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. *Journal of the Marine Biological Association of the United Kingdom* 81:873-878
- Scoulding B, Gastauer S, MacLennan DN, Fässler SMM, Copland P, Fernandes PG (2016) Effects of variable mean target strength on estimates of abundance: the case of Atlantic mackerel (*Scomber scombrus*). *ICES Journal of Marine Science* 74:822-831
- Simmonds J, MacLennan D (2005) *Fisheries Acoustics, Theory and Practice*. Blackwell Publishing, Oxford, UK
- Smith LA, Link JS, Cadrin SX, Palka DL (2015) Consumption by marine mammals on the Northeast U.S. continental shelf. *Ecological Applications* 25:373-389
- Stanton TK, Chu D (2000) Review and recommendations for the modelling of acoustic scattering by fluid-like elongated zooplankton: euphausiids and copepods. *ICES Journal of Marine Science* 57:793-807
- Stanton TK, Chu D, Wiebe PH (1998) Sound scattering by several zooplankton groups. II. Scattering models. *ICES Journal of Marine Science* 55:236-253
- Stanton TK, Dezhang C, Reeder DB (2004) Non-Rayleigh acoustic scattering characteristics of individual fish and zooplankton. *IEEE Journal of Oceanic Engineering* 29:260-268
- Trenkel VM, Berger L (2013) A fisheries acoustic multi-frequency indicator to inform on large scale spatial patterns of aquatic pelagic ecosystems. *Ecological Indicators* 30:72-79
- US Executive Order No. 13795 (2017) FR Doc 2017–09087. Federal Register, United States of America
- Waring G (1992) Cetaceans associated with Gulf Stream features off the northeastern USA shelf. *ICES Marine Mammals Comm.*
- Waring GT, Gerrior P, Payne PM, Parry BL, Nicolas JR (1990) Incidental take of marine mammals in foreign fishery activities off the northeast United States, 1977-88. *Fishery Bulletin* 88:347-360
- Watwood SL, Miller PJO, Johnson M, Madsen PT, Tyack PL (2006) Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *Journal of Animal Ecology* 75:814-825

- Wells RS, Scott MD (2009) Common Bottlenose Dolphin: *Tursiops truncatus*. In: Perrin WF, Würsig B, Thewissen JGM (eds) *Encyclopedia of Marine Mammals* (Second Edition). Academic Press, London
- Wiebe PH, Greene CH, Stanton TK, Burczynski J (1990) Sound scattering by live zooplankton and micronekton: Empirical studies with a dual-beam acoustical system. 88:2346-2360
- Wiebe PH, Mountain DG, Stanton TK, Greene CH, Lough G, Kaartvedt S, Dawson J, Copley N (1996) Acoustical study of the spatial distribution of plankton on Georges Bank and the relationship between volume backscattering strength and the taxonomic composition of the plankton. *Deep Sea Research Part II: Topical Studies in Oceanography* 43:1971-2001
- Wood SN (2003) Thin plate regression splines. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 65:95-114
- Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 73:3-36
- Wood SN (2017) *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC

