PELAGIC-BENTHIC COUPLING IN THE GULF OF MAINE:
MULTIDECADAL MOLECULAR ISOTOPE RECORDS OF
ZOOPLANKTON AND DEEP SEA CORALS BIOARCHIVES

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ABSTRACT

The export of organic matter from the surface to deep ocean has major implications for global biogeochemical cycles, the transfer of energy across food webs, and the sequestration of carbon through the biological pump. Therefore, understanding the physical and biological conditions that control these processes is important to understanding pelagic-benthic coupling and resulting controls on ocean productivity, fisheries production, and Earth's climate regulation. Equally important is consideration of and collaboration with diverse audiences that need to understand this information to make scientifically informed decisions about climate and environment policies that come from this research. Despite the importance of this knowledge, access to long-term data sets on the controlling mechanisms of export production are scarce and urgently needed to test assumptions about 1) the sources and transformations of organic matter through different food web pathways and 2) the variability of these processes across climatic, oceanographic, and ecological changes through time. This thesis applies recent advances in molecular isotope geochemistry approaches to biological archives of food web processes in the surface ocean (long term pelagic copepod archives) and deep ocean (benthic deep-sea coral archives) from the Gulf of Maine to shed new light on how changing ocean circulation, mixing, and stratification alter biogeochemical cycling, primary production, and metazoan and microbial heterotrophic processes leading to the formation of exported organic matter. Through strategic generalized additive modeling (GAM) approaches and transdisciplinary collaborations across
science, sculpture, video, educator, public media, and communication experts, this study was able to identify pronounced regimes changes in pelagic-benthic coupling and its underlying drivers over a multi-decadal time series. These regime changes were linked to a shift in proximate drivers from changes in water mass, mixing, and stratification to unprecedented warming in the recent decade, which related to changes in copepod abundance and pelagic food web dynamics. Surprisingly, there was a strong and persistent microbial loop geochemical signal recorded in *C. finmarchicus*, including evidence of multiple microbial trophic transfers in the food webs supporting these large copepods that were invisible to traditional geochemical food web metrics. Geochemical records of these microbial food web processes in pelagic system were directly exported to the benthic deep-sea coral record, which had a striking resemblance, in both magnitude and trend, to the geochemical record in the large-bodied copepod *Calanus finmarchicus*. Tight pelagic-benthic coupling, driven by the large, fast sinking fecal pellets of *C. finmarchicus*, provided a direct mechanism to export microbial loop production to the benthic system. We observed a long-term trend towards increasing reliance on microbially reprocessed organic matter that mirrored regional warming trends in both the pelagic and benthic food webs of the Gulf of Maine. Pelagic-benthic coupling in the Gulf of Maine was strongly influenced by variations in water mass nutrient delivery and mixed layer depth, which in the early rate of change periods drove physical-nutrient-production dynamics, though as the average mixed layer depth deepened in the most recent two decades, the closer proximity of the two systems facilitated the
continued pelagic-benthic coupling despite the recent decreases in *C. finmarchicus* abundance. These results provide a new critical framework for understanding the central role that copepods play in pelagic food webs and deep ocean export as well as how they may change in a warming future ocean. By transforming these complex physical, chemical, and biological ecosystem-level relationships into transdisciplinary data visualizations, we increased the collective reach and associated impact of this research through a more holistic and inclusive approach to presenting science.
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PREFACE

This dissertation uses Manuscript Format in accordance with guidelines established by the Graduate School of the University of Rhode Island with the exception of the 4th chapter, which is formatted for the Journal of Visualized Experiments.
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Chapter 1 Regional-scale water mass distribution and water column properties drive inversely oscillating copepod populations in the Gulf of Maine until warming overtakes the system as the dominant driver.

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ABSTRACT

Copepods act as key conduits of energy in ocean food webs, transferring bottom-up dynamics of biogeochemical cycling and productivity to upper trophic levels that include critical fisheries and endangered species like the North Atlantic right whale. Past studies have identified large oscillations in copepod species abundance and community composition associated with size class, where small-bodied copepods (e.g., *Centropages typicus*) had higher abundance during nutrient limited conditions (such as the 1990’s) associated with shifts in slope water mass composition and increases in winter stratification while large bodied copepods (e.g., *Calanus finmarchicus*) were most abundant in the 1980s and 2000s during times of high diatom production. Recent studies have implicated rapid warming in both the deep and surface waters of the Gulf of Maine over the last decade as a major driver of changes in these zooplankton population dynamics and associated food web dynamics. This study tested hypotheses around interdecadal trends in copepod abundance associated with seasonal life history and size class as well as the environmental drivers (slope water mass fraction, water column mixing, temperature, salinity, and climate indices). Using a combination of Generalized Additive Models and Markov Switching Models, we identified four Rate of Change (RoC) transitions in both *C. finmarchicus* and *C. typicus*, defined by the years 1986, 1997 (*C. finmarchicus*) /2000 (*C. typicus*), and 2006 around both seasonal (Winter/Fall *C. finmarchicus*) and annual (*C. typicus*) temporal dynamics. The mixed layer depth was identified as the most persistent relationship during the first three RoC periods in both species and
physical-nutrient-phytoplankton dynamics were the primary drivers of the interannual scale abundance changes. Then after 2006, the primary environmental correlations with abundance shifted to temperature related variables, including surface temperature and the Warm Slope Water fraction of bottom water in the Gulf of Maine, indicating a departure from previous multi-decadal environmental relationships driving interannual copepod community patterns. This change was unprecedented in the historical record (1977-2017), and predictive models based on only prior time frames (1977-2006) would have been unable to forecast this event. These data highlight the need to account for these shifting relationships when developing management tools and strategies in the Gulf of Maine as well as other regions where the rapid warming trend is expected to follow.

INTRODUCTION

Copepods act as a key conduit of energy at the intersection of lower and upper trophic levels (Pershing et al. 2005; Rose et al. 2010; Meyer-Gutbrod and Greene 2014). Changes in circulation patterns, primary productivity, and phytoplankton community composition propagate up the food web to impact secondary production (Pershing et al. 2005, 2010; Kane 2007; Bi et al. 2014; Record et al. 2019). Copepods then carry energy from the blooms of primary producers across both seasonal and generational time scales (days to years) (Record et al. 2010). Multi-decadal trends in copepod species abundance over the last 50 years have had cascading impacts on Gulf of Maine biogeochemical cycling, production, food web dynamics, and export (Pershing et al. 2015; Grieves et al. 2017; Pershing and Stamieszkin 2020). However, not all
copepods play the same ecological roles or respond to the same environmental
factors; and communities composed of different size classes with varying life
cycle strategies have different habitat ranges and phenological limits
(Reygondeau and Beaugrand 2011; Morse et al. 2017). This makes
understanding the underlying environmental and climatic drivers behind distinct
oscillations in copepod communities through time essential to assessing overall
ecosystem function and change.

The Gulf of Maine is a valuable system to study the environmental drivers
of copepod population dynamics. It is home to important commercial fisheries
and critically endangered species like the North Atlantic Right Whale
(*Eubalaena glacialis*), which fundamentally rely on copepod community
dynamics, particularly *Calanus finmarchicus*, for production (Kane 2007;
Greene et al. 2013; Meyer-Gutbrod and Greene 2014; Pershing et al. 2015).
Within the Gulf of Maine, small- and large- sized copepods have experienced
pronounced shifts in abundance and species composition with changes in
decaladal hydrographic-nutrient-phytoplankton dynamics (Pershing et al. 2005;
Kane 2007; Bi et al. 2014). Small bodied species (e.g., *Centropages typicus*,
*Metridia lucens*, *Temora longicornis*, *Oithona spp.*., and *Pseudocalanus spp.*)
follow similar abundance trends while larger-bodied species like *C. finmarchicus*
follow an inverse pattern (Pershing et al. 2005; Kane 2007; Morse et al. 2017).
For example, in the 1980s and 2000s, the large-bodied, subarctic *C. finmarchicus*
(late-stage CV and adult CVI) were more abundant than smaller-
bodied species, but during the fresher more stratified 1990s, the pattern
reversed (Pershing et al. 2005; Bi et al. 2014). The total range of *C. finmarchicus* has been contracting and shifting northward since the 1990s (Reygondeau and Beaugrand 2011).

Multidecadal transitions in copepod community structure reflect a combination of shifts in advective forces and bottom-up changes in food web dynamics. For example, *C. finmarchicus* relies heavily on periods with strong spring diatom blooms to accumulate lipids prior to entering diapause (Hansen et al. 1994; Hirsche 1996). In contrast, *C. typicus* feeds on smaller prey such as ciliates, picoeukaryotes, and dinoflagellates, which are more abundant when nutrient limitation in the euphotic zone selects for small-celled primary production and enhanced microbial loop food web dynamics (Calbet et al. 2007).

Studies have implicated climatic warming on both the deep and surface waters in the Gulf of Maine over the last decade with the observed changes in the copepod abundance (Kane 2007; Grieves et al. 2017; Record et al. 2019). Specifically, *C. finmarchicus* abundance is negatively correlated with bottom temperature (Record et al. 2019) and is therefore projected to decline as bottom temperatures continue to increase (Reygondeau and Beaugrand 2011; Grieves et al. 2017). Conversely, *C. typicus* and other small copepods have been found to flourish in the warmer waters (Kane 2007). Warming in the Gulf of Maine has been associated with climate indices such as the Atlantic Multi-decadal Oscillation (AMO) and Pacific Decadal Oscillation (PDO), as well as changes to the northern extent of the Gulf Stream (Chen et al. 2013; Pershing et al. 2015; Gonçalves Neto et al. 2021), making temperature a complicated variable to
interpret. Climate indices (AMO, PDO, and North Atlantic Oscillation [NAO]) are reflective of basin- to global-scale change and integrate multiple processes across the globe (Mantua et al. 1997; Enfield et al. 2001). These changes in ocean circulation result not only in changes to baseline temperature and salinity, but also nutrient profiles, advection of planktonic populations, and shifts in ecological niches, making the relationship between plankton populations and temperature highly complex. In addition to these shifts associated with climate oscillations, sea surface temperature in the Gulf of Maine has warmed faster than 99.9% of ocean regions worldwide since 2004, putting the region at the leading edge of marine heat waves that are expected to become more frequent and intense over the next century (Mills et al. 2013; Pershing et al. 2015; Saba et al. 2016). This makes the Gulf of Maine an exemplary place to study ecosystem change under climate warming through the lens of copepod community dynamics.

For most of the observational record, hydrographic characteristics and decadal scale ecosystem change in the Gulf of Maine have been modeled as a two-endmember “Coupled Slope Water System”, correlated with the winter NAO index (Greene and Pershing 2003; Wanamaker et al. 2008), where increased Gulf Stream water into the Gulf of Maine has been associated with zonal winds and positive NAO values. In Jordan Basin and the Northeast channel regions of the Gulf of Maine, there are three major water masses that can be broken down into temperature and salinity endmembers below 100m, and they each have distinct silicate (Si) and nitrate (N) concentrations detailed in Table 1.1: Warm
Slope Water (WSW), Labrador Slope Water (LSW) and Scotian Shelf Water (SSW). The higher the fraction of WSW entering the Gulf of Maine, the more diluted the ratio of silicate to nitrate becomes (Table 1.1). SSW has the highest Si:N and additional inflow has been found to significantly increase the overall Si:N ratio of bottom water in the Gulf of Maine (Townsend et al. 2014;2015, Zang et al. 2022, Balch et al. 2022). Changes in the relative fraction of these water masses to the Gulf of Maine have been associated with apparent shifts in primary production in the Gulf of Maine (Townsend et al. 2010; 2014; 2015; Balch et al. 2012, Zang et al. 2022). The spring bloom is dominated by diatoms which consume silicate and nitrate at a similar rate leading to a silicate-limited system and residual nitrate for other non-diatom phytoplankton to grow (Townsend et al. 2014; Zang et al. 2022). Townsend and Thomas (2001, 2002) identified silicate-limited blooms in the Gulf of Maine and Zang et al. (2022) provided evidence that the spring bloom magnitude is proportional to the inflow of SSW due to silicate concentrations. Additionally, beyond production alone, differences in nutrient ratios have likely influenced primary producer community composition and resulting copepod abundance dynamics (Townsend et al. 2010; Clark et al. 2019), as has been observed in other regions of the NW Atlantic (Li et al. 2006; Harrison and Li 2008; Fragoso et al. 2017).

*C. finmarchicus* and *C. typicus* have followed an inverse abundance pattern over the last four decades that has been associated with changes in primary productivity, which in turn has been associated with shifts in water mass dynamics. Lower production in the Gulf of Maine during the 1960s was attributed
to a dominance of nutrient deficient LSW (Pershing et al. 2001, 2005; Townsend et al. 2010). When the LSW retreated in the early 1970s, inflow of nutrient-rich WSW through the Northeast Channel increased, leading to mostly positive temperature and salinity anomalies for the next two decades, enhanced winter stratification (Head and Pepin 2010), and a pronounced increase in phytoplankton abundance during the 1990s (Kane et al. 2011). At this point, the two-endmember framework began to break down. SSW inflow events became increasingly common from the 1990s through the 2000s, augmenting surface freshening and stratification in the Gulf of Maine (Greene and Pershing 2007; Townsend et al. 2010, 2015), leading to hypothesized impacts on primary production, such as early nutrient uptake in the winter and depleted inorganic nutrients to fuel the spring boom (Pershing et al. 2005, 2010; Ji et al. 2017; Record et al. 2019). Around 2008, WSW appeared to return to the Gulf of Maine, evident from higher water column temperature and salinity anomalies than at any point since at least 1960 and from spatial-temporal correlations in sea surface height along the shelf (Gonçalves Neto et al. 2021). This increase in WSW and reduction of LSW and SSW would be expected to drive down the overall magnitude of the spring bloom (Zang et al. 2022), as well as increase the temperature baseline, shifting the environmental and ecological conditions in the Gulf of Maine to favor *C. typicus* over *C. finmarchicus*.

To identify the mechanistic links between copepod abundance and water mass dynamics of the Gulf of Maine ecosystem, studies have focused on variables associated with multiple ecosystem level functions (e.g. NAO, AMO,
PDO, bottom temperature, surface temperature), large spatial scales and varying temporal resolutions of both individual and community dynamics. As Ji et al. (2022) highlights, while each of these relationships are not necessarily causal, they can assist in hypothesis generation and aid in finding more focused mechanistic links. This study aims to characterize the temporal change between high and low abundance periods of *C. finmarchicus* and *C. typicus*, and to identify significant environmental parameters to further aid in hypothesis generation around what contributes to changes in the copepods’ decadal abundance patterns. We address two key hypotheses: 1) that copepod life history will be significant in explaining long term changes in abundance: *C. finmarchicus* rely on a seasonal diapause strategy that is linked to cohorts of populations, while *C. typicus* reproduce on a continuum and 2) that interdecadal oscillations of abundance trends will be influenced by changes in slope water mass fractions and their resulting high and low nutrient profiles in the early part of the time series, and in the early 2000’s, the relationship will break down and shift to a temperature driven regime associated with the rapid warming in the Gulf of Maine system.

To do this, we analyzed seasonal, annual, and decadal temporal trends in inverse *C. finmarchicus* and *C. typicus* abundance and tested a suit of environmental variables that may serve as more proximate drivers of abundance linked to large scale climate indices and temperature. By using *C. finmarchicus* and *C. typicus* as proxy species to represent distinct zooplankton abundance regimes in the Gulf of Maine, we can target phenological differences
in life cycles that are obscured in other size or community-based models, and we can gain additional insight into how the copepod community may be changing with time and environmental conditions. Here, we separated high and low abundance regimes by identifying statistically significant rate of change (RoC) periods that punctuated the regimes. Then we curated a suite of environmental variables across the entire time series (1977-2017) including: surface temperature and salinity, WSW/SSW/LSW, a stratification index (N2), the mixed layer depth, NAO, AMO, PDO, and AO. These variables were analyzed for significant seasonal and temporal lags to target different time scales of changes in copepod abundance and how they align with phenological and ecosystem level processes. Each RoC period was then separately analyzed to target the prevailing environmental drivers that captured the multi-year increase/decrease between high/low abundance regimes.

METHODS
Data Formatting
We collected hydrographic and integrated (0-200 m) copepod abundance data (count/100 m$^3$) spanning 1977 to 2017 from the NOAA-NEFSC Ecosystem Monitoring Program (Kane 2007). Additional hydrographic data from the World Ocean Database (WOD: https://www.ncei.noaa.gov/products/world-ocean-database) archive of CTD casts from the 1970s to present was used to calculate the mixed layer depth. Climate indices (NAO, PDO; AMO; AO) were collected from the NOAA Climate Data Archive (https://psl.noaa.gov/data/climateindices/list/).
Both the EcoMon and WOD data sets were temporally aggregated at a monthly resolution and spatially aggregated using the EcoMon Jordan Basin strata 42 (Figure 1.1; Figure 1.2) and vertically (depth) aggregated across 5-meter depth bins. From here, the mixed layer depth was calculated applying the methods in de Boyer Montégut et al. (2004) and the R package “gsw” (Kelly and Richards et al. 2021) using time points with more than 10 vertical depth bins. A stratification index (N2) was calculated from the Brunt–Väisälä frequency equation using the package “OCE” (Kelly and Richards 2021) with a surface water value (0-5 m) and a bottom water value (the average temperature and salinity data from below 100 m) to produce a general water column stability metric.

Variables were imputed to a monthly resolution using the “imputeTS” package in R (Moritz and Bartz-Beielstein 2017) to account for variable resolution of available data across the entire time series. Kalman smoothing was applied using the function na_kalman() and the auto.arima state space representation with an exception for the mixed layer depth and salinity variables, which required a structural time series model representation. These imputation methods apply the time structure from across the entire time series to resolve each missing point, rather than interpolating between two time points to resolve values. Working at a monthly resolution accommodates exploration of the different life cycle dynamics of each copepod species that occur on timescales finer than a seasonal or annual resolution. The data collected in this study spanned a period of rapid change in survey approaches in the region, and initial
surveys did not measure the hydrography in the same location as plankton tows and the methods and stations collected have evolved with time. The first RoC period (1977-1985) had limited data and while the mixed layer depth was imputed using the time structure of the entire series, it had few points for constraining the variation and trend during this time frame. Interpretation of this period should be with caution and in the context of how data availability has changed. In addition to the mixed layer depth, a proxy for stratification (N2) was calculated from temperature and salinity at 5m and 100 m using the brunt-väisälä frequency equation. This approach capitalizes on the available samples with a lower depth resolution from the EcoMon time series (surface/bottom) to gain more insight to the water column properties.

The relative contribution of Water mass endmembers (WSW, LSW, SSW) to bottom water in Jordan Basin was calculated from monthly temperature and salinity values averaged between 125-175 m using a three-point mixing triangle as originally described in Mountain (2012) and applied in Townsend et al. (2015). Water mass fractions for a depth range of 100-250 m were used to calculate WSW, LSW, and SSW (Table 1.1; Townsend et al. 2015; Figure 1.28). Estimates of the silicate (Si) and nitrate (N) concentrations in the three water masses and the relative contribution of the water masses to Jordan Basin bottom water were used to back calculate Si:N ratios in Jordan Basin bottom water over time.
Interpreting variable trends.

Monthly Anomalies

The monthly anomaly was taken for each variable to remove the seasonal trend in order to focus on interannual and multidecadal trends and to enable a relative comparison among different types of variables (Figure 1.3a). These monthly anomalies were calculated by subtracting the monthly average from each value and dividing by the monthly standard deviations across the entire time series.

Two state Markov Switching Models

Two state Markov Switching Models (MSM) were used to identify time regimes (Markov Switching Regimes, MSRs) within a variable and were built as linear models where the dependent variable was observed over time (Figure 1.3b). This method estimates the probability that each time point reflects one of two prevailing regimes that are defined around a mean and variance (identified by the hidden Markov Chains modeled by the MSM) using a maximum likelihood approach (Ailliot et al. 2015).

GAMS Time fits:

To identify when a variable is significantly moving from one regime to another (Figure 1.3c), each variable’s monthly anomalies were checked for a time trend by fitting a GAM vs time \((year + \frac{month−1}{12})\) from the R package “mgcv” using method “REML” and smoothing parameter \(K = 10\) (Figure 1.3d). Then to understand when the time additive GAM components were significantly changing with time, we assessed whether the first derivative (Figure 1.3e) was not equal to zero. This was done by checking that the upper and lower standard
deviation bounds (± 2*SD) for each of the GAMs additive time smooths points were either both above or both below zero. This is calculated using a modified version of the example code “Differentiating the smooths in a model (with CIs for derivatives)” from the function predict.gam() in the “mgcv” R package (Figure 1.3f). Time points where the standard deviation bounds were both positive (negative) are considered have a significantly increasing (decreasing) time trend.

Tying the Methods Together
By using the GAMs time fits, significant RoCs, and Markov Switching regimes, each variable was divided into periods of distinct conditions and transitions among them. To analyze the copepod abundance time structure, the monthly abundance anomalies for C. finmarchicus and C. typicus for each season were fitted for GAMs and MSM vs time (Figure 1.3a-f). Seasons where the abundance was driving the overall annual trends had MSM regimes where the mean and variance did not overlap, and GAMs additive time fits showed significant time transitions from one MSM regime into another. These periods of change were then used as the basis for assessing the environmental conditions behind the transitions between copepod abundance regimes.

Fitting environmental correlations by RoC period.
All variables were cross checked for correlations using the prewhiten() function from R package “TSA” (Chan and Ripley 2020), which applies a cross correlation function (CCF) to the bivariate time series that were prewhitened with independent variables Auto Regressive (AR) time series component. Variables with high CCF values at t = 0 were excluded from the model variable
selection process due to over correlation. Because temperature and salinity at 150m were used in calculating the water mass fractions, they were over correlated with the water mass fraction variables and therefore left out of the modeling process (Warm Slope water was highly correlated with bottom temperature and SSW was highly correlated with the bottom salinity). Additionally, the AO was over correlated with NAO and was therefore also not included in the modeling process.

Identify significant environmental lags.

The prewhiten() function was also applied to the C. finmarchicus and C. typicus abundance monthly anomaly for each RoC time period and the prior two years to check for significant lags in correlations with the prewhitened environmental variable monthly anomalies in order to account for ecological/phenological signals while also balancing the amount of truncated data that results when including a lagged variable. The lag with the max CCF value was then applied in the variable selection process (Figure 1.3h).

Fitting environmental GAMs Models

GAMs models were fit for each species’ abundance periods where the abundance increased or decreased into a different MSR during a specific season. The cutoff was defined by the inversion point (when the first derivative is equal to zero). Least absolute shrinkage and selection operator (LASSO) was used as an initial variable selection method, as it adjusts the coefficient for each variable based on the p-value and moves the least significant coefficients to zero (Figure 1.3i). Then each possible combination of the best $\frac{n_{points \ in \ model}}{2}$
variables with the highest coefficient were fit in a GAM for each environmental variable:

\[
GAM(\text{Copepod}_{season}) = \sum s(\text{environmental variable}, K = 3) + \text{intercept} ...
\]

The model with the lowest akaike information criterion (AIC) value was then selected. Smoothing parameter K was set to 3 to constrain the modeled relationships within realistic environmental conditions (Grieves et al. 2017) and to limit the degrees of freedom (Figure 1.3j).

Additive time fit assessment
Each variable included in the final models had an additive component that can be used to analyze the individual contribution to the overall model’s fit. This was used to assess its contribution to the time trend and the relationship with the copepod abundance. By applying the GAMs time fit and RoC approach to the additive component vs time, we assessed whether there was overlap between the two significant RoC trends and if the modeled environmental variable significantly contributed to the direction of the RoC in the copepod abundance (Figure 1.3k).

Test Density Distributions
The R package “ggstatsplot” was used to assess the density distributions differences between each regime within environmental variables. “type” was set to parametric to apply Welch’s one-way ANOVA test and the Games-Howell test. Results were visualized with a boxplot violin plot combination that displays the raw data (Patil 2021).
RESULTS
Time Trends

Multidecadal trends that move between periods of high and low abundance anomalies were identified in both annual (Figure 1.4) and seasonal (Figure 1.5) *C. finmarchicus* and *C. typicus* monthly abundance anomaly data using time smooth GAMs. Periods of higher (MSR1, dark gray shading) and lower (MSR2, light gray shading) abundance means and standard deviations were identified with MSMs. On a sub annual scale, monthly *C. finmarchicus* abundance anomaly values were classified in overlapping MSRs with little separation (Figure 1.4.a) indicating high interannual variability, while *C. typicus* had a strong annual scale trend with little sub annual variance in MSR classification at a monthly resolution (Figure 1.4.b). *C. finmarchicus* winter and fall smoothed time trends identified an interannual component to the overarching multidecadal trend between abundance anomaly regimes (Figure 1.5a and b); while spring and summer *C. finmarchicus* abundance anomalies showed little to no time trend or switches in MSRs (Figure 1.5c and d).

Identifying Significant Rates of Change (RoC)

Both *C. finmarchicus* and *C. typicus* transitions between MSRs occur over periods of years as opposed to no change, or an abrupt event on a monthly time scale (Figure 1.4, Figure 1.5). Therefore, we frame the following results using the periods where there are significant RoCs across zero to target our interpretation on shifts between high and low abundance MSRs. Four periods of change were defined for each species using the point where the first derivative of the time smooth (as demonstrated in Figure 1.3) was equal to zero.
before a significant RoC occurred as the time series transitions to the other MSR (years: 1986, 1997, 2006 C. finmarchicus; years: 1986, 1999, 2006 C. typicus); vertical lines Figure 1.4, Figure 1.5). This was done using annual data for C. typicus and with the winter months for C. finmarchicus because this season had the strongest trend with larger amplitudes in the smoothed time trend and a bigger separation between MSRs means (Winter diff in MSR: 1.53, Fall diff in MSR: 1.46).

Environmental Correlations

Here we present the environmental variables (WSW, LSW, SSW, mixed layer depth, brunt-väisälä frequency (N2) index, surface salinity, surface temperature, NAO, PDO, AMO) with additive components that have significant RoC time trends that fit the targeted abundance anomaly RoC period modeled. A detailed explanation of the relationships is presented first, followed by a summary of the results. All model results are also summarized in Figure 1.6.

MIXED LAYER DEPTH

The mixed layer depth had an overall positive relationship with C. finmarchicus abundance trends during the fall and winter seasons apart from a negative relationship during RoC3 in the fall (Figure 1.7; Figure 1.8). RoC2 also had a significant time lag relationship with the mixed layer depth at 9-11 months during both seasons. C. typicus generally had a negative relationship with the mixed layer depth during RoC1-3 (Figure 1.9; Figure 1.10; Figure 1.11; Figure 1.12). However, during RoC2 winter and summer, C. typicus abundance did have a positive relationship with the mixed layer depth (Figure 1.9; Figure 1.11).
Overall, deeper mixed layer depths were associated with higher abundance of *C. finmarchicus* and lower abundance of *C. typicus*.

**SOURCE WATER DYNAMICS**

During the winter RoC2, SSW had a positive relationship with *C. finmarchicus* abundance, while the relationship was negative relationship in RoC3 with a 12-month lag (Figure 1.38). Fall LSW fit both RoC periods where *C. finmarchicus* abundance decreased (RoC2 & 4) with opposite relationships, negative in RoC 2 and positive in RoC 4 (Figure 1.43); There was a positive relationship in RoC3 with a 2-month lag. SSW had an overall negative relationship with *C. typicus* abundance during RoC1-3 (and a lag of 0-7 months) with the exception of RoC2 during the summer (Figure 1.39; Figure 1.40; Figure 1.41; Figure 1.42). LSW had a more complicated relationship with *C. typicus* abundance. RoC1-2 had a positive relationship with lags of up to 16 months where RoC2&3 had over all negative relationships with Labrador slope water and time lags of 0-2 months (Figure 1.44; Figure 1.45; Figure 1.46; Figure 1.47). Source waters with higher Si:N input to the system were more often associated with higher abundances of *C. finmarchicus* and lower abundances of *C. typicus* than not.

**TEMPERATURE**

Surface temperature fit a negative relationship with winter *C. finmarchicus* abundance in RoC periods 2 and 4 with a 0-1-month lag (Figure 1.13). During RoC4, surface temperature was significantly correlated with the decreased abundance of *C. finmarchicus* and had a steeper negative slope than
the relationship fit during RoC2 in the winter and had a significant negative relationship, the fall RoC2 also had a negative surface temperature to abundance relationship at a 15-month lag. Surface temperature had an overall positive relationship with *C. typicus* abundance across all seasons (Figure 1.14; Figure 1.37; Figure 1.15; Figure 1.36); the only exception was RoC3 during the spring (Figure 1.37). WSW, which is over correlated positively with bottom water temperature, had a positive relationship with *C. finmarchicus* during RoC1; this changed to a negative relationship during the RoC3&4 time periods (Figure 1.48). *C. typicus* abundance was positively correlated with WSW at 0 and 10 month lags during the winter RoC1&3 time periods (Figure 1.16; Figure 1.49). Variables associated with warmer conditions were found to increase in significance when fitting the decrease the abundance of *C. finmarchicus* and increase *C. typicus* abundance during RoC3&4 relative to the first two RoC periods.

