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Beyond *Calanus*: changes to the copepod community in the northeast USA and implications for North Atlantic right whale foraging energetics

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ABSTRACT: Declines and shifts in the distribution of the Critically Endangered North Atlantic right whale *Eubalaena glacialis* since 2010 have underscored the need to better understand drivers of right whale habitat use. The influence of *Calanus finmarchicus* prey on right whale distribution is well established, but less is known about the relative importance of other prey taxa, especially in habitats south of the Gulf of Maine (GOM). We used data from NOAA's Ecosystem Monitoring Program (1980—2019) to assess spatiotemporal changes in the abundance of copepod prey and implications for right whale foraging energetics. Decadal-scale changes in copepods were most pronounced in the GOM, led by a marked summer increase of the copepod *Centropages typicus*. Spatiotemporal changes in right whale habitat use generally followed the estimated energy content of regional prey fields, driven mainly by the abundance of *C. finmarchicus*, which has an energy density approximately 10 times that of *C. typicus*. Increases in the abundance of smaller copepods in the GOM since 2010 have been insufficient to compensate energetically for the decline in *C. finmarchicus* in the eastern GOM in summer, where observations of foraging right whales have declined sharply. In southern New England, a site of increased right whale observations, the winter energy content of the sampled prey field was higher than in other subregions. Our analysis highlights that further ocean warming, predicted to negatively impact *C. finmarchicus* and positively impact smaller copepods, may influence whether traditional foraging grounds can support large numbers of foraging right whales.

KEY WORDS: *Eubalaena glacialis* · *Centropages typicus* · Prey abundance · Foraging · Climate change · Gulf of Maine

1. INTRODUCTION

North Atlantic right whales *Eubalaena glacialis* are harbingers of human impacts on wildlife. Historically depleted by whaling, *E. glacialis* are now beleaguered by entanglements in fishing gear and vessel strikes, resulting in Critically Endangered status (Cooke 2020) and a current population size estimate of approximately 340 individuals (as of 2022, Pettis et al. 2023). Effective management strategies and conservation efforts are dependent on an accurate understanding of *E. glacialis* habitat use to target areas and seasons with high right whale presence. In the past, the pres-

ence of right whales along the US coastline was treated as a repeating annual migration pattern, with a large portion of the breeding-age population spending winter months in the southern calving grounds offshore of Florida and Georgia before moving northward to spend spring, summer, and fall months feeding primarily in the Gulf of Maine (GOM) and western Scotian shelf (Winn et al. 1986, Baumgartner et al. 2003, Kraus & Rolland 2009, Davies et al. 2019). Spatiotemporal management strategies such as seasonal vessel speed restrictions and critical habitat designations were developed and implemented based on this understanding of *E. glacialis* habitat use (Asaro 2012,

Conn & Silber 2013, Davies & Brillant 2019). Detailed population records have been kept since the formation of the North Atlantic Right Whale Consortium in 1986, and a trend of population growth was observed until an estimated peak of 481 individuals in 2011 (Pettis et al. 2023). Recovery has since stalled, deteriorating into an ongoing unusual mortality event declared by National Marine Fisheries Services in 2017 after the death of at least 17 whales that year (Kraus et al. 2016, Pace et al. 2017, Stokstad 2017, Corkeron et al. 2018, Meyer-Gutbrod & Greene 2018).

The recent population decline of *E. glacialis* coincided with a shift in habitat use beginning in 2010, with right whales largely abandoning longstanding spring foraging grounds in the Great South Channel and summer foraging grounds in the eastern GOM and Scotian Shelf and subsequently favoring the Gulf of St. Lawrence from 2015 onwards (Davis et al. 2017, Simard et al. 2019, Crowe et al. 2021). Increased use of the western GOM and novel use of southern New England (SNE) has also been observed in this time period (Davis et al. 2017, 2019, Quintana-Rizzo et al. 2021, O'Brien et al. 2022, Meyer-Gutbrod et al. 2023). Use of new areas, in particular the Gulf of St. Lawrence, that did not previously have protections in place for right whales has likely contributed to increased mortality (Pettis et al. 2017, Stokstad 2017, Meyer-Gutbrod et al. 2018, Davies & Brillant 2019), highlighting the challenges and necessity of tailoring conservation efforts to changing patterns of right whale habitat use. In addition to distributional shifts, evidence that right whales can be found across the entirety of their range year-round is accumulating (Morano et al. 2012, Davis et al. 2017). These changes highlight the need to better understand drivers of *E. glacialis* habitat use outside of traditional hotspots in order to develop mitigation strategies for anthropogenic threats.

Changes in the abundance of *E. glacialis* preferred prey in US waters, *Calanus finmarchicus*, have been implicated in the observed changes to *E. glacialis* habitat use. *C. finmarchicus* is a large, subarctic copepod that dominates the Atlantic ecosystem from the GOM northward (Conover 1988, Grieve et al. 2017, Pershing & Stamieszkin 2020). Right whales feed on extremely dense aggregations of late stage (CV and CVI), lipid-rich *C. finmarchicus* that have historically occurred in spring and summer months in the GOM (Baumgartner et al. 2003, Pendleton et al. 2009). The seasonal regional abundance and distribution of *C. finmarchicus* is closely linked with use of foraging grounds by *E. glacialis* (Pendleton et al. 2012, Baumgartner et al. 2017, Meyer-Gutbrod et al. 2023) and with calving success (Meyer-Gutbrod et al. 2015). Waters of the

northeast USA, and particularly the GOM, have experienced rapid climate-driven warming in recent decades (Pershing et al. 2015), and this warming is predicted to cause severe declines in *C. finmarchicus* in the coming decades (Reygondeau & Beaugrand 2011, Grieve et al. 2017, Pershing et al. 2021). Within the GOM, an oceanographic regime shift characterized by advection of warmer slope water into the deep basins of the Gulf beginning in 2010 has led to summer declines in *C. finmarchicus* abundance in the eastern GOM and an increase in spring abundance, especially in the western GOM (Record et al. 2019, Sorochan et al. 2019, Meyer-Gutbrod et al. 2021). These changes in *C. finmarchicus* abundance are hypothesized to be driving the observed changes in *E. glacialis* habitat use (Record et al. 2019, Sorochan et al. 2019, 2021, Meyer-Gutbrod et al. 2021, 2023). However, prey changes have often been documented on a larger spatial scale than changes in right whale habitat use, obscuring the relationship between the two. For example, there have been record high spring abundances of *C. finmarchicus* documented post-2010 in the western GOM as a whole (Ji et al. 2017), whereas *E. glacialis* abundance has increased in Cape Cod Bay but decreased in the Great South Channel within that western region (Record et al. 2019). It is also unclear whether the presence of *E. glacialis* in other seasons and parts of their range, particularly in SNE (see Fig. 1), is driven by prey abundance.

While *C. finmarchicus* is considered the primary prey species of *E. glacialis* in the northeast USA, several smaller calanoid copepod taxa present in this region are thought to be facultative prey based on the filtering efficiency of right whale baleen and their abundance in the region, including *Centropages typicus*, *Pseudocalanus* spp., *C. hamatus*, and *Temora longicornis* (Mayo & Marx 1990, Pendleton et al. 2009, Lehoux et al. 2020, Sorochan et al. 2021). All of these species occur in right whale foraging habitat and have extensive distributional overlap with each other and *C. finmarchicus*, but they exhibit differing life histories that govern their seasonal and regional abundances. Like *C. finmarchicus*, *C. typicus* is a broadcast spawner (Ji et al. 2009). *Pseudocalanus* spp., comprised of 2 co-occurring species, *P. moultoni* and *P. newmani*, that are too morphologically similar to distinguish by eye (Bucklin et al. 1998, 2001, McGillicuddy & Bucklin 2002), carry their eggs, and *C. hamatus* and *T. longicornis* are able to lay resting eggs (Ji et al. 2009), traits which favor local population persistence over reliance on advection to supply and maintain the shelf population. *C. typicus*, *Pseudocalanus* spp., *C. hamatus*, and *T. longicornis* have more southerly distributions com-