TABLES

Table 1. Summary of marine mammal sightings by species or genus

Common Name	Scientific Name	Groups	Total Animals
Atlantic Spotted Dolphin	<i>Stenella frontalis</i>	1	56
Bottlenose Dolphin	<i>Tursiops truncatus</i>	22	181
Common Dolphin	<i>Delphinus delphis</i>	14	389
Risso's Dolphin	<i>Grampus griseus</i>	51	247
Striped Dolphin	<i>Stenella coeruleoalba</i>	10	413
Unidentified Dolphin	<i>Delphinidae</i>	29	474
Unidentified Small Whale	NA	2	2
Blainville's Beaked Whale	<i>Mesoplodon densirostris</i>	1	1
Cuvier's Beaked Whale	<i>Ziphius cavirostris</i>	8	21
Sowerby's Beaked Whale	<i>Mesoplodon bidens</i>	4	10
Unidentified Mesoplodont Whale	<i>Mesoplodont</i>	2	4
Unidentified Ziphiid Whale	<i>Ziphiid</i>	5	8
Pilot Whale (unidentified species)	<i>Globicephala</i>	24	325
Unidentified Medium Whale	NA	2	2
Blue Whale	<i>Balaenoptera musculus</i>	3	3
Fin Whale	<i>Balaenoptera physalus</i>	39	52
Fin/Sei Whale	<i>Balaenoptera physalus/Balaenoptera borealis</i>	11	11
Humpback Whale	<i>Megaptera novaeangliae</i>	6	8
Minke Whale	<i>Balaenoptera acutorostrata</i>	1	1
Right Whale	<i>Eubalaena glacialis</i>	1	1
Sperm Whale	<i>Physeter macrocephalus</i>	24	29
Unidentified Baleen Whale	<i>Mysticeti</i>	3	3
Unidentified Large Whale	NA	28	32
Unknown	Unknown	1	1

Table 2. Correlation matrix among echosounding organism classifications at depths of 0-50 m, 50-100 m, and 0-200 m. Red font indicates correlation ≥ 0.6 . Abbreviations in the table include PHY = phytoplankton, ZOO = zooplankton, NSB = non-swim bladder fish, and SBF = swim bladder fish

	PHY 0-50m	PHY 50-100m	PHY 0-200m	ZOO 0-50m	ZOO 50-100m	ZOO 0-200m	NSB 0-50m	NSB 50-100m	NSB 0-200m	SBF 0-50m	SBF 50-100m	SBF 0-200m
PHY 0-50m	1.000											
PHY 50-100m	0.255	1.000										
PHY 0-200m	0.882	0.430	1.000									
ZOO 0-50m	0.625	0.112	0.433	1.000								
ZOO 50-100m	-0.064	0.034	-0.046	-0.003	1.000							
ZOO 0-200m	-0.030	-0.021	-0.016	-0.029	0.064	1.000						
NSB 0-50m	0.099	0.015	0.046	0.627	0.005	-0.015	1.000					
NSB 50-100m	-0.028	0.013	-0.022	0.063	0.951	0.061	0.070	1.000				
NSB 0-200m	-0.033	-0.024	-0.021	-0.039	0.009	0.980	-0.021	0.010	1.000			
SBF 0-50m	0.774	0.372	0.842	0.333	-0.055	-0.021	-0.014	-0.044	-0.025	1.000		
SBF 50-100m	0.187	0.906	0.346	0.070	0.021	-0.014	-0.003	-0.012	-0.016	0.286	1.000	
SBF 0-200m	0.711	0.442	0.896	0.256	-0.042	-0.017	-0.018	-0.036	-0.021	0.954	0.371	1.000

Table 3. Generalized Additive Model (GAM) results showing variables included in each model, model degrees of freedom, deviance explained, and Mean Absolute Percentage Error (MAPE) Mean Absolute Error (MAE), and Spearman's Rank Correlation Coefficient (RHO) results from k -fold cross validation. Qualitative classifications of MAPE, MAE, and RHO are color-coded and provided below following the example of Kinlan et al. and Chavez et al 2019.

Species	Zooplankton	Phytoplankton & Fish Larvae	Swim Bladder Fish	Non-Swim Bladder Fish	Effective		MAPE	MAE	RHO
					Degrees of Freedom	Deviance Explained			
Common Dolphin	0-50 m *	0-50 m ***	0-50 m **		4.82	36.8%	98.89	0.2043	0.019
Bottlenose Dolphin	0-50 m **		0-50 m *		2.42	6.8%	96.25	0.0002	0.096
Striped Dolphin			0-200 m *		1.79	11.0%	98.56	0.0007	0.098
Risso's Dolphin			0-200 m **		1.81	3.6%	90.38	0.0002	0.060
Pilot Whale	50-100 m *				1.74	5.7%	96.56	0.0003	0.049
Sperm Whale	NA	NA	NA	NA	NA	< 1%	NA	NA	NA
Fin Whale	0-200 m ****	0-200 m ***			2.84	25.4%	95.23	0.00007	0.122

**** $p = 0$

*** $p < 0.001$

** $p < 0.05$

* $p \leq 0.10$

	RHO	MAE	MAPE
Excellent	$x > 0.3$	$x < 0.25$	$x > 150\%$
Fair to good	$0.05 \leq x < 0.3$	$1 > x > 0.25$	$150\% \geq x > 50\%$
Poor	$x < 0.05$	$x > 1$	$x < 50\%$

FIGURES

122

Figure 1. Marine mammal sightings and active echosounding locations along study area transects used for modeling.

