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North Atlantic right whale *Eubalaena glacialis* prey selection in Cape Cod Bay

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ABSTRACT: North Atlantic right whales *Eubalaena glacialis* have been observed feeding in Cape Cod Bay (CCB) for over 8 decades, making CCB the most consistent known feeding habitat under shifting ocean and climate conditions. Determining the composition of the right whales' prey resource in a stable feeding habitat during a period of environmental change will inform conservation efforts throughout their habitat range. We compared zooplankton sampled in the paths of skim-feeding right whales to the bay-wide zooplankton resource in CCB over 23 yr. The dominant zooplankton taxa in CCB were *Pseudocalanus* complex, *Calanus finmarchicus*, and *Centropages* spp. during the winter/spring seasons. The succession of these 3 dominant taxa — *Centropages* spp. to *Pseudocalanus* complex (day of the year [DOY] mean ± SD: 34 ± 3) to *C. finmarchicus* (DOY 92 ± 3) — has provided right whales with a stable, multi-month food resource in a small portion of their greater North Atlantic habitat. We found that right whales targeted aggregations of non-dominant prey groups: *Pseudocalanus* complex and *Centropages* spp. aggregations when *Centropages* spp. dominated the bay-wide zooplankton community; *Pseudocalanus* complex patches and *C. finmarchicus* patches when *Pseudocalanus* dominated; and primarily *C. finmarchicus* copepodite stage CIV and CV aggregations when CIII dominated bay-wide abundances. Over the time series, we found that *Centropages* spp. abundance increased and *C. finmarchicus* decreased only at the beginning of the season. CCB remains a critical foraging habitat for right whales due to the phenological cycle of their prey and limited inter-annual changes in prey abundance.

KEY WORDS: Zooplankton · North Atlantic right whale · Cape Cod Bay · Prey selection

1. INTRODUCTION

Cape Cod Bay (CCB) encompasses less than 3% of the North Atlantic right whales' (hereafter 'right whale') federally designated critical habitat in US waters (NOAA 2016), but this tidally mixed bay, fed by nutrient-rich Gulf of Maine waters, has been a key feeding area for the Critically Endangered right whale population since the first documented observations in the mid-1950s (Watkins & Schevill 1976, Mayo & Marx 1990, Pendleton et al. 2009). As a result of right whales returning to the Bay each winter/spring, a portion of CCB was designated a federal right whale critical habitat in 1994 (NOAA 1994) and was expanded to include the entire bay in 2016 (NOAA 2016). In recent years, some right whale habitats once identified as important aggregation and feeding areas (e.g. Bay of Fundy, Great South Channel) have shown a significant decline in right whale presence (Record et al. 2019) and others have become new centers of right whale sightings (Simard et al. 2019, Meyer-Gutbrod et al. 2022, O'Brien et al. 2022). In CCB, the abundance of right whales during the winter/spring season increased significantly between 1998 and 2017, resulting in an increasing proportion of the declining population feeding on the Bay's zooplankton resource (Mayo et al. 2018, Ganley et al. 2019). To understand why right whales con-

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tinue to return to CCB to feed, one must consider seasonal and inter-annual zooplankton dynamics through the lens of right whale nutritional requirements.

A reliable marine mammal foraging habitat must be underpinned by a productive ecosystem that provides sufficient prey to support metabolic and reproductive requirements; it must also provide dependable prey aggregations at a depth that allows sufficient feeding time to offset the energetic cost of diving (Kenney et al. 1986, DFO 2014, Plourde et al. 2019). The shallow ecosystem of CCB, with an average depth of 25 m (Anraku 1964), provides dense patches of zooplankton at an easily accessible depth (Watkins & Schevill 1976, Mayo & Marx 1990, Pendleton et al. 2009), which has attracted the large winter and spring right whale feeding aggregations observed over the last decade (Mayo et al. 2018).

In CCB, the fall phytoplankton bloom combined with strong winter/spring blooms supports the zooplankton resource throughout the year (Toner 1984). The majority of zooplankton species are permanent members of the Bay's zooplankton community. Their seasonal abundances are dependent upon temperature and salinity, which are driven by seasonal wind speed and direction as well as coastal processes such as the spring freshet (DeLorenzo Costa et al. 2006). However, some transient species (e.g. *Calanus finmarchicus*) are advected into the Bay each year (DeLorenzo Costa et al. 2006, Jiang et al. 2007) and are therefore strongly influenced by the wind-driven counter-clockwise circulation of the Massachusetts Bay-CCB system and the Maine Coastal Current (DeLorenzo Costa et al. 2006, Jiang et al. 2007, Record et al. 2019; see Fig. 1). Based on 102 µm mesh net collections, smaller taxa, such as copepod nauplii, *Oithona similis*, and *Pseudocalanus* spp. copepodites, dominate the zooplankton community variably throughout the year, with important seasonal occurrences of larger copepods such as *C. finmarchicus* and *Centropages* spp. (Turner 1994, Kropp et al. 2003, Libby et al. 2007, Hunt et al. 2010, Turner et al. 2011). Right whales are known to forage on particular zooplankton species of copepods and euphausiids (Watkins & Schevill 1976, Murison & Gaskin 1989, Mayo & Marx 1990, Beardsley et al. 1996, Baumgartner et al. 2003b). Based on right whale filtration efficiency (equivalent to 333 µm mesh; Mayo et al. 2001), 3 taxa are particularly important in CCB waters during the winter and early spring seasons (Jan–May): *C. finmarchicus*, *Pseudocalanus* spp., and *Centropages* spp. (Mayo & Marx 1990, Mayo et al. 2000).

The estimated population size of North Atlantic right whales started to decline after reaching a peak in 2009 (Pace et al. 2017). The seasonal distribution of right whales across the Gulf of Maine and the waters of the Canadian Maritimes began to shift around 2010 (Meyer-Gutbrod & Greene 2014, Davis et al. 2017) in the midst of a rapidly changing environment, with increasing water temperatures and changes in ocean circulation (Mills et al. 2013, Chust et al. 2014, Pershing et al. 2015, Greene 2016, Seidov et al. 2021). Changes in prey distribution are thought to be driving the changes in the whales' patterns of habitat use and possibly their overall health (Fortune et al. 2013, Meyer-Gutbrod & Greene 2014, Meyer-Gutbrod et al. 2015, O'Brien et al. 2022). In addition, while the whales are protected in historic habitats, they are more vulnerable to anthropogenic mortality in new habitats. Since a significant range shift occurred beginning in 2015, the population has declined by over 25.5% based on the Pace et al. (2017) estimate (Simard et al. 2019, Pettis et al. 2020, Meyer-Gutbrod et al. 2021). In CCB, while the percentage of the population that visited annually ranged from 3.9% (1998) to 56.9% (2013) (Mayo et al. 2018, Ganley et al. 2019), an average of 49.7% of the population returned each year between 2011 and 2020 (B. McKenna unpubl. data). Determining the composition and dynamics of the right whale's prey resource in CCB — one of a few known stable feeding habitats during a period of intense environmental change — is therefore essential for informing future conservation efforts throughout the whales' range. Using a unique data set collected between 1999 and 2022, we identified the seasonal dynamics of the right whales' prey that have made CCB a reliable feeding habitat, and we examined the fine-scale characteristics of zooplankton patches that right whales choose to consume within the context of the bay-wide resource.