pared to *C. finmarchicus* (Beaugrand et al. 2002, 2007, 2009), and right whale foraging habitat occurs at the middle or northern portion of their ranges compared to the southern end for *C. finmarchicus* (Reygondeau & Beaugrand 2011, Grieve et al. 2017). Due to their differing life histories and geographic ranges, it is likely that the smaller copepods will respond differently to changing conditions in key right whale foraging areas. Previous decadal-scale oceanographic regime shifts within the GOM have demonstrated swings in copepod community composition. Smaller copepods (particularly *C. typicus* and *Pseudocalanus* spp.) became more prevalent in the 1990s, corresponding with declines in *C. finmarchicus,* followed by a switch in the 2000s to elevated *C. finmarchicus* and comparatively lower levels of the smaller taxa (Pershing et al. 2005, Pershing & Kemberling 2023). This negative relationship between *C. finmarchicus* and a more diverse community of smaller copepods may be driven by increased stratification favoring the smaller copepods, which was correlated with an influx of cooler, fresher water in the 1990s, but likely tied to increased surface warming in the 2010s (Pershing & Kemberling 2023). In general, it is predicted that warmer conditions will favor the proliferation of the smaller taxa in the northeast USA, in particular *C. typicus* (Pershing et al. 2005, Stegert et al. 2010). Nonetheless, *C. finmarchicus* has been the sole focus of most assessments of foraging suitability for *E. glacialis*, especially in the northeast USA outside of Cape Cod Bay (Record et al. 2019, Meyer-Gutbrod et al. 2023, Ross et al. 2023). The implications of changes in the distribution and community composition of copepods for right whale foraging energetics have not been assessed in detail, and it remains unclear whether an influx of the smaller copepods in the northeast USA could compensate for a reduction in *C. finmarchicus* and sustain *E. glacialis* foraging. The other prey copepods have lower caloric density associated with their smaller size (DeLorenzo Costa et al. 2006, Lehoux et al. 2020). Thus, declines in the relative abundance of *C. finmarchicus* would likely diminish the energetic returns of prey patches for *E. glacialis*.

While oceanographic regime shifts affecting the abundance of copepods and right whales in the northeast US ocean have occurred in previous decades (Pershing et al. 2005, Greene et al. 2013, Meyer-Gutbrod & Greene 2014, Morse et al. 2017), the changes in the 2010s seem to be more intense than previous shifts, especially in terms of higher temperatures (Mills et al. 2024) and the decline of the right whale population (Pettis et al. 2023). The decline in right whale reproduction is in part driven by a decline in *C. finmarchicus*

in the eastern GOM, which in turn stems from an increased incursion of warmer slope water driven by a weakening Atlantic meridional overturning circulation beginning around 2010 (Record et al. 2019, Meyer-Gutbrod et al. 2021). *C. finmarchicus* may be uniquely vulnerable to warming at depth due to its cycle of diapause, particularly in the deep basin of the eastern GOM (Record et al. 2019). However, the other copepods consumed by right whales do not exhibit diapause, and thereby may be more affected by changes in surface temperature (SST), which in the GOM shifted into a much warmer regime beginning with the heatwave in 2012 (Pershing et al. 2018, Mills et al. 2024).

Here, we expand our focus beyond *C. finmarchicus* in known *E. glacialis* foraging hotspots in the northeast USA. We assess whether post-2010 changes in right whale habitat use can be explained more broadly across their range by assessing the dynamics of multiple copepod species, changes to the copepod community outside of known foraging hotspots, and spatiotemporal changes in the estimated energy density of available copepod prey. We summarize observed changes to *E. glacialis* habitat use from previous published studies and analyze 4 decades of copepod data collected by NOAA's Ecosystem Monitoring Program (EcoMon) surveys to assess links between changes to copepod prey species and changes in *E. glacialis* presence. Our specific objectives were to (1) summarize previously observed changes to *E. glacialis* habitat use, (2) quantify changes in the abundance and species composition of dominant copepod taxa, and (3) demonstrate the implications for the regional concentration of energy provided by prey species available to foraging right whales. Finally, we discuss whether observed shifts in *E. glacialis* habitat use may be related to our findings regarding changes to copepod abundance and composition.

2. MATERIALS AND METHODS

2.1. Spatial assignment of changes in *Eubalaena glacialis* habitat use and EcoMon data

EcoMon hosts oceanographic and plankton survey data collected from the northeast US shelf since 1977 (NOAA Fisheries Northeast Fisheries Science Center 2019). EcoMon surveys are assigned to 4 large management regions — GOM, George's Bank (GB), SNE, and Mid-Atlantic Bight (MAB) — which also encompass the range of *E. glacialis* in the northeast USA. To investigate more localized trends, we partitioned 3 of the 4 regions into smaller subregions, dividing GOM

and SNE into eastern and western halves to make GOME, GOMW, SNEE and SNEW, and dividing MAB into northern and southern halves to make MABN and MABS (Fig. 1). In order to maintain a consistent spatial extent between subregions, the GB management region was not subdivided. We then searched for papers describing changes in *E. glacialis* habitat use using any mode of detection that either encompassed data pre- and post-2010 or described trends after 2010 and assigned their described study areas to our subregions to create a summary of *E. glacialis* distribution changes across the northeast USA.

2.2. Copepod data

Plankton abundance data across 4 decades (1980–2019) were collated from EcoMon surveys conducted 4 to 6 times annually in the northeast USA, with each survey targeting 120 randomly selected plankton sta-
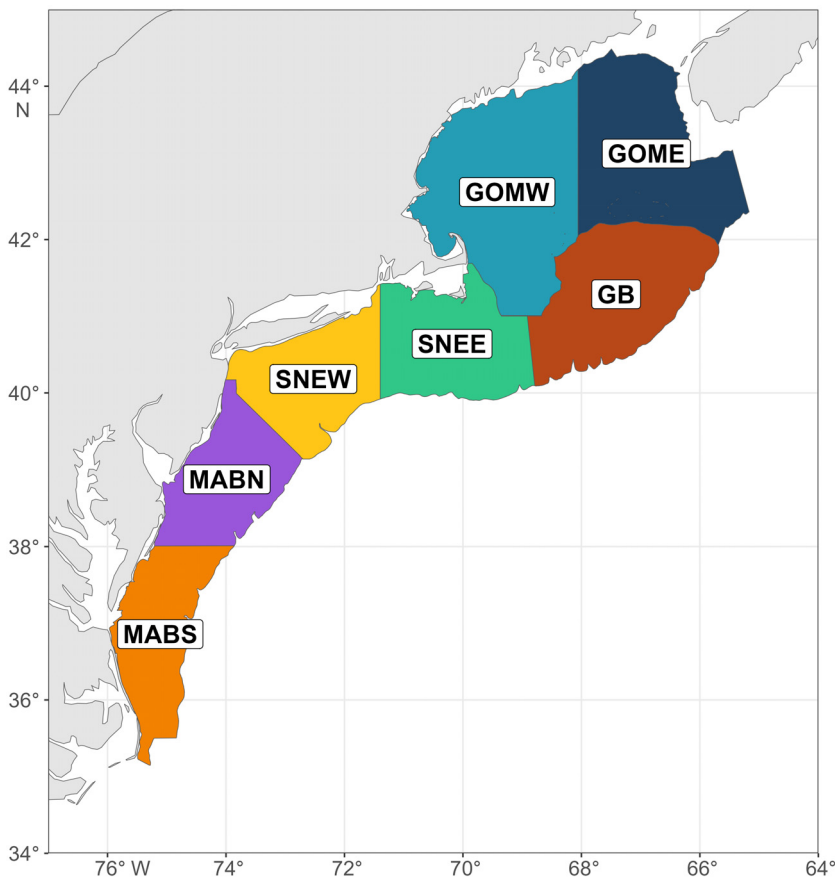

Fig. 1. Study range of the EcoMon dataset split into 7 subregions. GOME: Gulf of Maine east; GOMW: Gulf of Maine west; GB: Georges Bank; SNEE: southern New England east; SNEW: southern New England west; MABN: Mid-Atlantic Bight north; MABS: Mid-Atlantic Bight south

tions distributed across the region (NOAA Fisheries Northeast Fisheries Science Center 2019). EcoMon samples were collected using 61 cm bongo net fitted with 333 μm mesh (Kane 2007), which is comparable to *E. glacialis* filtering efficiency (Mayo et al. 2001), but likely misses smaller naupliar and copepodite stages for many taxa. Oblique tows lasted ≥5 min and ran from within 5 m of the seabed or 200 m depth. Zooplankton samples were reduced by subsampling into aliquots containing approximately 500 individuals, preserved in formalin, identified to the lowest possible taxa, and counted, with abundance normalized to the number of individuals beneath 10 m^2 of sea surface (Kane 2007). We rounded and reduced plankton counts to the number of individuals beneath 1 m^2 for analysis to be consistent with other *E. glacialis* studies (Meyer-Gutbrod et al. 2023, Ross et al. 2023) and assigned counts into quarterly seasonal bins to account for uneven sampling at the monthly scale over the decades of data collection (Kane 2007, Hare 2021; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n056p001_supp.pdf).