Figure 2. Example of echosounding transect data processing. A) Original 38 kHz data, B) cleaned 38 kHz data with noise processing applied, below bottom removed, and off-transect areas removed, C) 38 kHz data classified as swim-bladder fish, D) 38 kHz data classified as swim bladder fish and binned to 50 m (vertical) by 1000 m (horizontal) bins (scale is distorted in the y direction). Note: Data displayed is S_v (volume backscattering coefficient) (dB re 1 m^{-1}), or the mean volume backscattering strength. Data used for analysis was ABC (area backscattering coefficient) (m^2m^{-2}), where $ABC = (10^{S_v/10}) \times T$, and where T is the mean thickness of the integrated cell.

Figure 3. Example shelf edge transect in the area of Georges Bank that crosses canyon mouths. Marine mammal sightings overlaid with 38 kHz data is S_v (volume backscattering coefficient) (dB re 1 m⁻¹). Grid intervals are 50 m in depth and 1000 m horizontally.

Figure 4. Generalized Additive Model (GAM) plots showing the relationship between common (A) and bottlenose (B) dolphins and Area Backscatter Coefficient (ABC) from swim-bladder fish in the first 50 m of the water column.

A

B

Figure 5. Generalized Additive Model (GAM) plots for fin whale model truncated in the x-direction to exclude outliers and better display region with the vast majority of observations. Full plots can be seen in the supplemental appendix, Figure S5.

SUPPLEMENTAL FIGURES

Figure S1. Generalized Additive Model (GAM) plots for common dolphin model. The variables plotted are (from the top left going clockwise): the Area Backscatter Coefficient (ABC) for phytoplankton from 0-50 m, the ABC for swim bladder fish from 0-50 m, and the ABC for zooplankton from 0-50 m.

Figure S2. Generalized Additive Model (GAM) plots for bottlenose dolphin model. The variables plotted are the Area Backscatter Coefficient (ABC) for swim bladder fish from 0-50 m (left), and the ABC for zooplankton from 0-50 m (right).

Figure S3. Generalized Additive Model (GAM) plots of Area Backscatter Coefficient (ABC) for swim bladder fish from 0-200 m for Risso's dolphin (left) and striped dolphin (right) models

Figure S4. Generalized Additive Model (GAM) plot for pilot whales of Area Backscatter Coefficient (ABC) for zooplankton from 0-50 m (left), and ABC for zooplankton from 50-100 m (right).

Figure S5. Generalized Additive Model (GAM) plot for fin whale model of Area Backscatter Coefficient (ABC) for phytoplankton from 0-200 m (left), and ABC for zooplankton from 0-200 m (right).

CONCLUSIONS

This dissertation aimed to explore the role of marine mammal prey as a component of habitat, distribution, and bycatch in an attempt to provide data and insight that could prove useful for management. A number of factors influence marine mammal distribution such as migration, socialization, and breeding, but prey abundance is believed to be the primary driver of marine mammal distributions (Benoit-Bird et al. 2013b, Palacios et al. 2013). Yet, prey distribution rarely plays a direct role in designing regulations. This may be because it is difficult to assess for highly mobile and protected animals. The majority of species distribution models rely on physical characteristics of the surface or bottom of the ocean and use them as proxies for prey in the water column (e.g., Chavez-Rosales et al. 2019). Managers typically craft bycatch regulations driven by gear modifications and time-area fishing restrictions (Orphanides & Palka 2013) even though prey distribution primarily drives these time-area patterns. We need a better understanding of marine mammal distribution drivers and how they may shift with a changing climate to create more effective regulations that are adaptable to ecosystems in flux. This dissertation explores the relationships between prey and harbor porpoises, right whales, and a community of marine mammals south of New England.