2. MATERIALS AND METHODS

2.1. Zooplankton collection and sample parameters

A long-term zooplankton time series associated with right whale presence in CCB has been collected and curated by the Center for Coastal Studies' Right Whale Ecology Program in Provincetown, Massachusetts, since 1981. We queried the data set for samples collected between January and May, the period of residency for right whales in CCB (hereafter 'the season'), from 1999 to 2022. The number of samples available for analysis per year varied depending on weather conditions, whale presence, individual survey goals (e.g. full-bay survey versus targeted sampling with whales), personnel, funding, and sample quality, with a range of 39 (1999) to 279 samples (2005) and an average of 159 (n = 3821 total samples; Table S1 in the Supplement at www.int-res.com/articles/suppl/n051p015_supp.pdf). We included 2 types of zooplankton samples: (1) surface samples collected using a standard 30 cm diameter conical plankton net fitted with a mechanical flow meter, towed horizontally in a circular track around the central GPS coordinates of a station; and (2) upper water column samples (0–19 m) collected since 2003 using a standard 60 cm diameter net fitted with a mechanical flow meter, dropped vertically to 19 m then towed back to the surface obliquely. We only included samples collected with 333 µm Nitex mesh, to approximate right whale baleen filtration (Mayo et al. 2001). All collected samples were preserved in 10% pH-buffered formalin immediately after collection to minimize deterioration and predation. For this study, the composition of the bay-wide zooplankton resource (hereafter 'bay-wide resource') was based on zooplankton samples collected at regularly sampled, GPS-fixed locations (hereafter 'regular stations'; Fig. 1). To determine what right whales were potentially consuming, we used surface zooplankton samples taken behind and next to the direct fluke path (<3 m) of skim-feeding right whales (hereafter 'in-path'; Fig. 2). The term 'skim feeding' pertains to the act of skimming the surface of the water as the whale is filtering the zooplankton through its open mouth. This sampling technique enabled us to sample the non-depleted section of the patch that the right whales were consuming.

2.2. Laboratory analysis and zooplankton identification

We subsampled each preserved zooplankton sample with a 5 ml Hansen pipette. If the 5 ml subsample was too dense to count, the sample was first split with a Folsom plankton splitter before a subsample was taken. Each subsample was enumerated in its entirety to obtain the concentration of each taxonomic category. To ensure accurate representation of the composition and diversity of the zooplankton community, ≥200 organisms were counted and identified. If the 5 ml subsample contained fewer than 200 organisms, then additional subsamples were enumerated in their entirety until over 200 organisms were identified and counted. For each sample, concentrations were calculated as:

$$\text{organisms m}^{-3} = n\frac{V_S}{V_C}\frac{1}{(M_E - M_S)\ C} \qquad (1)$$

where n is the organism count, V_S is the volume of the whole sample, V_C is the volume of the counted subsample(s), M_E is the meter end, M_S is the meter start, and C is the flow meter calibration constant (m^3 revolution^{-1}).

Zooplankton were identified under a dissecting microscope and categorized to either species, genus, or taxonomic group (Smith & Johnson 1996, Todd et al. 1996, Gerber 2000, Johnson & Allen 2005). Species identification based on morphological characteristics can be hampered by morphological homogeneity in groups of genera or species, also known as 'cryptic species' (Frost 1989, Pershing et al. 2005, Thum & Derry 2008, McManus & Katz 2009, Kane 2014). *Pseudocalanus* spp. and *Paracalanus* spp. are considered cryptic species; therefore, we combined the dominant species of *Pseudocalanus moultoni* and *newmani* with *Paracalanus* spp. and the less common *Clausocalanus* sp. under the nomenclature '*Pseudocalanus* complex'. For the purposes of this paper,

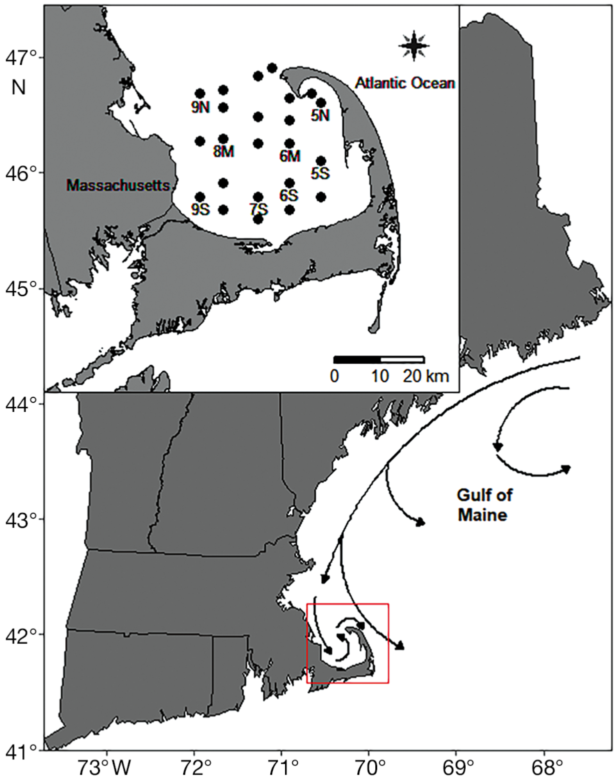

Fig. 1. Cape Cod Bay, located off the state of Massachusetts, USA, at the southern end of the Gulf of Maine. Arrows: dominant ocean currents in the coastal system. Adapted from Pettigrew et al. (2005). Inset: GPS-fixed, regularly sampled stations with example station names

Fig. 2. Center for Coastal Studies R/V 'Shearwater' collecting zooplankton behind a skim-feeding right whale in Cape Cod Bay. Photo credit: CCS, NOAA permit #14603

zooplankton identification was partitioned into 6 taxonomic categories based on the filtration capacity of right whale baleen (Mayo et al. 2001) and the dominant taxa in CCB (Mayo & Marx 1990, Turner 1994): (1) *Calanus finmarchicus*, (2) *Pseudocalanus* complex, (3) *Centropages* spp. (*C. typicus* and *C. hamatus*), (4) other copepods, (5) balanoids (barnacle larvae), and (6) other zooplankton (zooplankton not otherwise categorized in this study). *C. finmarchicus* were further identified by life history stages, from copepodite stage I (CI) to adult (CVI).

2.3. Statistical analysis

2.3.1. CCB zooplankton

We determined the bay-wide zooplankton resource concentration and composition across the time series in order to explore the relative importance of different taxa. We analyzed zooplankton data from oblique tows (0–19 m) taken at regular stations on sampling days with collections from 6–11 regular stations, ensuring comparable bay-wide coverage from sampling day to day and representing the zooplankton resource from the upper water column. While there were 22 regular fixed stations (Fig. 1), a maximum of 11 stations were sampled on any one day. Since oblique tow collections were started in 2003, we truncated the time series by 4 yr to look at gross taxonomic averages of the zooplankton community from the majority of the water column rather than just the surface. From this subset of samples, we calculated the proportion of the total community that each zooplankton category comprised. Taxonomic proportions were calculated from each day's sample collections, averaged to give a bay-wide mean per sampling day and then averaged together, yielding the mean proportion of each taxonomic group over the study period.