Each tow's GPS location was assigned to 1 of our 7 subregions (Fig. 1). We examined seasonal trends in abundance and species composition using the following seasons: winter, January–March; spring, April–June; summer, July–September; and fall, October–December.

To investigate the composition of the copepod community over time, we calculated the proportion of each potential *E. glacialis* prey species (*Calanus finmarchicus*, *Centropages typicus*, *Pseudocalanus* spp., *C. hamatus*, and *Temora longicornis*) out of the total zooplankton collected (ind. m^{-2}) for a given season and decade within each subregion. To check whether other potentially important zooplankton species occurred in large numbers, we also calculated the proportion for any other zooplankton that made up >10% of the total zooplankton sample in a given season, decade, and subregion. As *C. finmarchicus*, *C. typicus*, and *Pseudocalanus* spp. together made up the largest proportion of the copepod community and also exhibited the most change in their relative proportions across decades, further species-specific analyses focused on just these 3 copepod taxa.

We put recent changes in copepod abundance in a broader temporal context by comparing seasonal means ($\pm$SE) within each subregion for each taxon at the decadal scale (1980s, 1990s, 2000s, 2010s) to investigate the magnitude of changes in the 2010s compared to changes in abundance seen in previous decades. In order to place copepod counts in a context more directly tied to *E. glacialis* foraging behavior, we also calculated the proportion of tows that recorded total *C. finmarchicus* counts at or above a proposed threshold of 40 000 ind. m^{-2} needed to support high concentrations of *E. glacialis* foraging (Mayo & Marx 1990, Record et al. 2019) for each season within each subregion and decade. In addition, late-stage (CV and CVI) *C. finmarchicus* are highest in lipids and energy density (Michaud & Taggart 2007, Lehoux et al. 2020) and are known to be preferentially targeted by foraging *E. glacialis* (Baumgartner et al. 2003, Pendleton et al. 2009) and we therefore also examined abundances of stage (specifically CV–VI *C. finmarchicus*) specifically for each season, subregion, and decade.

2.3. Copepod prey taxa energy density and estimated energy content of subregions

We estimated the energy density (kJ ind.$^{-1}$) of the 3 main copepod prey taxa to assess whether changes in the relative abundance of *C. finmarchicus* in comparison to smaller copepod prey may have influenced the energy available to right whales. These estimates of energy density for each of our 3 main prey species were used to make a more direct connection between copepod count data and the ability of each subregion to support *E. glacialis* foraging. To calculate energy density for each prey species, we used published estimates of the carbon content of each of our focal copepod species (Table S1; DeLorenzo Costa et al. 2006), and multiplied the carbon content by a conversion factor of 46 kJ g^{-1} C (Salonen et al. 1976). Carbon content estimates came from samples taken in Cape Cod Bay and averaged across all stages commonly collected by 333 µm mesh: CII–VI for *C. finmarchicus*, and CV–VI for *C. typicus* and *Pseudocalanus* spp. (DeLorenzo Costa et al. 2006). We then used these taxa-specific energy density values to estimate taxa-specific energy content at the subregion scale from EcoMon count data (kJ m^{-2}) (DeLorenzo Costa et al. 2006). Hereinafter we use the terms 'energy content' or 'energy available in copepod prey' to describe estimated energy available from copepod prey given the estimated energy densities and observed abundances for each copepod taxa in a subregion. We calculated

the mean energy content of copepod prey in each combination of subregion, season, and decade.

To place our calculated energy density in the context of observed and potential future copepod community changes, we used the species-specific energy density estimates and simulated the energy available to foraging right whales for a given number of copepods across the range of observed copepod counts within the EcoMon dataset (0–100 000 individuals, see Fig. 3A, regardless of species). The range of 0–100 000 individuals of *C. finmarchicus* along with one of the smaller taxa were plotted as 2 axes, and the resulting plane was interpolated with the sum of the energy density provided by a given combination of abundances of each taxon. This was done for *C. finmarchicus* with *C. typicus* and *Pseudocalanus* spp. separately. In addition, for simplicity in visualizing the results, we show results for a generalized 'small copepod' calculated to be the mean energetic value between *C. typicus* and *Pseudocalanus* spp., as these taxa are both much smaller, with comparable energetic densities an order of magnitude less than *C. finmarchicus* (Table S1). A proposed energetic threshold needed to sustain high concentrations of right whales (~200 000 kJ m^{-2}, equivalent to the energy contained in 40 000 *C. finmarchicus* ind. m^{-2}, Record et al. 2019), was indicated on this visualization to demonstrate what combinations of *C. finmarchicus* and small copepod species would sustain high levels of right whale foraging. This threshold is in units of copepods m^{-2} to match earlier data analyses, but if converted is in range with other studies that calculated similar thresholds using units of copepods m^{-3} (Mayo & Marx 1990, Record et al. 2019, Ross et al. 2023). We then plotted the observed copepod counts for each species (counts of *C. typicus* and *Pseudocalanus* spp. were summed for the generalized small copepod) from the EcoMon dataset for each subregion in the 2010s and 2000s and marked the change between the 2 decades to demonstrate how changes in the abundance of *C. finmarchicus* in relation to smaller copepod prey may have influenced the energy available to right whales in the context of the proposed foraging threshold.

2.4. Statistical models

For each set of subregion, season, and species, we fitted generalized linear models (GLMs) to compare copepod abundance between the 2010s and the earlier decades of the study period. We utilized a Bayesian framework to handle the temporally and spa-

tially variable and overdispersed nature of the Eco-Mon count data without transformation. Copepod models were developed for each combination of season and subregion using a negative binomial distribution to address overdispersion in the count data. Time period was coded as a 2-level factor (pre- and post-2010) to highlight changes outside of previously seen fluctuations. Models with the same framework were also built with the estimated total energy content from all 3 focal copepod species as a response variable to quantify changes in energy content between decades as a result of changes in copepod species composition. Further GLMs were fit to compare 2010s-specific *C. finmarchicus* abundance between regions in each season, with subregion as a 7-level factor to enable between-subregion comparison of the contemporary copepod abundances. All models were given weakly informative priors (normal(0,10)) to balance avoiding unduly influencing the data while steering away from the most unreasonably extreme estimates. All GLMs in which the 95% credible interval did not contain zero were considered to show strong evidence that the change between the 2010s and prior decades was non-zero. All models were fit using the brms package (Bürkner 2017) in R v.4.3.1 (R Core Team 2023). Model fit and convergence was assessed using posterior predictive checks, traceplots, and Rhat diagnostics (Rhat = 1). Models were run for 5000 iterations over 4 chains, with a warm-up period of 500 iterations.

3. RESULTS

3.1. Changes to *Eubalaena glacialis* habitat use in the northeast USA

We found that studies of *E. glacialis* habitat use were concentrated in the GOM (7 studies), followed by SNEE (3 studies), and a single study based on passive acoustic monitoring in the other subregions (Table 1). Decreases in *E. glacialis* presence were evident in GOME in summer and fall. GOMW saw increased *E. glacialis* presence in spring. *E. glacialis* presence increased in SNEE, SNEW, MABN, and MABS in winter and spring, and also in SNEE and SNEW in fall.