**CLIMATE INDICIES**

During the winter, *C. finmarchicus* abundance and AMO had a parabolic relationship in RoC1, a negative relationship in RoC2 at a 11 month lag, and a positive relationship in RoC4 at a 12 month lag (Figure 1.17; Figure 1.18). AMO had a significant relationship with *C. finmarchicus* abundance during the fall months in RoC1-3 that was negative in the first two and transitioned to a negative parabolic relationship during RoC3. PDO was only significantly correlated with *C. finmarchicus* abundance during RoC4 with a negative relationship during both the winter and fall (Figure 1.23; Figure 1.24). AMO had
a positive relationship with *C. typicus* abundance during the winter (RoC1&2), summer (RoC 2), and fall (RoC2) and a negative relationship during RoC3 spring and fall (Figure 1.19; Figure 1.20; Figure 1.21; Figure 1.22). Spring (RoC2&3) and summer (RoC3) PDO had a negative relationship with *C. typicus* abundance that switched to a positive relationship during RoC4 (Figure 1.25; Figure 1.26). NAO had a positive relationship with *C. finmarchicus* abundance during RoC 2 and which flipped during RoC4 to a negative relationship (Figure 1.55; Figure 1.56). AMO was important for modeling interannual trends in both species abundance during the first three RoC periods, but then in RoC3&4 there was a transition from AMO to PDO in both significance and relationship fit for modeling the long-term trends in copepod abundance.

RESULTS SUMMARY

For *C. finmarchicus*, increases in abundance during RoC 1 and 3 were correlated with the mixed layer depth, AMO, and WSW and in addition, increases abundance in RoC3 were also correlated with surface salinity and SSW/LSW fraction in Jordan Basin bottom water. Decreases in abundance during RoC 2 and 4 were both correlated with surface temperature and salinity, LSW, AMO, and NAO. Additionally, decreases in abundance during RoC2 were correlated with the mixed layer depth, N2, and SSW; and RoC4 decrease in abundance were correlated with WSW and PDO. Over time there was a shift from the mixed layer depth being significant in modeling both species abundance to not all. Over the modeled time series (1977-2017), water mass
fraction and warming variables like surface temperature and PDO became more important in driving changes to the *C. finmarchicus* abundance trends.

For *C. typicus*, decreases in abundance during RoC1&3 were correlated with the mixed layer depth, WSW, SSW, LSW, and AMO. Additionally, decreases during RoC1 were correlated with spring N2; and decreases during RoC3 were additionally correlated with PDO, surface salinity and temperature. RoC2&4 were increased with changes in the mixed layer depth, surface temperature and surface salinity as well as PDO. Increases in RoC2 were correlated with SSW, LSW, and AMO; RoC4 was additionally correlated with WSW and N2.

During RoC4, the relationships between environmental variables and copepod abundance from the past three RoC’s broke down (Figure 1.7; Figure 1.8; Figure 1.9; Figure 1.10; Figure 1.11; Figure 1.12). The mixed layer depth no longer significantly contributed to abundance changes with time (it is also the deepest out of all of the RoC periods; Figure 1.65), indicating a shift in the relationship between copepods and water column primary production proxies. This breakdown of the relationship between abundance and nutrient-mixing dynamics from RoC1-3 is highlighted by a switch in significance of parameters that was associated with the influence of warming on each variable. WSW had a more significant time trend influence than LSW/SSW on both species abundance (Figure 1.48; Figure 1.16; Figure 1.49), which could indicate a bottom water temperature relationship or a decrease in the Si:N. Additionally, the relationship between surface salinity and the abundance of both copepods
flipped from negative to positive for *C. finmarchicus* and vice versa for *C. typicus* (Figure 1.13; Figure 1.14; Figure 1.37; Figure 1.15; Figure 1.36; Figure 1.30; Figure 1.31; Figure 1.33; Figure 1.34; Figure 1.32; Figure 1.35). Finally, across both species, the first three RoC periods were fit by the AMO (Figure 1.17; Figure 1.18; Figure 1.19; Figure 1.20; Figure 1.21; Figure 1.22), by RoC 4, this relationship was no longer identified, and the PDO began capturing the time trends in both species abundance (Figure 1.23; Figure 1.24; Figure 1.25; Figure 1.26).

**DISCUSSION**

This study identified interannual oscillation patterns in copepod abundance at a seasonal time scale in *C. finmarchicus* and at an annual time scale in *C. typicus* (Figure 1.5). From these oscillations, four different RoC periods emerged for the two species. Environmental models (Figure 1.3) were used to identify potential drivers of these temporal trends, which can best be understood by applying a conceptual water column framework (Figure 1.27). This figure highlights the interactions between the slope waters, the mixed layer depth, and the surface water system. The first three RoC periods were strongly correlated with the mixed layer depth (e.g., Figure 1.7; Figure 1.9). The mixed layer depth reflects the volume of water in the surface system, and therefore the dilution of phytoplankton and prey, as well as how much of the surface system is in the euphotic zone. This variable impacts density-dependent interactions between predators (e.g., copepods) and prey (e.g., phytoplankton and microzooplankton), as well as regulates light availability for light limited phytoplankton growth. Additionally, deeper mixed layer depths increase the
potential transport of nutrients from the slope water to the surface system to support surface primary production. The composition of that slope water concurrently alters the ratio of limiting nutrients in the system as slope water is the primary nutrient source in the Gulf of Maine (Townsend et al. 2015; Zhang et al. 2019; Whitney et al. 2020) and more LSW/SSW leads to better growth conditions for diatoms. Finally, the last RoC observed a breakdown in the prior relationships with interannual copepod abundance trends, and the surface temperature likely had direct impacts on the copepod phenology (Figure 1.13; Figure 1.14).

Decadal trends

When analyzing for decadal trends, different levels of sub annual variance in the oscillation trends between C. finmarchicus and C. typicus were associated with each species’ distinct life history (Figure 1.5a&b). C. finmarchicus had interannual trends in abundance in the winter and fall months (and no trend in the spring and summer), which coincided with the time frames when they are in diapause (Fiksen 2000; Johnson et al. 2007). This indicates that the number of adult C. finmarchicus that make it into and through diapause could be important to understanding the overarching decadal scale trend in their abundance. This disconnect between the diapausing populations, and the spring population has been identified in other studies (Ji et al. 2022), and while within a single year low winter and fall populations do not seem to propagate to other seasons, they do carry into the following years. In contrast to C. finmarchicus, C. typicus stays in the surface waters year-round continuously
reproducing (Carlotti and Harris 2007). At 15°C and high food concentrations, *C. typicus* have a lifespan of about half a month (15 ± 6 days for females and 16 ± 4 days for males) (Carlotti and Nival 1992; Carlotti and Harris 2007). This integration of cohorts across each season likely explains the minimal sub annual (month to month) variance that was observed in their population (Figure 1.4b). These RoC time periods were used to structure the modeling approach applied here, which aims to identify the role that shifts across in the environmental conditions play in these trends.

**MIXED LAYER DEPTH**

The mixed layer depth was found to be one of the most significant predictors of copepod abundance across the first three RoC periods in both species (Figure 1.6; Figure 1.7; Figure 1.8; Figure 1.9; Figure 1.10; Figure 1.11) even during periods with high Si:N compositions, such as RoC1 & RoC3 (Figure 1.62 and Figure 1.65) which were hypothesized to be influenced by the nutrient ratio. This implies that while the available nutrients to the system are important, the mixing depth matters too at these interannual time scales. *C. finmarchicus* abundance had an overwhelmingly positive relationship with mixed layer depth, while *C. typicus* had an opposite negative relationship during most RoC periods (see appendices for discussion on RoC2).

Light limitation and surface mixing layer dilution effect.

The inverse relationships between mixed layer depth and *C. finmarchicus* and *C. typicus* abundance were likely related to their life history and the dilution of the surface water system, as well as the nutrient connections
between the surface and deep-water system that change with the mixed layer depth (Figure 1.27). The “dilution coupling” and light limitation hypotheses are both controlled by stratification and the depth of the mixed layer (Figure 1.27). As presented in Behrenfeld (2010), the “dilution-coupling” hypothesis provides a possible explanation for the higher abundance of *C. finmarchicus* during winter and fall seasons with deeper mixed layer depths that is connected to *C. finmarchicus* life history (Figure 1.7; Figure 1.8). As the volume of the surface mixed layer increases with decreasing mixed layer depth, the likelihood that *C. finmarchicus* may encounter predators during diapause decreases. At the same time, the need for *C. finmarchicus* to find prey is negated by their available lipid storage. Unlike *C. finmarchicus*, *C. typicus* have a much shorter life span and do not have lipid storage to depend on during scarce food conditions. Thus deeper mixed layers would reduce the efficiency of their feeding and a shoaling mixed layer depth would increase potential prey density to support a larger population.

The Gulf of Maine has been identified as part of the light limited region in the North Atlantic (Henson et al. 2009), which may also contribute to the inverse relationship between the abundance of both copepods and the mixed layer depth (Figure 1.9; Figure 1.10; Figure 1.11; Figure 1.12). Deep vertical mixing removes phytoplankton from the euphotic zone (Figure 1.27), which in turn limits photosynthesis and reduces the potential growing season and therefore available biomass for consumption (Stramska and Dickey 1994; Doney 2006; Xu et al. 2011). In the subpolar North Atlantic, deeper mixed layers are attributed
to the delay of the spring bloom (Henson et al. 2009). This could lead to a mis-
mismatch in timing between larger copepods and the availability of food in the
surface ocean that leads to higher mortality and lower egg production (Campbell
et al. 2001), which in turn may be leading to the increased success of other
copepods such as *C. typicus* that are adapted to conditions like summer
stratification where increased nutrient cycling is required (Pershing et al. 2005;
Carlotti and Harris 2007; Pershing and Stamieszkin 2020). Both theories have
been linked to high mixing associated with zonal NAO periods and are hard to
separate from one another (Henson et al. 2009; Behrenfeld 2010).
The transport of nutrients associated with mixing dynamics.

The depth of the mixed layer could be increasing the connection between
the nutrient rich deep slope water and surface production (Figure 1.27). For the
nutrients advected into the Gulf of Maine via bottom slope water delivery to be
available to the surface production, they must be transported to the surface by
mixing (Zhang et al. 2019). *C. finmarchicus* and *C. typicus* had opposite
relationships with the mixed layer depth indicating that *C. finmarchicus*
abundance is higher under deeper winter/fall mixed layer depths. The
relationship between *C. finmarchicus* abundance and mixed layer depth may be
explained by the enhanced bloom that occurs when the mixed layer goes below
the Nutricline (~100m depth) during the winter (Henson et al. 2009; Zhang et al.
2019). This nutrient limitation likely impacted *C. typicus* differently than *C.
finmarchicus* in part because of their life cycle and phenological requirements.
*C. typicus* maturity and life stage is controlled by temperature rather than growth
and nutrition (Carlotti and Harris 2007) and their life stage and reproductive strategies may not be as interrupted in the same way under limiting feeding conditions as another species such as *C. finmarchicus* that depends on the size of the spring bloom to have enough energy to reproduce after diapause (Campbell et al. 2001).

**SOURCE WATER DYNAMICS**

Past studies have associated changes in NAO with Gulf of Maine copepod abundance by applying it as a proxy for changes in the mixing of WSW and LSW and associated advection of both nutrients and copepods into the region (Greene and Pershing 2003; Piontkovski et al. 2006; Bi et al. 2014). However, the relationship between NAO and water masses associated with copepod abundance broke down in the 2000s (Townsend et al. 2015). And applying NAO as a proxy for water masses is a larger generalization, by applying the water mass fraction of WSW, LSW, and SSW at 150 meters, this study gets a step closer to targeting the relationship between copepods and these larger scale circulation dynamics. Additionally, a time series of Si:N ratio in the Gulf of Maine was developed here to aid in the interpretation of the nutrient-water mass end member relationship. LSW and WSW were found to dominate most of the signal in the Si:N ratio, but influxes of SSW amplified the periods of especially high Si:N (Figure 1.32; Figure 1.62).

Advection as a driver of abundance.

Copepod abundance can be affected by resupply from advection of the water masses into the Gulf of Maine. Historically, *C. finmarchicus* abundance
was found to have a connection with along shore transport in the Gulf of Maine (Lynch et al. 1998; Greene and Pershing 2000; Bi et al. 2014) through shifts in the NAO, which were connected to changes in Gulf of Maine circulation (Greene and Pershing 2000; Conversi et al. 2001). A more recent study from Ji et al. (2022) modeled each Gulf of Maine basin numerically and showed that *C. finmarchicus* abundance dynamics emerge simultaneously and not lagged, suggesting independent populations in each basin, ruling out advection between populations. Additionally, the *C. finmarchicus* abundance magnitude at depth associated with each water mass is at least one order of magnitude smaller than the basin population, which also indicates that advection is likely a small source of population variation (Ji et al. 2022). This leads us to look at changes in water mass fractions as nutrient-phytoplankton shifts rather than changes to advection in this study.

Nutrient driven phytoplankton dynamics (Bottom water fraction term)

Our model results suggest that bottom water mass fractions conditions that support more biomass and diatoms in the phytoplankton blooms were connected to higher abundance of *C. finmarchicus* and lower abundance of *C. typicus*. The Si:N ratio, which is derived from the bottom water mass fractions, was used as a proxy for the nutrient pool available to primary production in the Gulf of Maine, as differences in Si:N ratio are linked to the size and composition of phytoplankton blooms (Townsend et al. 2015; Zang et al. 2022). Deep slope water is the primary source of nutrients entering the Gulf of Maine (Zhang et al. 2019; Whitney et al. 2020), and in addition to WSW and LSW driving the
composition of nutrients (Townsend et al. 2015), recently SSW has been attributed to significant influxes of Silicate into the system (Townsend et al. 2015; Zang et al. 2022). Influxes of SSW and LSW both drive up the Si:N ratio (Figure 1.28), creating better growth conditions for diatoms, which dominate the spring bloom and lead to a larger overall biomass of primary production (Zang et al. 2022). Conversely, periods of increased WSW likely led to smaller-celled phytoplankton communities that grow in silicate limited conditions (Townsend et al. 2015; Zang et al. 2022).

Modeled relationships between *C. finmarchicus* and *C. typicus* and water mass fractions identified LSW and SSW as long-term drivers of temporal abundance changes, suggesting that when conditions set up higher Si:N ratios, there will be a long-term increase in *C. finmarchicus* (Figure 1.38; Figure 1.43) and when the baseline conditions have a low Si:N ratio *C. typicus* abundance will increase (Figure 1.39; Figure 1.40; Figure 1.41; Figure 1.42; Figure 1.44; Figure 1.45; Figure 1.46; Figure 1.47). This could be linked to the necessary nutrition for *C. finmarchicus* to develop lipid storage to diapause or put into reproductive energy as food availability can impact both *C. finmarchicus* body size and egg production (Melle et al. 2014; Pershing and Stamieszkin 2020). Which water mass enters the Gulf of Maine has historically been framed as an important control on copepod abundance and while this was found to be significant in the model, there was inconsistency in the relationships between the water mass fractions and the copepod abundance (Figure 1.38b; Figure 1.47b Figure 1.43b, Figure 1.44b; Figure 1.45b; Figure 1.46b), suggesting that
additional mechanisms are occurring alongside the influence of bottom up
nutrient changes. Our model shows that changes in water mass fraction work
in concert with other factors, such as stratification, mixing, and temperature, to
control multiyear trends in copepod abundance in the Gulf of Maine.

TEMPERATURE

The Transition from hydrographic nutrient-phytoplankton dynamics to warming.

In 2008, the Gulf Stream migrated closer to the Tail of the Grand Banks
and cut off the supply of cool and fresh LSW to the Gulf of Maine, causing the
NE US shelf waters to warm more rapidly than previously documented
(Goncalves Neto et al. 2021). This hydrographic change was reflected in the
winter *C. finmarchicus* abundance models where during RoC2 surface
temperature had a weak effect on decreasing *C. finmarchicus* abundances but
one of the strongest correlations during RoC4 (Figure 1.13). During the winter,
stage CV *C. finmarchicus* would be in diapause and warmer temperatures may
have impacted phenological factors of energy demand. Warmer temperatures
could be increasing the speed through which *C. finmarchicus* consume lipids
leading to an early exit from diapause and migration to the surface during
unfavorable conditions or starvation at depth (Runge et al. 2015, Maps et al.
2012). These higher temperatures and lower primary production may also be
affecting *C. finmarchicus* abundance through decreased body size and egg
production (Melle et al. 2014).

This hydrographic shift in the Gulf Stream during 2008 (Goncalves Neto
et al. 2021) was also apparent in the *C. typicus* models as well, as WSW was
only significantly correlated with \textit{C. typicus} abundance during RoC4 (Figure 1.16). This suggests that with the cut off of water from the north, the magnitude of potential advection from the south in the Gulf Stream could have significantly increased (Bi et al. 2014). However, \textit{C. typicus} has a short life span of less than 1 month (Carlotti and Nival 1992; Carlotti and Harris 2007) and it is likely that the emerging relationship with WSW and surface temperature (Figure 1.14; Figure 1.37; Figure 1.15; Figure 1.36; Figure 1.16; Figure 1.49) is linked to other factors. \textit{C. typicus} development rate is strongly influenced by temperature (Carlotti and Harris 2007) and this modeled relationship with temperature could reflect an expansion in their ecological range/niche to areas further north that now reflect conditions that increase the rate at which \textit{C. typicus} matures.

CLIMATE INDICIES

Connecting basin scale climate indices to copepods on the Northwest Atlantic Shelf.

Both AMO and PDO were significant in modeling the RoCs in both species (Figure 1.18; Figure 1.19; Figure 1.20; Figure 1.21; Figure 1.22; Figure 1.23; Figure 1.24; Figure 1.25; Figure 1.26). Climate indices are used as proxies that integrate a series of environmental conditions and connections associated with zonal and meridional jet stream patterns, different warming and cooling conditions, shifts in western boundary currents, changes in upwelling and storm system tracks. Historically they have proved to be a useful tool for researchers to capture an integrated signal of multiple ecological links from primary production to zooplankton to fish and whales (Pershing et al. 2005, 2015; Kane
et al. 2007; Bi et al. 2014; Morse et al. 2017). For example, AMO and PDO are often used to capture biological relationships with global and basin scale temperature change, and they have been connected to “shifts” in ecosystem states through mechanisms that are often hard to directly test (Pershing et al. 2015). AMO and PDO are calculated using basin wide sea surface temperature data and capture long term trends/cycles in warming patterns. Enfield et al. (2001) found a high correlation between the AMO and the sea surface temperature North of 40 Degrees in the Pacific Ocean, suggesting some mechanistic link either through the tropospheric polar vortex or thermohaline circulation. Additionally, Kohyama et al. (2021) demonstrated that Pacific and Atlantic western boundary current sea surface temperature are correlated through zonally mirrored jet streams. These atmospheric links and correlations between the basin scale Pacific and Atlantic sea surface temperature might help explain why overall increasing surface temperatures in the Pacific Ocean would be significant in capturing the long term change in Atlantic copepod species we see in this study as well as others (Pershing et al. 2005, 2015; Kane et al. 2007; Bi et al. 2014; Morse et al. 2017).

Recent hydrograph changes break down historic relationships.

The results from this study suggest the historic interpretations of how PDO and AMO, as global scale warming trends (Pershing et al. 2015), relate to copepod communities has changed in recent decades. This study identified a transition from the significance of AMO capturing the time trend in copepod abundance (Figure 1.17; Figure 1.18; Figure 1.19; Figure 1.20; Figure 1.21;
Figure 1.22) to PDO capturing the time trends in our RoC periods (Figure 1.23; Figure 1.24; Figure 1.25; Figure 1.26). This may be a product of the warming in the western boundary currents - this variation in spatial warming may be captured differently in the PDO EOF approach and not in the AMO method and this western boundary current warming may be a significant factor in what is driving long term shifts in our species abundance and range. AMO is sea surface temperature data indexed with the 10-year running mean of sea surface temperature north of the equator and highly correlates to Empirical Orthogonal Function (EOF) methods (Enfield et al. 2001), while the PDO is an eigenvector from the EOF of the north Pacific Ocean sea surface temperature component (Mantua et al. 1997). Changes to these global sea surface temperature trends would be expected to, in turn, lead to shifts in the larger scale ecosystem functions and ecological niches associated with *C. finmarchicus* and *C. typicus*.

The Gulf of Maine is at the southern range of *C. finmarchicus* and northern range of *C. typicus* (Bi et al. 2014) and continued warming is expected to be associated with decreases in *C. finmarchicus* abundance in the Gulf of Maine (Grieves et al. 2017; Reygondeau and Beaugrand 2011) while likely increasing the range of *C. typicus* further north.

Temperatures in the Gulf of Maine are correlated with the position of the Gulf Stream (Pershing et al. 2015; Gonçalves Neto et al. 2021), which as a western boundary current is warming 2-3x faster than global mean surface ocean warming rate (Wu et al. 2012). The western boundary current sea surface temperatures are associated with meridional shifts in the jet streams driving
changes in the intensity and path of the ocean currents (Wu et al. 2012, 
Kohyama et al. 2021). Since 2008, the Gulf Stream has reduced the inflow of 
LSW based on sea surface height altimetry data (Gonçalves Neto et al. 2021) 
and as a result, the thermal environment across the northwest Atlantic shelf has 
changed sharply with an average warming rate of 0.95°C/decade across the 
time period of 2004-2018 (Freidland et al. 2020). Not only does this create a 
warmer environment further north for *C. typicus*, it also could increase the 
magnitude of *C. typicus* being advected further north, and decrease *C. finmarchicus* being advected further south (Beaugrand et al. 2009; Reygondeau 
and Beaugrand 2011)

NAO across mixing, advection, and nutrient supply

Up to this point, NAO has been applied as a proxy for: physical transport 
of copepods, nutrient advection, and wind driven mixing (Lynch et al. 1998; 
Greene and Pershing 2000; Greene and Pershing 2003; Piontkovski et al. 2006; 
Across the literature, these themes have been attributed to this “Coupled Slope 
Water System” that is often thought to result in different ecological systems that 
support small-celled phytoplankton and small-bodied zooplankton vs large-
celled phytoplankton and large-bodied zooplankton (Greene & Pershing 2003; 
Wanamaker et al. 2008). Our results here suggest that mixing was likely one of 
the major controls on the long-term inverse abundance trends between *C. finmarchicus* and *C. typicus*, and the restructuring of the water column 
associated with changes in hydrography on the shelf and warming is likely
driving the more recent decadal scale change. The direct inclusion of water mass fractions and other physical water column parameters in this study increased the potential explanatory power of our model and while the relationship found between NAO and copepod abundance was still significant, it was far less important than other parameters captured in the model. These results suggest that even during the earlier RoC periods, the major time trends that were previously explained using NAO can be described through other, more direct, in situ variables. This allows for more direct testing of the environmental and ecosystem changes occurring in the Gulf of Maine. We found that the relationships driving interannual patterns during RoC4 are significantly different from the three RoC periods that have been documented before. The change during RoC4 was unprecedented in the 50 year time series of this study, and the patterns from prior time frames would have been unable to predict these events in the current RoC4. This highlights the need to consider changes in significant links and chains of causality in the Gulf of Maine system as well as other regions where the rapid warming trend is expected to follow.
REFERENCES


Balch, W. M., Drapeau, D. T., Bowler, B. C., & Huntington, T. G. (2012). Step-changes in the physical, chemical and biological characteristics of the Gulf of Maine, as documented by the GNATS time series. Marine Ecology Progress Series, 450, 11-35.


new hypothesis about the persistence of Calanus finmarchicus in the Gulf of Maine. ICES Journal of Marine Science, 74(7), 1865-1874.


TABLES

Table 1.1 Water Mass characteristics for Warm Slope Water (WSW), Labrador Slope Water (LSW), Scotian Shelf Water (SSW) used to calculate the relative bottom water mass fraction and Si:N ratios in Jordan Basin bottom water. Data are from previous studies, working below 100m, in Jordan Basin and the Northeast Channel (Jones et al. 2003; Townsend et al. 2010, 2015; Mountain et al. 2012; Zang et al. 2022).

<table>
<thead>
<tr>
<th>Water Mass</th>
<th>Temperature (°C)</th>
<th>Salinity (PSU)</th>
<th>Si μM</th>
<th>N μM</th>
<th>Si:N</th>
</tr>
</thead>
<tbody>
<tr>
<td>WSW</td>
<td>12^1</td>
<td>35.4^1</td>
<td>13^4</td>
<td>24^3</td>
<td>0.54</td>
</tr>
<tr>
<td>LSW</td>
<td>6^1</td>
<td>34.6^1</td>
<td>13^4</td>
<td>16.5^2</td>
<td>0.79</td>
</tr>
<tr>
<td>SSW</td>
<td>4^2</td>
<td>32^1</td>
<td>17.56^3</td>
<td>16^3</td>
<td>1.1</td>
</tr>
</tbody>
</table>

Table 1.2 Table of final data products within Jordan Basin, Gulf of Maine from the years 1977-2017 used in each model development. Data sources are listed in parentheses: NOAA Ecological Monitoring Program (EcoMon); World Ocean Database (WOD).

**Biological Time Series**
- C. finmarchicus abundance (EcoMon)
- C. typicus abundance (EcoMon)

**Environmental Time Series**
- Surface/Bottom Temperature (EcoMon/WOD)
- Surface/Bottom Salinity (EcoMon/WOD)
- Brunt–Väisälä frequency (N2) (EcoMon/WOD)
- Mixed Layer Depth (MXLD) (WOD)
- Warm Slope Water Fraction (WSW) (EcoMon/WOD)
- Labrador Slope Water Fraction (LSW) (EcoMon/WOD)
- Scotian Shelf Water Fraction (SSW) (EcoMon/WOD)
- Climate Indices: North Atlantic Oscillation (NAO), Atlantic Multidecadal Oscillation (AMO), Artic Oscillation (AO), Pacific Decadal Oscillation (PDO) (NOAA)

Table 1.3 Seasonal and annual C. finmarchicus and C. typicus abundance at a monthly resolution vs time two state Markov switching models (MS2), model form, and Markov switching regimes (MSR) means, standard deviations, and switching probabilities. The numbers 1 and 2 refer to MSR1 and MSR2 for each model. 1-1 is the probability of being in MSR1 and staying in MSR1, 1-2 is the probability of being in MSR1 and switching to MSR2 and vice versa.
### Table 1.4 Winter C. finmarchicus abundance best fit GAMs. Rate of Change (RoC) time period modeled, final model equation, $R^2$, deviance explained, and number of total points (months) in model ($n$).

<table>
<thead>
<tr>
<th>C. finmarchicus</th>
<th>RoC Equation</th>
<th>$R^2$</th>
<th>dev.expl</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>$\text{C. finmarchicus, } W = s(\text{AMO}_w, k = 3) + s(\text{NAO}<em>w, k = 3) + s(\text{PDO}<em>w, k = 3) + s(\text{SS}</em>{15}, k = 3) + s(\text{SS}</em>{15}, k = 3)$</td>
<td>0.90</td>
<td>90.84</td>
<td>18</td>
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</tbody>
</table>

### Table 1.5 Fall C. finmarchicus abundance best fit models. See Table 1.4 for details.

<table>
<thead>
<tr>
<th>C. finmarchicus</th>
<th>RoC Equation</th>
<th>$R^2$</th>
<th>dev.expl</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fall</td>
<td>$\text{C. finmarchicus, } F = s(\text{AMO}<em>f, k = 3) + s(\text{MILD}</em>{11}, f, k = 3) + s(\text{MILD}_{f}, f, k = 3) + s(\text{NAO}<em>f, k = 3) + s(\text{PDO}<em>f, k = 3) + s(\text{ST}</em>{f}, k = 3) + s(\text{ST}</em>{f}, k = 3)$</td>
<td>0.90</td>
<td>90.86</td>
<td>42</td>
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<table>
<thead>
<tr>
<th>Mean</th>
<th>SD</th>
<th>Probability</th>
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<tbody>
<tr>
<td>$C. \text{ finmarchicus } \sim \text{ Annual Points}$</td>
<td>$[0.162, -0.035]$</td>
<td>$[1.312, 0.902]$</td>
</tr>
<tr>
<td>$C. \text{ finmarchicus } \sim \text{ Winter Months}$</td>
<td>$[-0.756, 0.769]$</td>
<td>$[0.612, 0.652]$</td>
</tr>
<tr>
<td>$C. \text{ finmarchicus } \sim \text{ Fall Months}$</td>
<td>$[-0.861, 0.599]$</td>
<td>$[0.799, 0.59]$</td>
</tr>
</tbody>
</table>
Table 1.6 Winter C. typicus abundance best fit models. See Table 1.4 for details.

<table>
<thead>
<tr>
<th>C. typicus Winter</th>
<th>ROC Equation</th>
<th>R²</th>
<th>dev.expl.</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>ROC C. typicus_W = (a(\text{AMO}_{w, k = 3}) + a(\text{MLD}_R, w, k = 3) + a(\text{N}_2, 15, w, k = 3) + a(\text{ST}<em>w, k = 3) + a(\text{WSW}</em>{1, w, k = 3}))</td>
<td>0.05</td>
<td>0.70</td>
<td>18</td>
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</table>

Table 1.7 Spring C. typicus abundance best fit models. See Table 1.4 for details.

<table>
<thead>
<tr>
<th>C. typicus Spring</th>
<th>ROC Equation</th>
<th>R²</th>
<th>dev.expl.</th>
<th>n</th>
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<tbody>
<tr>
<td>1</td>
<td>ROC C. typicus_Sp = (a(\text{AMO}_{w, k = 3}) + a(\text{MLD}_R, w, k = 3) + a(\text{N}_2, 15, w, k = 3) + a(\text{ST}<em>w, k = 3) + a(\text{WSW}</em>{1, w, k = 3}))</td>
<td>0.08</td>
<td>0.44</td>
<td>10</td>
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Table 1.8 Summer C. typicus abundance best fit models. See Table 1.4 for details.