Recent harbor porpoise bycatch in the northwest Atlantic has decreased, but regional bycatch has shifted to southern New England where little was known about harbor porpoise diet (Orphanides & Palka 2013, Orphanides 2019). The research in this dissertation suggests that diet in this region differs substantially from other previously studied regions (Smith & Gaskin 1974, Recchia & Read 1989, Smith &

Read 1992, Gannon et al. 1998). Stomach samples in this region suggested a greater reliance on true hakes (*Urophycis*) and squids, and less of a dependence on herrings. We found an overall diversification of prey with a general shift towards smaller and less calorie dense prey. Clupeids, true hakes, cephalopods, and silver hake (*Merluccius bilinearis*) constituted 85.5% of all estimated consumed biomass. Surprisingly, we found small cusk eels and flatfish were consumed in large numbers, although given their small size they constituted a tiny overall portion of biomass consumed.

Much of this shift appears to have occurred in the latter half of the time series (2007-2017) and aligns with declines of herring and mackerel in the region. Despite this shift in prey, porpoises appear to select their prey preferentially. This was based on comparison with the best available dataset, although it is better suited to bottom feeding animals than those that feed on schooling fish. At minimum, porpoise have clear prey size selection criteria. Both the prey species and the prey sizes have little overlap with the gillnet catch. This suggests that porpoises and the fish species caught in gillnets may be feeding on the same prey. Many of the species fed on by porpoises in this study have demonstrated recent shifts in distribution that may have influenced prey choice (Nye et al. 2009, Kleisner et al. 2017).

North Atlantic right whales have also demonstrated recent shifts in distribution (Pace et al. 2017) and their primary prey is forecasted to shift its distribution with a changing climate (Grieve et al. 2017). These whales have also recently been found to consistently occupy areas previously thought to be migratory corridors or non-preferred foraging habitat, including the continental shelf south of New England (Davis et al. 2017, Leiter et al. 2017). Our opportunistic study of right whale potential

prey resources proved surprising and suggested a prey profile more similar to that in Cape Cod Bay with an increased reliance on *Pseudocalanus* (DeLorenzo Costa et al. 2006a).

Our study also hinted at the possible consumption of ctenophores by right whales. Consumption of gelatinous prey by right whales has been documented previously (Winn & Wishner 1987, Kenney 2008), although most researchers assume that they are consumed incidentally while attempting to prey on copepods. Recent research has shown that a large number of marine species consume gelatinous prey on a regular basis, many of which have high caloric needs (Hays et al. 2018). In our study, the Video Plankton Recorder (VPR) and echosounder data both suggested a layer of ctenophores at ~35-40 m depth. These two instruments differed substantially in the calculated density of ctenophores in this layer. Nevertheless, if the echosounder estimate was correct, the observed ctenophore density falls into the range of suspected caloric needs for right whales (Fortune et al. 2013). The layer closest to the right whale sightings was also far larger than where the VPR was towed.

It is possible that the right whales were feeding on copepods observed in the bongo nets that were missed on the echosounders and the VPR because of the patchy distribution of copepods, inappropriate echosounder frequencies, and concentrations of copepods close to the bottom. Although, given climate driven changes in circulation and preferred right whale prey (Record et al. 2019), combined with health compromised whales that may be nutritionally stressed (Rolland et al. 2016), consumption of alternate prey resources should be considered realistic.

A better understanding of the oceanographic factors aggregating prey is needed to better assess right whale prey aggregations. Our study pointed to possible tidal fronts in this region that may aggregate zooplankton, but much more research would be needed to confirm that hypothesis. The source of plankton is also important for this region. If copepods are coming from the Gulf of Maine, that source may be reduced by climate changes, while if copepods are being supplied from offshore, that theoretically could be sustained as the Gulf of Maine warms.