3.2. Plankton community

Out of the 5 potential *E. glacialis* copepod prey, *Calanus finmarchicus*, *Centropages typicus*, and *Pseu-*

Table 1. Reported seasonal trends in *Eubalaena glacialis* habitat use since 2010 across the northeast USA. Subregions are those shown in Fig. 1. PAM: passive acoustic monitoring

Subregion	Winter (JFM)	Spring (AMJ)	Summer (JAS)	Fall (OND)	Detection Mode	Notes	References
GOME			Decrease	Decrease	PAM, aerial surveys, shipboard surveys		Davis et al. (2017), Record et al. (2019), Meyer-Gutbrod et al. (2021, 2023)
GOMW		Increase			PAM, aerial surveys, shipboard surveys	Contains Cape Cod Bay, which has seen increased use, and Great South Channel, which has seen decreased use	Record et al. (2019), Charif et al. (2020), Meyer-Gutbrod et al. (2021, 2023), Ganley et al. (2019), Pendleton et al. (2022)
GB					PAM	Limited data, no PAM before 2010	Davis et al. (2017)
SNEE	Increase	Increase		Increase	PAM, aerial surveys, shipboard surveys	Effort focused on Nantucket Shoals area	Quintana-Rizzo et al. (2021), Meyer-Gutbrod et al. (2023), O'Brien et al. (2022)
SNEW				Increase	PAM	PAM effort uneven before and after 2010	Davis et al. (2017)
MABN	Increase	Increase			PAM		Davis et al. (2017)
MABS	Increase	Increase			PAM		Davis et al. (2017)

docalanus spp. comprised the largest proportion (up to 85% of all zooplankton) of seasonal decadal counts in the more northerly study subregions (GOME, GOMW, GB, and SNEE). In the more southerly regions (SNEW, MABN, and MABS), *C. finmarchicus* made up a notably lower proportion of zooplankton (<25%), while *C. typicus* made up a large proportion of zooplankton (>25%) during winter months only (Fig. 2). In the summer and fall in these more southerly regions, other species not known to be tar-

geted by *E. glacialis* foraging were dominant, notably echinoderm larvae and the ctenopod *Penilia* spp. (Fig. S2). Due to the much higher prevalence of *C. finmarchicus*, *C. typicus*, and *Pseudocalanus* spp. compared to other proposed *E. glacialis* prey, further analyses focused on these 3 species.

The relative proportions of *C. finmarchicus* and *C. typicus* in the summer copepod community in the GOM changed markedly in the 2010s compared to previous decades (Fig. 2). Beginning in 2010, *C. typ-*
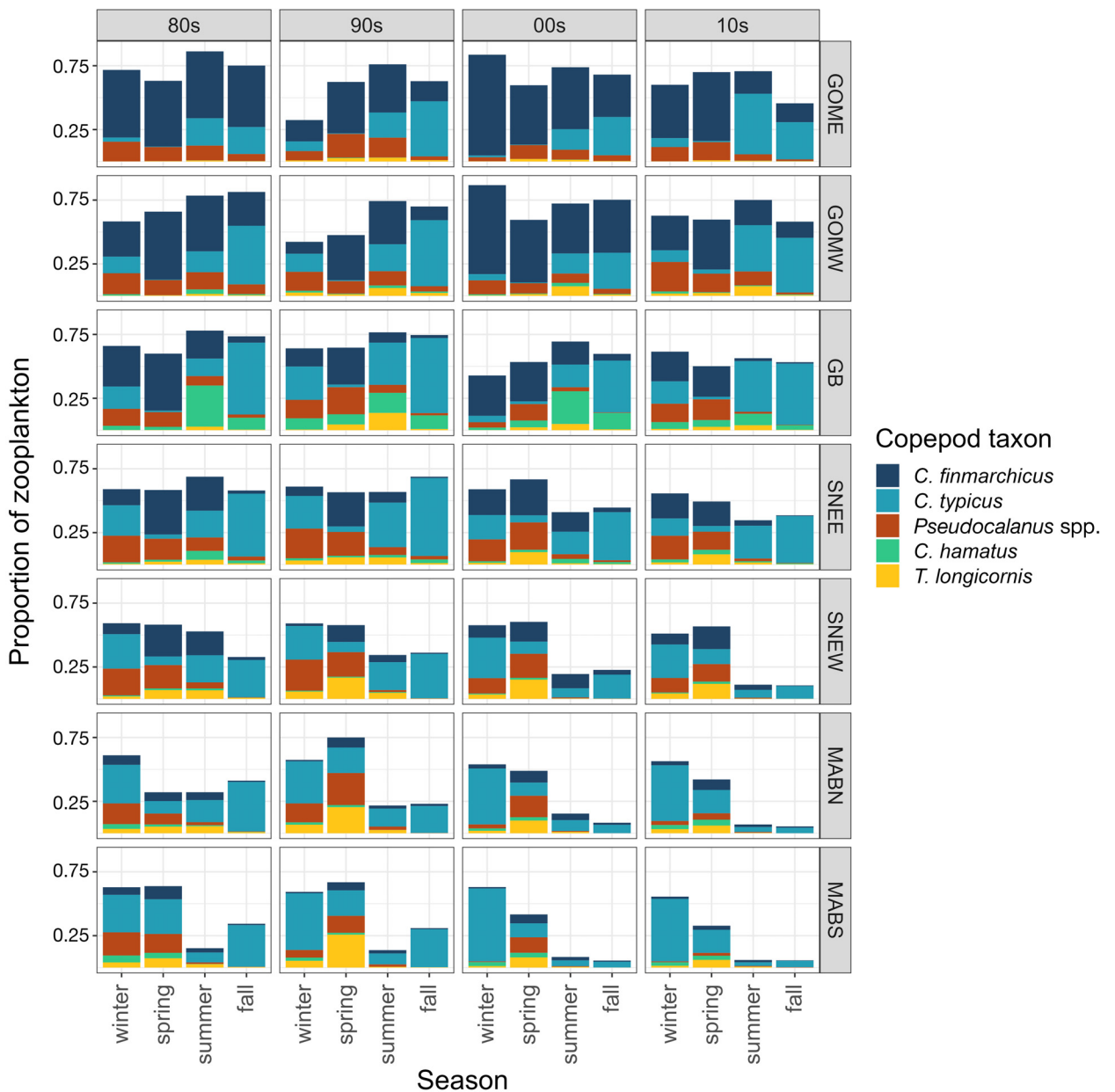

Fig. 2. Average proportion of zooplankton comprised of copepod species (*Calanus finmarchicus*, *Centropages typicus*, *Pseudocalanus* spp., *C. hamatus*, *Temora longicornis*) categorized as potential *Eubalaena glacialis* prey within EcoMon samples, shown across study regions by decade and season. Subregions are as shown in Fig. 1

icus dominated the zooplankton community, in contrast to previous decades where *C. finmarchicus* made up the majority of the zooplankton community. This summer trend was seen in both the eastern and western halves of the GOM. Other seasons and subregions did not appear to exhibit major decadal shifts in the ratio of these 2 species in the 2010s.

3.3. Spatiotemporal changes in copepod abundance

Decadal means of seasonal copepod abundance highlighted changes in *C. finmarchicus* in the 2010s for several subregions (Fig. 3A). Spring abundance of *C. finmarchicus* increased in the 2010s compared to all previous decades in both GOME and GOMW but decreased markedly in SNEE (Table 2, Fig. 3A). *C. finmarchicus* abundances were lower in GOME and GB in summer and fall, and lower in fall in SNEE in the 2010s (Table 2, Fig. 3A). In all other seasons and subregions, there were no changes to this species' abundance outside of decadal oscillations. These decadal patterns were generally mirrored in the proportion of tows at or above the *E. glacialis* feeding threshold (Fig. S3) and in the abundance of late-stage *C. finmarchicus* (CV and CVI, Fig. S4). Within the 2010s, *C. finmarchicus* was most abundant in GOME and GOMW for spring, summer, and fall. In winter, however, there was no difference in *C. finmarchicus* abundance between regions north of MABN, and SNEE had the highest recorded average *C. finmarchicus* abundance (Fig. 3A, Table 3, Fig. S5A).