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<tr>
<th>C. typicus Summer</th>
<th>ROC Equation</th>
<th>R²</th>
<th>dev.expl.</th>
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<tr>
<td>1</td>
<td>ROC C. typicus_Su = (a(\text{AMO}_{w, k = 3}) + a(\text{MLD}_R, w, k = 3) + a(\text{N}_2, 15, w, k = 3) + a(\text{ST}<em>w, k = 3) + a(\text{WSW}</em>{1, w, k = 3}))</td>
<td>0.07</td>
<td>0.53</td>
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Table 1.9 Fall C. typicus abundance best fit models. See Table 1.4 for details.

<table>
<thead>
<tr>
<th>C. typicus Fall</th>
<th>ROC Equation</th>
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<th>dev.expl.</th>
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<tr>
<td>1</td>
<td>ROC C. typicus_F = (a(\text{AMO}_{w, k = 3}) + a(\text{MLD}_R, w, k = 3) + a(\text{N}_2, 15, w, k = 3) + a(\text{ST}<em>w, k = 3) + a(\text{WSW}</em>{1, w, k = 3}))</td>
<td>0.07</td>
<td>0.53</td>
<td>18</td>
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Table 1.10 Winter C. finmarchicus abundance estimated parametric and smoothed effects, effective degrees of freedom (edf), standard error (Std.Error), reference degrees of freedom (Ref.df), test statistic critical values (t-value/F), and p-values with significance ("." < 0.1, "*" < 0.05, "**" < 0.01, "***" < 0.001) for best fit model of abundance.

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<tr>
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<th>RoC.2</th>
<th>RoC.3</th>
<th>RoC.4</th>
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**Table 1.11 Fall C. finmarchicus, see Table 1.10 for details.**

RoC.1

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Winter C. typicus, see Table 1.10 for details.

RoC.1

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**Table 1.12 Spring C. typicus, see Table 1.10 for details.**

RoC.1

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**Table 1.13 Summer C. typicus, see Table 1.10 for details.**

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Fall C. typicus, see Table 1.10 for details.

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Figure 1.1 EcoMon Copepod stations by Rate of Change (RoC) time period as defined by winter *C. finmarchicus*. Sample region is defined by Jordan Basin EcoMon strata 42.
Figure 1.2 World Ocean Data (+) and Ecomon (X) environmental stations by RoC period. (RoC period defined by winter C. finmarchicus. Sample region is defined by Jordan Basin EcoMon strata 42.

Figure 1.3 Schematic of modeling approach, with each panel illustrating a method applied within the overall data flow. Panels a-c explain how abundance regimes are identified using Markov Switching Models (MSM) and Panels d-e explain how the transitions between regimes are constrained by the derivative of the generalized additive model (GAM) additive time.
component. The bottom panel lays out the approach to variable selection, and identifying if an additive component fits the interannual direction of change.

Figure 1.4 Applies steps A-F in Figure 1.3 to monthly anomaly abundance data (black points) of a) C. finmarchicus and b) C. typicus from 1977 to 2017 in Jordan Basin. In both panels, the continuous line is a GAMs time smooth and the color shading on the line represents the first derivative, with ranges from -0.5/month (blue) to +0.5/month (red). Black shading behind the continuous line highlights when the confidence interval for the first derivative does not include zero, indicating periods with a significant rate of change. Dark and light grey shaded regions represent Markov Switching Regimes (MSRs), the middle line is drawn through the average monthly anomaly of the regime, and the thinner horizontal lines and shading show the MSR standard deviation.
Figure 1.5 Applies steps A-F in Figure 1.3 to seasonal level monthly anomaly abundance data for copepods (Calanus finmarchicus and Centropages typicus) collected in the NOAA EcoMon program from 1977-2017 in Jordan Basin. Figure formatting follows the same structure from Figure 1.4 (Winter: Dec–Feb; Spring: Mar–May; Summer: Jun–Aug; Fall: Sep–Oct). Vertical lines indicate when the first derivative of C. finmarchicus winter abundance (Panels a-d) or C. typicus annual abundance (Panels e-f) are equal to zero and just before a switch to the other Markov Switching Regime (MSR).
Figure 1.6 Summary figure of results from all models of species abundance during each RoC period by variable, species, and season. Red represents positive relationships, and blue negative relationships. Dark to light gradient is scaled to the nRSS values where darker values fit the abundance variance closer, and lighter shades fit less abundance variance.
Figure 1.7 Mixed layer depth (MXLD) relationship with winter C. finmarchicus abundance anomaly. \_w indicates winter (\_sp: Spring, \_su: Summer, \_f: Fall) and \_# indicates the number of lagged months. A, shows the abundance anomaly relationship with time. The small gray points are original C. finmarchicus winter monthly anomaly values (Figure 1.5a) and the thin continuous line is the smoothed GAMs time fit on the original abundance anomaly data. Color shading is the first derivative of the smoothed time fit and ranges from -0.5/month (blue) to +0.5/month (red). Black shading behind the continuous line indicates when the confidence interval for the first derivative does not include zero, indicating periods with a significant rate of change. The model additive component and GAM time fit from each Rate of Change (RoC) model fit (1-4) are indicated by large black points and thick lines. Bottom panels show C. finmarchicus abundance anomaly relationships with the environmental variable (also a monthly anomaly value), MXLD. Each RoC is shown (from left to right: RoC.1, RoC.2, RoC.3, RoC.4). Color shading and black shading are the same as for the top panel. Tick marks on the x and y axes represent the original anomaly values. Interpreting this figure is as follows: MXLD has both a significant positive relationship with C. finmarchicus abundance anomalies across the entire time series and fits the direction of change in C. finmarchicus abundance anomalies for RoC 1-3.
Figure 1.8 (MXLD) relationship with Fall C. finmarchicus abundance. See Figure 1.7 for full description.

Figure 1.9 Mixed Layer Depth (MXLD) relationship with winter C. typicus abundance. See Figure 1.7 for full description.
Figure 1.10 Figure R: (MXLD) relationship with Spring C. typicus abundance. See Figure 1.7 for full description.

Figure 1.11 (MXLD) relationship with summer C. typicus abundance. See Figure 1.7 for full description.
Figure 1.12 (MXLD) relationship with Fall C. typicus abundance. See Figure 1.7 for full description.

Figure 1.13 Surface Temperature (ST) relationship with winter C. finmarchicus abundance. See Figure 1.7 for full description.
Figure 1.14 Surface Temperature (ST) relationship with winter C. typicus abundance. See Figure 1.7 for full description.

Figure 1.15 (ST) relationship with summer C. typicus abundance. See Figure 1.7 for full description.
Figure 1.16 (WSW) relationship with Summer C. typicus. See Figure 1.7 for full description.
Figure 1.17 Atlantic Multidecadal Oscillation (AMO) relationship with winter C. finmarchicus abundance. See Figure 1.7 for full description.

Figure 1.18 (AMO) relationship with Fall C. finmarchicus abundance. See Figure 1.7 for full description.
Figure 1.19 Atlantic Multidecadal Oscillation (AMO) relationship with winter *C. typicus* abundance. See Figure 1.7 for full description.

Figure 1.20 (AMO) relationship with Spring *C. typicus* abundance. See Figure 1.7 for full description.
Figure 1.21 (AMO) relationship with summer C. typicus abundance. See Figure 1.7 for full description.

Figure 1.22 (AMO) relationship with fall C. typicus abundance. See Figure 1.7 for full description.
Figure 1.23 (PDO) relationship with winter *C. finmarchicus* abundance. See Figure 1.7 for full description.
Figure 1.24 (PDO) relationship with Fall C. finmarchicus abundance. See Figure 1.7 for full description.

Figure 1.25 (PDO) relationship with Spring C. typicus abundance. See Figure 1.7 for full description.
Figure 1.26 (PDO) relationship with summer C. typicus abundance. See Figure 1.7 for full description.
Figure 1.27 Example of winter water column properties and dynamics. The GAMs Surface temperature anomaly during the winter additive time component is plotted at 0 meters, the color bar ranges from anomaly values -2.77 (purple) to 2.77(yellow). The euphotic zone is marked at the average winter depth in Jordan Basin as according to Bisagni 2003. The GAMs mixed layer depth time component is plotted using actual values, with dark blue indication 130.0m and light-yellow indicating 69.1m. The silicate to nitrate ratio represents the source water signal and is plotted in reference to depths below 100m where the lightest green reflects the anomaly value of -2.2 and the darkest green 2.2 as it is calculated from the composition of slope water at and below this depth. The dilution, and therefore resulting volume of the surface layer and water in the euphotic zone is a function of the mixed layer depth. Additionally, it is hypothesized that the deeper the mixed layer depth is, the more connected the surface water will be with the bottom slope water system.
Figure 1.28 Temperature and Salinity mixing triangle, based on water mass endmember properties (described in Table 1.1) from Mountain et al. (2012) Fig. 2 and Townsend et al. (2015) Fig. 12: Warm Slope Water (WSW), Labrador Slope Water (LSW), and Scotian Shelf Water (SSW). Two SSW points are plotted here. The higher SSW point, as proposed by Townsend et al. (2015) to represent more recent (2004-2014) higher temperature SSW values in Jordans Basin, was applied in this study for calculating water mass fractions), and the lower SSW point reflects Gulf of Maine water at depth in the Northeast Channel from 1964-2008 (Mountain 2012). Symbol shapes are defined by the dominant water mass fraction, WSW: triangles, LSW: circles, and SSW: squares. Shading reflects the Si:N ratio calculated directly from the water mass fractions using the estimated Silicate and Nitrate concentrations in Table 1.1.
APPENDICES

Surface Salinity and RoC2.

During the fall *C. finmarchicus* and surface salinity had a positive relationship during RoC2&3 at a lag of 0-1 months and during RoC4 SS had a negative relationship at a 15-month lag during the winter and fall (Figure 1.30; Figure 1.31). N2 had a negative correlation with *C. finmarchicus* during the second RoC period (Figure 1.50). N2 had a positive relationship with *C. typicus* (Figure 1.51; Figure 1.52; Figure 1.53; Figure 1.54). During RoC2 across all seasons surface salinity had a negative relationship with *C. typicus* abundance, and then during winter spring (RoC4) and the fall (RoC3&4) surface salinity had a positive relationship with *C. typicus* abundance at a lag of 3 months (Figure 1.33; Figure 1.34; Figure 1.32; Figure 1.35). In RoC2 &3, surface salinity was most likely a proxy for SSW intrusions in the surface water, and then in RoC4 it could be reflecting the warming from the bottom up and the saltier WSW mixing into the surface water or evaporation due to warming in the surface water.

Changes in the temperature and salinity profiles in the water column can also alter seasonal stratification (Zhang et al. 2019) and it is likely that the lower surface salinity in RoC2 (Figure 1.65) increased stratification during the winter (Figure 1.64) and these relationships are related to the divergence with the mixed layer depth relationship observed in *C. typicus* discussed in the main text. This change in salinity and stratification led to an increase in *C. typicus* across all seasons, and a decrease in *C. finmarchicus* (Figure 1.30; Figure 1.31; Figure 1.33; Figure 1.34; Figure 1.32; Figure 1.35; Figure 1.50; Figure 1.51; Figure 1.52; Figure 1.53; Figure 1.54). This trend has been identified before in past
literature and associated with influxes of SSW into the surface water capping off the winter mixing and leading to an early bloom (Durbin et al. 2003; Pershing et al. 2005). A mis-match of feeding opportunities occurs and species like *C. typicus* that do well in low nutrient conditions thrive - all before *C. finmarchicus* comes out of diapause in late winter early spring. So then *C. finmarchicus* missed out on their feeding window, or experienced a smaller bloom as a result of the diminished nutrient pool during the spring. The model also suggests that when this larger than normal population of *C. typicus* carries into the summer months, it is further supported by higher nutrient fluxes associated with increases in deep SSW under the absence of higher *C. finmarchicus* populations (Figure 1.41).

![Diagram](image)

**Figure 1.29** Two state Markov Switching models MSM and GAM time additive component on the Si:N ratio calculated from bottom water mass fractions in Jordan Basin identified a separate regime with periods where Scotian Shelf Water (SSW) is high in the deep water (when values are above the Labrador Slope Water (LSW) Si:N ratio line). Horizontal lines in the middle of the shaded regions reflect the mean of the Markov switching regime, while the shading and outside horizontal line represents the standard deviation; darker
shading reflects the Markov switching regime with the higher mean and lighter the one with the lower regime. See Figure 1.4 for more details on reading Markov Switching model and GAM time plots.

Figure 1.30 Surface Salinity (SS) relationship with winter C. finmarchicus abundance. See Figure 1.7 for full description.
Figure 1.31 (SS) relationship with Fall C. finmarchicus abundance. See Figure 1.7 for full description.

Figure 1.32 (SS) relationship with summer C. typicus abundance. See Figure 1.7 for full description.
Figure 1.33 Surface Salinity (SS) relationship with winter C. typicus abundance. See Figure 1.7 for full description.

Figure 1.34 (SS) relationship with Spring C. typicus abundance. See Figure 1.7 for full description.
Figure 1.35 (SS) relationship with Fall C. typicus abundance. See Figure 1.7 for full description.

Figure 1.36 (ST) relationship with fall C. typicus abundance. See Figure 1.7 for full description.
Figure 1.37 Surface Temperature (ST) relationship with spring C. typicus abundance. See Figure 1.7 for full description.

Figure 1.38 Scotian Shelf Water (SSW) relationship with winter C. finmarchicus abundance. See Figure 1.7 for full description.
Figure 1.39 (SSW) relationship with winter *C. typicus* abundance. See Figure 1.7 for full description.

Figure 1.40 (SSW) relationship with spring *C. typicus* abundance. See Figure 1.7 for full description.
Figure 1.41 (SSW) relationship with summer C. typicus abundance. See Figure 1.7 for full description.

Figure 1.42 (SSW) relationship with fall C. typicus abundance. See Figure 1.7 for full description.
Figure 1.43 (LSW) relationship with Fall C. finmarchicus abundance. See Figure 1.7 for full description.

Figure 1.44 (LSW) relationship with winter C. typicus abundance. See Figure 1.7 for full description.
Figure 1.45 (LSW) relationship with spring C. typicus abundance. See Figure 1.7 for full description.

Figure 1.46 (LSW) relationship with summer C. typicus abundance. See Figure 1.7 for full description.
Figure 1.47 (LSW) relationship with Fall C. typicus abundance. See Figure 1.7 for full description.
Figure 1.48 (WSW) relationship with Winter C. finmarchicus. See Figure 1.7 for full description.

Figure 1.49 (WSW) relationship with Winter C. typicus. See Figure 1.7 for full description.
Figure 1.50 (N2) relationship with winter C. finmarchicus abundance. See Figure 1.7 for full description.

Figure 1.51 (N2) relationship with winter C. typicus abundance. See Figure 1.7 for full description.
Figure 1.52 (N2) relationship with spring C. typicus abundance. See Figure 1.7 for full description.
Figure 1.53 (N2) relationship with summer C. typicus abundance. See Figure 1.7 for full description.

Figure 1.54 (N2) relationship with Fall C. typicus abundance. See Figure 1.7 for full description.
Figure 1.55 (NAO) relationship with winter C. finmarchicus abundance. See Figure 1.7 for full description.

Figure 1.56 (NAO) relationship with Fall C. finmarchicus abundance. See Figure 1.7 for full description.
Figure 1.57 Residuals winter *C. finmarchicus* GAM.

Figure 1.58 Residuals fall *C. finmarchicus* GAM.
Figure 1.59 Residuals winter C. typicus GAM.

Figure 1.60 Residuals spring C. typicus GAM.
Figure 1.61 Residuals summer *C. typicus* GAM.

Figure 1.62 Residuals fall *C. typicus* GAM.
Figure 1.63 Density of Water Mass Fractions as defined by the four RoC periods identified in C. finmarchicus winter abundance trend (Figure 1.5). Figure was generated with the “ggstatsplot” R package (Patil 2021), “type” was set to parametric to apply Welch’s one-way Anova test and the Games-Howell Test. Results are visualized with a boxplot violin plot combination that displays the raw data.
Figure 1.64 Density of Water Column stability metrics, see Figure 1.63 for details.
Figure 1.65 Density of Surface water, see Figure 1.63 for details.
Figure 1.66 Density of Climate Indexes, see Figure 1.63 for details.
Figure 1.67 Density of Water mass estimated nutrient endmembers, see Figure 1.63 for details.
Chapter 2 Large-bodied Calanus finmarchicus rely more heavily on the microbial loop food web than small bodied Centropages typicus over a multi-decadal time series.

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ABSTRACT

Copepods are the most numerous metazoans in the ocean and they play a key role in transferring energy from primary production to higher trophic levels and into deep ocean. We lack long term historical records of food web dynamics supporting copepod production to test classic hypotheses about the roles that large- and small-bodied copepods play in traditional (fueled by new nutrients) and microbial loop (fueled by recycled nutrients) food webs, as well as how copepod trophic dynamics may be restructuring around recent environmental warming and hydrographic changes on multi-decadal scales. Therefore, this study applied compound-specific stable nitrogen isotope analysis of amino acids to a 21-year (1996-2017) time series of copepods in the Gulf of Maine, a region leading in the global warming trend and at the interface of multiple major ocean current systems that alter key bottom-up drivers of food web structure. This study reconstructed key aspects of the food web ecology supporting large-bodied *Calanus finmarchicus* and small-bodied *Centropages Typicus*, hypothesized to occupy traditional and microbial loop food webs respectively, including: the water mass nitrogen source ($\delta^{15}N_{\text{MSA}}$), heterotrophic microbial reworking on organic matter ($\sum V$), and both metazoan ($TP_{\text{Glx-Phe}}$) and microbial ($TP_{\text{Ala-Phe}}$) trophic transfer indices. For both species, $\sum V$ showed significant interannual oscillations with a long-term increase by 0.6 units from 1996 to 2017 that coincided with a 9% overall reduction in the relative contribution of microbial trophic transfers to the total trophic position in both species. While it was hypothesized that *C. finmarchicus* would occupy a short “traditional” food chain, *C. finmarchicus* actually had a higher trophic position, owing to additional microbial trophic
transfers \( \text{TP}_{\text{Ala-Phe}} 4.1 \pm 0.3 \) and a higher proportion of \( \Sigma V \) \( 2.2 \pm 0.5 \) than \( C. \) typicus \( \text{TP}_{\text{Ala-Phe}} 3.5 \pm 0.3; \Sigma V 1.6 \pm 0.4 \). We observed key transitions in the relationships between these trophic dynamics and their environmental drivers in 2003 (relative microbial contribution to trophic transfers), 2006 \( \Sigma V \), and 2012 \( \delta^{15}N_{\text{SAa}} \) that line up with not only rapid warming and hydrographic change in the Gulf of Maine, but also recent shifts in copepod abundance and community dynamics that indicate recent deviation from historic drivers to warming and hydrographic changes. The increase in importance of the microbially reworked organic matter in Jordan Basin and the unexpected microbial trophic linkages supporting \( C. \text{finmarchicus} \) production provide a new critical framework for understanding how the central role that copepods play in pelagic food webs may change in the future ocean.

INTRODUCTION

Copepods are the most numerous metazoans in the ocean (Fenchel 1988) and are generally considered secondary grazers of primary production, making them key conduits of energy and organic matter to upper trophic levels (Pershing et al. 2005; Meyer-Gutbrod & Greene 2014), and to export of surface ocean production to depth via their sinking fecal pellets and carcasses (Steinberg & Landry 2017; Halfter et al. 2022). By consuming primary production, copepods integrate bottom-up signals of changing biogeochemical cycles, plankton community dynamics, and microbial reprocessing of organic matter, manifested in their population dynamics and recorded in the chemical composition of their tissue. Variations in the factors that impact the sources and
cycling of organic matter supporting copepods can exert strong controls over
the zooplankton production in the surface ocean, and ultimately the fate of that
production to higher trophic levels and export to the deep ocean. Large-scale
environmental factors (e.g. stratification and mixed layer depth, water mass
nutrient delivery), biological factors (e.g. phytoplankton community composition,
the rates and timing of primary production, microbial degradation of particulate
organic matter - POM), and small-scale physical factors (e.g. POM aggregation-
disaggregation dynamics) interact with one another, exert bottom-up influence
on zooplankton size, abundance, and feeding strategies, and therefore shape
copepod food web dynamics (Frederiksen et al. 2006; De la Rocha & Passow
2007; Greene and Pershing 2007; Passow & Carlson 2012; Pershing et al.
2015). Understanding these pan-ecosystem forces and mechanisms driving
copepod trophic dynamics is critical to understanding how the central role that
copepods play in pelagic food webs may change in the future ocean.

There has been tremendous work looking at past relationships between
environmental and climate drivers of copepod population dynamics, but we lack
long term historical records of how those drivers impact the food web dynamics
supporting copepod production. The Gulf of Maine, with its long history of
climatic, oceanographic, and biological study, is a model system for linking
environmental and climatic variation with bottom up forcing of copepod trophic
dynamics. This system is warming faster than 99.9% of the rest of the world’s
oceans and sits at the complex hydrodynamic interface of multiple major ocean
current systems that alter key bottom-up drivers of food web structure, including
temperature, salinity, stratification, nutrient concentration and stoichiometry, and biogeochemical cycling (Townsend et al. 2010; Pershing et al. 2005, 2015; Kane 2007; Bi et al. 2014; Saba et al. 2014). The long-term copepod population dynamics needed to build historical perspective on changing pelagic food web structure have also been recorded in the Gulf of Maine region (Richardson et al. 2010). For example, the NOAA EcoMon time series, and the Gulf of Maine Continuous Plankton Recorder (CPR) Transect provide half a century of critical data and zooplankton sample collections to test outstanding hypotheses about decadal-scale bimodal oscillations of large-bodied vs. small-bodied plankton dynamics in the region (Record et al. 2019; Greene & Pershing 2003; Wanamaker et al. 2008; Balch et al. 2012; Kane 2007; Pershing et al. 2010).

Substantial fluctuations in plankton community population dynamics have been identified and correlated with hydrographic and biogeochemical variability in the Gulf of Maine, often modeled as a two-end member “Coupled Slope Water System”, correlated with (and therefore predictable from) the winter North Atlantic Oscillation (NAO) index (Greene & Pershing 2003; Wanamaker et al. 2008). For much of the last 50 years, documented oscillations have occurred between well-known cold periods when Labrador Slope Water (LSW: T = 6°C, S = 34.6 PSU, NO3 = 16 uM; Table 2.1) extended far southwestward along the Scotia-Maine continental slope, flooding the deep waters of Jordan Basin via the NE Channel (Petrie & Drinkwater 1993; Townsend et al. 2010) and warm periods when inflow of Warm Slope Water (WSW: T = 12°C, S = 35.4 PSU; Table 2.1) through the NE Channel increased, leading to mostly positive T&S
anomalies and higher NO3 concentrations (>23 µM; Figure 2.2A; Townsend 2015) and Atlantic-like nutrient (i.e., Redfield) N:P (16:1) and Si:N (1:1.1) ratios (Capone et al. 2005; Jenkins et al. 2015). However, the slope water-NAO relationship began to break down in the 1990s; this disruption accelerated during the 2000s with increasing Scotian Shelf Water (SSW, T = 2°C, S = 32.0 PSU; Table 2.1) inflow events, which had significant effects on surface freshening and stratification in the Gulf of Maine (Greene & Pershing 2007; Townsend et al. 2010, 2015). SSW has the lowest NO3 concentrations (<12 µM), and distinct N:P and Si:N signals (Townsend et al. 2010), which originate from sedimentary denitrification and terrestrial runoff on the western Arctic (Bering and Chukchi Seas) shelves, where Arctic halocline water, one of the principal source waters for SSW, is formed (Jones et al. 2003; Yamamoto-Kawai et al. 2008; Tremblay et al. 2015). Water mass shifts have had significant effects on surface freshening and stratification in the Gulf of Maine (Greene and Pershing 2007; Townsend et al. 2010, 2015), with hypothesized impacts on primary production shifting to communities dominated by smaller species (Pershing et al. 2005, 2010; Ji et al. 2017). Townsend and Thomas (2001, 2002) have identified Si:N ratios as a major limiting factor large-celled diatom spring blooms in the Gulf of Maine; and Zang et al. (2022) provided evidence that the spring bloom magnitude is proportional to the inflow of SSW (highest Si:N ratio of the three water masses). Differences in nutrient ratios may also have influenced primary producer community composition (Townsend et al. 2010;
Clark et al. 2019), as has been observed in other regions of the NW Atlantic (Li et al. 2006; Harrison & Li 2008; Fragoso et al. 2017).

Changes in Gulf of Maine circulation patterns, primary productivity, and phytoplankton community composition propagate up the food web to impact secondary production as well as biological carbon pump processes (Pershing et al. 2005, 2010; Kane 2007; Bi et al. 2014; Record et al. 2019; Stamieszkin et al. 2015; Pershing et al. 2015b). Copepod body size is a controlling factor in the interaction of zooplankton with phytoplankton communities and related environmental conditions (Stamieszkin et al. 2015; Michaels and Silver 1988). Conventionally, size-dependent copepod trophic dynamics have been described in the framework of traditional vs. microbial loop food web dynamics. In the traditional food web, new production fueled by large phytoplankton (e.g., diatoms) supports short food chains dominated by large copepods (e.g., Calanus finmarchicus) with efficient energy transfer up the food web and into the deep ocean, while the microbial loop food web is dominated by small celled phytoplankton production and microbial recycling that supports small bodied copepods (e.g., Centropages typicus) in long food chains with inefficient energy transfer through the food web and into the deep ocean (Figure 2.1; Layman et al. 2015). In the Gulf of Maine, large-bodied C. finmarchicus and small-bodied C. typicus exhibit juxtaposed abundance patterns on decadal time scales linked to warming NAO, and a increase in the influx of WSW into the Gulf of Maine (Chapter 1; Pershing et al. 2005; Bi et al. 2014; Grieve et al. 2017; Morse et al. 2017; Record et al. 2019). For example, in the 1980s and 2000s, the large-
bodied, sub-arctic *C. finmarchicus* (late-stage CV and adult CVI) were more abundant than smaller, temperate *C. typicus*, but during the fresh, stratified 1990s, the pattern reversed (Figure 2.4C; Pershing et al. 2005; Bi et al. 2014). These transitions between zooplankton community state likely reflect a combination of shifts in advective forces and bottom up changes in food web dynamics as *C. finmarchicus* relies heavily on periods with strong spring diatom blooms to accumulate lipids prior to entering diapause (Hansen et al. 1994; Hirsche 1996), whereas *C. typicus* consumes production fueled by recycled N with a higher degree of microbial reworking such as smaller-celled prey based food webs selected for by nutrient limitation in the euphotic zone (Calbet et al. 2007). These changes in food web dynamics, coupled with factors like phenology (e.g., temperature change and age of maturity) and advection, are hypothesized to have significant impacts on temporal trends in copepod population dynamics (Campbell et al. 2001; Pershing and Stamieszkin 2020). Documented changes to *C. finmarchicus* abundance have been linked to the calving rates and range of critically endangered North Atlantic Right Whales *Eubalaena glacialis* (Record et al. 2019; Meter-Gutbrod and Greene 2017), as well as changes in the magnitude of export production to the deep ocean (Brun et al. 2019).