Distribution of offshore marine mammals also appears to be driven by prey resources. Models presented in this dissertation reflected predicted prey-mammal relationships. Model fits scaled with preferred prey and depth preferences. Marine mammals that are thought to feed shallower with a diet rich in fish showed stronger model fits, and those whales and dolphins believed to feed deeper and rely more heavily on squid showed poorer fits. These model fits reflected limitations of the applied echosounding algorithm in regards to depth and the lack of an explicit squid classification. The potential of this approach was validated by the model fits as expressed in terms of explained deviances. The models presented here had similar fits to published models using a variety of variables serving as proxies for water column prey characteristics. In the future, combining echosounding-derived prey variables with traditional oceanographic and bathymetric variables should result in better model predictions that may be more responsive to changes in the environment.

An effective application of prey information for assessing habitat, distribution, bycatch, and entanglement issues requires higher resolution spatial and temporal prey data than we currently have. Regional prey distributions are primarily driven by spring

and fall bottom trawl surveys. For a better understanding of prey distribution, surveys may have to be undertaken with different gear or technology and at different times of year. Alternatively, knowledge of species distribution may be improved through laboratory studies combined with habitat models. Understanding the drivers behind prey distribution is going to become increasingly important as offshore energy development proceeds and regional climate changes. The previous spatial-temporal patterns that underlie many marine management regulations are not going to persist, and are in fact already changing.

The research in this dissertation has spawned additional research to further investigate these marine mammal-prey issues. In 2020 we will undertake another cruise on the Endeavor to examine right whale prey choices and oceanographic drivers in southern New England. This research will be complimented by a US-Canadian collaboration during the 2020 winter and spring season. As part of this collaboration, very similar research will be conducted in Canadian waters and on the shelf south of New England to try to understand the drivers behind right whale prey aggregations in these two regions. A pilot project is underway to get improved harbor porpoise and seal diet data by comparing traditional hard-part stomach content analysis with DNA analysis from those same stomach contents. Plans are also in place to expand the marine mammal distribution modelling using echosounding prey classification to additional years of data. Additional modelling is planned using multiple years of data to relate echosounding data to traditional oceanographic and bathymetric surfaces so that prey layer surfaces could be created and used to improve marine mammal distribution and abundance models. It is hoped that we can get closer to incorporating

prey considerations into marine mammal management through these continued analyses generated from this dissertation.

LITERATURE CITED

- Benoit-Bird KJ, Battaile BC, Nordstrom CA, Trites AW (2013) Foraging behavior of northern fur seals closely matches the hierarchical patch scales of prey. *Marine Ecology Progress Series* 479:283-302
- Chavez-Rosales S, Palka DL, Garrison LP, Josephson EA (2019) Environmental predictors of habitat suitability and occurrence of cetaceans in the western North Atlantic Ocean. *Scientific Reports* 9:5833
- Davis GE, Baumgartner MF, Bonnell JM, Bell J, Berchok C, Bort Thornton J, Brault S, Buchanan G, Charif RA, Cholewiak D, Clark CW, Corkeron P, Delarue J, Dudzinski K, Hatch L, Hildebrand J, Hodge L, Klinck H, Kraus S, Martin B, Mellinger DK, Moors-Murphy H, Nieukirk S, Nowacek DP, Parks S, Read AJ, Rice AN, Risch D, Širović A, Soldevilla M, Stafford K, Stanistreet JE, Summers E, Todd S, Warde A, Van Parijs SM (2017) Long-term passive acoustic recordings track the changing distribution of North Atlantic right whales (*Eubalaena glacialis*) from 2004 to 2014. *Scientific Reports* 7:13460
- DeLorenzo Costa A, Durbin EG, Mayo CA (2006) Variability in the nutritional value of the major copepods in Cape Cod Bay (Massachusetts, USA) with implications for right whales. *27:109-123*
- Fortune SME, Trites AW, Mayo CA, Rosen DAS, Hamilton PK (2013) Energetic requirements of North Atlantic right whales and the implications for species recovery. *Marine Ecology Progress Series* 478:253-272
- Gannon DP, Craddock JE, Read AJ (1998) Autumn food habits of harbor porpoises, *Phocoena phocoena*, in the Gulf of Maine. *Fishery Bulletin* 96:428-437
- Grieve BD, Hare JA, Saba VS (2017) Projecting the effects of climate change on *Calanus finmarchicus* distribution within the U.S. Northeast Continental Shelf. *Scientific Reports* 7:6264
- Hays GC, Doyle TK, Houghton JDR (2018) A Paradigm Shift in the Trophic Importance of Jellyfish? *Trends in Ecology & Evolution*