2.3.2. Seasonal regimes

We explored the phenological and interannual dynamics of total zooplankton and the dominant taxonomic categories by (1) identifying seasonally dominant taxa during the CCB right whale season; (2) calculating the period of dominance for these taxa (hereafter 'seasonal regime') and the date when dominance transitioned from one taxon to the next (hereafter 'seasonal regime shift'); and (3) analyzing inter-annual variation in these transitions over the time series. We defined the dominant taxonomic category as the taxa with the majority abundance (≥50%) in each sample. We first calculated monthly mean concentrations of each taxonomic category for the duration of the time series to determine their seasonal shifts. We then chose the top 3 categories of the cumulative taxonomic proportions over the time series. To obtain the overall succession of the 3 dominant zooplankton categories in CCB, we used surface tows collected at regular stations to encompass a longer period than oblique tows (1999–2022 vs. 2003–2022 respectively); using surface tows did not yield significantly different mean taxonomic proportions than when using oblique tows (paired *t*-test: $t = 0.012$, df = 5, $p > 0.05$). We applied Loess regressions to the average proportions of the 3 dominant categories per day of the year (DOY) through the right whale season (R Core Team 2022). We used the 'reconPlots' R package (Heiss 2022) to obtain the seasonal regimes by applying Loess regressions and fitting predictive Loess curves to their proportions by DOY for each year and located the DOY when 2 curves intercepted in the seasonal succession of the 3 taxonomic categories, hence creating 2 columns of DOY intercept points. We then applied linear regressions to the intercept points to test for trends in the timing of seasonal regime shifts through the times series based on DOY. Next, we tested whether there was a change in the timing of seasonal regime shifts of taxa in CCB before and after 2010, a period of significant change when the previously increasing right whale population started to decline, according to population models (Pace et al. 2017, Pettis et al. 2021). We separated the seasonal regime transition dates into 2 periods: pre-2010 (1999–2009) and post-2010 (2011–2022) and applied Welch's 2-sample *t*-test to the mean transitional DOY during each time frame.

2.3.3. Regime zooplankton concentrations

We calculated the median bay-wide zooplankton concentrations of total zooplankton and the 3 dominant taxa in the oblique tow data set (2003–2022) per sampling day, then averaged by year and separated by regime to observe the shifts in concentrations within each regime over the time series. We used the oblique tow data to encompass the zooplankton community from the majority of the water column. Linear regressions were performed to obtain trends in total zooplankton and each of the 3 main taxa. We used multiple regression analysis to determine which main taxa influenced the total zooplankton concentration in each regime.

2.3.4. Right whale food resource

We focused on what right whales directly consumed in CCB during the 23 yr of the study based on in-path surface tows of skim-feeding right whales. We first calculated monthly mean concentrations of each taxonomic category for the duration of the time series to determine their seasonal shifts. Taxonomic proportions were averaged from each day's sample collections to give a mean per sampling day, divided into the 3 bay-wide taxonomic seasonal regimes described above, and then averaged, yielding the mean proportion per regime. We focused on zooplankton proportions for the following comparison analysis, rather than concentrations, to minimize the variability in the contrasting patterns of the bay-wide resource and the in-path samples. We compared the taxonomic proportions of the general bay-wide zooplankton resource to the in-path data in each seasonal regime. We used the calculated taxonomic averages from the oblique tows (0–19 m) to account for the zooplankton resource from the majority of the water column and limited the in-path taxonomic averages to 2003–2022 to match. A Fisher's exact test was used to determine the difference in the taxonomic proportions between the bay-wide resource and in-path resource for each regime.

Because the late copepodite stages of *C. finmarchicus*, in particular the lipid-rich stage V (CV), have been documented as the primary prey for right whales throughout most of their range (Murison & Gaskin 1989, Baumgartner et al. 2003a,b, McKinstry et al. 2013), we analyzed the *C. finmarchicus* life stages right whales were consuming in CCB. We calculated the proportions of the *C. finmarchicus* copepodite stages (CI–CV) and adult stage (CVI) from in-path surface samples when *C. finmarchicus* was the dominant species in the sample. We compared the composition of the in-path samples with the composition of the bay-wide zooplankton resource. Specifically, we analyzed *C. finmarchicus* copepodite stage composition (CIII–CV) from *C. finmarchicus*-dominant samples collected during the *C. finmarchicus* seasonal regime, comparing in-path samples to bay-wide samples taken within 8 d of each other. A Fisher's exact test was used to determine the significant association between the sample groups and the copepodite stages.

Before parametric analyses, data were checked using the Shapiro-Wilk test for normality and the Levene test for homogeneity of variances. All analyses were performed in the statistical software R version 4.2.2 (R Core Team 2022), with $\alpha = 0.05$.

3. RESULTS

3.1. Bay-wide zooplankton community

Zooplankton samples from 1291 oblique upper water column tows (0–19 m) collected at regular stations during the CCB right whale season (January–May) between 2003 and 2022 gave a contextual picture of the seasonal prey resource in the Bay. The bay-wide zooplankton community was composed of *Pseudocalanus* complex (33.9%), *Calanus finmarchicus* (22.2%), *Centropages* spp. (14.6%), other copepods (11.5%), balanoids (10.0%), and other zooplankton (7.8%). Over the study period (2003–2022), the monthly mean (±SD) total zooplankton concentrations in CCB ranged from 1729.4 ± 1179.4 organisms m^{-3} in February to 4244.8 ± 3125.0 organisms m^{-3} in April, with an overall mean of 3125.4 ± 2330.8 organisms m^{-3} through the season. The mean highs and lows for each taxon differed, with *C. finmarchicus*, other copepods, balanoids, and other zooplankton peaking later in the season (April–May), while *Centropages* spp. peaked earliest (January) and *Pseudocalanus* complex peaked in March (Table 1). The seasonality of the taxonomic categories varied independently from the seasonal trend of the total zooplankton (Fig. 3).

3.2. Seasonal regimes

We examined zooplankton data from surface tows (n = 2028) to determine the transition of taxonomic dominance through the season between 1999 and 2022. The succession of dominance transitioned from *Centropages* spp. in the early winter (Fig. 4a) to *Pseudocalanus* complex in late winter (Fig. 4b), and finally to *C. finmarchicus* in early spring (Fig. 4c). Hereafter the seasonal regimes were abbreviated to *Centropages* spp. regime (Cs), *Pseudocalanus* complex regime (Pc), and *C. finmarchicus* regime (Cf). The mean (±SE) DOY for the seasonal regime shift from Cs → Pc was day 34 ± 3, while the mean DOY shift from Pc → Cf was day 92 ± 3 (Fig. 3). The overall trends of the 2 yearly seasonal regime shifts were not statistically significant over the study period (Cs → Pc: $r^2 = 0.013$, $p = 0.713$; Pc → Cf: $r^2 = 0.008$, $p = 0.605$; Fig. 5), signifying that the transitional period between these dominant taxa remained stable through the study period. We further analyzed the seasonal regime shifts in CCB, comparing the years before the estimated right whale population decline (1999–2009) and after the onset of the decline (2011–2022). There was no significant difference in taxonomic phenology between the 2 periods (Welch's 2-sample *t*-test, 1999–2009: $t = -0.997$, df = 9.49, $p = 0.344$; 2011–2022: $t = 0.981$, df = 17.98, $p = 0.340$).