To accurately link bottom up forcing of copepod food web structure and population dynamics to environmental and climatic drivers, we need long-term historical records of copepod trophic dynamics. Previously, much of the stable isotope analysis of zooplankton bioarchives has focused on total ("bulk")
organic material, revealing information about past changes in surface ocean conditions, productivity, and biogeochemical cycling (e.g., Fry and Quinones 1994; Trueman et al. 2012; Kurten et al. 2013). However, a main challenge to interpreting bulk stable isotope data in a historical context is determining whether isotopic changes are due to changes in (1) baseline dissolved inorganic nitrogen ($\delta^{15}N_{NO_3}$) values, (2) trophic transformations of organic matter, (3) microbial reworking of particulate organic matter (POM), or (4) some combination of all of these factors (Altabet 1988; Wakeham & Lee 1989; Hofmann et al. 2000; Lehmann et al. 2002). Compound specific stable isotope analysis of Amino Acids (CSIA-AA) offers a powerful analytical tool kit to disentangle these potentially confounding factors and to trace the sources and cycling of organic matter to copepod production (reviewed in Ohkouchi et al. 2017). This approach relies on differential isotope fractionation of individual amino acids, which have yielded a number of robust, quantitative metrics of organic matter transformation, including: 1) the Source Nitrogen Index (Mompeán et al. 2016), reflecting baseline nitrogen biogeochemical cycling that supports food web architecture, 2) the $\Sigma V$ Index (McCarthy et al. 2007) reflecting the degree of microbial reworking of organic matter, and 3) the Trophic Transfer Index (Hannides et al. 2009) revealing metazoan trophic processing of organic matter that is internally indexed to the baseline nitrogen sources. Characterizing these key food web parameters from historical copepod archives offers the opportunity to quantitatively link changes in copepod trophic dynamics with records of historic environmental and climatic change.
In this study, we generated a 21 year (1996-2017), annually resolved time series of Gulf of Maine baseline biogeochemical cycling, microbial reprocessing of organic matter, and trophic dynamics, manifested as CSIA-AA signals in the tissues of two dominant Northwest Atlantic copepods: large-bodied *C. finmarchicus* and small-bodied *C. typicus*. With juxtaposed abundance trends and life history characteristics, these two copepod species constitute ~40% of the total zooplankton abundance in the region (Kane 2008; Bi et al. 2014), making them ideal candidates for studying ecosystem drivers of biological variability in the region. We then identified temporal trends in isotope-based food web metrics, and used Generalized Additive Models (GAMs) to determine the significance of 18 environmental drivers in explaining those trends, elucidating the underlying mechanisms of historic changes in the organic matter and food webs supporting dominant copepods in the Gulf of Maine. We explicitly test classic hypotheses that that: 1) large-body *C. finmarchicus* depend on environmental conditions that support a “traditional food web” with diatom production (high Si:N ratio), a short food chain, and low microbial reworking of organic matter, while small-body *C. typicus* utilize production fueled by recycled N with a high degree of microbial reworking leading to longer food chains, and 2) are these CSIA-AA food web patterns are consistent with changing oceanographic conditions, which result in the observed seesaw trend between *C. finmarchicus* and *C. typicus* populations in recent decades.
METHODS
Zooplankton Sample Collection
We sampled *C. finmarchicus* and *C. typicus* that were collected and archived by the NOAA Northeast Fisheries Science Center Oceanography Branch between 1996 and 2017 during surveys of Jordan Basin, Gulf of Maine as part of the Ecosystem Monitoring (EcoMon) Program (Figure 2). Samples were collected using a 61 cm, 333 μm mesh bongo net that was towed obliquely to a maximum depth of 200m, or 5m from the bottom (Kane 2007), and preserved in 5% formalin. Recent work has shown that formalin does not have significant effects on individual amino acid δ15N values, which lends confidence to using CSIA-AA on historical, fixed archives (Ogawa et al. 2013; Hetherington et al. 2019). *C. finmarchicus* stage five copepodids (CV) were picked from samples collected in May and June each year, ensuring that those individuals hatched that year (Gen1) and assimilated that year's spring phytoplankton bloom. *C. typicus* adults (CVI) were picked from samples collected in September and October each year when they are most abundant, reflecting foraging over the summer (Pershing et al. 2005). Samples were aggregated across multiple stations, which were randomly selected from every cruise within the Jordan Basin strata each year to reach a dry weight average of 11.94mg ± 6.71mg of *C. finmarchicus* (minimum 20 individuals' total; minimum of 3 individuals per station) and 2.53mg ± 0.50 of *C. typicus* (minimum 60 individuals) (Table 2.13).
CSIA-AA Methods

*C. finmarchicus* and *C. typicus* tissue were acid-hydrolyzed in 0.5mL of 6 N HCl at 110°C for 20 h to isolate the total free amino acids. Samples were passed through 0.45 μm Millipore glass-fiber filters and then derivatized by esterification with acidified isopropanol followed by acylation with trifluoroacetic anhydride (Silfer et al. 1991). Derivatized samples were extracted using a P-buffer (KH2PO4 + Na2HPO4 in Milli-Q water, pH 7) – chloroform solution two times with centrifugation (600 g) and organic phase extraction between each round (Ueda et al., 1989) and then acylated once again.

Derivatized amino acids were injected on column (1μl in ethyl acetate) in splitless mode at 250°C and separated on a BPX5 column (60 m 0.32 mm ID, 1.0 m film thickness) in a Thermo Trace Ultra gas chromatograph (GC), and the separated amino acid peaks were analyzed on a Finnegan MAT DeltaPlus XL isotope ratio mass spectrometer (IRMS) interfaced to the GC through a GC-IsoLink II and reduction furnace (1000°C) with liquid nitrogen trap. Copepod samples were analyzed in triplicate along bracketed by a mixed amino acid standard of known isotopic composition (Sigma-Aldrich Co.) and homogeneous algal lab working standard included as a known-unknown for quality assurance and quality control purposes (Yarnes and Herszage 2017). The long-term reproducibility of 15N values in the algal lab working standard was ± 0.3‰ (mean across all individual amino acids for >100 separate full analyses), which provides an estimate of full protocol reproducibility (hydrolysis, wet chemistry, and isotope analysis).
We measured 13 individual amino acids with sufficient peak size and well-defined baseline chromatographic separation, which we classified as trophic amino acids: glutamic acid/glutamine (Glx), aspartic acid/asparagine (Asx), alanine (Ala), leucine (Leu), isoleucine (Ile), proline (Pro), valine (Val), and source amino acids: phenylalanine (Phe), Methionine (Met), and Lysine (Lys) (McMahon and McCarthy 2016). Glycine (Gly), serine (Ser), and threonine (Thr) were kept as separate groups given the lack of consensus on degree of trophic fractionation (reviewed in McMahon and McCarthy, 2016). Note, acid hydrolysis converts glutamine (Gln) and aspartamine (Asn) into glutamic acid and aspartic acid, respectively, due to cleavage of the terminal amine group, resulting in the measurement of combined Gln + Glu (referred to hereby as Glx), and Asn+Asp (referred to hereby as Asx). Stable isotope ratios are expressed relative to Air in standard delta (δ) notation in per mil units (‰).

CSIA-AA Metrics
The Source Nitrogen Index, calculated as the mean δ^{15}N value of source amino acids (δ^{15}N_{\text{SAA}} value of Phe, Lys), reflects the nitrogen isotope signal of biogeochemical cycling at the base of the food web supporting copepod production, which can be used, for example, to constrain variation in nutrient source (e.g., water mass contribution) and biogeochemical cycling (e.g., N2-fixation and nitrification) (McClelland et al. 2003; Sherwood et al. 2011; Whitney et al. 2020). Source amino acids undergo minimal nitrogen isotope discrimination during trophic transfers, such that δ^{15}N_{\text{SAA}} values provide a robust proxy for the isotopic value of nitrogen cycling at the base of the food
web, without the confounding factor of trophic modification (McMahon and McCarthy 2016).

\[ \Sigma V \] Index
The degree of heterotrophic microbial reworking of organic matter supporting copepod production (e.g., Wakeham et al., 1997; Calleja et al. 2013) was calculated using the \( \Sigma V \) Index, which reflects the cumulative increased variance of trophic amino acid \( \delta^{15}N \) values during microbial degradation relative to predictable patterns from metazoan trophic discrimination (McCarthy et al. 2007): \[ \Sigma V = \frac{1}{n} \sum_{i=1}^{n} |X_{AA}^i|, \] where \( X_{AA} \) is the deviation of each trophic amino acid \( \delta^{15}N \) value from the mean of all sampled trophic amino acids (Ala, Asx, Glx, Ile, Leu, and Pro) and \( n \) = the total number of amino acids used in the calculation. The degree of heterotrophic microbial reworking differentiates between zooplankton feeding on fresh algal-based production (\( \Sigma V < 2 \)) and microbially re-mineralized organic matter (\( \Sigma V > 2 \)) (McCarthy et al. 2007).

Trophic Transfer Index
The trophic transfer index provides information about the number of trophic transfers of energy and organic matter between trophic levels and thus the length of food chains supporting copepod production. Food chain length is a classic ecological parameter with implications for the efficiency of energy transfer to higher trophic levels (McMahon and McCarthy 2016). As an important ecological metric of ecosystem structure, food chain length plays a central role in the function of ecological communities by modulating energy transfer from primary productivity to apex predators (Degerman et al. 2018; Décima 2022). We calculated a metazoan trophic transfer index (\( TP_{Glx-Phe} \)) that
is internally indexed to the isotopic baseline (Chikariashi et al. 2009):

\[ TP_{\text{Glx-Phe}} = 1 + \frac{\delta^{15}N_{\text{Glx}} - \delta^{15}N_{\text{Phe}} - \beta_{\text{Glx-Phe}}}{TDF_{\text{Glx-Phe}}} \]

where the \( \delta^{15}N_{\text{Glx}} \) and \( \delta^{15}N_{\text{Phe}} \) are the nitrogen isotope values of copepod heavily fractionating trophic amino acid (Glx) and minimally fractionating source amino acid (Phe) of the copepod annual samples, \( \beta_{\text{Glx-Phe}} \) (3.3 ± 1.8‰) is the difference in Glx and Phe \( \delta^{15}N \) value in marine microalgae (Ramirez et al. 2021), and \( TDF_{\text{Glx-Phe}} \) is the diet to consumer nitrogen isotope trophic discrimination factor of Glx and Phe (7.6 ± 1.4‰) (McMahon & McCarthy 2016). Previous work has suggested that the trophic amino acid Glx may not register microbial trophic transfers (TDF ~ 0‰; Gutiérrez-Rodríguez et al. 2014) and thus underestimate trophic position in food chains that contain microbial loop trophic dynamics. Therefore, we also calculated a second trophic transfer index using Ala as the trophic amino acid (\( TP_{\text{Ala-Phe}} \)), which has been shown to be more sensitive to microbial transfers (Décima et al. 2017; Bode et al. 2021)

\[ TP_{\text{Ala-Phe}} = 1 + \frac{\delta^{15}N_{\text{Ala}} - \delta^{15}N_{\text{Phe}} - \beta_{\text{Ala-Phe}}}{TDF_{\text{Ala-Phe}}} \]

where \( \beta_{\text{Ala-Phe}} \) is 3.2 ± 1.2 (Ramirez et al. 2021) and \( TDF_{\text{Ala-Phe}} \) is 4.5 ± 2.1‰ (McMahon & McCarthy 2016). Calculating both \( TP_{\text{Glx-Phe}} \) and \( TP_{\text{Ala-Phe}} \) gives information about if the number of trophic transfers are changing at the microbial or the metazoan levels, and aids in reconstructing the trophic structure at lower levels. The change in relative percent of trophic position due to microbial trophic transfer was calculated by taking the fraction of \( TP_{\text{Glx-Phe}} \) and \( TP_{\text{Ala-Phe}} \) allowing for the relative comparison of the two trophic transfer indexes (Bode et al. 2021).

Error propagation was iterated across 100,000 times using the function propagate() from the R package “propagate” (Spiess 2018). Samples were not
run in replication due to limited resources, and the analytical error from triplicate injections is propagated across each CSIA-AA index.

Modeling environmental drivers of foodweb dynamics
The model design was constructed to test the hypotheses around 1) the differences between environmental conditions that support a “traditional food web” (*C. finmarchicus*) and high microbial reworking with a longer food chain (*C. typicus*) and 2) how physical processes and nutrient conditions influence biogeochemical cycling recorded in the pelagic system. First, we targeted the difference between species CSIA-AA index values, and how those differences may have changed throughout the time periods by testing the linear fixed and mixed effects, as well as by modeling the GAMs additive time component. Then the GAMs predictor models were used to analyze the correlations between the CSIA-AA indexes and key environmental variables, and to test if those relationships experienced a change around known environmental events in the Gulf of Maine. Gaussian, Lognormal and Gamma distributions were tested for each index, and a gaussian distribution was found to be the appropriate for all.

Test by species
To test if the three CSIA-AA food web metrics 1) The \(\delta^{15}N_{\text{SAA}}\) Source Nitrogen Index, 2) \(\Sigma V\) Index, and 3) Trophic Transfer Index for *C. finmarchicus* and *C. typicus* had the same mean values and followed the same overarching time trend, a series of linear models were fit and the best was selected using the lowest Akaike Information Criterion (AIC) value. The first was a simple linear model using the \texttt{lm()} function and the next three were all linear mixed-effects models fit with the \texttt{lmer()} function from the “\texttt{Lme4}” package (Douglas et al. 2015),
of which, one fit separate intercepts and the same slope: "lmer(var ~ year + (1 | species), data = data)”, another fit separate slopes and the same intercept: “lmer(var ~ year + ( 0 + year | species), data = data)” and the third fit both separate intercepts and slopes: “lmer(var ~ year + ( 1 + year | species), data = data)”. 

Test Interdecadal Trends
To test if there was interdecadal variability in the three CSIA-AA food web metrics of the two copepod species, generalized additive models (GAMs) were fit to annual anomaly values \((\frac{x - \text{mean}(x)}{sd(x)})\) as a function of time using the “mgcv” package and the method “REML” with smoothing parameter \(K = 10\) (Wood 2011) and are identified as GAMtime here and throughout. We identified when the time additive component was significantly changing as the first derivative was not equal to zero, i.e., 95% of each of the upper and lower quantiles for each spline were either all above or below zero. This was calculated using a modified version of the example code “Differentiating the smooths in a model (with CIs for derivatives)” from the function predict.gam() in the “mgcv” R package. Time points where the standard deviation bounds were both positive/negative were considered to have a significantly increasing/decreasing time trend.

Format Environmental Data
Environmental and copepod abundance data products were going back to the start of the copepod time series (1991) are limited, but the NOAA-NEFSC EcoMon program provided hydrographic and integrated (0-200 m) zooplankton abundance data (count/100m³) earlier then our sampled time frame (1977), and additional CTD hydrographic data was queried from Jordan Basin obtained from
the World Ocean Database (https://www.ncei.noaa.gov/products/world-ocean-database) and additional climate index data was from the National Oceanic and Atmospheric Administration (NOAA) (https://psl.noaa.gov/data/climateindices/list/), as collated in Chapter 1.

Data was first aggregated to a monthly resolution and missing months were imputed using methods described in Chapter 1. The environmental data was then aggregated to an annual resolution, defined by the season in which the samples were collected. For *C. finmarchicus* this included the collection year spring as well as prior summer, fall, and winter months. For *C. typicus* this included the collection year fall as well as prior winter, spring, and summer months. Annual anomalies were then calculated by species to facilitate comparable coefficients. Co-predictor variables were analyzed for co-variance using the cor() function in R and variables with correlations above 0.5 were not included in the model selection process together. Co-predictor variables that were found to not covary significantly were Si:N, the mixed layer depth, a Brunt–Väisälä frequency based stratification index (N2), and abundances for *C. finmarchicus* and *C. typicus*. Si:N was found to co-vary with BT, ST, SS, WSW, LSW, SSW, and BS, mixed layer depth was highly correlated with AMO, and N2 was highly correlated with the NAO.

When testing environmental variables to assess drivers of copepod food web parameters, many were correlated and thus limited inclusion in the models. However, the Si:N ratio, mixed layer depth, N2, and *C. finmarchicus* and *C. typicus* abundance all were not over correlated with one another. The Si:N ratio,
mixed layer depth, and N2 were all calculated applying the in-situ temperature and salinity data and including them in the model increases the interpretation of the environmental dynamics associated with changes in temperature and salinity.

GAMs for Fitting Parameters

To identify correlations for each CSIA-AA index a modeling process was developed to address variable selection and to identify parameters that capture the temporal autocorrelation. For variable selection, a least absolute shrinkage and selection operator (LASSO) method was applied; the method adjusts the coefficient for each variable based on the p-value and moves the least significant coefficients to zero. To apply a fixed effects model framework, each variable was multiplied by a (0,1) categorical variable to generate a separate term for each species and a categorical vector was included to model separate intercepts. The highest coefficient for each separate environmental variable were then selected as initial variables using a cutoff that defines the maximum degrees of freedom that can be fit with n points in the model: $\frac{n}{(n+k)k}$ where k is the smoothing parameter (k = 3 here).

Each combination of variables was fit in a GAM of the form: $GAM(y \sim s(x_1, by = species, k = 3) + ... + species)$. The smoothing parameter K was set to 3 to constrain the modeled relationships within realistic environmental conditions (Grieves et al. 2017) and to limit the degrees of freedom. The model with the lowest AIC value was selected as the final model. We calculated a normalized residual sum of squares (RSS) value to assess how well the environmental variables fit the copepod abundance. Because the metric was...
normalized, values could be compared across models where the closer the value was to zero, the better the model fit. These relationships are then used to identify connections between the isotope metrics and different environmental mechanisms that occur in the Gulf of Maine and to test the hypothesized connections we expect to see. For instance, if the $\delta^{15}N_{SA\text{A}}$ values are identified to have a positive relationship shape fit with the Si:N ratio derived from in situ observations of water mass temperature and salinity, that would suggest that the $\delta^{15}N_{SA\text{A}}$ values align with the expected water mass endmembers, and if additional variables are significant, other biogeochemical processes are also potentially influencing the $\delta^{15}N_{SA\text{A}}$ values.

To identify time changes in the additive components for each environmental model, the same GAM method above was applied, but instead of using the actual values for the isotope indexes for the dependent variable, the anomaly values were applied to remove the intercepts associated with each species. Then instead of applying species as a fixed effect, a categorical time variable was applied to test the significance of a shift at every time point after the first $K + 2$ data points and before the last $K + 2$ data points to account for degrees of freedom. The lowest AIC value was used to select the significant change point (Method modified from Gonçalves Neto et al. 2021).

RESULTS

Means and temporal trends of the three CSIA-based food web indexes were compared between the two copepod species. The CSIA-AA $\delta^{15}N$ amino acid profile for both species (Figure 2.9) was found to follow classic metazoan CSIA-AA trophic and source separation patterns (McMahon and McCarthy
Results of the CSIA-AA index vs. environmental predictor data sets were compared by species, including before and after an identified time change in each CSIA-AA index. Residuals for each predictor model were examined (see supplemental) and found to have no significant remaining structure apart from the $\Sigma V$ by species model. Below we describe first the trends in CSIA-AA indexes, followed by the results of modeling the index time series using environmental and biological variables (Table 2.2).

Trophic Transfer Index

Both *C. finmarchicus* and *C. typicus* were found to have the same TP$_{\text{Glx-Phe}}$ ($2.3 \pm 0.1$ *C. finmarchicus*; $2.3 \pm 0.2$ *C. typicus*; (Figure 2.3a). Both species registered a 0.24 increase in trophic level across the 21 year time frame (Table 2.3), which was classified as an increasing trend as fit by the GAM$_{\text{time}}$ (Figure 2.4a). *C. finmarchicus* had a higher TP$_{\text{Ala-Phe}}$ ($4.1 \pm 0.3$) than *C. typicus* ($3.5 \pm 0.3$) by 0.7 trophic levels (calculated from fitted linear model) (Table 1, 2; Figure 2.3a). The TP$_{\text{Ala-Phe}}$ linear slope did not exceed the standard error (Table 2.3) and it was also not found to have a significant GAM$_{\text{time}}$ rate of change for either species, indicating no significant change over the time series (Figure 2.4a). When including species as a categorical model variable, the relative percent of trophic position due to microbial trophic transfer was 11% higher for *C. finmarchicus* than *C. typicus* (Table 2.3; Figure 2.3b). The slope of change in relative percent of trophic position due to microbial trophic transfer over time was the same for both species, which decreased by 9% over the 21-year time frame (Table 2.3; Figure 2.4b).
When modeling the percent microbial contribution to trophic transfers including species as a categorical variable in the model, 55.5% of the deviance was captured (Table 2.4). In this model we found a negative relationship between mixed layer depth and microbial trophic transfer contribution such that when the mixed layer was deeper, there were less trophic transfers within the microbial food web (Table 2.5; Figure 2.5a). When using percent microbial contribution to trophic transfers anomaly values, and no differentiation between species the predictor variables (Table 2.9) captured 79.3% of the deviance of this microbial contribution to the trophic index, over the entire time frame (Table 2.8). Additionally, a time change – spring of 2004 – was identified across the predictor variables and anomalies of microbial trophic transfer contribution (Figure 2.10). During the first time frame (1996-2004), the water mass Si:N ratio in Jordan Basin had a positive relationship (edf 1.92; Table 2.9) with the microbial contribution to the trophic transfer index (RSS Shading Figure 2.6b). During the second time frame (2004-2017), $\delta^{15}N_{\text{SA2}}$ value and stratification index N2 were positively correlated (Figure 2.6a,c), and the Si:N ratio and C. typicus abundance were negatively correlated with this microbial contribution to trophic position (Figure 2.6b,d).

\[ \sum v \]

Index

Linear trends of $\sum V$ had the same positive slope over time for both species (Figure 2.3c), indicating that the proportion of reworked organic matter consumed by both species, whether directly or indirectly, increased by 0.6 units from 1996 to 2017 (Table 2.3). However, the linear trend line intercept for C. finmarchicus was 0.49 units higher than for C. typicus (Table 2.3; Figure 2.3c),
indicating that the food web supporting *C. finmarchicus* had more microbially reworked organic matter at its base than that supporting *C. typicus*. ∑V showed an oscillating pattern over time, with significant interdecadal changes that occurred in the spring of 2001 and the fall of 2007, followed by a period of increasing ∑V that ended in fall of 2012 (Figure 2.4c).

When modeling ∑V and including species as a categorical variable, each species had similar additive terms across each predictor relationship with an offset between species of 0.5 units (Table 2.4; Table 2.6). *C. finmarchicus* ∑V had a negative parabolic relationship (edf 1.86; Table 2.6) with δ¹⁵N_SAA value (Figure 2.5b). ∑V for both species had a positive relationship with mixed layer depth (*C. finmarchicus* linear, *C. typicus* edf 1.32; Table 2.6) and a negative linear relationship with the Si:N ratio (Figure 2.5c,d; Table 2.6). In the time change model where anomaly values are applied in the dependent variable, and no differentiation between species is used, ∑V was positively correlated with the shallowest mixed layer depth values prior to the fall of 2005 (Table 2.8, Table 2.10; Figure 2.6 e-i). From 1996-2005, the shallow mixed layer depth values, *C. finmarchicus* abundance, and the δ¹⁵N_SAA values fit the increasing time structure identified with the GAM_time (Figure 2.7; Table 2.10), and the Si:N fit the decreasing time structure identified in the GAM_time (Figure 2.7; Figure 2.6). Then from 2005-2017, δ¹⁵N_SAA values switched to a positive relationship with ∑V (Figure 2.6e) indicating that higher source water isotope values are related to more heterotrophic microbial reworking, and the deepest mixed layer depth values had a positive relationship with the high ∑V values (Figure 2.6f).
correlating deeper mixed layers with more heterotrophic microbial reworking. The Si:N, N2, and *C. finmarchicus* abundance had similar relationships and ranges across both time frames with $\sum V$(Figure 2.6 5 g-i). The Si:N fit the oscillating $\sum V$ time structure from the GAM$_{time}$ during 2005-2017 (Figure 2.7; Figure 2.6).

Source Nitrogen Index
The slope of $\delta^{15}N_{\text{SAA}}$ value did not exceed the standard error, and thus $\delta^{15}N_{\text{SAA}}$ value was not found to change significantly over time for either species (Table 2.3; Figure 2.4). However $\delta^{15}N_{\text{SAA}}$ values did have significantly different intercepts between species, with *C. finmarchicus* having a higher intercept than *C. typicus* by 1.0‰ (Table 2.3; Figure 2.3).

When included species as a categorical variable in the $\delta^{15}N_{\text{SAA}}$ model, 50.6% of the deviance was captured (Table 3, 6; Figure 2.5) The mixed layer depth and Si:N ratio modeled deviance in each species, but *C. finmarchicus* had relatively high overall RSS values compared to *C. typicus* (Figure 2.5) indicating that more deviance was left in the *C. finmarchicus* residuals than in the *C. typicus* residuals (RSS shading in Figure 2.3). Then when modeling the $\delta^{15}N_{\text{SAA}}$ values with anomalies, and not differentiating between species, a time change was identified in the best fit parameters during the fall of 2012 that captured 61.6% of the deviance (Table 2.8). 1996-2012 was explained by a negative relationship with the mixed layer depth and a positive relationship with the Si:N (Table 2.8, 10; Figure 2.6). And from 2012-2017 the $\delta^{15}N_{\text{SAA}}$ value was fit with deep mixed layer depth values (-0.14 to 2.08 anomaly values) and the low Si:N values (-1.45 to 0.24 anomaly values) (Figure 2.6j,k).
Time Changes
The significant trend changes in $\Sigma V$ (Figure 2.4c) lined up with a significant time change identified by modeling the CSIA-AA indices vs. the predictor variables while also using a sliding categorical variable and selecting for the lowest AIC (Figure 2.10). The start of the rate of change decrease in the $\Sigma V$ (Figure 2.4c) lined up with the time change identified in the percent microbial contribution to trophic transfers (Figure 2.4b). The change in the $\Sigma V$ relationship occurred during the decreasing period of $\Sigma V$ (Figure 2.4c) and at the end of the second increasing rate, the change in the $\delta^{15}N_{\text{AA}}$ value occurred (Figure 2.4d).

**DISCUSSION**
This study tested classic hypotheses about the roles that large- and small-bodied copepods play in traditional (fueled by new nutrients) and microbial loop (fueled by recycled nutrients) food webs and explored how copepod trophic dynamics and their environmental drivers correlate with multi-decadal population trends. Contrary to our hypothesis, we found that the large-bodied *C. finmarchicus* relied more heavily on the microbial loop food web than small-bodied *C. typicus*. We predicted that *C. finmarchicus* would occupy a shorter food chain with fewer trophic transfers starting with large diatom production, in contrast with a longer food chain with more trophic transfers between small-celled primary production and *C. typicus*. Instead, both copepods appeared to feed at the same trophic position, based on the compound-specific trophic position estimate ($\text{TP}_{\text{Glx-Phe}}$). In fact, additional microbial trophic transfers were identified using Ala isotope fractionation patterns, which revealed that *C. finmarchicus* was actually supported by a longer,
microbial loop-fueled food chain compared to that supporting *C. typicus*. Furthermore, *C. finmarchicus* fed on organic matter that had undergone more extensive microbial reworking than *C. typicus*.

Changes in these trophic dynamics – increasing trophic level and microbial reworking of organic matter – were driven by the water mass source and mixing with major shifts in time that propagated up through the food web metrics starting with the $\delta^{15}N_{\text{SA}}$ in 2003, to the $\Sigma V$ in 2006 and finally the percent microbial contribution to trophic transfers in 2012. These changes lined up with the rapid warming and hydrographic change in the Gulf of Maine. Together these results suggest that we need to rethink the Gulf of Maine copepod trophic dynamics across species and time and the resulting implications they have for energy transfers up the food chain as well as export into the deep ocean.

**TROPHIC DYNAMICS**

We hypothesized, based on classic food web theory (Michaels and Silver 1988; Legendre and Rassoulzadegan 1995; Layman et al. 2015), that the large-bodied *C. finmarchicus* would rely on a “traditional” short food chain system supported by fresh phytoplankton associated with high nutrient growth conditions, for example diatoms, which are thought to fuel *C. finmarchicus*’ lipid accumulation and support a diapause life history strategy (Johnson et al. 2007; Pershing and Stamieszkin 2020). Conversely, we hypothesized that *C. typicus* would utilize production fueled by recycled N with a higher degree of microbial reworking, leading to more microbial trophic transfers and a longer food chain (Calbet et al. 2007). However, using a metazoan-based compound-specific
trophic position equation \((TP_{\text{Glx-Phe}})\) that is internally indexed to baseline biogeochemical cycling, we found that both *C. finmarchicus* \((TP_{\text{Glx-Phe}} = 2.3 \pm 0.1)\) and *C. typicus* \((TP_{\text{Glx-Phe}} = 2.3 \pm 0.2)\) occupied the same trophic position (Figure 2.3a). While surprising given ecological theory about predator to prey size ratios (Wirtz 2012; Boyce et al. 2015), there has been increasing evidence that individual trophic interactions observed across a natural community structure show that impacts of mesozooplankton grazing on plankton prey is proportional to the abundance of what is available, rather than the size, and that established individual plankton predator-prey dynamics may not linearly transfer to the community level (Stamieszkin et al. 2017). There is also seasonal-resolution zooplankton bulk stable isotope trophic position data that suggested that trophodynamic plasticity in other *Calanus* spp. can allow for both significant herbivore and microbial diet contributions (Kurten et al. 2013). Our results show that at the population level over multi-decadal timescales, large-bodied *C. finmarchicus* and smaller-bodied *C. typicus* are not following conventional traditional vs microbial loop food web paradigms based on body size differences.

**Heterotrophic Microbial Reworking**

While both *C. finmarchicus* and *C. typicus* occupied the same metazoan trophic position, estimates of the degree of microbial reworking of consumed organic matter based on \(\Sigma V\) data indicate that these two copepod species are not feeding in the same food web system. Surprisingly, *C. finmarchicus* \((\Sigma V = 2.2 \pm 0.5)\) had a higher proportion of reworked organic matter in their diets than in *C. typicus* \((\Sigma V = 1.6 \pm 0.4)\) by \(0.6\ \Sigma V\) units (Table 2.3; Figure 2.3). *C. finmarchicus* was expected to feed on fresh diatom production (Hansen et al.
while *C. typicus*, which is typically associated with the microbial loop based on its phenology, smaller size, was expected to rely on more microbiially reworked organic matter (Calbet et al. 2007; Wirtz 2012; Boyce et al. 2015). This observed difference in reliance on microbially reworked organic matter was likely not a function of seasonal difference in food web structure as we would have expected fall periods when *C. typicus* were sampled to have lower nutrient levels and higher small cell plankton production/microbial reworking of organic matter than during the spring bloom period when *C. finmarchicus* were collected (Anderson 2009; Fischer et al. 2014). Furthermore, the higher reliance on microbially reworked organic matter in *C. finmarchicus* was consistent across the entire 21-yr time frame, lending confidence that this is a robust ecological phenomenon (Figure 2.3c). *C. typicus* and *C. finmarchicus* have both been documented to be omnivorous feeders (Calbet et al. 2007; Saage et al. 2008; Leiknes et al. 2014). While *C. typicus* has been shown to be broadly omnivorous and a selective ambush feeder with a wide range of prey from small algae to yolk-sack fish (Calbet et al. 2007; Sell et al. 2001) *C. finmarchicus* have been shown in lab settings to select for ciliates even when phytoplankton was in excess concentrations except for periods of overwhelming diatom abundance (Leiknes et al. 2014); it is possible that *C. typicus* is feeding on a wider range of prey than *C. finmarchicus*, which could explain the difference in their diet composition of heterotrophic microbial reworking.