Seasonal means for *C. typicus* showed strong changes in both GOM subregions in the 2010s compared to previous decades (Fig. 3A). In spring and summer, *C. typicus* was much more abundant in the 2010s than in the previous decades (Fig. 3A, Table 2). In the 2010s for all other seasons and subregions, *C. typicus* abundance remained within the bounds of previous decadal variability (Fig. 3A, Fig. S5B).

Pseudocalanus spp. also exhibited abundance changes in several subregions in the 2010s. Abundance increased in the 2010s in spring and summer in GOMW compared to previous decades (Fig. 3A, Table 2). In spring in the MAB subregions, *Pseudocalanus* spp. decreased in the 2010s. The taxa also exhibited a decrease in summer in SNEE and GB in the 2010s, and in fall in both GOM subregions and SNEE in this decade (Fig. 3A, Table 2). For all other seasons and subregions, *Pseudocalanus* spp. abundance in the 2010s was within the range of abundances seen in previous decades (Fig. 3A, Fig. S5C).

3.4. Estimated copepod energy density and subregional energy content

The energy density of individual *C. typicus* and *Pseudocalanus* spp. were calculated to be 10× and 6× less than that of *C. finmarchicus*, respectively (Table S1). When these values were applied to the mean abundance data, the estimated energy available in the copepod samples was dominated by *C. finmarchicus* across subregions (Fig. S6), and the changes in overall energy content correspondingly mirrored changes in *C. finmarchicus* (Fig. 3B). Models assessing changes to the estimated energetic content of copepod prey in subregions before and after 2010 revealed that even the large increases observed in smaller copepods did not have a large influence on the energy available to foraging right whales (Fig. 4). Visualizing the changes in energy based on maximum observed values for copepod counts further emphasized that the estimated energy content of copepod prey in spring and summer increased from the 2000s to the 2010s in the GOMW and exceeded the energetic threshold for sustained right whale foraging (Figs. 3B & 5, Fig. S7). While the subregional estimated energy content of copepod prey increased between the 2000s and 2010s in GOME in spring, summer values in GOME decreased in this time frame despite the observed increase in small copepods, and fell below the energetic threshold needed to sustain right whale foraging in summer (Fig. 5, Fig. S7). Areas outside the GOM did not exceed the energetic threshold in any season, even with increases in smaller copepods in the 2010s (Fig. 5, Fig. S7).

4. DISCUSSION

The copepod community in the northeast USA showed considerable changes in 2010–2019 in comparison to previous decades, with particularly notable changes in species composition and abundance concentrated in the GOM. The entire GOM saw increases in *Calanus finmarchicus* in spring and large spring and summer increases in *Centropages typicus*. But the eastern and western halves of the GOM have diverged in terms of changes to other copepods and changes in other seasons, with GOMW showing spring and summer increases in *Pseudocalanus* spp. and GOME showing a summer decline in *C. finmarchicus* and less change in other taxa. Converting copepod counts to species-specific energy density emphasized the importance of *C. finmarchicus* as a resource in comparison to *C. typicus* and *Pseudocala-*
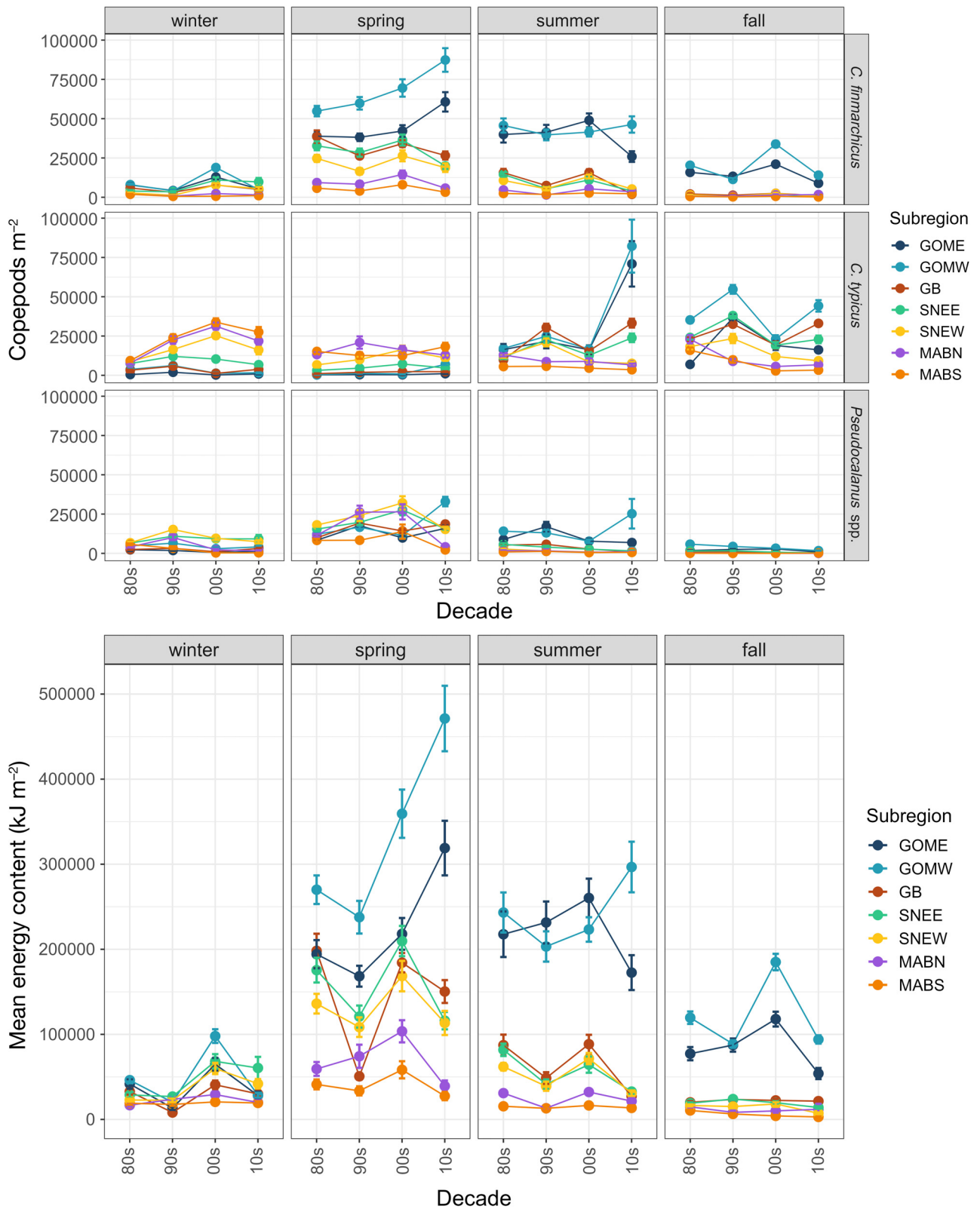
Fig. 3. (A) Decadal mean abundances of *Calanus finmarchicus*, *Centropages typicus*, and *Pseudocalanus* spp. within each season and subregion. (B) Mean energy content of copepod prey across decades within each season and subregion based on the energy density and abundance of each taxon. Subregions are as shown in Fig. 1

Table 2. Model estimates of changes in plankton abundance in the 2010s compared to the previous 3 decades. Note: only species, subregions, and seasons that exhibited strong evidence of changes outside of previous fluctuations (as seen in Fig. 3) are reported here. Estimates are in units of ln(ind. m^{-2}). Subregions are as shown in Fig. 1