3.3. Regime zooplankton concentrations

We examined the median zooplankton concentrations taken via oblique tows (n = 1640) per sampling day averaged per year to determine the trend of the total zooplankton and the 3 dominant taxa in each regime between 2003 and 2022 (Table 2). During the Cs regime, only the negative trend of *C. finmarchicus* was significant ($r^2 = 0.213$, $p = 0.047$), while during the Pc and Cf regimes, only *Centropages* spp.'s positive trends were significant ($r^2 = 0.571$, $p < 0.001$; $r^2 = 0.427$, $p = 0.002$ respectively). Based on multiple regressions, *Centropages* spp. ($t = 10.244$, $p < 0.001$) and *Pseudocalanus* complex ($t = 5.205$, $p < 0.001$) influenced the total zooplankton in the Cs regime. All 3 main taxa influenced the total zooplankton in the Pc regime (*Centropages* spp.: $t = 4.667$, *Pseudocalanus*: $t = 10.403$, *C. finmarchicus*: $t = 6.363$; $p < 0.001$), while only *C. finmarchicus* ($t = 3.65$, $p = 0.002$) and *Pseudocalanus* complex ($t = 3.005$, $p = 0.009$) influenced the total zooplankton in the Cf regime.

3.4. Right whale food resource

Total monthly zooplankton concentrations from zooplankton samples collected behind feeding right whales were 3–5 times higher than the bay-wide concentrations. The monthly mean (±SD) total zooplankton con-

Table 1. Monthly mean (±SD) concentrations (organisms m^{-3}) of the total zooplankton and taxonomic categories in Cape Cod Bay based on oblique samples from 2003 to 2022 (n = 1291). Numbers in parenthesis represent number of samples per month

Taxonomic category	Month				
	January (249)	February (211)	March (272)	April (306)	May (253)
Total zooplankton	2367.3 ± 1401.8	1729.4 ± 1179.4	3099.9 ± 3587.7	4244.8 ± 3125.0	4185.5 ± 2360.2
Calanus finmarchicus	11.4 ± 18.0	33.7 ± 28.7	373.3 ± 461.5	2266.9 ± 2591.0	1884.9 ± 1781.9
Pseudocalanus complex	836.5 ± 468.6	950.5 ± 849.3	2008.1 ± 3517.2	942.0 ± 1066.6	732.3 ± 614.2
Centropages spp.	1202.8 ± 1310.5	351.9 ± 334.3	170.8 ± 273.4	103.5 ± 210.6	184.4 ± 297.9
Other copepods	166.2 ± 171.9	128.3 ± 102.1	139.8 ± 98.7	258.9 ± 277.2	516.5 ± 465.0
Balanoids	107.7 ± 170.4	192.9 ± 445.6	324.6 ± 374.9	349.0 ± 430.0	134.7 ± 148.4
Other zooplankton	42.7 ± 46.2	72.2 ± 137.1	82.9 ± 114.0	324.0 ± 540.1	731.3 ± 1242.0

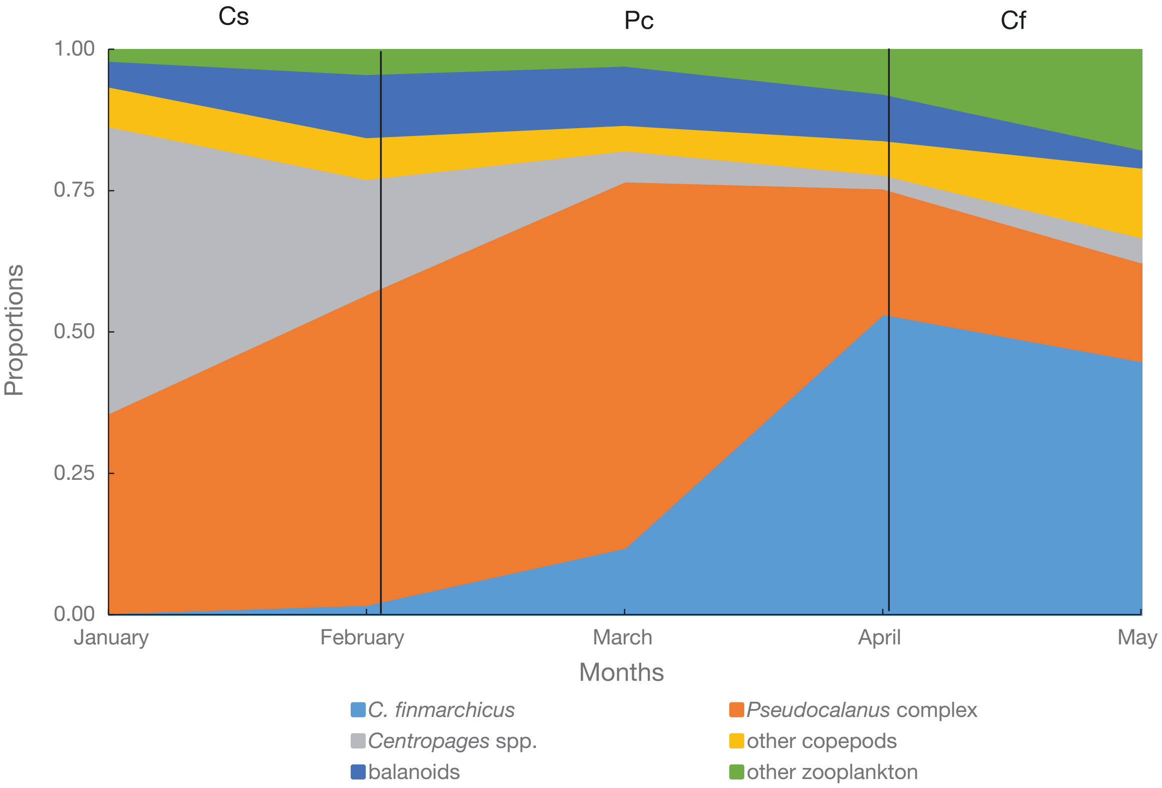

Fig. 3. Monthly proportions of the taxonomic categories in Cape Cod Bay through the season of typical right whale residency (Jan–May), with samples averaged by day, then combined by month for the study period (2003–2022; n = 1291). Vertical lines: mean regime shifts (early February and early April) from one taxon-dominant regime to the next; regimes are labeled above the figure (Cs: *Centropages* spp.; Pc: *Pseudocalanus* complex; Cf: *Calanus finmarchicus*)

centrations over the study period from in-path samples (1999–2022) varied from 9287.2 ± 9181.2 organisms m^{-3} in February to 16 264.3 ± 23 971.2 organisms m^{-3} in March, with an overall mean of 13 438.0 ± 13 678.4 organisms m^{-3} for the season (Table 3). The variability of the mean concentrations for the total zooplankton and individual taxonomic categories can be attributed to the high variability of the zooplankton patches, the seasonal aspect of the taxonomic categories, and the right whales' prey selection. Right whales were observed feeding in all 3 taxonomic seasonal regimes in CCB (Murison & Gaskin 1989, Mayo & Marx 1990, McGillicuddy & Franks 2019, Staudinger et al. 2019). During the Cs regime of the bay-wide zooplankton resource (DOY 1–34), right whales fed on zooplankton aggregations dominated by *Pseudocalanus* complex (74.0 %), with the subdominant taxon *Centropages* spp. (23.5 %; Table S2). As the succession of the bay-wide resource progressed from the Cs regime into the Pc regime (DOY 35–92), *Pseudocalanus* complex (62.3 %) dominated the in-path samples of skim-feeding right whales, with a sub-dominance of *C. finmarchicus* (25.7 %). During the Cf regime (DOY 93–150), right whales fed primarily on aggregations dominated by *C. finmarchicus* (80.0 %).