Additionally, the microbial reworking (∑V) signal measured in the copepods in this study were on average higher than the typical value measured
in zooplankton (1.4 +/- 0/19) (Mompean et al. 2016; McCarthy et al. 2007; Calleja et al. 2013) suggesting that Jordan basin has a relatively high level of bacterial resynthesis (combined species: 1.94, +/- 0.56, *C. finmarchicus*: 2.20 +/- 0.53, *C. typicus*: 1.64 +/- 0.44) supporting pelagic copepod production. Thus, while we would expect *C. finmarchicus* to be selectively grazing on diatoms, this result suggests that there must be a high abundance of reworked organic matter available for them to feed on, and that *C. typicus* are omnivorously feeding on prey in a shorter food chain, during a fall phytoplankton bloom (Durbin and Kane 2007).

Microbial Trophic Position

We found additional support for our observation that large-bodied *C. finmarchicus* relied more heavily on a microbial loop food web than small bodied *C. typicus* using an alternative CSIA-AA trophic position calculation (TP_{Ala-Phe}) that is sensitive to microbial trophic transfers which are undetectable using the more common metazoan TP_{Glx-Phe} approach (Gutierrez-Rodriguez et al. 2014). Gutierrez-Rodriguez et al. (2014) found that trophic fractionation of Glx between diet and microbial consumers is close to 0‰, meaning that the trophic position estimates based on Glx as a trophic amino acid may not accurately record trophic transfers within the microbial loop food web. Décima et al. (2017) supported those conclusions and suggested an Ala as an alternative trophic amino acid that shows trophic fractionation through both protist and metazoan trophic transfers. This method has been applied to communities of zooplankton in the Pacific where a large range of microbial trophic transfers were identified by species (Décima and Landry 2020) as well as in piscivores species where 6-
21% of the trophic transfers were attributed to protistan processes (Bode et al. 2021). In this study, the $T{P}_{\text{Ala-Phe}}$ estimate of *C. finmarchicus* was 2 trophic transfers higher than observed with metazoan-based trophic position estimate ($T{P}_{\text{Glx-Phe}}$) indicating that *C. finmarchicus* does indeed rely significantly on a microbial loop food web (Table 2.3; Figure 2.4). In fact, $T{P}_{\text{Ala-Phe}}$ estimates for *C. finmarchicus* were 0.65 trophic units higher than *C. typicus*. As with $T{P}_{\text{Glx-Phe}}$ estimates, these offsets were consistent across the entire 21-year time series, lending independent support for our conclusions that springtime *C. finmarchicus* production is fueled by a food web containing more microbial activity than that supporting *C. typicus*. The additional trophic transfers supporting *C. finmarchicus* at the microbial level could be the result of a “multivorous food web” as described in Décima and Landry 2020 first figure, in which protistan consumers graze on phytoplankton and are then consumed by mesozooplankton. And in fact, Décima and Landry 2020 identified this multivorous food web structure inside of an eddy-constrained diatom bloom, where a classical short food chain was expected. The higher level of microbial transfers inside the eddy, measured by $T{P}_{\text{Ala-Phe}}$, suggested that the microbial community reorganized around the high nutrient influx/bloom event, and that the metazoan community grazed opportunistically on the increased protist prey, rather than selecting diatoms. Similar observations were made within our data set, where a greater contribution of microbial trophic steps in both copepod species were identified early in the time series when nutrient conditions were more likely to support bigger blooms, and by the end of the study period, when
the silicate limitation in the Gulf of Maine had increased, and smaller over all blooms were expected, microbial trophic transfers within the food web supporting these copepods had decreased by 9% in both species (Table 2.3). Over the course of the 21-year time series, we observe a 0.25 unit increase in metazoan trophic level increase in the copepods, which when coupled with the 9% decrease in microbial contribution, suggests that the planktonic trophic structure in Jordan Basin is changing. These examples highlight that a significant amount of energy moving through oceanic food webs is through microbial trophic transfers at the base of the food web, even during seasonal (as in the Gulf of Maine) or episodic diatom blooms.

*C. finmarchicus* are critical to subarctic food webs like that in the Gulf of Maine (Pershing and Stamieszkin 2020) and our finding that microbial production is key to copepod trophic dynamics, particularly for *C. finmarchicus*, is important for understanding how these copepod species link bottom-up food web processes to higher trophic level consumers. For example, the increase in metazoan trophic position ($T_{\text{Glx-Phe}}$), and constant value of the microbial trophic position ($T_{\text{Alx-Phe}}$) suggests that the copepods are shifting their diet to a metazoan based organic matter, with similar microbial trophic transfers and a $T_{\text{Glx-Phe}} < 3$. This could suggest a shift to consuming more mesozooplankton fecal pellet matter, which has been shown to have a lower $T_{\text{Glx-Phe}}$ than the animal's body (Doherty et al. 2021); and may also support the observed increase in overall heterotrophic microbial reworking. These findings have implications for diet quality, which is likely decreasing as more food for both
copepod species is getting reworked by heterotrophic microbes. The relative increase in foraging on microbial food web components by *C. finmarchicus* compared to fresh, presumably diatom, production over the last two decades may reduce capacity of *C. finmarchicus* to put on critical lipid supplies needed for diapause. This may, in turn, have implications for higher trophic level species, like Atlantic herring (*Clupea harengus*), sand lance (*Ammodytes spp.*), and capelin (*Mallotus villosus*) and the top predators like cod, tuna, seabirds, and whales that are dependent on a high lipid content that comes from *C. finmarchicus* (Pershing and Stamieszkin 2020). These findings also have implications for thinking about the efficiency of energy transfer to these higher trophic levels. Trophic transfer efficiency is low, meaning that longer food chains result in lower relative energy and biomass at the top of the food chain (McMahon and McCarthy 2016; Layman et al. 2015). As such, energy budget models will likely need to consider the longer than expected food chain with higher microbial trophic transfers supporting *C. finmarchicus* and how that is changing over time. These results shift the way we think about what is occurring at the base of the food web around these characteristic species, both by highlighting the importance bacterial trophic steps have in moving energy up to the system as well as the potential impact that the decrease in microbial trophic transfers observed across the timeseries may have.

**NUTRIENT DYNAMICS**

The proposed framework for thinking about how nitrogen moves through the biological and physical processes in Jordan Basin and becomes incorporated into the copepods sampled for this study is shown in Figure 2.8
and is as follows: 1) what was the nutrient composition of the slope water entering the Gulf of Maine and how does that impact potential primary production, 2) are the nutrients available to surface production, i.e., was there sufficient mixing to bring the slope water from depth to the surface, and 3) did stratification occur to relieve light limitation conditions to facilitate a primary production bloom event. This framework ties together past literature that has focused on slope water regime changes driving shifts in long term copepod abundance (Chapter 1; Pershing et al. 2001; 2005; Greene and Pershing 2003; Piontkovski et al. 2006; Townsend et al. 2010; Bi et al. 2014), as well as theory on productivity driven by the seasonal mixing and stratification dynamics (Pershing and Stamieszkin 2020). Conventionally, winter mixing brings nutrients to the surface, followed by stratification, driven by both decreases in wind and increases in warming, that increases light access and allows phytoplankton to grow rapidly; then in the summer, stratification is strong, which terminates spring productivity as oligotrophic conditions set in; in the fall, wind driven mixing picks up and resurgence of nutrients leads to a second bloom. Our goal is to frame established fundamental biological and physical processes that influence production, in a way that aids in tracing these processes through the water column with a biogeochemical isotope lens.

Nutrient Baseline

While C. finmarchicus and C. typicus did not appear to follow the classic food web structure we hypothesized based on body size, there was evidence that C. finmarchicus are still eating a diet that was derived in a diatom-fueled system, and C. typicus in one with a microbially reworked baseline. The higher
\( \delta^{15}N_{SAA} \) values identified in *C. finmarchicus* (4.4 ± 1.0‰) were consistent with the Labrador Slope water values (Marconie et al. 2015; Sherwood et al. 2011) and higher silicate concentration water masses (Zang et al. 2022; Townsend et al. 2015), indicative of feeding in a system where production is fueled by a higher fraction of diatoms that grow in high nutrient conditions supplied by slope water from depth (Zang et al. 2022; Townsend et al. 2015; Zhang et al. 2019). Conversely, the lower \( \delta^{15}N_{SAA} \) values identified in *C. typicus* (3.4 ± 0.6‰) likely indicates a diet that is supported by production with higher rates of recycling and remineralization of nitrogen through nitrification that takes place in almost all Gulf of Maine waters above 100m (Whitney et al. 2020). In addition, some of the low \( \delta^{15}N_{SAA} \) values may also be attributed to nitrogen fixation, which has recently been identified as a more significant contributor than considered in the past in both coastal and shelf waters in the western North Atlantic (Conley et al. 2009; Marconie et al. 2015; Whitney et al. 2020). These species-specific \( \delta^{15}N_{SAA} \) values also coincide with expected seasonal differences in nitrogen biogeochemical processes associated with the seasons *C. finmarchicus* (spring) and *C. typicus* (fall) were collected during. Elevated spring \( \delta^{15}N_{SAA} \) values are expected with upwelling during the winter fueling the spring bloom, while elevated nitrification occurs during the fall, associated with the limited fall surface ocean N pool. Again, these findings align with the observations presented in Décima and Landry (2020), where zooplankton inside a Pacific eddy-constrained diatom event fed on production fueled by upwelled nutrients were found to have a higher source amino acid 15N baseline values while
copepods feeding on active microbial communities outside of the eddy had lower source amino acid $\delta^{15}N$ baseline values.

Source Water Signature
The impact of the fraction of different slope waters that enter the Gulf of Maine on baseline nitrogen and resulting primary production is evident from the relationships identified between the Si:N ratio and both the $\delta^{15}N_{\text{SAA}}$ and $\sum V$ indices recorded in both copepod species (Figure 2.5 3 f & b, respectively). The $\delta^{15}N_{\text{SAA}}$ for each water mass separated around high and low Si:N ratios according to the expected nutrient signatures in each water mass: higher Si:N would lead to more LSW, and lower Si:N indicates more WSW. In addition to being a proxy for source water mass fractions, the Si:N also indicates conditions that may support different levels of spring bloom biomass, which are dominated by (silicate limited) diatoms in the Gulf of Maine system (Townsend et al. 2015; Zang et al. 2022). Because Si:N is a proxy for both water mass and primary productivity, the correlation of elevated heterotrophic microbial reworking (high $\sum V$) with lower Si:N (WSW signature) and increased fresh algal production (low $\sum V$) in the copepods diet alongside a higher Si:N (LSW/SSW signature) (Figure 2.5d) further confirms that the source nutrient baseline measured in the copepods does incorporate the original water mass source.

Upwelling of Nutrients
While the composition of the slope water entering the Gulf of Maine was important in driving the baseline nitrogen composition and the proportion of heterotrophically reworked organic matter consumed by the copepods, physical processes associated with transporting the slope water to the surface were also
necessary to support the observed copepod food web dynamics (Koeve, 2001). Deeper mixed layer values ( > -0.2 anomaly value) led to an increase in the $\delta^{15}N_{\text{SAA}}$ values (Figure 2.5e) indicating that the slope water (> 5%o 15N value) was mixed into the surface system, and the higher nitrate waters were available for primary production (Zhang et al. 2019). This is further supported by the negative relationship between heterotrophic microbial reworking and $\delta^{15}N_{\text{SAA}}$ values (> -1.0 anomaly value) in *C. finmarchicus* (Figure 2.5b), where higher $\delta^{15}N_{\text{SAA}}$ values (< 1.0 anomaly value) aligned with low heterotrophic microbial reworking, and indicated a water mass signature similar to that of the slope waters where high $\delta^{15}N_{\text{SAA}}$ values coincide with LSW and a higher Si:N that would increase diatom production.

Surface Stratification and Mixed Layer Depth

Following from our understanding of water mass intrusion into the Gulf of Maine and resulting mixing of nutrients into the surface water, adequate access to both nutrients and light are needed for phytoplankton to grow. The Gulf of Maine has been identified as a light limited system (Follows and Dutkiewicz 2001) and observations of deep mixed layer depths have been associated with light limiting conditions that decrease the chlorophyll-a values in the region (Henson et al. 2009). We observed a positive relationship between the mixed layer depth and the degree of heterotrophic microbial reworking of organic matter ($\Sigma V$) consumed by both copepod species (Figure 2.5c), indicating that shallow mixing layers are associated with the consumption of more algal production, and deeper mixed layer depths lead to copepod diets based on a higher proportion of microbiially reworked POM. We interpret our data to indicate
that as the mixed layer depth shoals, the phytoplankton concentration in the euphotic zone increases, but when mixing is deeper, production is light limited, and their biomass is diluted (Behrenfeld 2010). These deeper periods of mixing have also been associated with lower encounter rates between the phytoplankton and their microzooplankton predators (Behrenfeld and Boss 2014; Lindemann and St. John 2014; Pershing and Stamieszkin 2020). Thus we interpret the negative relationship between the relative microbial contribution of trophic transfers at the base of the food web and mixed layer depth found in this study (Figure 2.5a) to indicate a multivorous-type food web (see “Microbial Trophic Position” in Discussion above) supported by higher primary production, under shallower mixed layer depth conditions. In summary, when mixed layer depths were shallower, we suggest that copepods were part of a multivorous food web supported by less microbially reworked organic matter and more new primary production, but were composed of more trophic levels taking advantage of the bloom conditions.

Remineralization of Baseline Nitrogen

When the physical processes of nutrient rich LSW/SSW water mass intrusion, vertical mixing, and enhanced stratification were not found to coincide, there was added evidence for the remineralization of the baseline nitrogen source identified in the relationship between water column mixing and the degree of heterotrophic reworking of organic matter supporting copepod production. Shallow mixed layer values had a negative correlation with the $\delta^{15}N_{SAA}$ value (Figure 2.5e), which could be attributed to nitrification fractionation patterns that have been shown to occur above 100 meters in the
Gulf of Maine (Whitney et al. 2020). At the same time, the high $\Sigma V$ values of C. finmarchicus, indicating enhanced reliance on microbially reworked POM, correlated with low $\delta^{15}N_{\text{SAAN}}$ values (Figure 2.5b), which together indicate that microbial processes that lead to resulting fractionation of lower $\delta^{15}N_{\text{SAAN}}$ values occurred in shallower mixed layers and that on top of the source water mass values, additional biogeochemical cycling is altering the overall $\delta^{15}N_{\text{SAAN}}$ signature.

The Gulf of Maine has undergone major oceanographic changes in recent decades (Pershing et al. 2015; Pershing et al. 2018; Record et al. 2019). The rate of warming in the system notably increased starting in 2004 (Pershing et al. 2015) and the northward movement of the Gulf Stream in 2008 cut off the supply of LSW around the tail of the Grand Banks (Gonçalves Neto et al. 2021) and has been associated with changes to major fisheries in the region (Pershing et al. 2015). Over the last two decades, this study observed steady increases across both copepod species in the reliance on microbially reworked organic matter ($\Sigma V$) and metazoan-based trophic position ($\text{TP}_{\text{Glx-Phe}}$), and decreases in the relative contribution of microbial trophic transfers to copepod trophic position (Figure 2.4). These data suggest a steady, region-wide transition to a system that is more reliant on microbially reprocessed organic matter but passed through fewer microbial trophic transfer steps. At the same time, we observed significant changes in the relationship between the nitrogen biogeochemical cycling ($\delta^{15}N_{\text{SAAN}}$) and environmental predictor variables, particularly the mixed layer depth and Si:N, that coincide with the timeframe of documented physical
changes in the Gulf of Maine system (Pershing et al. 2015; Gonçalves Neto et al. 2021). For example, from 2005-2017, there was deeper mixing that coincided with elevated levels of heterotrophic microbial reworking of organic matter supporting copepod production in the system (Figure 2.6f,h), and then during 2006-2017, the relative contribution of microbial trophic transfers to copepod trophic position was strongly associated with shifts in the balance of WSW/LSW water mass signal from the baseline nitrogen fueling the system (Figure 2.6a). In the fall of 2012, the time change predictor model indicated that WSW (Figure 2.6k) was effectively mixed up into the surface (Figure 2.6j) suggesting that the low $\delta^{15}N_{\text{SAO}}$ values in both copepod species can be attributed to this advection of WSW. These conditions fit into the framework outlined above as follows: 1) the decrease in LSW/SSW into the Gulf of Maine (after the $\delta^{15}N_{\text{SAO}}$ 2012 time change; Figure 2.8) supports hypotheses that there was an increase in the silicate limitation, which would lead to lower levels of large-celled, diatom primary production (Figure 2.6g; 2005-2017 time frame); 2) deep mixing from 2012-2017 transported slope water to the surface (Figure 2.6j); and 3) deeper mixing could be a result of either longer periods of mixing increasing the annual average of the mixed layer depth, or deeper mixing during the shorter periods, either of which would cause changes in light availability that limited the supply of phytoplankton to the copepods. Over the entire time series, we observed an increase in metazoan trophic steps, which suggests that there is a steady transition in the copepod's trophic structure as they adjust to the increases in
the available heterotrophic microbially reworked organic matter and lower phytoplankton biomass conditions.

Connections to Abundance

The trophodynamic patterns of the juxtaposed copepods, *C. finmarchicus* and *C. typicus*, were strikingly different in this system, though not in the way we originally hypothesized. Furthermore, we hypothesized that the observed trophodynamic patterns of these two copepod species would be consistent across changing oceanographic conditions, and thus driving in the observed inversely oscillating population trends between these two species in recent decades based on "good" and "bad" food web conditions for these pelagic consumers. We found here that the CSIA-AA indexes did not have a significant relationship with abundance until after 2003/2006 (Figure 2.6 5 d&j), suggesting that the 2006 transition to temperature-related drivers of copepod abundance in Chapter 1 was also related to the changes in overarching food web dynamics. Lower abundances of *C. finmarchicus* were associated with high heterotrophic microbial reworking and higher *C. typicus* abundance correlated with a lower percent microbial contribution to trophic transfers, which suggests periods of lower overall production. These changes quantified with CSIA parameters are having an impact on the copepods’ populations, and therefore on the ecology of the system.

This study identified a system where the food web dynamics of large and small copepods did not follow the classic traditional vs. microbial loop food web model. Large-bodied *C. finmarchicus* participated in a longer, more microbial reworked food web, while the smaller bodied *C. typicus* fed at a lower trophic
position and relied on less production that underwent less microbial reworking. We found that both variation in the source water intrusion into the Gulf of Maine with characterized by distinct biogeochemical properties, as well as water column mixing and stratification dynamics were important drivers of variability in copepod food web dynamics and population abundance. Much of previous research in this region has connected bottom temperature to copepods as a significant driver of change through a multitude of different mechanisms (Pershing et al. 2010; Kane 2007; Bi et al. 2014; Record et al. 2019; Chapter 1). By deconvolving temperature and salinity data into: the mixed layer depth, a stratification index, and the different water mass fractions with their distinct nutrient signatures, we have provided a proximate mechanistic link for previous literature correlations between bottom temperature and copepod population and food web dynamics. These results provide new details to the growing body of literature that suggests we need to revise the way food web dynamics in the Gulf of Maine are conceptualized, as well as the framework for potential temporal drivers behind them. Our approach increases the strength of predictor variables such as temperature and salinity that have both historically been collected in the field across a temporal and spatial ranges like those applied here in this study, and can also be contemporary modeled in regional and global climate models (unlike climate indexes) and applied to other long term ecological field surveys to project and assess future scenarios of global warming.
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**TABELS**

*Table 2.1* Water Mass characteristics for Warm Slope Water (WSW), Labrador Slope Water (LSW), Scotian Shelf Water (SSW) used to calculate the relative bottom water mass fraction and Si:N ratios in Jordan Basin bottom water. Data are from previous studies, working below 100m, in Jordan Basin and the Northeast Channel (Jones et al. 2003; Townsend et al. 2010, 2015; Mountain et al. 2012; Zang et al. 2022).

<table>
<thead>
<tr>
<th>Water Mass</th>
<th>Temperature (°C)</th>
<th>Salinity (PSU)</th>
<th>Si μM</th>
<th>N μM</th>
<th>Si:N</th>
</tr>
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<tbody>
<tr>
<td>WSW</td>
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<td>35.4(^1)</td>
<td>13(^4)</td>
<td>24(^3)</td>
<td>0.54</td>
</tr>
<tr>
<td>LSW</td>
<td>6(^1)</td>
<td>34.6(^1)</td>
<td>13(^4)</td>
<td>16.5(^2)</td>
<td>0.79</td>
</tr>
<tr>
<td>SSW</td>
<td>4(^2)</td>
<td>32(^1)</td>
<td>17.56(^3)</td>
<td>16(^3)</td>
<td>1.1</td>
</tr>
</tbody>
</table>

*Table 2.2* Table of final data products within Jordan Basin, Gulf of Maine from the years 1977-2017 used in each model development. Data sources are listed in parentheses: NOAA Ecological Monitoring Program (EcoMon); World Ocean Database (WOD).

**Biological Time Series**
- *C. finmarchicus* abundance (*EcoMon*)
- *C. typicus* abundance (*EcoMon*)

**Zooplankton CSIA-AA**
- Source Nitrogen Index (*EcoMon zooplankton*)
- Trophic Transfer Index (*EcoMon zooplankton*)
- Sigma V Index (*EcoMon zooplankton*)

**Environmental Time Series**
- Surface/Bottom Temperature (*EcoMon/WOD*)
- Surface/Bottom Salinity (*EcoMon/WOD*)
- Brunt–Väisälä frequency (N2) (*EcoMon/WOD*)
- Mixed Layer Depth (MXLD) (*WOD*)
- Warm Slope Water Fraction (WSW) (*EcoMon/WOD*)
- Labrador Slope Water Fraction (LSW) (*EcoMon/WOD*)
- Scotian Shelf Water Fraction (SSW) (*EcoMon/WOD*)
- Climate Indices: North Atlantic Oscillation (NAO), Atlantic Multidecadal Oscillation (AMO), Artic Oscillation (AO), Pacific Decadal Oscillation (PDO) (NOAA)

*Table 2.3* Summary of the best fit linear CSIA-AA index models from Table 2.1. Std.err is the error term associated with the slope value, T0_Value is the value at the first time point, and Tn_Value is the value at the end of the
timeseries. \( T\_diff \) is the change that occurred over the time series, and \( \text{intercept\_diff} \) is the offset between the two species.

Table 2.4: GAMs equation by species, \( R^2 \), deviance explained, and number of samples in model (n) for the best fit models by species. Terms in all models are as follows: Si:N: Silicate:Nitrate; N2: Stratification Index; MXLD: Mixed layer depth; calanus: C. finmarchicus abundance; centyp: C. typicus abundance; \( s\_\text{mean} \): \( \delta^{15}N \_{\text{SAAS}} \); sum\_v: \( \sum V \); per\_micro: relative contribution to microbial trophic transfers.

<table>
<thead>
<tr>
<th>Species Models</th>
<th>R2</th>
<th>dev.expl</th>
<th>AIC</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>( s_\text{mean} = s(\text{MXLD}, by = \text{Species} k = 3) + s(\text{Si:N}, by = \text{Species} k = 3) )</td>
<td>0.39</td>
<td>50.64</td>
<td>103.78</td>
<td>39</td>
</tr>
<tr>
<td>( \text{sum_v} = s(\text{mean_v}, by = \text{Species} k = 3) + s(\text{Si:N}, by = \text{Species} k = 3) + s(\text{MXLD}, by = \text{Species} k = 3) )</td>
<td>0.43</td>
<td>55.42</td>
<td>51.37</td>
<td>39</td>
</tr>
<tr>
<td>( \text{per_micro} = s(\text{MXLD}, by = \text{Species} k = 3) )</td>
<td>0.50</td>
<td>55.46</td>
<td>-77.04</td>
<td>29</td>
</tr>
</tbody>
</table>

Table 2.5: Relative Microbial Contribution to trophic transfers modeled by species (speciescal: C. finmarchicus, speciesty: C. typicus). Estimated parametric and smoothed effects, effective degrees of freedom (edf), standard error (Std.Error) and reference degrees of freedom (Ref.df), test statistic critical values (t-value/F) and p-values are shown by significance (‘.”’ < 0.1, ‘*’ <0.05, ‘***’ < 0.01, ‘****’ <0.001) for best fit model of tropic position by species. See Table 2.4 for full description of variable terms.

<table>
<thead>
<tr>
<th>Estimate/edf</th>
<th>Std.Error/Ref.df</th>
<th>t/F</th>
<th>P/S</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>0.43</td>
<td>0.01</td>
<td>29.34</td>
<td>P</td>
</tr>
<tr>
<td>speciesty</td>
<td>-0.12</td>
<td>0.02</td>
<td>-5.45</td>
<td>P</td>
</tr>
<tr>
<td>s(MXLD):speciescal</td>
<td>1.00</td>
<td>1.00</td>
<td>2.53</td>
<td>S</td>
</tr>
<tr>
<td>s(MXLD):speciesty</td>
<td>1.00</td>
<td>1.00</td>
<td>0.19</td>
<td>S</td>
</tr>
</tbody>
</table>

Table 2.6: \( \sum V \) modeled by species (speciescal: C. finmarchicus, speciesty: C. typicus). See Results Table 2.5.
Table 2.7 $\delta^{15}N_{\text{SAA}}$ modeled by species (speciescal: C. finmarchicus, speciesty: C. typicus). See Results Table 2.5.

<table>
<thead>
<tr>
<th></th>
<th>Estimate/edf</th>
<th>Std.Error/Ref.df</th>
<th>t/F</th>
<th>P/S</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>2.18</td>
<td>0.09</td>
<td>23.43</td>
<td>P</td>
<td>***</td>
</tr>
<tr>
<td>speciesty</td>
<td>-0.51</td>
<td>0.14</td>
<td>-3.75</td>
<td>P</td>
<td>***</td>
</tr>
<tr>
<td>s(Smeananom):speciescal</td>
<td>1.86</td>
<td>1.98</td>
<td>4.11</td>
<td>S</td>
<td>*</td>
</tr>
<tr>
<td>s(Smeananom):speciesty</td>
<td>1.00</td>
<td>1.00</td>
<td>0.00</td>
<td>S</td>
<td>.</td>
</tr>
<tr>
<td>s(SIN):speciescal</td>
<td>1.00</td>
<td>1.00</td>
<td>0.92</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(SIN):speciesty</td>
<td>1.00</td>
<td>1.00</td>
<td>3.10</td>
<td>S</td>
<td>.</td>
</tr>
<tr>
<td>s(MXLD):speciescal</td>
<td>1.00</td>
<td>1.00</td>
<td>2.85</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(MXLD):speciesty</td>
<td>1.32</td>
<td>1.54</td>
<td>1.91</td>
<td>S</td>
<td></td>
</tr>
</tbody>
</table>

Table 2.8 Anomaly model equation by time change, R2, deviance explained and number of samples in model (n) for the best fit models by species. See Table 2.4 for full description of variable terms.

<table>
<thead>
<tr>
<th>Equation</th>
<th>R2</th>
<th>dev.expl</th>
<th>AIC</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Smeananom + s(N2, by = Chg_Pat, k = 3) + s(MXLD, by = Chg_Pat, k = 3) + s(SIN, by = Chg_Pat, k = 3)</td>
<td>0.47</td>
<td>61.56</td>
<td>99.35</td>
<td>39</td>
</tr>
<tr>
<td>Smeananom + s(N2, by = Chg_Pat, k = 3) + s(MXLD, by = Chg_Pat, k = 3) + s(Smeananom, by = Chg_Pat, k = 3) + s(SIN, by = Chg_Pat, k = 3)</td>
<td>0.54</td>
<td>71.09</td>
<td>103.17</td>
<td>39</td>
</tr>
<tr>
<td>s(meananom, by = Chg_Pat, k = 3)</td>
<td>0.63</td>
<td>70.34</td>
<td>66.10</td>
<td>39</td>
</tr>
</tbody>
</table>
Table 2.9 Percent Microbial Contribution anomaly by time change. See Results Table 2.5.

<table>
<thead>
<tr>
<th></th>
<th>Estimate/edf</th>
<th>Std.Error/Ref.df</th>
<th>t/F</th>
<th>P/S</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-0.58</td>
<td>0.56</td>
<td>-1.02</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>catsecond</td>
<td>-0.12</td>
<td>0.59</td>
<td>-0.20</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>s(cenyp):catfirst</td>
<td>1.00</td>
<td>1.00</td>
<td>2.30</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(cenyp):catsecond</td>
<td>1.83</td>
<td>1.97</td>
<td>4.18</td>
<td>S *</td>
<td></td>
</tr>
<tr>
<td>s(N2):catfirst</td>
<td>1.32</td>
<td>1.53</td>
<td>0.51</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(N2):catsecond</td>
<td>1.81</td>
<td>1.96</td>
<td>2.76</td>
<td>S **</td>
<td></td>
</tr>
<tr>
<td>s(SIN):catfirst</td>
<td>1.92</td>
<td>1.98</td>
<td>6.56</td>
<td>S *</td>
<td></td>
</tr>
<tr>
<td>s(SIN):catsecond</td>
<td>1.00</td>
<td>1.00</td>
<td>2.37</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(Smeananom):catfirst</td>
<td>1.06</td>
<td>1.12</td>
<td>5.76</td>
<td>S *</td>
<td></td>
</tr>
<tr>
<td>s(Smeananom):catsecond</td>
<td>1.38</td>
<td>1.62</td>
<td>6.67</td>
<td>S **</td>
<td></td>
</tr>
</tbody>
</table>

Table 2.10 ΣV anomaly by time change. See Results Table 2.5.