Species	Subregion	Season	Intercept (95% CI)	Estimate (95% CI)
Calanus finmarchicus	GOME	Spring	10.59 (10.50, 10.69)	0.43 (0.21, 0.65)
		Summer	10.70 (10.57, 10.84)	−0.53 (−0.88, −0.16)
		Fall	9.74 (9.63, 9.86)	−0.64 (−0.90, −0.37)
	GOMW	Spring	11.01 (10.94, 11.09)	0.37 (0.21, 0.52)
	GB	Summer	9.56 (9.43, 9.69)	−2.00 (−2.32, −1.67)
		Fall	7.51 (7.42, 7.61)	−0.68 (−0.89, −0.45)
	SNEE	Spring	10.40 (10.29, 10.52)	−0.50 (−0.70, −0.28)
		Fall	7.03 (6.90, 7.16)	−0.92 (−1.25, −0.58)
Centropages typicus	GOME	Summer	9.79 (9.59, 10.01)	0.83 (0.24, 1.50)
	GOMW	Summer	9.84 (9.70, 9.97)	0.89 (0.45, 1.37)
Pseudocalanus spp.	GOME	Fall	7.75 (7.61, 7.91)	−1.04 (−1.39, −0.67)
	GOMW	Spring	9.48 (9.39, 9.57)	0.93 (0.74, 1.12)
		Summer	9.38 (9.24, 9.52)	0.98 (0.53, 1.49)
		Fall	8.46 (8.39, 8.54)	−1.02 (−1.22, −0.81)
	GB	Summer	8.39 (8.29, 8.51)	−1.42 (−1.70, −1.14)
	SNEE	Summer	8.39 (8.22, 8.56)	−1.00 (−1.38, −0.60)
		Fall	7.26 (7.13, 7.40)	−1.66 (−2.00, −1.30)
	MABN	Spring	9.76 (9.62, 9.90)	−1.42 (−1.69, −1.15)
	MABS	Spring	9.18 (9.02, 9.35)	−1.46 (−1.83, −1.06)

nus spp. Analyses of energy density of copepod prey suggested that higher energy density in GOMW and declines in energy density below the *Eubalaena glacialis* foraging threshold in GOME in summer may be contributing to recent changes in *E. glacialis* habitat use. Energy content of copepod prey may also play a role in the observations of *E. glacialis* in SNEE in winter given the higher estimated energy content of prey in that subregion in comparison to other subregions during winter. Placing the changes within the GOM in context of the broader northeast USA gives a more detailed view of how a large-scale phenological shift in prey dynamics throughout the year may be driving changes in *E. glacialis* habitat use.

Our results suggest that the observed increases in small copepods observed in the GOM do not make up for the loss of available energy driven by declines in *C. finmarchicus*, which constitutes the vast majority of energy available to foraging right whales. The energy density of *C. typicus* is approximately 10× lower than *C. finmarchicus*, thus even the record high counts of *C. typicus* recorded in the GOM replaced only a small fraction of energy lost to the decline of *C. finmarchicus*. *Pseudocalanus* spp. contain approximately 6× less energy than *C. finmarchicus*, and so smaller increases

in these species in the GOM similarly do not contribute meaningfully to the overall energy content of the region. Thus, despite the influx of smaller copepods, the energy density of copepod prey showed no significant change in summer in the GOM in the 2010s compared to previous decades, even falling below the right whale foraging threshold in the eastern half. Our visualization demonstrates that it would take increases of small copepods far beyond what has been recorded, and even more than the ~100 000 maximum seen for any species in the EcoMon dataset, to match the energy provided by *C. finmarchicus*. This is likely a conservative estimate, as we used carbon content values averaged across life history stages for our 3 taxa; accounting for the very high energy density of late-stage *C. finmarchicus* targeted by right whales would likely increase the estimate further. Warming ocean temperatures are predicted to degrade the overall quality of *C. finmarchicus* (Helenius et al. 2024), calling into question whether the northeast USA can support large numbers of foraging *E. glacialis* over the long term. Further, in Cape Cod Bay, *E. glacialis* appear to preferentially target dense aggregations of *Pseudocalanus* spp. and/or *C. finmarchicus* more than *C. typicus* (Hudak et al. 2023), suggesting that the observed change in copepod ratios in favor of *C. typicus* could be detrimental to *E. glacialis* foraging. In the GOMW, the higher abundance of *Pseudocalanus* spp. in the 2010s extended into the summer months while *C. finmarchicus* remained stable between decades in summer, perhaps fortifying the area's ability to support the increased numbers of *E. glacialis* observed in this region in recent years (Ganley et al. 2019, Charif et al. 2020, Pendleton et al. 2022) even through an increase in *C. typicus*, as right whales appear to be extending their annual residency time in this region (Charif et al. 2020).

Patterns of *E. glacialis* habitat use generally followed patterns in the abundance and estimated energy content of *C. finmarchicus* between subregions, agreeing with studies at finer spatial scales (Pendleton et al. 2009, Record et al. 2019, Meyer-Gutbrod et al. 2023). In winter during the 2010s, the abundance of *C. finmarchicus* was extremely low in MABN and MABS, and slightly higher (but still low compared to

Table 3. Recent (2010−2019) *Calanus finmarchicus* comparisons between subregions within each season. Estimates are in reference to GOME. **Bold**: the 95% credible interval does not cross zero. Subregions are as shown in Fig. 1

Season	Term	Estimate (95% CI)
Winter	Intercept	8.60 (8.11, 9.16)
	GOMW	−0.10 (−0.74, 0.52)
	GB	−0.06 (−0.68, 0.51)
	SNEE	0.61 (−0.04, 1.23)
	SNEW	0.02 (−0.60, 0.60)
	MABN	**−1.28 (−1.89, −0.69)**
	MABS	**−1.64 (−2.26, −1.07)**
Spring	Intercept	11.02 (10.78, 11.28)
	GOMW	**0.36 (0.05, 0.66)**
	GB	**−0.83 (−1.12, −0.55)**
	SNEE	**−1.11 (−1.44, −0.79)**
	SNEW	**−1.17 (−1.51, −0.84)**
	MABN	**−2.35 (−2.70, −2.00)**
	MABS	**−2.92 (−3.30, −2.54)**
Summer	Intercept	10.22 (9.60, 10.94)
	GOMW	0.56 (−0.32, 1.41)
	GB	**−2.66 (−3.45, −1.94)**
	SNEE	**−1.92 (−2.73, −1.18)**
	SNEW	**−1.64 (−2.44, −0.93)**
	MABN	**−2.05 (−2.83, −1.34)**
	MABS	**−2.49 (−3.29, −1.77)**
Fall	Intercept	9.12 (8.76, 9.52)
	GOMW	0.44 (−0.04, 0.91)
	GB	**−2.28 (−2.73, −1.86)**
	SNEE	**−3.01 (−3.51, −2.53)**
	SNEW	**−2.89 (−3.41, −2.36)**
	MABN	**−1.67 (−2.23, −1.12)**
	MABS	**−3.71 (−4.30, −3.11)**

other seasons) in more northerly subregions. The highest average winter abundance occurred in SNEE, where increased winter presence of *E. glacialis* has been observed since 2010 (Quintana-Rizzo et al. 2021, O'Brien et al. 2022). The small, increasing trend in *C. finmarchicus* in winter in SNEE corresponded to a significant increase in available energy, another example of the dominance of this species for foraging returns. The lipid content of *C. finmarchicus* in SNEE remains constant through the winter season, and prey quality (in terms of energetic content) is comparable to the GOM (Carlowicz Lee et al. 2024), further highlighting the importance of this subregion for foraging. In all other seasons, *C. finmarchicus* abundance was higher in GOME and GOMW compared to other subregions. In spring in the 2010s, the GOMW had significantly higher abundance of *C. finmarchicus* than even the GOME and showed a large increase in energy density of copepod prey, corresponding to a period when *E. glacialis* used this region heavily (Charif et al. 2020, Meyer-Gutbrod et al. 2023). Spring

in GOMW also saw increases in *Pseudocalanus* spp., which may have increased the favorability of this foraging ground and season. Summer in this region, while showing an increase in both *Pseudocalanus* spp. and *C. typicus*, did not show a significant change in energy density, as the abundance of *C. finmarchicus* remained relatively stable.