We compared the proportions of the taxonomic categories between the bay-wide zooplankton resource to the in-path prey resource for each regime during the shortened 2003–2022 time series (Table S2). As the overall season progressed through the 3 regimes, the right whale prey proportions (*C. finmarchicus*, *Pseudocalanus* complex, *Centropages* spp.) in the in-path samples followed a dominance of *Pseudocalanus* complex and *Centropages* spp. in the Cs regime, which transitioned to *Pseudocalanus* complex and *C. finmarchicus* in the Pc regime, and then to *C. finmarchicus* in the Cf regime, while the bay-wide resource followed a dominance progression of *Centropages* spp. and *Pseudocalanus* complex, to only *Pseudocalanus* complex, and then to *C. finmarchicus* (Table S2). During all 3 regimes, 'other copepods', 'balanoids', and 'other zooplankton' categories had lower proportions (0.1–3.8 %) in the in-path samples than in the bay-wide resources (2.4–13.8 %). We found significant differences in all 3 bay-wide versus in-path comparisons (Fisher's exact test, $p < 0.001$) (Fig. 6).

Based on in-path samples, the average *C. finmarchicus* stage composition (i.e. when *C. finmarchicus* was the dominant taxon in the sample; n = 110), was composed of 0 % CI, 2.7 % CII, 20.0 % CIII, 66.4 % CIV,

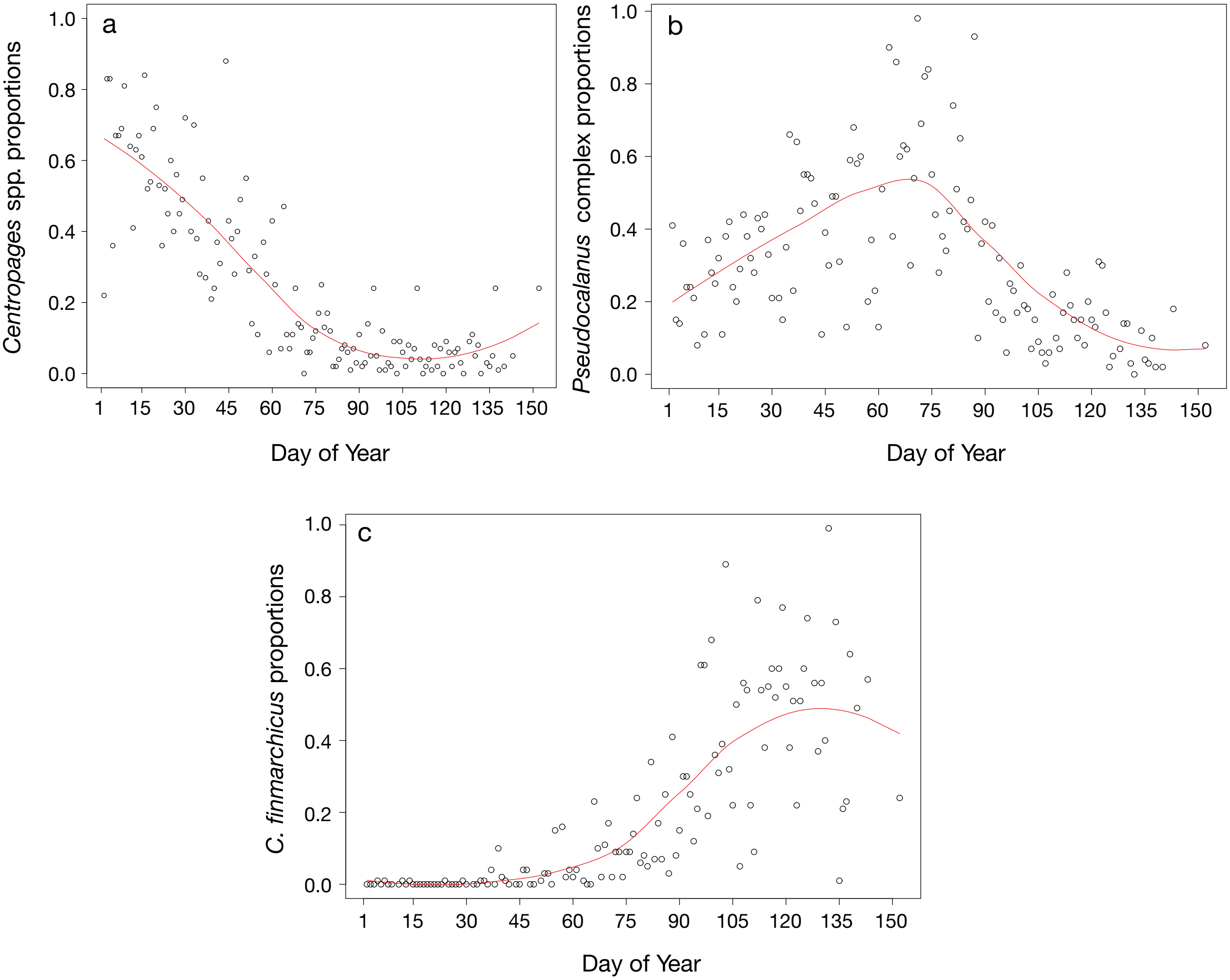

Fig. 4. Loess regressions on proportions of (a) *Centropages* spp., (b) *Pseudocalanus* complex, and (c) *Calanus finmarchicus* from zooplankton samples taken at the surface at regular stations through the study period (1999–2022) in Cape Cod Bay

9.1% CV, and 1.8% CVI. When comparing the *C. finmarchicus* stage compositions (CIII–CV) that right whales were feeding on to the bay-wide stage composition during the Cf seasonal regime, we found that right whales fed on zooplankton patches with higher concentrations of CIVs and CVs than were present in the bay-wide zooplankton resource (75.0 and 9.4% versus 21.3 and 2.2% respectively). The high proportions of CIV and CV in the in-path samples suggest right whales were finding and feeding upon patches of CIV and CV (Fisher's exact test, $p < 0.001$; Fig. 7).

4. DISCUSSION

This study provides a unique view of right whale prey in CCB, a small yet vital area of the known right whale critical feeding habitat. Previous studies of right whales' prey have focused on short time frames (i.e. hours, days, or months) or limited prey species (Murison & Gaskin 1989, Mayo & Marx 1990, Beardsley et al. 1996, Baumgartner et al. 2003a,b, Pendleton et al. 2009, Plourde et al. 2019). Our observations provide an in-depth examination of the zooplankton community based on the right whale's filtration capabilities (333 µm; Mayo et al. 2001), while also focusing on the intricacies of all prey targeted by the whales in this major feeding habitat. This analysis of the total zooplankton community composition in CCB over 19+ yr revealed the contribution of multiple taxa at different times throughout the winter and spring (Table 1), with 3 copepod taxa dominating: *Calanus finmarchicus*, *Pseudocalanus* complex, and *Centropages* spp., all known as right whale prey (Watkins &