<table>
<thead>
<tr>
<th></th>
<th>Estimate/edf</th>
<th>Std.Error/Ref.df</th>
<th>t/F</th>
<th>P/S</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>0.85</td>
<td>0.45</td>
<td>1.88</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>catsecond</td>
<td>-0.64</td>
<td>1.03</td>
<td>-0.62</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>s(calanus):catfirst</td>
<td>1.00</td>
<td>1.00</td>
<td>2.93</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(calanus):catsecond</td>
<td>1.88</td>
<td>1.98</td>
<td>3.81</td>
<td>S *</td>
<td></td>
</tr>
<tr>
<td>s(MXLD):catfirst</td>
<td>1.00</td>
<td>1.00</td>
<td>4.12</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(MXLD):catsecond</td>
<td>1.64</td>
<td>1.87</td>
<td>1.57</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(Smeananom):catfirst</td>
<td>1.74</td>
<td>1.93</td>
<td>2.15</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(Smeananom):catsecond</td>
<td>1.00</td>
<td>1.00</td>
<td>0.90</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(N2):catfirst</td>
<td>1.78</td>
<td>1.95</td>
<td>2.73</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(N2):catsecond</td>
<td>1.00</td>
<td>1.00</td>
<td>1.28</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(SIN):catfirst</td>
<td>1.00</td>
<td>1.00</td>
<td>3.64</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(SIN):catsecond</td>
<td>1.67</td>
<td>1.88</td>
<td>3.58</td>
<td>S *</td>
<td></td>
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</tbody>
</table>
Table 2.11 $\delta^{15}N_{\text{SAA}}$ Value anomaly by time change. See Results Table 2.5.

<table>
<thead>
<tr>
<th></th>
<th>Estimate/edf</th>
<th>Std.Error/Ref.df</th>
<th>t/F</th>
<th>P/S</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>0.15</td>
<td>0.14</td>
<td>1.06</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>catsecond</td>
<td>-1.43</td>
<td>0.98</td>
<td>-1.46</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>s(N2):catfirst</td>
<td>1.86</td>
<td>1.98</td>
<td>3.61</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(N2):catsecond</td>
<td>1.87</td>
<td>1.98</td>
<td>3.42</td>
<td>S</td>
<td>*</td>
</tr>
<tr>
<td>s(MXLD):catfirst</td>
<td>1.93</td>
<td>1.99</td>
<td>7.60</td>
<td>S</td>
<td>**</td>
</tr>
<tr>
<td>s(MXLD):catsecond</td>
<td>1.00</td>
<td>1.00</td>
<td>0.36</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(SiN):catfirst</td>
<td>1.80</td>
<td>1.96</td>
<td>2.47</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>s(SiN):catsecond</td>
<td>1.00</td>
<td>1.00</td>
<td>0.55</td>
<td>S</td>
<td></td>
</tr>
</tbody>
</table>
Figure 2.1 Schematic depiction of the connections between plankton and the flow of organic matter in the surface ocean. Green arrows reflect the pathway of primary production, and orange arrows reflect the pathway of different nutrient sources. a) simplifies the flow of different pathways and is modified from Sigman et al. (2012) while b) breaks the pathways into the hypothesized flow of organic matter through different size classes. Original artwork by C. Nowakowski.
Figure 2.2 The study region is located in Jordan Basin, Gulf of Maine, and was defined by the EcoMon strata 42. Points reflect individual station locations where *C. finmarchicus* (red) and *C. typicus* (blue) were collected from across years 1996-2017. Contours fall on the 100m (light grey) and 200m (dark grey) depth.
Figure 2.3 CSIA-AA Indices (mean ± SD pf propagated analytical error) for C. finmarchicus (red diamonds and lines) and C. typicus (blue triangles and lines) vs time: a) Trophic position: Metazoan reflects trophic position calculated with Glu as the trophic amino acid (Black line is the linear trend in both species as there was no difference between species here) and Microbial reflects trophic position calculated with Ala as the trophic amino acid, b) Relative contribution of microbial trophic transfers (as determined by trophic position calculated using Ala as the trophic amino acid) to copepod trophic position, c) copepod reliance on degree of microbial reworked organic matter (ΣV) and d) mean source amino acid nitrogen isotope value (δ15N_SAA). Lines reflect linear models from Table 2.3.
Figure 2.4 GAMs time modes on anomaly values for a) Trophic position, b) relative microbial contribution to trophic transfers, c) \(\sum V\), c) \(\delta^{15}N_{\text{SAA}}\). The y axis reflects anomaly values, which were calculated by species. Shading represents the first derivative of the GAMs time smooth; purple is 0.15 units/year and light blue is -0.15 units/year. Black shading behind the GAMs time smooth represents the periods where the first derivatives is not equal to zero and reflects significant change. Horizontal lines reflect the time change associated with the predictor relationships.
Figure 2.5 Predicted CSIA-AA index values based on best-fit GAMs including species categorical terms and intercepts and 95% CIs represented by shading. The alpha value (degree of transparency) is proportional to the RSSn value normalized to 0.8 where less transparent indicates smaller residual deviance, and more transparent indicates larger residual deviance. Orange are C. finmarchicus samples, and blue are C. typicus samples, points are the original values, and lines are the GAMs additive fit. See Table 2.4 for full description of variable terms.

Figure 2.6 Each row of plots reflects the best fit model for each CSIA-AA index. Points are the original values, and lines are the GAMs additive fit.
Orange is the first-time frame and blue is the second time frame as identified by the AIC values in Figure 2.10: The relative microbial contribution to trophic transfers model had a change in the fall of 2003, $\Sigma V$ had a change in the spring of 2006, the $\delta^{15}N_{SAX}$ had a change in the spring of 2012. The alpha value (degree of transparency) is proportional to the RSSn value normalized to 1.4, where less transparency indicates smaller residual deviance, and more transparency indicates larger residual deviance. See Table 2.4 for full description of variable terms.

Figure 2.7 $\Sigma V$ GAM’s Additive fits vs time. Continuous line in the background and light gray points reflect the GAMs additive time component of the original values, and the foreground broken line represents the additive component of
each variable as modeled in Table 2.10. See Table 2.4 for full description of variable terms.

Figure 2.8 Example of winter water column properties and dynamics. The GAMs Surface temperature anomaly during the winter additive time component is plotted at 0 meters, the color bar ranges from anomaly values -2.77 (purple) to 2.77(yellow). The euphotic zone is marked at the average winter depth in Jordan Basin as according to Bisagni 2003. The GAMs mixed layer depth time component is plotted using actual values, with dark blue indication 130.0m and light-yellow indicating 69.1m. The silicate to nitrate ratio represents the source water signal and is plotted in reference to depths below 100m where the lightest green reflects the anomaly value of -2.2 and the darkest green 2.2 as it is calculated from the composition of slope water at and below this depth. The dilution, and therefore resulting volume of the surface layer and water in the euphotic zone is a function of the mixed layer depth. Additionally, it is hypothesized that the deeper the mixed layer depth is, the more connected the surface water will be with the bottom slope water system.
Table 2.12 Akaike Information Criterion (AIC) values for linear model fixed and mixed effects testing. Index is the CSIA-AA index being tested, model is the equation form tested, AIC_Diff is the AIC of each model equation – the AIC of the linear model. Lowest values of AIC_Diff reflect the best fit linear trend.

<table>
<thead>
<tr>
<th>Index</th>
<th>model</th>
<th>AIC_val</th>
<th>AIC_Diff</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trophic Position Microbial Contribution</td>
<td>Index ~ Time + (1</td>
<td>Species)</td>
<td>213.2181</td>
</tr>
<tr>
<td>Trophic Position Microbial Contribution</td>
<td>Index ~ Time + (0 + Time</td>
<td>Species)</td>
<td>213.2637</td>
</tr>
<tr>
<td>Trophic Position Microbial Contribution</td>
<td>Index ~ Time + (1 + Time</td>
<td>Species)</td>
<td>217.2213</td>
</tr>
<tr>
<td>Trophic Position Microbial Contribution</td>
<td>Index ~ Time</td>
<td>440.4236</td>
<td>0.00000</td>
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<td>Index ~ Time</td>
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<td>0.00000</td>
</tr>
<tr>
<td>Trophic Position Metazoan</td>
<td>Index ~ Time + (1</td>
<td>Species)</td>
<td>-335.6783</td>
</tr>
<tr>
<td>Trophic Position Metazoan</td>
<td>Index ~ Time + (0 + Time</td>
<td>Species)</td>
<td>-335.6783</td>
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<td>Species)</td>
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<td>Species)</td>
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</tr>
<tr>
<td>Percent Microbial Contribution</td>
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<td>Species)</td>
<td>-1028.7404</td>
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<td>Percent Microbial Contribution</td>
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<td>Species)</td>
<td>-1024.7619</td>
</tr>
<tr>
<td>Percent Microbial Contribution</td>
<td>Index ~ Time</td>
<td>-797.3912</td>
<td>0.00000</td>
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<td>Sum V</td>
<td>Index ~ Time + (1</td>
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<tr>
<td>Sum V</td>
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<td>Species)</td>
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<td>Sum V</td>
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<td>Species)</td>
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<td>Sum V</td>
<td>Index ~ Time</td>
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<td>Mean Source Amino Acid</td>
<td>Index ~ Time + (1</td>
<td>Species)</td>
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<td>Species)</td>
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</tr>
<tr>
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<td>Species)</td>
<td>1111.7973</td>
</tr>
<tr>
<td>Mean Source Amino Acid</td>
<td>Index ~ Time</td>
<td>1221.7090</td>
<td>0.00000</td>
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</table>
Table 2.13 Number of individual copepods within each composition year by species. Zooplankton sample weight in mg by taxa, year, and number of individuals.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Year</th>
<th>n individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. finmarchicus</td>
<td>1996</td>
<td>30</td>
</tr>
<tr>
<td>C. typicus</td>
<td>1996</td>
<td>60</td>
</tr>
<tr>
<td>C. finmarchicus</td>
<td>1997</td>
<td>25</td>
</tr>
<tr>
<td>C. typicus</td>
<td>1997</td>
<td>63</td>
</tr>
<tr>
<td>C. finmarchicus</td>
<td>1998</td>
<td>28</td>
</tr>
<tr>
<td>C. finmarchicus</td>
<td>1999</td>
<td>28</td>
</tr>
<tr>
<td>C. typicus</td>
<td>1999</td>
<td>64</td>
</tr>
<tr>
<td>C. finmarchicus</td>
<td>2000</td>
<td>28</td>
</tr>
<tr>
<td>C. typicus</td>
<td>2000</td>
<td>60</td>
</tr>
<tr>
<td>C. finmarchicus</td>
<td>2001</td>
<td>28</td>
</tr>
<tr>
<td>C. typicus</td>
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<td>50</td>
</tr>
<tr>
<td>C. finmarchicus</td>
<td>2002</td>
<td>35</td>
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Figure 2.9 $\delta^{15}N$ values (‰) of individual amino acids in a) C. finmarchicus samples and b) C. typicus. Amino acid names are presented in standard three letter abbreviations. Figure symbols represent each composite sample analyzed by year.
Figure 2.10 AIC values plotted vs time from each time change tested as a categorical variable in GAMs predictor models. Horizontal lines are the AIC value of a model fit without a time change; vertical lines reflect the best fit model with the lowest AIC value. a) Relative microbial contribution to trophic transfers, b) heterotrophic microbial reworking c) $\delta^{15}N_{\text{SAA}}$ value.
Chapter 3 Multidecadal molecular isotope records of pelagic plankton bioarchives and deep-sea corals indicated strong pelagic-benthic coupling in the Gulf of Maine driven by slope water dynamics, Si:N ratios, and mixed layer depth.

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ABSTRACT

In continental shelf ecosystems, pelagic-benthic coupling provides essential ecosystem functions, including energy transfer in surface and deep ocean food webs, regulation of biogeochemical cycling, and climate feed-back mechanisms through carbon sequestration. Yet despite its importance, access to long-term data sets of export production are scarce and urgently needed to test assumptions about 1) the sources and transformations of organic matter through different food web pathways, and 2) the variability of these processes across climatic, oceanographic, and ecological changes through time. This study applied compound-specific stable nitrogen isotope analysis of amino acids to a 38 year (1981-2019) time series of pelagic copepod bioarchives (large-bodied *Calanus finmarchicus* and small-bodied *Centropages typicus*) and deep ocean bioarchives (deep-sea coral *Primnoa resedaeformis*) in the Gulf of Maine, to fill a critical data gap in our understanding of the patterns and drivers of variation in export production on ecologically relevant time scales. This is a region leading in the global warming trend and at the interface of multiple major ocean current systems that alter key bottom-up drivers of food web structure. We calculated multiple key metrics of food web dynamics that regulate export production, including: water bass nitrogen source ($\delta^{15}N_{SAA}$), degree of heterotrophic microbial reworking on organic matter ($\Sigma V$), and relative contribution of metazoan ($TP_{Glx-Phe}$) and microbial ($TP_{Ala-Phe}$) trophic transfers to food chain length, all of which revealed strong pelagic-benthic coupling in both magnitude and temporal trend. As hypothesized, there was particularly strong agreement across all metrics between large-bodied *C.*
**finmarchicus** and deep-sea *P. resedaeformis*, including a steady increase in the heterotrophic microbial reworking trend. The strong reliance of *C. finmarchicus* on microbial loop processes, including elevated $T_{\text{Ala-Phe}}$ transfers (4+/− 0.3) and a high level of $\sum V$ (2.0 ± 0.5), was mirrored in *P. resedaeformis*, creating a direct mechanism to link surface microbial loop food web dynamics to the deep ocean through the biological pump. Generalized additive models revealed key relationships among distinct deep slope water masses entering the Gulf of Maine, water column mixing and stratification processes, surface ocean biogeochemical and trophic dynamic processes reflected in the isotopic values of export production recorded in deep sea corals. Identifying the strong microbial loop connectivity between the pelagic and benthic systems will greatly improve our understanding of Gulf of Maine export dynamics and ability to better parameterize new mechanistic General Ecosystem Models, which management and conservation strategies for regional fisheries and protected marine mammal species depend on.

**INTRODUCTION**

Within continental shelf ecosystems, pelagic-benthic coupling provides essential ecosystem functions, including energy transfer in surface and deep ocean food webs, regulation of biogeochemical cycling, and climate feed-back mechanisms through carbon sequestration (Griffiths et al. 2017). Primary production in the euphotic zone is transformed by food web processes into sinking particulate organic matter (POM) that is exported from the upper ocean into the ocean interior constituting the ocean’s Biological Pump (e.g., Buesseler & Boyd, 2009; Steinberg & Landry, 2017; Boyd et al. 2019). As such, variations
in the factors that impact the pelagic food web, including physical (e.g., stratification; mixed layer depth), chemical (e.g., water mass nutrient delivery), and biological (e.g., plankton community production and composition; microbial degradation of POM) processes, can exert strong controls over export production (De la Rocha & Passow 2007; Passow & Carlson 2012). Yet the scarcity of long-term data sets of the sources and transformations of export production presents a major impediment to testing assumptions about 1) the roles different plankton food web pathways play in linking pelagic and benthic ecosystems, and 2) the variability of these processes across different climatic, oceanographic, and ecological changes through time.

The Gulf of Maine is an ideal natural laboratory for investigating historic bottom-up drivers of export production dynamics. The Gulf of Maine region lies at the confluence of sub-tropical (Gulf Stream – Warm Slope Water [WSW]) and sub-Arctic (Labrador Slope Water [LSW] and Scotian Slope Water [SSW]) current systems (Balch et al. 2012; Peterson et al. 2017; Gonçalves Neto et al. 2021), the dynamic interplay among which has triggered a series of decadal-scale hydrographic, biogeochemical, and biological step-changes over the last half century (Petrie & Drinkwater 1993; Greene et al. 2013). Jordan Basin, which sits along the path of slope water intrusion into the Gulf of Maine via the Northeast Channel (Record et al. 2019), has a multidecadal history of oceanographic observations (Bigelow 1926), with concurrent physical, chemical, and biological data that can be pieced together from the mid-1960s onward, including the long-term EcoMon oceanographic and zooplankton monitoring
program, and continuous data from instrumented moorings and satellites since the late 1990s (e.g., Townsend et al. 2010).

Long-term, high resolution biological archives (bioarchives) can fill a critical data gap in our understanding of the patterns and drivers of variation in export production on ecologically relevant time scales. Proteinaceous deep-sea corals act as “living sediment traps,” providing century scale, annually-resolved geochemical records of changes in surface biogeochemical cycling and plankton community dynamics transported to depth via export production (Sherwood et al. 2011, 2014; Robinson et al. 2014; McMahon et al. 2015a). P. resedaeformis, one of the dominant deep-sea coral species in the NW Atlantic, can live for hundreds of years and records geochemical signals in its diet, sinking POM, in the annual growth rings of its diagenetically resistant protein-calcite skeleton (Sherwood et al. 2005a,b, 2006; Sherwood and Edinger 2009). At the same time, long-term zooplankton monitoring programs, such as the NOAA Ecosystem Monitoring Program (EcoMon; Richardson et al. 2010) in the NW Atlantic provide historic records of pelagic food web processes fueling the sources and transformations of organic matter that becomes export production. Copepods are the most numerous metazoans in the ocean and are key conduits of energy from primary producers to upper trophic levels as well as variable but important contributors to export production via fecal pellet production (Pershing et al. 2005; Meyer-Gutbrod & Greene 2014; Steinberg & Landry 2017). Variations in body size, prey preferences, past population fluctuations in response to climate oscillations and warming trends can all modulate the roles
that these heterotrophic metazoans play in the timing and composition of export production.

In the 1980s and 2000s *C. finmarchicus* (late-stage CV and adult CVI) were more abundant than small, temperate Centropages typicus, but during the fresh, stratified 1990s, the pattern reversed (Pershing et al. 2005; Bi et al. 2014). These transitions reflect a combination of shifts in advective forces and bottom-up changes in food web dynamics as *C. finmarchicus* relies heavily on periods with strong spring diatom blooms to accumulate lipids prior to entering diapause (Hansen et al. 1994; Hirsche 1996), whereas a smaller species like *C. typicus* consumes smaller prey such as ciliates, picoeukaryotes, and dinoflagellates when nutrient limitation in the euphotic zone selects for small-celled food webs (Calbet et al. 2007). Variations in copepod body size, prey preferences, responses to climate oscillations and warming trends, and population fluctuations in response to physical-chemical shifts can all modulate the roles that these heterotrophic metazoans play in the timing and composition of export production.

For decades, large phytoplankton have been assumed to typically be grazed by large zooplankton, which together produce ballasted, fast sinking particles leading to enhanced export production and stronger pelagic-benthic coupling (Billett et al., 1983; Michaels and Silver, 1988; Boyd and Stevens, 2002; Aksnes and Wassmann, 1993). In the Gulf of Maine, recent observations suggest that periods typified by large-bodied *C. finmarchicus* often coincide with stronger pelagic-benthic coupling (Wanamaker et al. 2009; Stamieszkin et al. 2014).
Yet, increasing sea surface temperatures have been implicated in ecosystem shifts towards small-cell, microbial loop-dominated food webs with potentially reduced energy transfer to higher trophic levels and benthic systems (Karl et al. 2001; Li et al. 2009), coinciding with projected decreases in *C. finmarchicus* abundance as the Gulf of Maine warms (Grieves et al. 2017; Record et al. 2019). Yet recent work has indicated that *C. finmarchicus* may in fact play a larger role in microbial loop food web dynamics than typically assumed (Nowakowski Chapter 2), which may serve as an important mechanism by which microbially reworked organic matter from pelagic systems is exported to the deep ocean, and in turn linking export dynamics to the processes of warming, stratification, and nutrient limitation that regulate microbial loop food web dynamics (Close et al. 2013).

By comparing multidecadal geochemical records of the sources and transformations of organic matter supporting pelagic (copepod) and benthic (coral) production in a system with dramatic and well documented shifts in regional climate, oceanography, and biogeochemical cycling, we can greatly expand our understanding of historic changes in coupling of pelagic-benthic systems through export production. Previously, much of the stable isotope analysis of bioarchives has focused on total (“bulk”) organic material, revealing information about past changes in surface ocean conditions, productivity, and biogeochemical cycling (e.g., Heikoop et al. 2002; Sherwood et al. 2005a, 2009; Williams et al. 2007; Hill et al. 2014). However, a main challenge to interpreting bulk stable isotope data in a paleo-context is determining whether isotopic
changes are due to changes in 1) baseline nitrogen (15NO3) values, 2) trophic transformations of organic matter, 3) microbial reworking of POM, or 4) some combination of all of these factors (Altabet 1988; Wakeham & Lee 1989; Hofmann et al. 2000; Lehmann et al. 2002).

Recent advances in compound-specific isotope analysis of amino acids (CSIA-AA) can disentangle key geochemical information about the sources and transformations of organic matter recorded in long-term, high resolution pelagic (e.g., copepod) and benthic (e.g., deep-sea coral) bioarchives, thus filling a critical data gap in our understanding of the patterns and drivers of variation in export production on ecologically relevant time scales (Hannides et al. 2009; Décima et al. 2013; Sherwood et al. 2011, 2014). These approaches rely on differential isotope fractionation of individual amino acids, which have yielded a number of robust, quantitative metrics of organic matter transformation that link pelagic and benthic components of export production (reviewed in Ohkouchi et al. 2017). The trophic transfer index can help differentiate between short traditional food webs and long microbial food webs in the pelagic system and export production from fresh sinking algal production vs zooplankton fecal pellet production (Décima et al. 2017; Doherty et al. 2021), heterotrophic microbial reworking can identify the degree of fresh organic matter export vs microbial remineralization of sinking organic matter (McCarthy et al. 2007), and the source water index tracks changes in nitrogen cycling among WSW/LSW/SSW water masses with distinct nutrient ratios and d15N signatures entering the Gulf of Maine (Sherwood et al. 2011). Together, these CSIA-AA metrics have the
potential to greatly improve our understanding of the fate of organic matter and biogeochemical cycling across the water column (McMahon et al. 2018).

This study quantifies the proximate drivers of and temporal variations in the sources and transformations of marine export production in a highly variable oceanographic region. By comparing geochemical records of metazoan and microbial trophic dynamics and biogeochemical cycling supporting pelagic (copepod) and benthic (coral) production in a statistical modeling framework, we test the classic pelagic-benthic coupling hypothesis: 1) there is strong pelagic-benthic coupling in this system, defined here as geochemical proxies in deep-sea corals that mirror the magnitude and temporal dynamics of pelagic copepod geochemical proxies, particularly large bodied *C. finmarchicus*, and 2) stronger pelagic-benthic coupling occurs under environmental conditions that support higher large body copepod populations (*C. finmarchicus*) (e.g., higher Si:N ratios, shorter food chains, less microbial reworking of organic matter) and weaker pelagic-benthic coupling occurs under environmental conditions that support higher small body copepod populations (*C. typicus*) (e.g., lower Si:N ratios, longer food chains, more microbial reworking of organic matter). As increasing warming has been implicated in ecosystem shifts towards small-cell, microbial loop-dominated food webs with potentially reduced energy transfer to higher trophic levels (Karl et al. 2001; Li et al. 2009), developing historic time series of the relationships between oceanographic condition, pelagic food web dynamics, and export production will improve our ability to predict how these systems will respond in the future.
METHODS

Processing the Coral Colonies

Colonies of *P. resedaeformis* were collected using a remotely operated vehicle in Jordans Baisn 2019 (Figure 3.1). Samples were frozen at the time of collection and sections from 1cm to 2cm thick were cut from the coral base with an IsometTM low speed saw. The polyp tissue was then removed, and thick sections were polished using 1500-3000 grit sandpaper and cleaned ultrasonically using deionized water to reveal banding patterns. Imaging was done using a retrofitted GoPro Hero 10, 24mp on a dissection microscope under ultraviolet light to highlight the contrast between the growth rings (Figure 3.14). The final images were used for both aging the growth bands and guiding the sampling process for CSIA-AA. Individual growth bands were isolated from the coral thick sections by placing the sections in 5% HCL to dissolve carbonate and then peeling individual growth rings using dissection tools (e.g., Sherwood et al. 2005). Individual growth bands were fully submerged in 5% HCL for 24 hrs to dissolve any remaining calcite. Finally, samples were tripled rinsed in deionized water and dried in an oven at 50°C overnight. Annual growth rings were identified by counting the transitions between dark (proteinaceous) and light (calcite) bands (Sherwood and Edinger 2008). The outside band that was initially covered with living polyp tissue is assumed to be dated to the time of collection.

Bulk Isotope Analysis

For bulk stable isotope analysis, 0.6mg subsamples of the annual growth bands of the dried proteinaceous skeleton were weighed into capsules and analyzed for 15N and 13C values on an Elementar VarioEL Cube Elemental
Analyser followed by "trap and purge" separation and on-line analysis by continuous-flow with a DeltaPlus Advantage isotope ratio mass spectrometer coupled with a ConFlo III interface at Laboratoire d'isotopes Stables Ján Veizer, Ontario Canada. All isotope values are expressed relative to the standards: $^{15}$Nair (-3.9) and $^{13}$Cvdpdb(-28.5) using standard delta notation ($\delta$) in permil units (‰).

CSIA-AA Methods

Each entire sample band of *P. resedaeformis* proteinaceous skeleton was acid-hydrolyzed in 0.5mL of 6 N HCl at 110°C for 20 h to isolate the total free amino acids. Samples were passed through 0.45 µm Millipore glass-fiber filters and then derivatized by esterification with acidified isopropanol followed by acylation with trifluoroacetic anhydride following McMahon et al. (2018). Derivatized samples were extracted using a P-buffer (KH$_2$PO$_4$ + Na$_2$HPO$_4$ in Milli-Q water, pH 7) – chloroform solution two times with centrifugation (600 g) and organic phase extraction between each round (Ueda et al., 1989) and then acylated once again.

Derivatized amino acids were injected on column (1µl in ethyl acetate) in splitless mode at 250°C and separated on a BPX5 column (60 m 0.32 mm ID, 1.0 m film thickness) in a Thermo Trace Ultra gas chromatograph (GC), and the separated amino acid peaks were analyzed on a Finnegan MAT DeltaPlus XL isotope ratio mass spectrometer (IRMS) interfaced to the GC through a GC-IsoLink II and reduction furnace (1000°C) with liquid nitrogen trap. Coral skeleton samples were analyzed in triplicate, bracketed by a mixed amino acid standard of known isotopic composition (Sigma-Aldrich Co.) and homogeneous
algal lab working standard included as a known-unknown for quality assurance and quality control purposes (Yarnes and Herszage 2017). The long-term reproducibility of 15N values in the algal lab working standard was ± 0.3‰ (mean across all individual amino acids for >100 separate full analyses, which provides an estimate of full protocol reproducibility (hydrolysis, wet chemistry, and isotope analysis).

We measured 13 individual amino acids with sufficient peak size and well-defined baseline chromatographic separation, which we classified as trophic amino acids: glutamic acid/glutamine (Glx), aspartic acid/asparagine (Asx), alanine (Ala), leucine (Leu), isoleucine (Ile), proline (Pro), valine (Val), and source amino acids: phenylalanine (Phe), Methionine (Met), and Lysine (Lys) (McMahon and McCarthy 2016). Glycine (Gly), serine (Ser), and threonine (Thr) were kept as separate groups given the lack of consensus on degree of trophic fractionation (reviewed in McMahon and McCarthy, 2016). Note, acid hydrolysis converts glutamine (Gln) and aspartamine (Asn) into glutamic acid and aspartic acid, respectively, due to cleavage of the terminal amine group, resulting in the measurement of combined Gln + Glu (referred to hereby as Glx), and Asn + Asp (referred to hereby as Asx). Stable isotope ratios are expressed relative to Air in standard delta (δ) notation in per mil units (‰).

CSIA-AA Metrics
Source Nitrogen Index
The Source Nitrogen Index, calculated as the mean $\delta^{15}N_{\text{SAA}}$ value of source amino acids ($\delta^{15}N_{\text{SAA}}$ value of Phe, Lys), reflects the nitrogen isotope signal of biogeochemical cycling at the base of the food web supporting copepod
production, which can be used, for example, to constrain variation in nutrient source (e.g., water mass contribution) and biogeochemical cycling (e.g., N2-fixation and nitrification) (McClelland et al. 2003; Sherwood et al. 2011; Whitney et al. 2020). Source amino acids undergo minimal nitrogen isotope discrimination during trophic transfers, such that $\delta^{15}N_{SA}$ values provide a robust proxy for the isotopic value of nitrogen cycling at the base of the food web, without the confounding factor of trophic modification (McMahon and McCarthy 2016).