Not all observed changes to the copepod community matched directly with observed changes in *E. glacialis* habitat use. In the 2010s, spring *C. finmarchicus* abundance and estimated copepod energy content increased in GOME, possibly as a result of longer and more sustained spring phytoplankton blooms following earlier spring transition (Friedland et al. 2015, 2023), but decreased in SNEE in the 2010s, an area with lower bloom frequencies. Yet observations of *E. glacialis* have increased in spring in SNEE (Quintana-Rizzo et al. 2021, O'Brien et al. 2022; Table 1) but not GOME (Davis et al. 2017, Meyer-Gutbrod et al. 2021, 2023, Record et al. 2019; Table 1). Observations of socio-sexual behavior in SNEE suggest that *E. glacialis* may use this part of their migratory corridor for non-foraging activity (Rickard et al. 2022), in which case, use of this subregion might not be driven by prey abundance. The GOMW, which experiences by far the highest concentration of prey in spring, is directly adjacent to both GOME and SNEE. So despite an increase in prey in GOME, the huge amount of energy available in GOMW may be enough to support the small right whale population, and preclude any need to exploit other foraging areas in spring. Observed increases of *E. glacialis* presence in MABN and MABS (Davis et al. 2017) did not show clear links with changes in copepods, and the only decadal-scale change we observed in these subregions was a decrease in *Pseudocalanus* spp. in spring. *E. glacialis* use of both of these regions may be tied to migratory behavior rather than foraging.

We observed a marked increase in *C. typicus* during summer in GOME and GOMW, both in terms of counts and the relative abundance within the copepod community. Importantly, the summer increase in average *C. typicus* was in part driven by anomalously high counts in 2012, a year which saw a particularly strong marine heat wave (Mills et al. 2013). As heat waves become more common under climate change (Mills et al. 2024), this pattern could repeat and intensify, making it likely that *C. typicus*, which is better adapted to warm summer low-food conditions than *C. finmarchicus* (Ji et al. 2009, Stegert et al. 2012), could further dominate summer zooplankton communities in the GOM. The apparent resilience of *C. finmarchicus* in GOMW (which did not see declines in summer
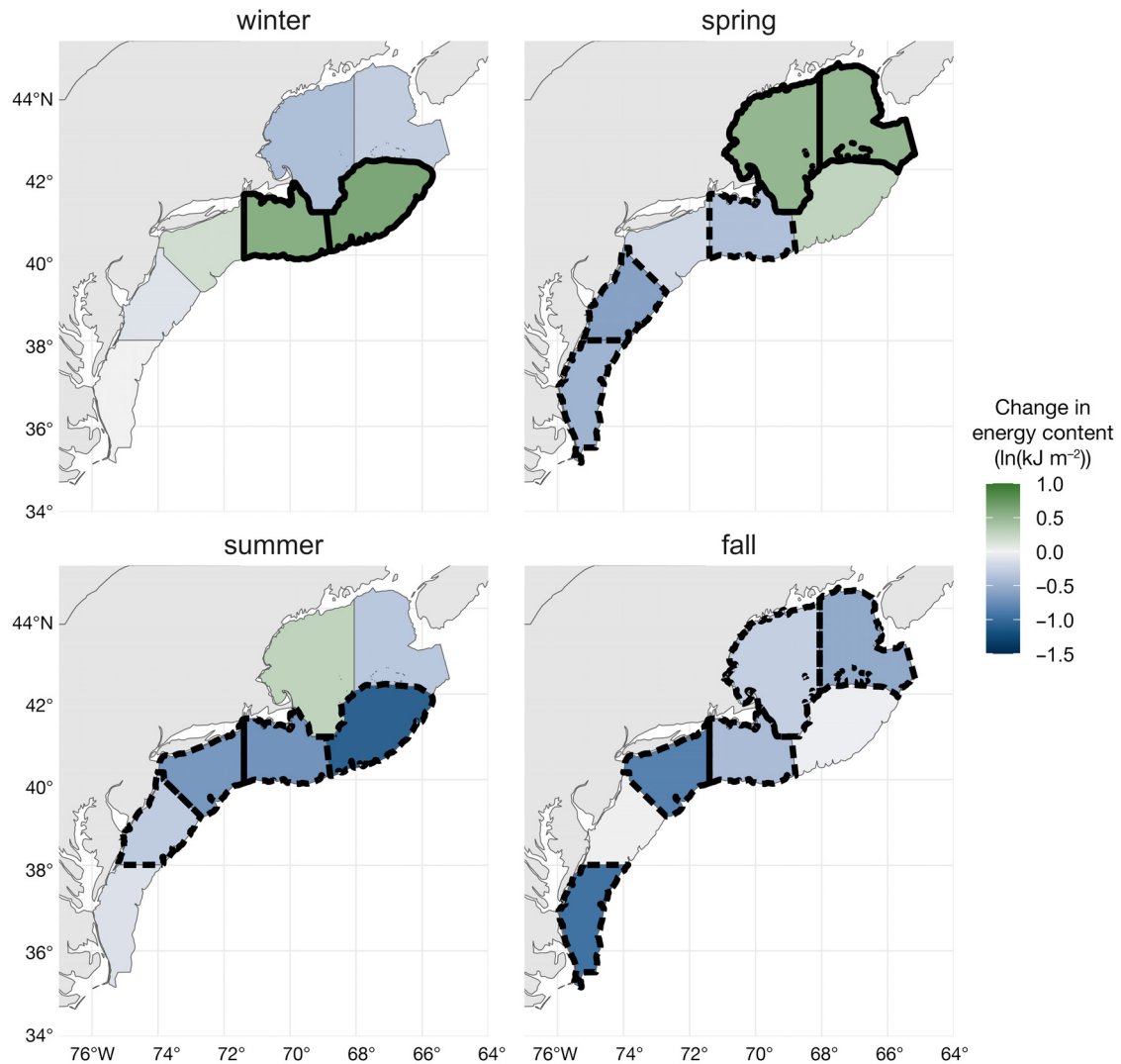
Fig. 4. Changes in seasonal mean energy content of copepod prey within subregions in the 2010s vs. 1980s–2000s estimated using generalized linear models. Solid bold borders: strong evidence of an increase in mean energy content of copepod prey in the 2010s compared to previous decades; dashed bold borders: strong evidence of a decrease (i.e. 95% CI does not cross 0)

in the 2010s in comparison to previous decades) relative to GOME could be tied to the coastal amplification of supply and transport (CAST), where *C. finmarchicus* is advected into the subregion through the nutrient-rich Maine Coastal Current (Ji et al. 2017). Changes in *Pseudocalanus* spp. exhibited a different response to the changing climate; this taxa increased seasonally only in the GOMW, while decreasing over the entire Gulf and SNEE in fall, on top of spring and summer declines south of the GOM. Perhaps akin to *C. finmarchicus*, *Pseudocalanus* spp. benefits from favorable conditions created by the Maine Coastal Current in GOMW while responding negatively to warming temperatures and the extended warm season brought by delayed fall transition elsewhere (Ji et

al. 2009, 2017). This pattern follows predictions that compared to *Pseudocalanus* spp., *C. typicus* will be better able to take advantage of the longer growing season predicated by climate change due to its shorter generation times, while *Pseudocalanus* spp. population growth will slow as temperatures warm (Stegert et al. 2010).