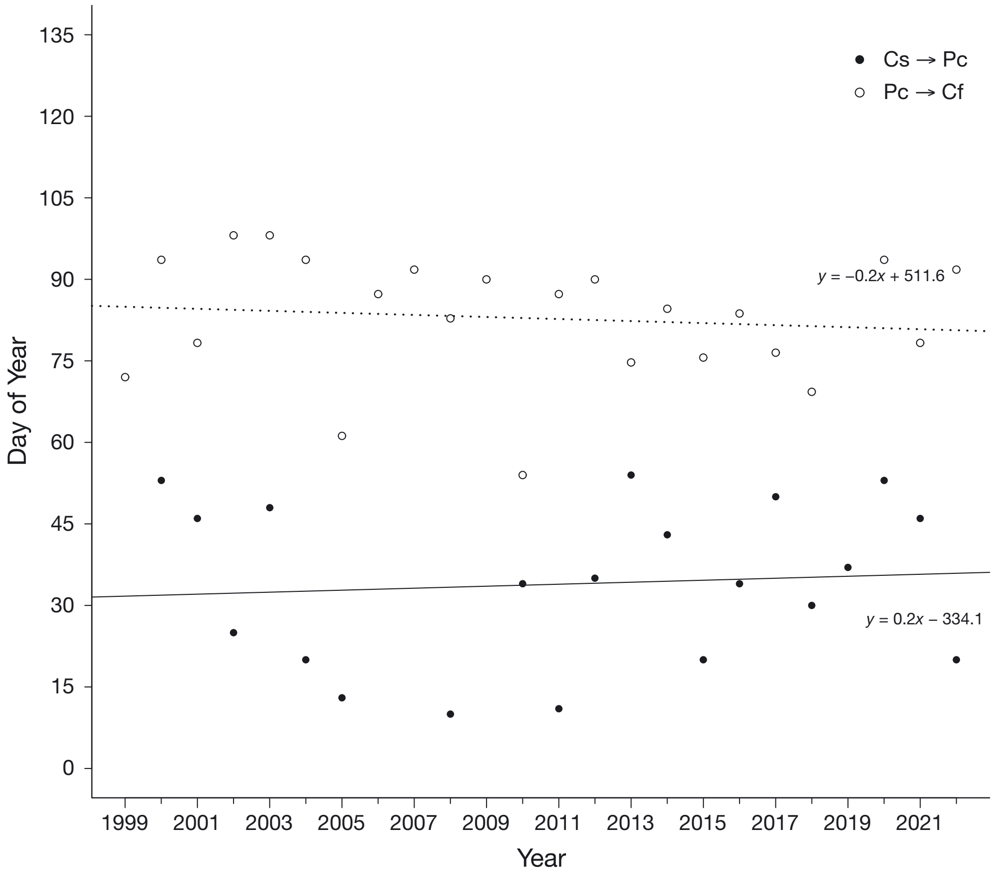

Fig. 5. Day of the year intercept points of Loess curves for each seasonal regime shift per year indicating the change in dominance between *Centropages* spp. and *Pseudocalanus* complex (Cs → Pc), and *Pseudocalanus* complex and *Calanus finmarchicus* regime (Pc → Cf). Solid line: Cs → Pc linear regression ($r^2 = 0.013$, $p > 0.05$); dashed line: Pc → Cf linear regression ($r^2 = 0.008$, $p > 0.05$)

Schevill 1976, Murison & Gaskin 1989, Mayo & Marx 1990, Beardsley et al. 1996, Baumgartner et al. 2003b). Right whales rely on substantial seasonal aggregations of zooplankton prey associated with cycles of productivity (Baumgartner et al. 2007). The succession of the 3 dominant copepods in this study (*Centropages* spp. to *Pseudocalanus* complex to *C. finmarchicus*) has provided a stable food resource for a substantial portion of the remaining right whale population during nearly half of the year in a relatively small portion (<3%) of their broad habitat range. Given that the right whale prey resources have been shifting and changing in other known feeding habitats (Chust et al. 2014, Record et al. 2019, Brennan et al. 2021), the stability of the zooplankton resource may partially explain the increase in the number of individual right whales visiting and feeding in CCB over the years (Mayo et al. 2018).

Table 2. Linear regression analyses on the median concentrations of total zooplankton and the 3 main taxa averaged by year, with number of years (n) per regime. **Bold** text denotes statistically significant categories ($p < 0.05$)

Regime	Taxonomic category	n	r^2	*t*	p
Centropages spp.	Total zooplankton	19	0.156	1.772	0.094
	Calanus finmarchicus		**0.213**	**−2.147**	**0.047**
	Pseudocalanus complex		0.002	−0.194	0.848
	Centropages spp.		0.153	1.753	0.098
Pseudocalanus complex	Total zooplankton	20	0.158	1.841	0.082
	Calanus finmarchicus		0.008	0.378	0.710
	Pseudocalanus complex		0.001	0.104	0.918
	***Centropages* spp.**		**0.571**	**4.891**	**<0.001**
Calanus finmarchicus	Total zooplankton	20	0.040	0.865	0.399
	Calanus finmarchicus		0.025	−0.683	0.503
	Pseudocalanus complex		0.035	0.810	0.428
	***Centropages* spp.**		**0.427**	**3.659**	**0.002**

Right whales are filter-feeders that rely on physical and behavioral processes to aggregate their prey into

Table 3. Monthly mean (±SD) concentrations (organisms m^{-3}) of the total zooplankton and taxonomic categories from in-path samples of skim-feeding right whales in Cape Cod Bay from 1999 to 2022 (n = 153). Numbers in parenthesis represent number of samples collected per month

Taxonomic category	Month				
	January (9)	February (9)	March (19)	April (97)	May (19)
Total zooplankton	12 428.5 ± 6260.8	9287.2 ± 9181.2	16 264.3 ± 23 971.2	13 310.5 ± 12 387.3	13 707.2 ± 8564.1
Calanus finmarchicus	54.9 ± 127.3	979.9 ± 1431.2	885.9 ± 1175.2	10 361.4 ± 10 292.2	12 332.3 ± 8292.4
Pseudocalanus complex	9176.6 ± 4708.4	6392.5 ± 8863.8	14 607.8 ± 24 307.0	1787.8 ± 3492.7	664.7 ± 765.8
Centropages spp.	2900.2 ± 4057.3	1610.7 ± 887.7	479.7 ± 825.0	138.7 ± 353.8	159.5 ± 338.0
Other copepods	233.7 ± 170.1	59.7 ± 35.7	153.8 ± 185.6	605.4 ± 1679.3	274.5 ± 340.1
Balanoids	4.8 ± 13.6	182.9 ± 378.7	105.5 ± 252.3	327.0 ± 873.2	142.1 ± 222.8
Other zooplankton	58.3 ± 93.3	59.3 ± 126.0	31.6 ± 71.4	89.2 ± 244.3	134.2 ± 171.4