$\sum V$ Index

The degree of heterotrophic microbial reworking of organic matter supporting copepod production (e.g., Wakeham et al., 1997; Calleja et al. 2013) was calculated using the $\sum V$ Index, which reflects the cumulative increased variance of trophic amino acid $\delta^{15}N$ values during microbial degradation relative to predictable patterns from metazoan trophic discrimination (McCarthy et al. 2007): $\sum V = \frac{1}{n} \sum |X_{AA}|$, where $X_{AA}$ is the deviation of each trophic amino acid $\delta^{15}N$ value from the mean of all sampled trophic amino acids (Ala, Asx, Glx, Ile, Leu, and Pro) and $n =$ the total number of amino acids used in the calculation. The degree of heterotrophic microbial reworking differentiates between zooplankton feeding on fresh algal-based production ($\sum V < 2$) and microbially re-mineralized organic matter ($\sum V > 2$) (McCarthy et al. 2007).

Trophic Transfer Index

The trophic transfer index provides information about the number of trophic transfers of energy and organic matter between trophic levels and thus the length of food chains supporting copepod production. Food chain length is
a classic ecological parameter with implications for the efficiency of energy transfer to higher trophic levels (McMahon and McCarthy 2016). As an important ecological metric of ecosystem structure, food chain length plays a central role in the function of ecological communities by modulating energy transfer from primary productivity to apex predators (Degerman et al. 2018; Décima 2022). We calculated a metazoan trophic transfer index (TP\textsubscript{Glx-Phe}) that is internally indexed to the isotopic baseline (Chikariashi et al. 2009; McMahon et al. 2018): 

\[ TP_{Glx-Phe} = 1 + \frac{(\delta^{15}N_{Glx} - \delta^{15}N_{Phe}) - \delta^{15}N_{Phe} - \beta_{Glx-Phe}}{TDF_{Glx-Phe}}, \]

where the the \( \delta^{15}N_{Glx} \) and \( \delta^{15}N_{Phe} \) are the nitrogen isotope values of copepod heavily fractionating trophic amino acid (Glx) and minimally fractionating source amino acid (Phe) of the coral samples, \( \beta_{Glx-Phe} \) (3.3 ± 1.8‰) is the difference in Glx and Phe \( \delta^{15}N \) value in marine microalgae (Ramirez et al. 2021), TDF\textsubscript{Glx-Phe} is the diet to consumer nitrogen isotope trophic discrimination factor of Glx and Phe (7.6 ± 1.4‰) (McMahon & McCarthy 2016), and \( \delta^{15}N_{Phe} \) (3.4 +/- 0.1) reflects the offset between the proteinaceous skeletons and polyp tissue (McMahon et al. 2018). Previous work has suggested that the trophic amino acid Glx may not register microbial trophic transfers (TDF ~ 0‰; Gutiérrez-Rodríguez et al. 2014) and thus underestimate trophic position in food chains that contain microbial loop trophic dynamics. Décima et al. (2017) supported those conclusions and suggested an Ala as an alternative trophic amino acid that shows trophic fractionation through both protist and metazoan trophic transfers. This method has been applied to communities of zooplankton in the Pacific where a large range of microbial trophic transfers were identified by
species (Décima and Landry 2020) as well as in piscivores species where 6-21% of the trophic transfers were attributed to protistan processes (Bode et al. 2021). Therefore, we also calculated a second trophic transfer index using Ala as the trophic amino acid (TP\textsubscript{Ala-Phe}), which has been shown to be more sensitive to microbial transfers (Décima et al. 2017; Bode et al. 2021) and modified it to include the offset (Ala Phe 5.12 +/- 0.45) between the proteinaceous skeleton and polyp tissue from McMahon et al. 2018:

$$TP_{Ala-Phe} = 1 + \frac{(\delta^{15}N_{Ala} - \delta_{Ala-Phe}^{15}N_{Phe} - \beta_{Ala-Phe}^{15}N_{Phe})}{TDF_{Ala-Phe}}$$

where $\beta_{Ala-Phe}$ is 3.2 ± 1.2 (Ramirez et al. 2021) and $TDF_{Ala-Phe}$ is 4.5 ± 2.1‰ (McMahon & McCarthy 2016). The change in relative percent of trophic position due to microbial trophic transfer was calculated by take the fraction of $TP_{Glx-Phe}$ and $TP_{Ala-Phe}$ allowing for the relative comparison of the two trophic transfer indexes (Bode et al. 2021).

Error propagation was iterated across 100,000 times using the function propagate() from the R package “propagate” (Spiess 2018). Samples were not run in replication due to limited resources, and the analytical error from triplicate injections is propagated across each CSIA-AA index.

Modeling Environmental Drivers of Food Web Dynamics
The model design was constructed to test the hypotheses: 1) there is strong pelagic-benthic coupling in this system linked to large bodied $C.~finmarchicus$, and 2) stronger pelagic-benthic coupling occurs under environmental conditions that support $C.~finmarchicus$. First, we targeted the difference between species CSIA-AA index values, and how those differences changed throughout the time series by testing the linear fixed and mixed effects, as well as by modeling the
GAMs additive time component. Then the GAMs predictor models were used to analyze the correlations between the CSIA-AA indices and key environmental variables and to test if those relationships experienced a change around known environmental events in the Gulf of Maine. Gaussian, Lognormal, and Gamma distributions were tested for each index, and a gaussian distribution was found to be the appropriate for all.

Test by Species
To test if the three CSIA-AA food web metrics 1) Source Nitrogen Index, 2) ΣV Index, and 3) Trophic Transfer Index for each species had the same mean values and followed the same overarching time trend, a series of linear models were fit, and the best was selected using the lowest Akaike Information Criterion (AIC) value. The first was a simple linear model using the lm() function and the next three were all linear mixed-effects models fit with the lmer() function from the “lme4” package (Douglas et al. 2015), of which, one fit separate intercepts and the same slope: “lmer(var ~ year + (1 | species), data = data)”, another fit separate slopes and the same intercept: “lmer(var ~ year + ( 0 + year | species), data = data)” and the third fit both separate intercepts and slopes: “lmer(var ~ year + ( 1 + year | species), data = data)”.

Testing Interdecadal trends
To test if there was interdecadal variability in the three CSIA-AA food web metrics, generalized additive models (GAMs) were fit to annual anomaly values \( \frac{(x - \text{mean}(x))}{sd(x)} \) as a function of time using the “mgcv” package and the method “REML” with smoothing parameter K = 10 (Wood 2011) and are identified as GAMtime here and throughout. We identified when the time smooth was
significantly changing as the first derivative was not equal to zero, i.e., 95% of each of the upper and lower quantiles for each spline were either all above or below zero. This was calculated using a modified version of the example code “Differentiating the smooths in a model (with CIs for derivatives)” from the function predict.gam() in the “mgcv” R package. Time points where the standard deviation bounds were both positive/negative were considered to have a significantly increasing/decreasing time trend.

Data were first aggregated to a monthly resolution and missing months were imputed using methods as follows from chapter 1. The environmental data were then aggregated to the resolution of the coral samples. Anomalies were then calculated to facilitate comparable coefficients. Co-predictor variables were analyzed for co-variance using the cor() function in R and variables with correlations above 0.5 were not included in the model selection process together. Co-predictor variables that were found to not covary significantly were Si:N, the mixed layer depth, a Brunt–Väisälä frequency based stratification index (N2), and abundances for C. finmarchicus and C. typicus. Si:N was found to co-vary with BT, ST, SS, WSW, LSW, SSW, and BS, mixed layer depth was highly correlated with AMO, and N2 was highly correlated with the NAO.

When testing environmental variables to assess drivers of the coral food web parameters, many were correlated and thus limited inclusion in the models. However, the Si:N ratio, mixed layer depth, N2, and C. finmarchicus and C. typicus abundance all were not over correlated with one another (see supplemental). The Si:N ratio, mixed layer depth, and N2 were all calculated
applying the in situ temperature and salinity data, and including them in the model increases the interpretation of the environmental dynamics associated with changes in temperature and salinity.

GAMs for fitting parameters

To identify correlations for each CSIA-AA index a modeling process was developed to address variable selection and to identify parameters that capture the temporal autocorrelation. For variable selection, a least absolute shrinkage and selection operator (LASSO) method was applied; the method adjusts the coefficient for each variable based on the p-value and moves the least significant coefficients to zero. To apply a fixed effects model framework, each variable was multiplied by a (0,1) categorical variable to generate a separate term for each species and a categorical vector was included to model separate intercepts. The highest coefficient for each separate environmental variable were then selected as initial variables using a cutoff that defines the maximum degrees of freedom that can be fit with n points in the model: \[ \frac{n}{(n+k)k} \] where k is the smoothing parameter (k = 3 here).

Each combination of variables was fit in a GAM of the form: \( GAM(y \sim s(x_1, by = species, k = 3) + ... + species) \). The smoothing parameter K was set to 3 to constrain the modeled relationships within realistic environmental conditions (Grieves et al. 2017) and to limit the degrees of freedom. The model with the lowest AIC value was selected as the final model. We calculated a normalized residual sum of squares (RSS) value to assess how well the environmental variables fit the copepod abundance. Because the metric was
normalized, values could be compared across models where the closer the value was to zero, the better the model fit.

To identify time changes in the additive components for each environmental model, the same GAM method above was applied, but instead of using the actual values for the isotope indexes for the dependent variable, the anomaly values were applied to remove the intercepts associated with each species. Then instead of applying species as a fixed effect, a categorical time variable was applied to test the significance of a shift at every time point after the first $K + 2$ data points and before the last $K + 2$ data points to account for degrees of freedom. The lowest AIC value was used to select the significant change point (Method modified from Gonçalves Neto et al. 2021).

RESULTS
The CSIA-AA 15 N amino acid profile for both species (Figure 3.2) was also found to follow classic metazoan CSIA-AA trophic and source separation patterns (McMahon and McCarthy 2016). The most significant decadal change in the coral was identified in the Heterotrophic microbial reworking which increased linearly by 0.41 units across the time series (Table 3.1; Figure 3.3). None of the other coral indexes had a linear slope that was larger than the associated error (Table 3.1). The coral was found to have a long microbial food chain, the $TP_{\text{Ala-Phe}} (4+/\text{-} 0.3)$ was found to be 1.6 trophic transfers higher than the $TP_{\text{Glx-Phe}} (2.4 +/- 0.1)$ and the average relative microbial contribution to trophic transfers was 0.41 +/- 0.04. While other indexes did not have steady decadal scale changes, all but the trophic position had interannual trends (Figure 3.3). The relative contribution of microbial trophic transfers decreased
from 1988-1992 and rose back up to the initial state from 1997-2000; the Heterotrophic microbial reworking increased over the time frame, and the $\delta^{15}N_{\text{SAA}}$ experienced a steady increase at the start of the time series until 1991 (Figure 3.3).

Comparing Coral and Copepod CSIA-AA

The coral and copepod CSIA-AA data sets were evaluated for differences and similarities on both decadal and interannual levels and strong pelagic benthic coupling was identified across all species, and a direct connection between the coral and *C. finmarchicus* was identified. When testing linear, fixed, and mixed effects models across all indexes, each species was identified to be more likely to share a slope than not by comparing the AIC (a criteria that weights both the degrees of freedom as well as the maximum likelihood of the model estimate) (Table 3.13; Table 3.2; Figure 3.4), and in particular, *P. resedaeformis* was found to be more likely to share an intercept with *C. finmarchicus* (Table 3.13; Table 3.2; Figure 3.4). $\text{TP}_{\text{Glx-Phe}}$ had the same intercept across all species (2.3 +/- 0.2) (Table 3.13; Table 3.2) and $\text{TP}_{\text{Ala-Phe}}$, the relative contribution of microbial trophic transfers, $\sum V$, and $\delta^{15}N_{\text{SAA}}$ were all identified to have different intercepts by species (Table 3.13). *C. typicus* was found to have a lower intercept than *P. resedaeformis* in both the $\text{TP}_{\text{Ala-Phe}}$ (0.46 Trophic Transfers), the relative contribution of microbial trophic transfers (8%), $\sum V$ (0.57 units), and the $\delta^{15}N_{\text{SAA}}$ (2.2‰) (Table 3.2). While *C. finmarchicus* was found to have values closer to the *P. resedaeformis*; both the relative contribution of microbial trophic transfers and $\sum V$ had a very small differences, and the *C. finmarchicus* $\text{TP}_{\text{Ala-Phe}}$ was 0.16 trophic transfers higher than *P.
resedaeformis and the $\delta^{15}N_{\text{SAA}}$ value was 1.1‰ lower (Table 3.2). When directly testing linear correlations between C. finmarchicus and P. resedaeformis and leaving out the C. typicus samples, only the $\delta^{15}N_{\text{SAA}}$ was found to have a significantly different intercept (C. finmarchicus 1.1‰ lower) and the only significant linear trend was in $\Sigma V$, where the samples increased by 0.47 units across 39 years. Nonlinear trend testing on anomaly values calculated by species identified that C. finmarchicus and C. typicus $\delta^{15}N_{\text{SAA}}$ both share an interannual trend with the P. resedaeformis $\delta^{15}N_{\text{SAA}}$ value with a small peak in the early 1990’s (Figure 3.17) and that just C. finmarchicus shares an increasing trend with the $\Sigma V$ (Figure 3.18 b).

Coral Bulk $\delta^{15}N$ Isotope Relationships

The Bulk $\delta^{15}N$ measurements were found to follow the $\delta^{15}N_{\text{SAA}}$ closer than any other CSIA-AA parameter. Because the Bulk $\delta^{15}N$ and CSIA-AA P. resedaeformis data are irregular and not measured on directly the same bands, the relationships were analyzed by fitting the time structure using GAMs models both including and excluding a measurement method term (Figure 3.19). Using the difference in AIC values, the $\delta^{15}N_{\text{SAA}}$ and relative contribution of microbial trophic transfers had more similar time structure than not to the bulk $\delta^{15}N$ measurements, and the peak in the mid 1990’s was captured in both without parameterizing the measurement method.

When modeling the Bulk $\delta^{15}N$ Coral data with the environmental parameters, deeper mixed layer depths was found to have the greatest influence on increased bulk $\delta^{15}N$ values. The model fit 93.8% of the deviance (Table 3.4) and a time change was identified in the year 2001, and the mixed
layer depth captured the $GAM_{time}$ structure both before (1981-2001) and after the time change (2001-2017) (Figure 3.6d). The N2 captured additional $GAM_{time}$ structure in the first time period (1981-2001) (Figure 3.6c). The mixed layer depth had a positive relationship with 1.87 estimated degrees of freedom in the first time period (1981-2001) that connected deeper mixed layer depths with higher 15 N values. This relationship with the mixed layer depth then switched to a negative parabolic relationship with a lower intercept (0.32) during 2001-2017 (Figure 3.5d; Table 3.4). From 1981-2001, the N2 had a positive linear relationship with the bulk $\delta^{15}N$ measurements that associated more mixing potential with higher $\delta^{15}N$ values. Similar to the mixed layer depth, from 2001-2019 this relationship changed signs, an even became less significant and no longer fit the $GAM_{time}$ structure in the data (Figure 3.5c & Figure 3.6c; Table 3.4).

$C. finmarchicus$ and $C. typicus$ abundance fit additional variance in the bulk $\delta^{15}N$ data but did not capture overarching $GAM_{time}$ structure (Figure 3.5 a&b Figure 3.6 a&b; Table 3.4).

Relative Microbial Contribution to Trophic Transfers

The coral CSIA-AA relative microbial contribution to trophic transfers model that was fit including both copepod CSIA-AA indexes and environmental parameters in the variable selection captured 70.44% of the deviance (Table 3.5). The significant increase in the $GAM_{time}$ structure for the percent microbial contribution to the trophic position was fit by a positive linear relationship with the $C. finmarchicus$ abundance, and a negative relationship with copepod $\Sigma V$ anomaly (Results figure 10 a-c). This indicated that higher abundances of $C. finmarchicus$ were associated with more microbial contribution to the trophic
position in the coral, and when the copepod's diet consisted of a higher proportion of reworked organic matter. Additional variance was captured by a positive slope with Si:N that had 1.49 degrees of freedom (Table 3.6). The coral CSIA-AA model fit using only the coral CSIA-AA indexes and environmental parameters captured 92.36% of the deviance with a time change in the year 1997 (Table 3.9). The first \( \text{GAM}_\text{time} \) decrease in the percent microbial contributions to trophic transfers was captured by the coral \( \delta^{15}N_{\text{SAA}} \) with negative slope that has 1.93 degrees of freedom (Results Figure 12 a & 13c; Table 3.10) indicating that higher \( \delta^{15}N_{\text{SAA}} \) values are associated with less percent microbial contributions to trophic transfers. During (1997-2017) the mixed layer depth fit the increase in the relative contribution of microbial trophic transfers with a positive linear slope (Results Figure 12c & 13b; Table 3.10). Additional variance was captured by a negative Si:N slope with 1.93 degrees of freedom from 1981-1997, and a linear positive relationship SiN from 1997-2017 (Results Figure 12 b; Table 3.10).

\( \Sigma V \) Relationships

The Coral CSIA-AA \( \Sigma V \) model that included Copepod CSIA-AA in the variable selection fit a low amount of the variance only capturing 33.05% (Table 3.5). The \( \Sigma V \) had a negative linear relationship with the copepods relative contribution of microbial trophic transfers and a positive linear relationship with \( C. \ typicus \) abundance (Figure 3.7; Table 3.7) such as that the lower the percent microbial contribution to the copepods trophic transfers and the lower the \( C. \ typicus \) abundance the lower the coal \( \Sigma V \) is as well. When the coral \( \Sigma V \) was fit vs the other coral CSIA-AA parameters and included a time change at 1994,
89.10% of the deviance was captured (Table 3.9). The increasing GAM<sub>time</sub> trend during 1981-1994 was fit by a positive relationship with the mean source (1.64 degrees of freedom; Results Figure 12d &13c; Table 3.11) and the variance was captured well by a positive relationship with <i>C. typicus</i> abundance (Results Figure 12g shading). Then from 1994-2017 the mixed layer depth fit the increasing GAM<sub>time</sub> trend with a positive relationship and 1.91 degrees of freedom (Results Figure 12e & 13b; Table 3.11), and the <i>C. finmarchicus</i> captured the most variance (Results Figure 12 e shading).

δ<sup>15</sup>N<sub>SAA</sub> Relationships
The Coral CSIA-AA δ<sup>15</sup>N<sub>SAA</sub> value modeled with Copepod CSIA-AA captured 62.92% of the deviance (Table 3.5). The δ<sup>15</sup>N<sub>SAA</sub> value had a negative relationship with both the copepod ΣV index (linear; Figure 3.7; Table 3.8) such that low δ<sup>15</sup>N<sub>SAA</sub> values are associated with periods of higher proportions heterotrophic microbial reworking in the copepods diet. There was also a negative relationship with N2 in the same model (1.37 degrees of freedom; Figure 3.7g; Table 3.8). Modeling the coral CSIA-AA δ<sup>15</sup>N<sub>SAA</sub> value with environmental parameters and a time change at 1990 fit 66.57 % of the deviance (Table 3.9). The Si:N ratio had a positive relationship in both time periods (1981-1990 & 1990-207), but the slope was steeper in the second time frame (Results Figure 12h) indicating that higher Si:N ratios occur alongside higher δ<sup>15</sup>N<sub>SAA</sub> values. The mixed layer depth had a positive linear relationship in the time frame from 1981-1990, which became a positive parabolic relationship with 1.85 degrees of freedom in 1990-2017 (Results Figure 12 i;
Table 3.12). The $\delta^{15}N_{\text{SAA}}$ values had a 0.8‰ lower intercept from 1981-1990 compared to 1991-2017 (Table 3.12).

**DISCUSSION**

**STRONG PELAGIC-BENTHIC COUPLING**

Multidecadal time series of CSIA-AA indices reflecting metazoan and microbial trophic transfers, microbial reworking of POM, and source water biogeochemical cycling in deep sea corals and pelagic copepod bioarchives provide clear evidence of strong pelagic-benthic coupling in the Gulf of Maine. All three CSIA-AA indices in benthic corals matched the magnitude and trend identified in the same indices in pelagic copepods; this was especially true between large-bodied *C. finmarchicus* and *P. resedaeformis*. *C. finmarchicus*, which relies heavily on microbially reprocessed organic matter (Ch. 2), thus provide a direct link between surface microbial loop food web dynamics and benthic food web dynamics via the biological pump. Variations in water mass delivery into the Gulf of Maine and their distinct nutrient profiles (e.g., Si:N ratio), coupled with shifting stratification and mixed layer depth, played critical roles in regulating interannual and interdecadal trends in surface food web dynamics and associated pelagic-benthic coupling. These results, in the context of decades of long-term observation programs in the Gulf of Maine, enable us to identify complex ecosystem states and establish new mechanistic understandings of the relationships between pelagic food webs, export production, and region oceanography and climate.

**Metazoan Trophic Structure**

We found geochemical evidence of strong pelagic-benthic coupling in the Gulf of Maine over the last two decades. There was strong alignment in both
magnitude and temporal trends of three CSIA-AA indices the sources and transformation of organic matter linking pelagic and benthic production in the Gulf of Maine. For example, benthic deep-sea corals (2.4 ± 0.1) and surface ocean copepods, *C. finmarchicus* (2.3 ± 0.1) and *C. typicus* (2.3 ± 0.2) all had the same metazoan trophic position (Figure 3.4a; Table 3.13; Table 3.2), indicating linked trophic dynamics of surface and benthic food webs. While we expected to observe pelagic benthic coupling between *C. finmarchicus* and *P. resedaeformis*, under the expectation that the larger larger-bodied copepod, *C. finmarchicus*, would be more efficient at transferring organic matter to the coral due to their larger, faster sinking fecal pellets and overall body size (Stamieszkin et al., 2015; Wanamaker et al., 2009); we did not expect them to share the same trophic position, or for *C. typicus* to have a similar food chain length as well. This result suggest that each animal feeds on prey with a similar amount of metazoan trophic transfers, disputed the fact that we expected that *P. resedaeformis* would be one step above *C. finmarchicus*, and that *C. typicus* would have the longest food chain length. For the *P. resedaeformis* to have a trophic position of 2.4 ± 0.1 in Jordan Basin over the past two decades it is likely that they have been feeding on recently exported sinking POM composed of phytoplankton and zooplankton fecal pellets (a metric of zooplankton diet) rather than sinking zooplankton themselves. Zooplankton fecal pellets have been shown to have a lower trophic position than the rest of the animal due to widely ranging dietary adsorption efficiencies (Doherty et al. 2021), which is a likely explanation for why the coral trophic position was not higher than the copepod trophic position.
The strong reliance of Gulf of Maine *P. resedaeformis* on phytodetritus and fecal pellets is in stark contrast to trophic position estimates of *P. resedaeformis* in the Northwest Atlantic outside of the Gulf of Maine, whose trophic position (~3.5 Sherwood et al. 2005a) indicates that they were feeding more directly on zooplankton themselves (*TP_{bulk} ~2-2.5*; Sherwood 2005a). The Gulf of Maine *P. resedaeformis* trophic position estimates agree with trophic position estimates of *P. pacifica* from the Gulf of Alaska (2.4 ± 0.2; McMahon et al. 2018), which were also shown to feed on phytodetritus and fecal pellet POM with an estimated TP of 1.5 (McCarthy et al. 2007). In both the Gulf of Alaska and Gulf of Maine, bomb radiocarbon curve reconstruction from *Primnoa spp.* skeleton time series indicates that these species are feeding on recently exported POM rather than resuspended POM from the benthos (Sherwood et al. 2005; 2007). This makes sense as current understanding of gorgonian coral growth indicates that annual gorgonian skeleton accretion happens largely during periods like the spring bloom (Schiff et al. 2014; Sherwood et al. 2005a; 2005b), where primary production out paces the demand of grazers and excess production skinks from the surface into the deep ocean (Pershing and Stamieszkin 2020).

**Multivorous Trophic Structure**

Recent developments in our ability to measure microbial trophic transfers applying a *TP_{Ala}* calculation (Décima et al. 2017) have enhanced our ability to reconstruct the trophic structure at lower trophic levels, especially when applied alongside the metazoan *TP_{Glx}* calculation (Décima & Landry 2020). The *TP_{Ala}* calculation revealed an “invisible” microbial trophic transfer that shows the coral recorded the same microbial transfer (*TP_{Ala} = 4.0 ± 0.3*) that was identified in *C.*
*finmarchicus* (*TP_{Ala} = 4.1 ± 0.3*). The coral *TP_{Ala}* value being 1.6 trophic transfers higher than the *TP_{Glx} (2.4 +/-0.1*) may aid in explaining the CSIA-AA discrepancies with past bulk measurements of about 3.5 TP in *P. resedaeformis* (Sherwood et al. 2008) as the bulk δ^{15}N method provides an integrated signal across all trophic transfers. The fact that this invisible microbial trophic transfer shows up in both the coral and *C. finmarchicus* while a lower value was measured in the *C. typicus* (*TP_{Ala} = 3.4 +/-0.3*) is significant because it provides more evidence for the tight pelagic-benthic coupling with the large copepods. The offset in the coral and *C. finmarchicus* *TP_{Ala} also suggest it is plausible that the pelagic-benthic coupling is occurring through the corals feeding on fecal pellets produced by *C. finmarchicus* as a proportion of the POM consumed, which have a lower trophic position than the animal bodies (Doherty et al. 2021). A major ecological difference between the two species is the size of *C. finmarchicus* larger fecal pellets compared to those of *C. typicus*. Larger fecal pellets have a faster sinking rate (Stamieszkin et al. 2015) and have been attributed as a mechanism for other relationships identified between benthic animal growth and *C. finmarchicus* abundance such as growth bands on ocean quahogs in the Gulf of Maine (Wanamaker et al. 2009). The comparable *TP_{Ala} values between surface ocean *C. finmarchicus* and benthic *P. resedaeformis* suggest that there were minimal additional microbial trophic transfers that occurred during transit of POM and fecal pellets from the mixed layer to the corals. This likely reflects the fast-sinking rate of large calanoid fecal pellets coupled with the relatively shallow collection depths of *P. resedaeformis* in
Jordan Basin (218 m). Notably, this relationship was consistent across the entire 21-year time series, indicating surprisingly minimal variation in microbial trophic transfer dynamics through time.

$\delta^{15}N_{\text{SAA}}$ Primary Production Coupling

Comparison of mean source amino acid $\delta^{15}N$ values ($\delta^{15}N_{\text{SAA}}$) between surface ocean copepods and benthic corals as a geochemical proxy for the source water in which these species were feeding also indicates strong pelagic-benthic coupling, particularly between the coral and *C. finmarchicus*. Both coral ($\delta^{15}N_{\text{SAA}} = 5.6 \pm 0.6\%$) and *C. finmarchicus* (4.4 ± 1.1‰) had $\delta^{15}N_{\text{SAA}}$ values indicating feeding on production from nitrate sourced in LSW/SSW bottom water that is conducive to high diatom production, while the notably lower $\delta^{15}N_{\text{SAA}}$ values measured in *C. typicus* (3.4 ± 0.6‰) indicate they are feeding in a food web where the relative nitrogen is more reworked by processes such as nitrification and nitrogen fixation (Décima & Landry 2020; Whitney et al. 2020) than the other two species. These reworking signals coincided with shallow mixed layer depths having a negative relationship in the $\delta^{15}N_{\text{SAA}}$ values of both the coral (Results Figure 12j & 7; Table 3.12 & 6) and the copepods (Chapter 2). This relationship suggests a potential for processes like nitrification or nitrogen fixation to decrease the water column $\delta^{15}N$ values, and it is likely that this is a signature from oligotrophic periods such as the summer and late fall (Anderson 2009) where production depends on recycled nutrients (Pershing and Stamieszking 2020). Higher $\delta^{15}N_{\text{SAA}}$ values reflect advection of LSW/SSW into the Gulf of Maine off the Northeast US continental shelf (Sherwood et al. 2011) which carry in higher amounts of nitrate and depending on the
composition (more LSW/SSW), increased levels of Silicate (Townsend et al. 2015; Zang et al. 2019). The Gulf of Maine is considered to be both Nitrogen- (Zhang et al. 2019) and silicate-limited system (Zang et al. 2019) and both the mixing of the slope water to the surface during the winter, and influxes of LSW/SSW are important in creating conditions for high biomass diatom-based blooms (Zhang et al. 2019; Zang et al. 2022). These blooms are considered to be an essential part of the success of *C. finmarchicus* and in particular, their ability to produce lipid storage for diapause (Johnson et al. 2007; Pershing and Stamieszkin 2020). Thus, these data support our hypothesis that slope water conditions with high Si:N ratios (LSW/SSW) that support high diatom production and favor high *C. finmarchicus* production also support strong pelagic-benthic coupling. However, if *P. resedaeformis* were directly consuming diatoms, $T_P_{Ala}$ would be significantly lower than the observed 4.0 ± 0.3. This indicates that the high nutrient (diatom production) is going through about 2 additional trophic transfers before it reaches the coral. It is likely that protists are first feeding on diatoms and associated POM, which are then in turn being grazed on by zooplankton or die and may even go through additional reworking before being consumed by the coral. As discussed earlier, the third transfer is more likely to be either consumption of microbially reworked organic matter or zooplankton fecal pellets and not zooplankton carcasses themselves. This again, supports the theory that *C. finmarchicus* fecal pellets are an important component of deep-sea coral diet and thus pelagic-benthic coupling. The strong correlation between *C. finmarchicus* and *P. resedaeformis* may also help to constrain the
time frames that *P. resedaeformis* are able to lay down gorgonian growth bands to the spring period of high export production.