- Kenney RD (2008) Right Whales *Eubalaena glacialis*, *E. Japonica*, *E. australis*. In: Perrin W, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Academic Press
- Kleisner KM, Fogarty MJ, McGee S, Hare JA, Moret S, Perretti CT, Saba VS (2017) Marine species distribution shifts on the U.S. Northeast Continental Shelf under continued ocean warming. *Progress in Oceanography* 153:24-36
- Leiter SM, Stone KM, Thompson JL, Accardo CM, Wikgren BC, Zani MA, Cole TVN, Kenney RD, Mayo CA, Kraus SD (2017) North Atlantic right whale *Eubalaena glacialis* occurrence in offshore wind energy areas near Massachusetts and Rhode Island, USA. *Endangered Species Research* 34:45-59
- Nye JA, Link JS, Hare JA, Overholtz WJ (2009) Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Marine Ecology Progress Series* 393:111-129
- Orphanides CD (2019) Estimates of cetacean and pinniped bycatch in the 2016 New England sink and Mid-Atlantic gillnet fisheries. In: Commerce UDo (ed). NOAA Fisheries, Woods Hole, MA, USA
- Orphanides CD, Palka DL (2013) Analysis of harbor porpoise gillnet bycatch, compliance, and enforcement trends in the US northwestern Atlantic, January 1999 to May 2010. *Endangered Species Research* 20:251-269
- Pace RM, Corkeron PJ, Kraus SD (2017) State–space mark–recapture estimates reveal a recent decline in abundance of North Atlantic right whales. *Ecology and Evolution* 7:8730-8741
- Palacios DM, Baumgartner MF, Laidre KL, Gregr EJ (2013) Beyond correlation: integrating environmentally and behaviourally mediated processes in models of marine mammal distributions. *Endangered Species Research* 22:191-203
- Recchia CA, Read AJ (1989) Stomach contents of harbour porpoises, *Phocoena phocoena* (L.), from the Bay of Fundy. *Canadian Journal of Zoology* 67:2140-2146
- Record NR, Runge JA, Pendleton DE, Balch WM, Davies TA, Pershing AJ, Johnson CL, Stamieszkin K, Ji R, Feng Z, Kraus SD, Kenney RD, Hudak CA, Mayo CA, Chen C, Salisbury JE, Thompson CRS (2019) Rapid Climate-Driven Circulation Changes Threaten Conservation of Endangered North Atlantic Right Whales. *Oceanography*
- Rolland RM, Schick RS, Pettis HM, Knowlton AR, Hamilton PK, Clark JS, Kraus SD (2016) Health of North Atlantic right whales *Eubalaena glacialis* over three

decades: from individual health to demographic and population health trends.
Marine Ecology Progress Series 542:265-282

Smith GJD, Gaskin DE (1974) The diet of harbor porpoises (*Phocoena phocoena* (L.))
in coastal waters of Eastern Canada, with special reference to the Bay of Fundy.
Canadian Journal of Zoology 52:777-782

Smith RJ, Read AJ (1992) Consumption of euphausiids by harbour porpoise
(*Phocoena phocoena*) calves in the Bay of Fundy. Canadian Journal of Zoology
70:1629-1632

Winn HE, Wishner KF (1987) Why whales eat ctenophores. Tenth Biennial
Conference on the Biology of Marine Mammals, Miami, FL