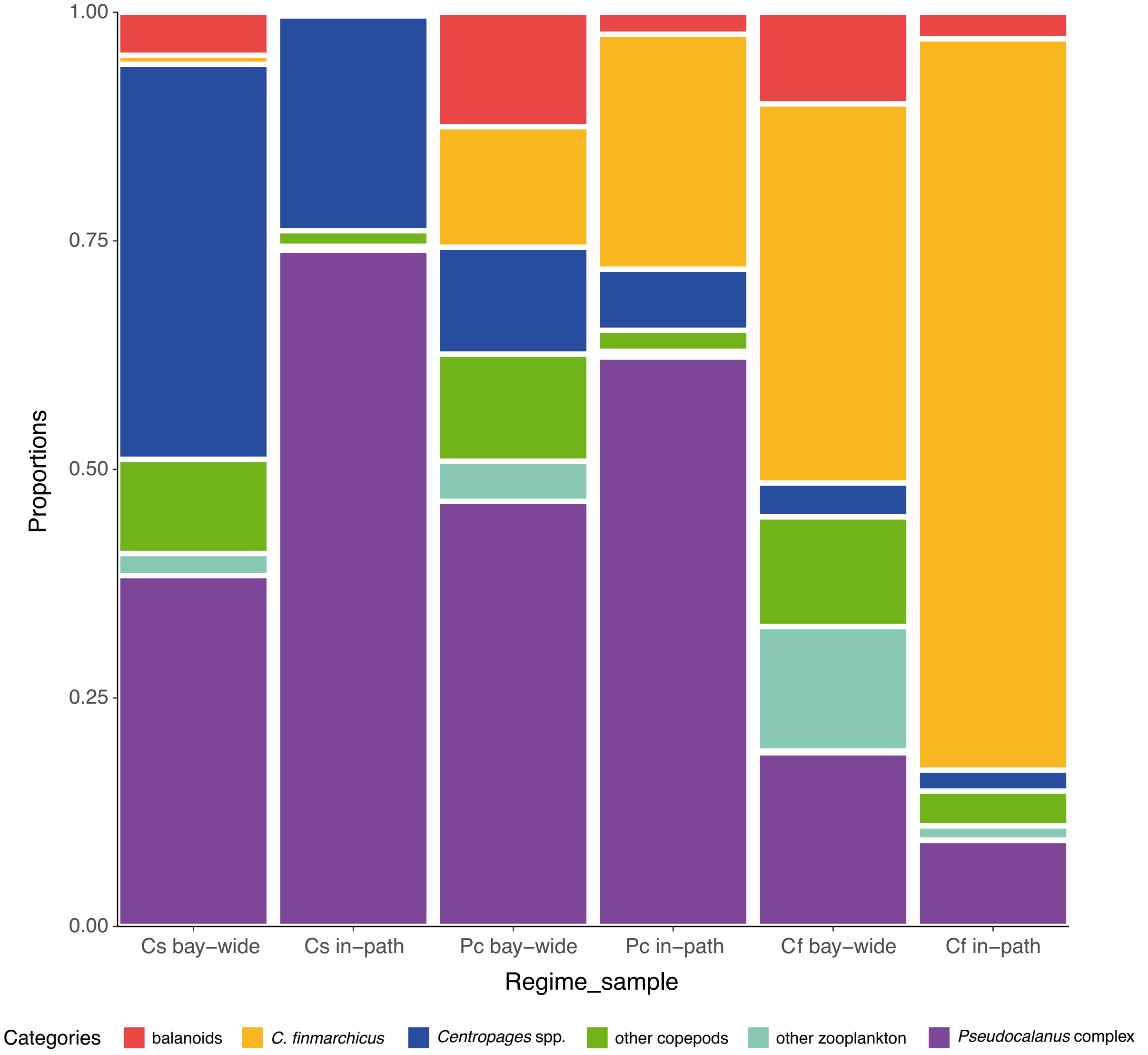

Fig. 6. Comparison of proportions of the taxonomic categories in bay-wide and in-path samples for each regime: Cs: *Centropages* spp. regime, bay-wide (n = 32 d), in-path (n = 3 d); Pc: *Pseudocalanus* complex regime, bay-wide (n = 66 d), in-path (n = 23 d); Cf: *Calanus finmarchicus* regime, bay-wide (n = 66 d), in-path (n = 58 d). Taxonomic percentages of categories can be found in Table S2 in the Supplement

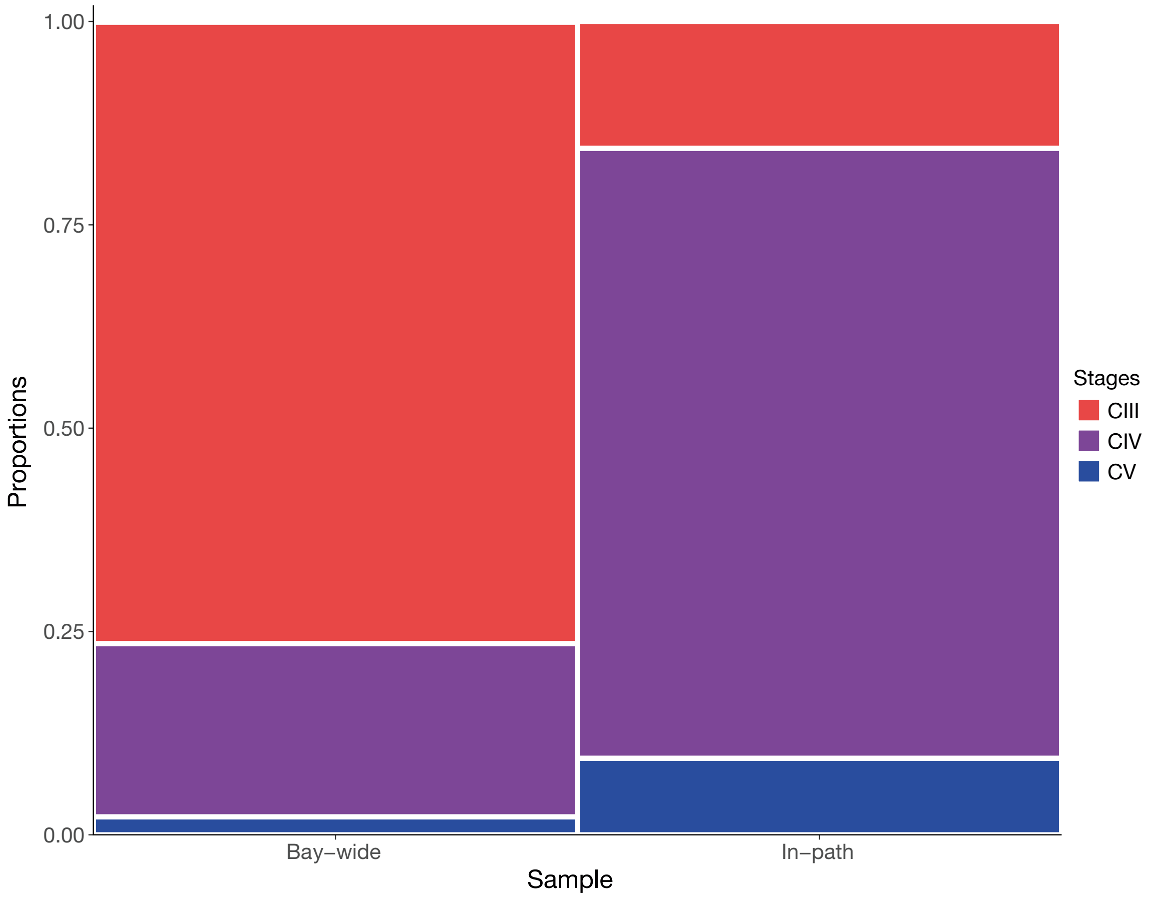

Fig. 7. Comparison of proportions of in-path *Calanus finmarchicus* copepodite stages (CIII–CV) collected during the *C. finmarchicus* seasonal regime (n = 64 samples) versus bay-wide zooplankton samples (n = 89 samples)

high-density patches on which to feed, unlike humpback whales, which can actively aggregate their prey through behaviors such as bubble-feeding (Baumgartner et al. 2007, Greer et al. 2016). Therefore, right whales require patches of zooplankton prey that are orders of magnitude more dense than background concentrations (Mayo & Marx 1990) and are able to focus on discrete slicks of concentrated plankton (Watkins & Schevill 1976). The right whales' consumption of high concentrations of *Pseudocalanus* complex during the seasonal *Centropages* spp. regime as well as the increase in *C. finmarchicus* intake during the *Pseudocalanus* complex regime reveals that right whales can target particular species among the bay-wide resource composition, and can also target dense patches of prey.