The sampling protocol of the EcoMon dataset has disadvantages for studying copepods relative to *E. glacialis* foraging. The EcoMon dataset measures individual copepod counts and integrates their counts across the entire water column, which does not necessarily correlate to what a feeding whale encounters at a particular depth. *E. glacialis* targets extremely dense, patchy aggregations of prey, and this
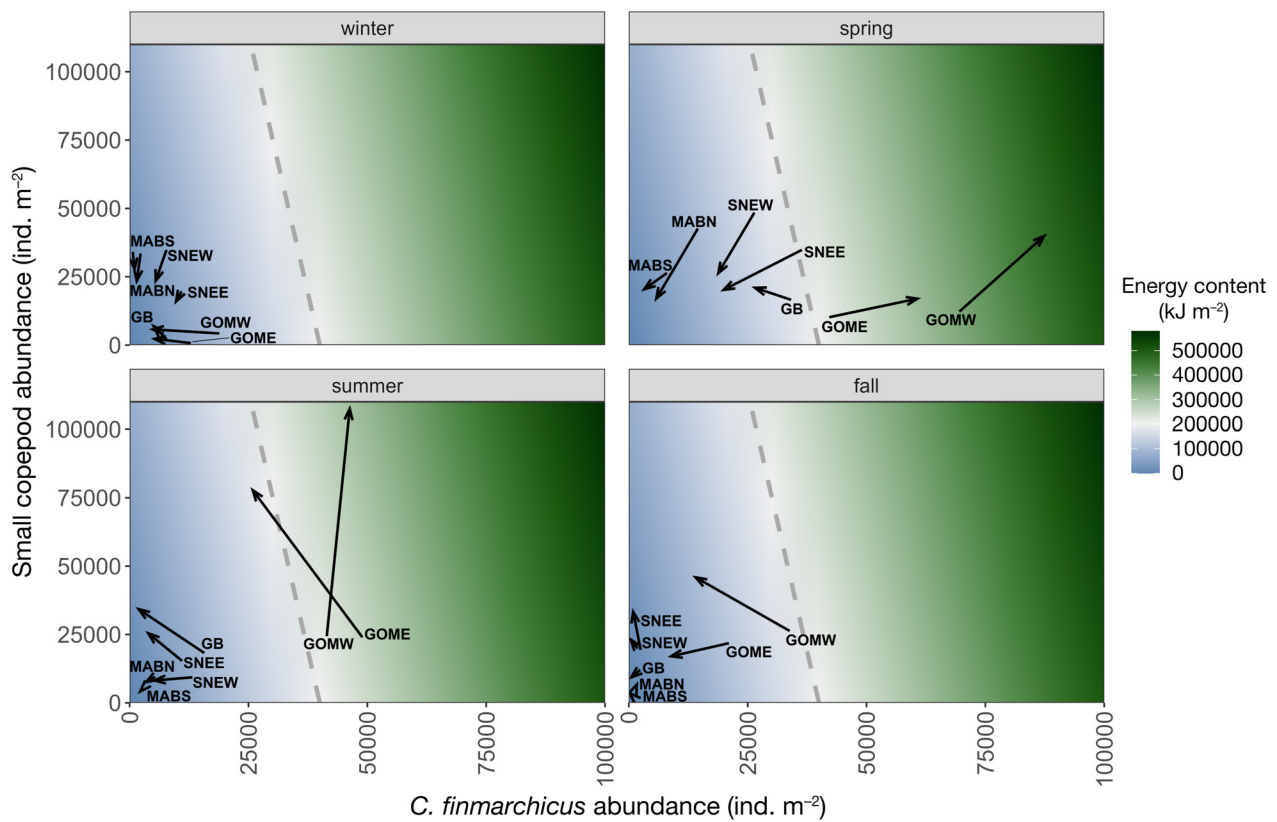
Fig. 5. Estimated energy content of copepod prey across the r ange of observed copepod abundances from Fig. 3 (0—100 000 individuals). Small copepods: the sum of *Centropages typicus* and *Pseudocalanus* spp. counts from the EcoMon dataset together. Color gradient: the summed energy content for a given abundance of *Calanus finmarchicus* and small copepods. Dashed line: the hypothesized threshold that needs to be exceeded to sustain significant right wh ale foraging, equivalent to the energy contained in 40 000 *C. finmarchicus* (Mayo & Marx 1990, Record et al. 2019). Arrows: decadal changes in estimated summed energy density within each subregion and season from the 2000s (the base of the arrow) to the 2010s (the point of the arrow). Subregions are as shown in Fig. 1

may not be captured in vertically integrated tows. For example, it is possible for depth-integrated tow data in deep waters to show high quantities of *C. finmarchicus* in areas that do not see high foraging use by right whales, as the copepods are spread out over too great of an area to suit right whale foraging (Plourde et al. 2019). Integrating EcoMon data with depth-stratified tows targeting aggregated copepods would be helpful for resolving fine-scale copepod drivers of *E. glacialis* habitat use. However, *E. glacialis* energetic needs are so high, especially for nursing females (Fortune et al. 2013), that abundance even on relatively large spatial scales is correlated with presence and calving success (Pendleton et al. 2009, Meyer-Gutbrod et al. 2015), making broad changes in copepod abundance a useful metric for informing conservation and management.

Effective protection of *E. glacialis* will depend on a thorough understanding of where and when the species is occurring, contingent on knowledge of the drivers of these patterns of habitat use. Given the rapid climate-driven oceanographic change occurring in foraging habitat (Record et al. 2019, Pershing & Kemberling 2023) and associated impacts on copepod communities, *E. glacialis* may be selecting foraging habitat that is not optimal in terms of prey abundance or energy content, but that is preferable to other regions showing comparably rapid oceanographic changes or declines in prey quality, as seen in the 2 halves of the GOM in this study. Additionally, since habitat is contiguous, treating subregions as discrete areas may not capture the fact that individuals must travel through adjacent areas when moving to preferred foraging grounds. Whales may be present in an area because they are traveling to an adjacent region rather than for a reason specific to the area they are sighted in.

By incorporating species beyond *C. finmarchicus* and comparing seasonal prey availability and energetic content across subregions in 4 decades, our re-

sults provide more detailed insight into potential drivers of observed shifts in *E. glacialis* habitat use. Patterns of *E. glacialis* habitat use in the 2010s generally followed patterns in the abundance and energy provided by *C. finmarchicus* between subregions, agreeing with studies at finer spatial scales. The energy density of copepod prey increased in GOMW in spring, where right whale observations have increased, whereas declines in *C. finmarchicus* have pushed the overall copepod energy density below the right whale foraging threshold in GOME, where observations of foraging right whales have declined sharply in summer despite large increases in smaller copepod taxa. SNEE had the highest prey abundance and energy density of any subregion in the winter season, aligning with increased right whale presence in winter. In general, *C. finmarchicus* abundance dominated the energy density of prey samples, and it would take increases in the abundance of smaller prey species far beyond what has been observed in the northeast USA to match the energy provided by *C. finmarchicus*. Observed increases in *Pseudocalanus* spp. and *C. typicus* do not make up for the energy loss represented by the decline of *C. finmarchicus* in the GOM in summer. Continuing shifts towards *C. typicus* dominance in the northeast USA would likely degrade the viability of right whale foraging grounds even if counts were able to match the energy density of *C. finmarchicus*, given evidence that right whales preferentially target *C. finmarchicus* and *Pseudocalanus* spp. even during periods of high *C. typicus* abundance (Hudak et al. 2023). Further, *C. typicus* will likely be better able to take advantage of the longer growing season predicated by climate change, while warming ocean temperatures are predicted to degrade the overall quality of *C. finmarchicus* (Helenius et al. 2024), calling into question whether the northeast USA can support large numbers of foraging *E. glacialis* over the long term.

Gaps in knowledge that are central to *E. glacialis* management will require a deeper understanding of drivers of *E. glacialis* habitat use outside of these traditional hotspots. For example, the question of where roughly half of all *E. glacialis*, which do not forage in the Gulf of St. Lawrence (Crowe et al. 2021), go in the summer and fall months can only be answered by collecting robust time series of *E. glacialis* occurrence in regions throughout the northeast USA. Assessing prey availability and environmental drivers of prey abundance is key to understanding and predicting patterns of *E. glacialis* habitat use in these regions. It has been hypothesized that unobserved whales may either be diffusely spread across their range, aggre-gating in previously unknown prey hotspots, or that survey effort is insufficient to identify all whales within known foraging areas (Meyer-Gutbrod et al. 2023). Our results did not identify new areas with high *C. finmarchicus* densities at the subregional scale, so any unknown prey hotspots may only be resolved at higher spatial resolutions. Past work on right whale prey dynamics has focused on regions where *E. glacialis* occur in high numbers, and if *E. glacialis* are more dispersed in other regions, lower average prey abundances may still be able to support foraging by low numbers of *E. glacialis*. Thus, broad assessments of prey abundance and distribution, beyond traditional foraging areas, may be critical to understanding current patterns of *E. glacialis* habitat use and to developing and implementing effective protections in new foraging areas.

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