C. finmarchicus has been considered the primary prey of right whales, with emphasis on the late copepodite stages CIV and CV (Watkins & Schevill 1976, Wishner et al. 1988, Beardsley et al. 1996, Mayo et al. 2001, Baumgartner et al. 2003a), due to the energy-rich lipid stores which make them a high-quality food source (Lee et al. 2006, Davies et al. 2012). In CCB, the bay-wide *C. finmarchicus* resource is dominated by CIII during both the *Pseudocalanus* complex and *C. finmarchicus* regimes; however, we found that right whales seek aggregations of CIVs, and to a lesser extent CVs, suggesting that right whales target not only patches of particular species but larger and therefore more energy-rich life stages as well.

The rapidly changing environment, along with anthropogenic threats, has had a negative impact on the right whale population over the last decade (Rolland et al. 2012, Greene 2016, Meyer-Gutbrod & Greene 2018, Record et al. 2019, Meyer-Gutbrod et al. 2021, 2022, Garrison et al. 2022). Over the last 5 decades, the Gulf of Maine and Scotian Shelf water temperatures have been slowly rising, with a rapid increase in the past 10 yr (Greene 2016, Seidov et al. 2021). Ocean circulation patterns have been changing, with the Gulf Stream shifting further north and changes to the Atlantic meridional overturning circulation altering the deep-water dynamics of the Gulf of Maine ecosystem over the last decade (Pershing et al. 2015, Meyer-Gutbrod et al. 2021). These changes in oceanographic conditions have rendered much of the right whales' Gulf of Maine–Scotian Shelf foraging habitat less productive in terms of right whale prey, due to an apparent negative relationship between warming deep water and *C. finmarchicus* abundance (Record et al. 2019). The changes in the whales' prey distribution have led the whales to explore new habitats, such as the Gulf of St. Lawrence and southern New England shelf waters, where they are less protected from anthropogenic harm (Meyer-Gutbrod et al. 2021, Pershing & Pendleton 2021, O'Brien et al. 2022). The estimated North Atlantic right whale population has declined since 2010 (Pettis et al. 2021), likely due to a downward trend in the number and fecundity of breeding females (Reed et al. 2022) and decreasing body size due to chronic stressors (Stewart et al. 2022), including unreliable foraging grounds (Record et al. 2019, Brennan et al. 2021). However, despite changes in their prey distribution elsewhere, the phenology of right whales' copepod prey in CCB has not changed before or after the onset of their population decline. In addition, except for the decline in the already low *C. finmarchicus* concentrations during the *Centropages* regime, the total zooplankton and the 3 dominant taxa concentrations have remained stable or increased in each of the regimes. This stability may explain why an increasing proportion of the right whale population uses CCB as an early season foraging ground. Furthermore, CCB may act as a potential seasonal 'waiting room' until other habitat areas develop richer resource aggregations that are more energetically profitable (Pendleton et al. 2022).

While this phenological stability is encouraging, it is dependent upon continued production of the 3 dominant copepod taxa. The range of *Centropages hamatus* and *typicus* extends into warmer waters south beyond Cape Hatteras, they are confined mainly to shallow coastal regions, and their population is maintained by local production (Durbin & Kane 2007), making them likely candidates to remain abundant in CCB even if waters warm significantly; indeed, we found that their abundance has increased over the time series of this study (Table 2). Their abundance in CCB peaks between September and December, making the *Centropages* spp. resource that right whales encounter a 'carry-over' from the past season's annual production. Furthermore, right whales seem to seek *Pseudocalanus* complex taxa during the *Centropages* spp. regime, raising the question as to whether more *Centropages* in CCB would bolster right whale feeding opportunities. *Pseudocalanus* complex are also considered coastal taxa whose March–April peak in abundance in the southern Gulf of Maine/CCB is more similar to their seasonal peak in the Mid-Atlantic Bight than the rest of the Gulf of Maine (Kane 2014), suggesting the potential resilience of *Pseudocalanus* complex resource to future warming. However, their persistence is also dependent upon the spring phytoplankton bloom, to which their lifecycle is tuned. Decreases in phytoplankton production caused by changing oceanographic conditions — mainly warming surface waters — has been deleterious to *Pseudocalanus* spp. on the NE Shelf (Kane 2014), making the availability of *Pseudocalanus* complex taxa to right whales uncertain in the future.

Unlike *Centropages* spp. and *Pseudocalanus* complex, the *C. finmarchicus* resource in CCB is dependent upon advection via the western Maine Coastal Current system rather than local production. The strength of this current system is driven in the winter and early spring by northwesterly winds that push nutrient-rich water along the Maine coast and carry *C. finmarchicus* from elsewhere in the Gulf of Maine and Scotian Shelf (Jiang et al. 2007). For example, when southwesterly winter winds prevailed in 2002, CCB saw some of its lowest *C. finmarchicus* concentrations as well as reduced right whale sightings and residence times (DeLorenzo Costa et al. 2006, Jiang et al. 2007). The persistence of *C. finmarchicus* in the Gulf of Maine despite significant warming has been attributed to relatively high year-round phytoplankton biomass found in the Maine Coastal Current, supported by nutrients supplied by tidal and wave-driven mixing (Runge et al. 2015, Ji et al. 2017). A recent study found a decline in *C. finmarchicus* in Jordan Basin correlated with warmer winter temperatures in the deep water (Record et al. 2019). We found that in CCB, *C. finmarchicus* concentrations were declining in the earlier part of the right whale season (Table 2), which was likely not impacting right whales foraging because they target *Pseudocalanus* complex during that period. As long as the supply of *C. finmarchicus* from the Maine Coastal Current continues and the changing environmental conditions in CCB are minimal, there is potential for right whales to be supported by the CCB prey resource.

In summary, our study shows that CCB has remained an essential foraging habitat for the critically endangered North Atlantic right whale population over the last 19+ yr, with the whales taking advantage of the persistent cyclic pattern and stable concentrations of the 3 dominant taxa — *C. finmarchicus*, *Pseudocalanus* complex, and *Centropages* spp. — during the winter/spring season. While in the Bay, the whales appear to actively seek out and forage on concentrated aggregations of *Pseudocalanus* complex and *C. finmarchicus*, further targeting the larger, more nutrient-dense life stages of the latter. Whether this habitat continues to support right whales depends both upon local conditions and the supply of *C. finmarchicus* from elsewhere in the Gulf of Maine. Therefore, continued monitoring and modeling of the CCB habitat is critical to interpreting the movement and fate of the whales as well as identifying other areas that may become critical feeding habitats for the few remaining right whales.

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