**Microbial Reworking Coupling**

While the $\delta^{15}N_{SAA}$ values of *C. finmarchicus* and *P. resedaeformis* do suggest pelagic-benthic coupling in Jordan Basin is linked to spring diatom production and the source waters that support it, the relatively long food chain with additional microbial trophic transfers of organic matter fueling both the *C. finmarchicus* and *P. resedaeformis* was not our original hypothesis. Additional evidence from the CSIA-AA index $\Sigma V$, which measures the degree of microbial reprocessing of organic matter, and the associated but independent assessment of the relative percent contribution of microbial vs. metazoan trophic transfers supporting *C. finmarchicus* and *P. resedaeformis* both support the conclusion that *C. finmarchicus* plays an important role in exporting microbial loop production to the deep sea. Both *C. finmarchicus* and *P. resedaeformis* consumed organic matter that exhibited the same degree heterotrophic microbial reworking ($\Sigma V$) in magnitude and temporal trend. For both species, $\Sigma V$ values between 1.5-2.5 indicate consumption of organic matter consumed by zooplankton and resynthesized by heterotrophic bacteria (McCarthy et al. 2007; Calleja paper 2013). Similarly, *C. finmarchicus* and *P. resedaeformis* relied on organic matter that had the same elevated contribution of microbial trophic transfers compared to *C. typicus* (Figure 3.4c; Table 3.13; Table 3.2) with a value of 0.41 +/- 0.04. Décima & Landry (2020) identified a similar range in microbial trophic transfer contributions to food webs supporting a community of zooplankton in an evolving eddy in the Pacific Ocean. They
proposed that the microbial community restructured around an eddy constrained diatom event, which supported a multivorous food web - as described in Décima and Landry 2020 first figure to be a trophic structure which include a trophic link in which protistan consumers graze on phytoplankton and are then consumed by mesozooplankton. While the Décima & Landry (2020) study was on a relatively short time frame of weeks, our study covered a 38-year time period and applied tissues that integrate isotopic signals across entire seasons, suggesting that these microbial trophic transfers through a diatom bloom system are not just a short-term restructuring of the microbial community, but are also an important link in the overall spring bloom trophic structure in the Gulf of Maine. Furthermore, Li et al. 2006 identified changes in bacterioplankton on the continental shelf of Nova Scotia and the Labrador Sea that were coherent with changes in phytoplankton biomass and suggested that the two trophic levels (primary production and microbial) were coupled on a multi-year time frame.

**TEMPORAL DYNAMICS**

We expected to see that changes to the Jordan Basin nutrient baseline, consistent with both warming and hydrographic shifts over the last several decades, would alter pelagic process and lead to enhanced small-cell, microbial loop dominated food webs (Stemann & Boss 2012; Close et al. 2013; Turner 2015; Bisson et al. 2020; Li et al. 2009). While we did observe an increase in the heterotopic microbial reworking over the entire 38-year time series, the other CSIA-AA metrics indicative of microbial loop food web dynamics, including both metazoan and microbial trophic transfer indices, did not have significant decadal
trends (Figure 3.3; Table 3.1). Instead, we found a more complex series of relationships that were best traced to nutrient dynamics through the deep slope water entering the Gulf of Maine and regulated by water column mixing, primary production, and biogeochemical processes, before being exported to the deep ocean and consumed by the deep-sea coral.

Δ Decadal Increase and Warming

The multi-decadal increase in heterotrophic microbial reworking of organic matter supporting *P. resedaeformis* production in this study lines up with the Gulf of Maine warming trend and the hypothesized shift to more microbial loop food web dynamics (Pershing et al. 2015; DeVries and Weber 2017; Karl et al. 2001; Li et al. 2009). This indicates that in recent years there is a smaller proportion of fresh production being exported to depth. This is most likely the result of a combination of two processes: 1) under warming conditions, the smallest phytoplankton that are associated with warmer, fresher/more stratified waters, are expected to survive (Li et al. 2009) and these conditions are then expected to lead to smaller amounts of organic matter both moving up the food web and reduced efficiency of export to depth (Li et al. 2009; DeVries and Weber 2017). And 2) under these warming conditions, *C. finmarchicus* abundances on the Northeast US continental shelf are projected to decline (Grieve et al. 2017; Record et al. 2019; Chapter 1). This would reduce the efficiency of the export associated with *C. finmarchicus* ability to repackage organic matter into larger, faster sinking, fecal pellets (Wanamaker et al. 2009; Stamieszkin et al. 2015). As discussed in more detail in the relative contribution
of microbial trophic transfers section below, the coral and *C. finmarchicus* pelagic-benthic coupling does not diverge as the *C. finmarchicus* abundance decreases, and this may be due to the deepening of the mixed layer depth physically increasing the connection of the pelagic and benthic systems and decreasing the sinking transit time and distance.

Interannual $\Sigma V$ Dynamics between the coral and copepods

The magnitude and temporal trend in *P. resedaeformis* $\Sigma V$ values track very closely with *C. finmarchicus* $\Sigma V$ values, indicating that they are in the same baseline reworking system. However, there were larger interannual variations in the *C. finmarchicus* $\Sigma V$ value than in the *P. resedaeformis* $\Sigma V$ value. Some of this interannual variance may reflect differences in integration time of the tissues analyzed in this study. *C. finmarchicus* were measured as aggregated whole organisms, which reflect approximately three months of isotope integration time (Schmidt et al. 2003; Chapter 2) that includes the preceding late winter and spring bloom. For *P. resedaeformis*, we measured annual growth rings at one to two years resolution. Thus, the $\Sigma V$ values in *P. resedaeformis* may reflect a slightly longer time-averaged signal of export that dampens variance relative to *C. finmarchicus*. That said, we do think there are real signals of differences in the degree of pelagic-benthic coupling across this multidecadal time series. For instance, it is also important to consider that the abundance of dominant copepod species in Jordan Basin, and thus their relative proportion in the copepod community, is fluctuating between periods dominated by large vs. small-bodied copepods on an interannual time scale (CH 1; Greene & Pershing 2003; Kane 2007; Wanamaker et al. 2008; Pershing et al. 2010; Balch et al.
2012; Record et al. 2019). As such, the expected proportion of reworked microbial material exported from the surface ocean via large vs small copepod communities is also expected change with time. Generally, the degree of heterotrophic microbial reworking ($\sum V$) supporting *P. resedaeformis* closely mirrored, in magnitude and temporal trend, that of *C. finmarchicus*. However, during periods when $\sum V$ measured in *C. finmarchicus* exceeded the value measured the *P. resedaeformis* (Figure 3.4c; post 2009), *C. finmarchicus* abundance was low relative to *C. typicus* (Results figure 12f). We hypothesize that during these periods, there was enhanced export of organic matter from the more abundant small-bodied copepod community, represented by *C. typicus* in this study, which had a lower relative $\sum V$ value (Results figure 12g); (Close et al. 2013). Conversely, in phases where $\sum V$ measured in *P. resedaeformis* exceeded that of *C. finmarchicus* and *C. typicus* (Figure 3.4c; 2002-2009), this could indicate that smaller, slower skinning particles, are undergoing additional microbial reworking as they sink to the benthos.

**Decadal warming increase $\sum V$**

While the decadal increase in heterotrophic microbial reworking in both the pelagic food web and the associated export production is likely correlated to system wide changes associated with the warming trend in the Gulf of Maine, there are additional trophic and environmental mechanisms at play. This study applies two diet and consumer metabolic pathways ($\text{TP}_{\text{Glx-Phe}}$ and $\text{TP}_{\text{Ala-Phe}}$) that we can calculate, as well as the overall heterotrophic microbial reworking ($\sum V$) which quantifies the isotopic fractionation deviance across all trophic amino acids separate from that of the metazoan biogeochemical pathways (McCarthy...
et al. 2007). And while the degree of heterotrophic microbial reworking of POM observed here in the Gulf of Maine increased steadily across the entire time series – the relative contribution of microbial and metazoan trophic transfers didn’t have a significant decadal trend. This suggests that the $\sum V'$ trend is capturing additional metabolic pathways that are occurring separate from the metazoan food web as well as the protistan microzooplankton based trophic transfers (Décima et al. 2017).

This increase in $\sum V'$ is likely originating in bottom-up processes, like the warming water, but also local water column structure changes, as indicated by the associations among both the coral $\sum V$ and $\delta^{15}N_{\text{SA}}$ with the mixed layer depth. The Gulf of Maine has been identified as a region where light limitation is more prevalent than nutrient limitation (Henson et al. 2009) and primary production requires light (Zhang et al. 2019), and therefore stratification for phytoplankton blooms (Li et al. 2006). If the mixing is too deep, phytoplankton are mixed out of the euphotic zone and net production is reduced. Prior to 2004, mixing was comparatively shallow relative to recent years, and the relationship between mixed layer depth and the coral heterotrophic microbial reworking indicated that more fresh production occurred during more shallow mixing years aligning with the light limitation hypothesis and deeper periods of mixing indicated an increased opportunity for microbial reworking of organic matter.

Chapter 2 attributed shallow mixed layer depths with both fresher organic matter and a greater relative contribution of microbial trophic transfers to the copepods diet - and this process was found to be a factor that increases the $P$. 

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resedaeformis $\Sigma V$ trend (Figure 3.7d). In addition to the mixed layer depth, it was found in chapter 2 that the relative microbial contribution to trophic transfers in the copepods was associated with a small, 0.2 trophic transfer increase in $TP_{Glu}$ over the 21-year time frame. This change in copepod trophic structure, to consuming more metazoan derived material with a $TP_{Glx} < 3$ was likely associated with an increase in fecal pellets consumption. It is possible that that heterotrophic gut bacterial in copepods (and the ambient waters) could be a potential pathway for additional microbial metabolic processes to alter the coral $\Sigma V$ values (Doherty et al. 2021).

$\delta^{15}N_{SAA}$ Values
$\delta^{15}N_{SAA}$ values can be influenced by a number of processes from biological primary production in the surface ocean to the physical transport and mixing of nutrients (Whitney et al. 2020; Sherwood et al. 2011; Marconi et al. 2015). This study hypothesized that the isotopic nutrient baseline in the corals would be driven by the source water signature of water masses mixing on the shelf. The dominant mode of nitrogen supply to the Gulf of Maine is in the slope water that enters through the deep water in the Northeast Channel (Green and Pershing 2000, 2003; Smith et al. 2001; Townsend et al. 2010;2015; Mountain 2012; Zhang et al. 2019) and the inflow in intermediate and surface waters such as the Scotian shelf water (Zhang et al. 2019; Townsend et al. 2015) has been identified as a secondary source. Both are large scale advective sources and are dominant over riverine and atmospheric inputs (Zhang et al. 2019). The slope waters have the following nitrate signatures: WSW $< 5\%$ and LSW $6\%$ (Sherwood et al. 2011). P. resedaeformis $\delta^{15}N_{SAA}$ values (5.6±0.6) were within...
the range of WSW and LSW, and were positively correlated the Si:N ratio (Figure 3.9), which is a proxy for the mixing water masses in Jordan Basin. So as the Si:N is higher, we see the higher $\delta^{15}N$ values associated with LSW as expected, and similarly, the lower Si:N ratio a lines with WSW $\delta^{15}N$ values. However, if the source water was the sole driver of variance in the baseline $\delta^{15}N_{\text{SAA}}$ value, we would have expected to observe interannual oscillations that reflect the increase in WSW to the Gulf of Maine in more recent years in the $\delta^{15}N_{\text{SAA}}$. In 2008, there was a northward shift in the gulf stream identified in the sea surface height altimetry data (Gonçalves Neto et al. 2021) and the resulting poleward retreat of the Labrador current may indicate the weakening of AMOC under climate change, which may increase the amount of slope water entering the Gulf of Maine (Zhang et al. 2019; Saba et al. 2016; Pershing et al. 2015). This pronounced water mass shift was not observed in the interannual trends of $P.\ resedaeformis$ $\delta^{15}N_{\text{SAA}}$ values (Figure 3.3d). Instead, there was no temporal trend after 1993. This may be partially explained by the complex relationship identified between the mixed layer depth and $\delta^{15}N_{\text{SAA}}$ values (Figure 3.9i). This relationship is consistent with deeper mixed layers (> -1.31 anomaly value) injecting ($\delta^{15}N > 5\%$) slope water from depth into the surface, which is necessary for it to be incorporated into the primary production (Zhang et al. 2019). This same relationship was identified in the $P.\ resedaeformis$ bulk $\delta^{15}N$ record provided further support for the mixing relationship between the nitrogen source and $\delta^{15}N_{\text{SAA}}$ values. Additionally, a time change in the $\delta^{15}N_{\text{SAA}}$ occurred in 1991 (Figure 3.9; Figure 3.20), which coincides with the accelerated warming
trend and deepening mixed layer. Then a second time change occurred in the bulk $\delta^{15}N$ relationship with the environmental parameters during 2001 (Figure 3.20) marking the year when the mixed layer depth became anonymously high (Figure 3.13). These trends also overlap with the accelerated warming trend as well as a shift in the nutrient profile to a lower Si:N (Figure 3.13) caused by an increase in WSW on the US northeastern continental shelf (Gonçalves Neto et al. 2021) entering the Gulf of Maine (Chapter 1). These patterns imply that while the relative contribution of source water mass to the nutrient budget of the Gulf of Maine is important in setting baseline nitrogen isotope dynamics in the system, water column mixing is also a major control on the available nutrients to primary production. And that this additional mixed layer signal may influence the interpretation and application of $\delta^{15}N_{SAA}$ in other long term paleo records with limited environmental data (Rahmstorf et al. 2015)

Relative contribution of microbial transfers

Large relative contribution of microbial vs metazoan trophic transfers to *P. resedaeformis* trophic position aligned with similar high nutrient/primary productivity as identified in the pelagic system (Chapter 2). The second chapter found that a decrease in Si:N ratio of water masses entering the Gulf of Maine would lead to less fresh organic matter suggesting lower bloom biomass (Townsend et al. 2015; Zang et al. 2019), which in turn leads to less contribution of the microbial community to trophic structure and production (Li et al. 2006; Décima and Landry 2020; Chapter 2). This same relationship was identified both between *P. resedaeformis* relative contribution of microbial trophic
transfers and Si:N ratio after 1997 (Figure 3.9b) as well as by the correlation between copepod $\sum V$ values that associated a higher proportion of fresh material in the pelagic system with a high relative microbial contribution to trophic transfers (Figure 3.7a). And while the $P. resedaeformis$ relative contribution of microbial trophic transfers relationship with the mixed layer depth (Figure 3.9 c) did not align with the same light limitation hypothesis as the copepods (Chapter 2), it suggested that either: 1) the sufficient upwelling of high slope water nutrients from depth lead to increases in the phytoplankton biomass as well as the microbial community biomass available for surface consumers and sequestration to the deep ocean, or 2) the closer the pelagic processes and organic matter are to the sea floor, the more connected they are to the benthic system. This is consistent with the export that occurs during diapause and diel vertical migration when mesozooplankton and micronekton respire, defecate, and excrete organic matter at the bottom of the mixed layer (Pinti et al. 2023; Pershing and Stamieszkin 2020; Steinberg et al. 2000). This deeper mixing could be a proxy for how connected the benthic and the surface ecosystems are. Excretion during diurnal vertical migration at depth is more likely to leave the surface mixing layer and be exported to the deep ocean (Pinti et al. 2023; Pershing and Stamieszkin 2020; Steinberg et al. 2000) providing a potential mechanism for how even under decreasing $C. finmarchicus$ abundance after 2006 (Chapter 1) (and by proxy a decrease in large fecal pellet production), the coupling of the CSIA-AA indexes between the coral and $C. finmarchicus$ is maintained. The surface and benthic systems are physically
closer, and the export that does occur would reach the coral more efficiently. Whether it is the vertical transport of nutrients, or more effective export of available organic matter, it is clear that the physical processes connecting the pelagic and benthic systems play a key role in the trophic structure of exported organic matter.

Multidecadal molecular isotope records from pelagic and benthic bioarchives revealed strong pelagic-benthic coupling, particularly linked to large-bodied *C. finmarchicus* food web dynamics. The proteinaceous coral skeleton preserved a long-term record of increasing microbial reworking in exported organic matter that matched the magnitude and trend in the pelagic system. In addition, water mass nutrient dynamics, mixing, and stratification were key to regulating biogeochemical cycling and trophic dynamics supporting pelagic-benthic coupling. And while deeper mixing is creating a stronger pelagic-benthic connection as *C. finmarchicus* abundance decreases, a future shoaling in the mixed layer depth could have consequences for the fate of organic matter to the benthic system. The results of this study will help to better parameterize new mechanistic General Ecosystem Models, facilitating hypothesis testing across a wide range of future modeling, observational, and experimental studies to quantify the magnitude, timing, and mechanisms of past ecosystem changes, greatly improving our ability to forecast future changes in Gulf of Maine ecosystem dynamics, upon which management and conservation strategies for regional fisheries and protected marine mammal species depend (Record et al. 2019; Pershing & Stamieszkin 2020)
REFERENCES


Balch, W. M., Drapeau, D. T., Bowler, B. C., & Huntington, T. G. (2012). Step-changes in the physical, chemical and biological characteristics of the Gulf of Maine, as documented by the GNATS time series. Marine Ecology Progress Series, 450, 11-35.


warming leads to collapse of the Gulf of Maine cod fishery. Science, 350(6262), 809-812.


TABLES

Table 3.1 Linear trends in *P. resedaeformis* for both CSIA-AA and bulk nitrogen isotope data sets. Slope is the coefficient fit for the time variable, std.err is the error associated with the slope term, T0_value is the value at the start of the respective data set, and Tn_Value is the value at the end of the respective data set. T_diff is the difference between the Tn_value and T0_values.

<table>
<thead>
<tr>
<th>Index</th>
<th>Model</th>
<th>slope</th>
<th>std.err</th>
<th>T0_Value</th>
<th>Tn_Value</th>
<th>T_diff</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trophic Position Microbial Contribution</td>
<td>Index ~ Time</td>
<td>-0.002</td>
<td>0.005</td>
<td>4.04</td>
<td>3.95</td>
<td>-0.09</td>
</tr>
<tr>
<td>Trophic Position Metazoan</td>
<td>Index ~ Time</td>
<td>-0.002</td>
<td>0.002</td>
<td>2.40</td>
<td>2.32</td>
<td>-0.08</td>
</tr>
<tr>
<td>Percent Microbial Contribution</td>
<td>Index ~ Time</td>
<td>0.000</td>
<td>0.001</td>
<td>0.40</td>
<td>0.41</td>
<td>0.01</td>
</tr>
<tr>
<td>Sum V</td>
<td>Index ~ Time</td>
<td>0.011</td>
<td>0.003</td>
<td>1.97</td>
<td>2.38</td>
<td>0.41</td>
</tr>
<tr>
<td>Mean Source Amino Acid</td>
<td>Index ~ Time</td>
<td>0.007</td>
<td>0.010</td>
<td>5.49</td>
<td>5.74</td>
<td>0.25</td>
</tr>
<tr>
<td>All Bulk Colonies</td>
<td>Bulk ~ Time</td>
<td>0.004</td>
<td>0.004</td>
<td>10.07</td>
<td>10.23</td>
<td>0.16</td>
</tr>
</tbody>
</table>

Table 3.2 Best linear fit models between all species (coral and copepods) according to Table 3.13. Model is the best equation form, Species is the level on which indexes and slope are separated by, and T0_value is the value at the start of the time frame, Tn_value is the value at the end of the time frame, and T_diff is the difference between Tn_value and T0_value. Intercept_Diff is the intercept difference between each copepod and the coral.

<table>
<thead>
<tr>
<th>Index</th>
<th>Model</th>
<th>Species</th>
<th>slope</th>
<th>std.err</th>
<th>T0_Value</th>
<th>Tn_Value</th>
<th>T_diff</th>
<th>Intercept_Diff</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trophic Position Microbial Contribution</td>
<td>Index ~ Time</td>
<td>(1</td>
<td>Primnoa resedaeformis</td>
<td>-0.002</td>
<td>0.003</td>
<td>4.04</td>
<td>3.95</td>
<td>-0.09</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C. finmarchicus</td>
<td>4.10</td>
<td>4.11</td>
<td>-0.05</td>
<td>0.16</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>C. typicus</td>
<td>3.54</td>
<td>3.49</td>
<td>-0.05</td>
<td>0.46</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trophic Position Metazoan</td>
<td>Index ~ Time</td>
<td>All</td>
<td>0</td>
<td>0.002</td>
<td>2.30</td>
<td>2.30</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td>Percent Microbial Contribution</td>
<td>Index ~ Time</td>
<td>(1</td>
<td>Primnoa resedaeformis</td>
<td>-0.083</td>
<td>0.077</td>
<td>0.42</td>
<td>0.39</td>
<td>-0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C. finmarchicus</td>
<td>0.43</td>
<td>0.42</td>
<td>-0.01</td>
<td>0.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>C. typicus</td>
<td>0.32</td>
<td>0.31</td>
<td>-0.01</td>
<td>0.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sum V</td>
<td>Index ~ Time</td>
<td>(1</td>
<td>Primnoa resedaeformis</td>
<td>0.016</td>
<td>0.006</td>
<td>1.79</td>
<td>2.39</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C. finmarchicus</td>
<td>2.05</td>
<td>2.36</td>
<td>0.33</td>
<td>0.63</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>C. typicus</td>
<td>1.49</td>
<td>1.82</td>
<td>0.33</td>
<td>0.57</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean Source Amino Acid</td>
<td>Index ~ Time</td>
<td>(1</td>
<td>Primnoa resedaeformis</td>
<td>-0.001</td>
<td>0.012</td>
<td>5.60</td>
<td>5.58</td>
<td>-0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C. finmarchicus</td>
<td>4.45</td>
<td>4.45</td>
<td>-0.03</td>
<td>-1.13</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>C. typicus</td>
<td>3.43</td>
<td>3.46</td>
<td>-0.03</td>
<td>-2.18</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3.3 Test to identify if coral and *C. fin* have the same linear trend and intercept. According to Table 3.14 Test to identify if coral and *C. fin* have the same linear trend and intercept. See Table 3.13.
Table 3.4 Bulk Isotope nitrogen values GAMs model fit vs the environmental data. Estimated parametric and smoothed effects, effective degrees of freedom (edf), standard error (Std.Error) and reference degrees of freedom (Ref.df), test statistic critical values (t-value/F) and p-values are shown by significance ("." < 0.1, "*" <0.05, "**" < 0.01, "***" <0.001) for best fit model of tropic position by species. Terms in all models are as follows: Si:N: Silicate:Nitrate; N2: Stratification Index; MXLD: Mixed layer depth; calanus: C. finmarchicus abundance; centyp: C. typicus abundance; s_mean: $\delta^{15}N_{\text{SSA}}$; sum_v: $\sum V$; per_micro: relative contribution to microbial trophic transfers. Any CSIA-AA index with “cope” on the end of a term refers to zooplankton values, and with out “cope” refers to coral values.

<table>
<thead>
<tr>
<th>Estimate/edf</th>
<th>Std.Error/Ref.df</th>
<th>t/F</th>
<th>P/S</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>10.42</td>
<td>0.01</td>
<td>715.30</td>
<td>P</td>
</tr>
<tr>
<td>catsecond</td>
<td>0.32</td>
<td>0.14</td>
<td>2.21</td>
<td>P</td>
</tr>
<tr>
<td>s(calanus):catfirst</td>
<td>1.89</td>
<td>1.99</td>
<td>4.37</td>
<td>S</td>
</tr>
<tr>
<td>s(calanus):catsecond</td>
<td>1.82</td>
<td>1.96</td>
<td>2.42</td>
<td>S</td>
</tr>
<tr>
<td>s(centyp):catfirst</td>
<td>1.00</td>
<td>1.00</td>
<td>0.45</td>
<td>S</td>
</tr>
<tr>
<td>s(centyp):catsecond</td>
<td>1.08</td>
<td>1.16</td>
<td>3.76</td>
<td>S</td>
</tr>
<tr>
<td>s(N2):catfirst</td>
<td>1.00</td>
<td>1.00</td>
<td>26.83</td>
<td>S</td>
</tr>
<tr>
<td>s(N2):catsecond</td>
<td>1.00</td>
<td>1.00</td>
<td>3.90</td>
<td>S</td>
</tr>
<tr>
<td>s(MXLD):catfirst</td>
<td>1.87</td>
<td>1.98</td>
<td>10.71</td>
<td>S</td>
</tr>
<tr>
<td>s(MXLD):catsecond</td>
<td>1.93</td>
<td>1.99</td>
<td>10.32</td>
<td>S</td>
</tr>
</tbody>
</table>

Table 3.5 Coral CSIA-AA GAMs mode fit vs environmental and Copepod CSIA-AA parameters. See Table 3.4 for a full description of variable notations.

<table>
<thead>
<tr>
<th>Equation</th>
<th>R2</th>
<th>dev.expl</th>
<th>AIC</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>per_micro = s(SiN, k = 3) + s(calanus, k = 3) + s(sumvCope, k = 3)</td>
<td>0.60</td>
<td>70.44</td>
<td>-56.20</td>
<td>14</td>
</tr>
<tr>
<td>sum_v = s(centyp, k = 3) + s(permicroCope, k = 3)</td>
<td>0.21</td>
<td>33.05</td>
<td>-5.96</td>
<td>14</td>
</tr>
<tr>
<td>s_mean = s(N2, k = 3) + s(sumvCope, k = 3)</td>
<td>0.55</td>
<td>62.92</td>
<td>18.80</td>
<td>14</td>
</tr>
</tbody>
</table>

Table 3.6 Relative microbial contribution to trophic transfers Coral CSIA-AA values GAMs model fit vs environmental and copepod CSIA-AA parameters. See Table 3.4 for details. See Table 3.4 for a full description of variable notations.
<table>
<thead>
<tr>
<th>Estimate/edf</th>
<th>Std.Error/Ref.df</th>
<th>t/F</th>
<th>P/S</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>0.41</td>
<td>0.01</td>
<td>80.59</td>
<td>P ***</td>
</tr>
<tr>
<td>s(SiN)</td>
<td>1.49</td>
<td>1.74</td>
<td>0.87</td>
<td>S</td>
</tr>
<tr>
<td>s(calanus)</td>
<td>1.00</td>
<td>1.00</td>
<td>6.18</td>
<td>S *</td>
</tr>
<tr>
<td>s(sumvCope)</td>
<td>1.00</td>
<td>1.00</td>
<td>11.68</td>
<td>S **</td>
</tr>
</tbody>
</table>

Table 3.7 $\sum V$ Coral CSIA-AA value GAMs model fit vs environmental copepod CSIA-AA parameters. See Table 3.4 for details.

<table>
<thead>
<tr>
<th>Estimate/edf</th>
<th>Std.Error/Ref.df</th>
<th>t/F</th>
<th>P/S</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>2.24</td>
<td>0.04</td>
<td>50.48</td>
<td>P ***</td>
</tr>
<tr>
<td>s(centyp)</td>
<td>1.00</td>
<td>1.00</td>
<td>3.28</td>
<td>S</td>
</tr>
<tr>
<td>s(permicroCope)</td>
<td>1.00</td>
<td>1.00</td>
<td>2.45</td>
<td>S</td>
</tr>
</tbody>
</table>

Table 3.8 $\delta^{15}N_{SAA}$ Coral CSIA-AA value GAMs model fit vs environmental Copepod CSIA-AA parameters. See Table 3.4 for details.

<table>
<thead>
<tr>
<th>Equation</th>
<th>R²</th>
<th>dev.resid</th>
<th>AIC</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>par_micro = s(SiN, by = Chg_Pat, k = 3) + s(MLD, by = Chg_Pat, k = 3) + s(Smeanam, by = Chg_Pat, k = 3)</td>
<td>0.87</td>
<td>62.85</td>
<td>-124.48</td>
<td>23</td>
</tr>
<tr>
<td>sum_cal = s(calanus, by = Chg_Pat, k = 3) + s(MLD, by = Chg_Pat, k = 3) + s(centyp, by = Chg_Pat, k = 3) + s(Smeanam, by = Chg_Pat, k = 3)</td>
<td>0.75</td>
<td>89.10</td>
<td>-28.01</td>
<td>23</td>
</tr>
<tr>
<td>S mean = s(MLD, by = Chg_Pat, k = 3) + s(SiN, by = Chg_Pat, k = 3)</td>
<td>0.54</td>
<td>66.57</td>
<td>30.52</td>
<td>23</td>
</tr>
</tbody>
</table>

Table 3.9 Coral CSIA-AA models fit vs environmental and coral CSIA-AA parameters. See Table 3.4 for a full description of variable notations.

**Table 3.10 Relative contribution of microbial trophic transfers**: Coral CSIA-AA models fit vs environmental and coral CSIA-AA parameters. See Table 3.4 for a full description of variable notations.
Table 3.11 $\sum V$ Coral CSIA-AA models fit vs environmental and coral CSIA-AA parameters. See Table 3.4 for details.

<table>
<thead>
<tr>
<th>Estimate/edf</th>
<th>Std.Error/Ref.df</th>
<th>t/F</th>
<th>P/S</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>0.39</td>
<td>0.01</td>
<td>69.89</td>
<td>P ***</td>
</tr>
<tr>
<td>catsecond</td>
<td>0.02</td>
<td>0.01</td>
<td>2.09</td>
<td>.</td>
</tr>
<tr>
<td>s(SiN):catfirst</td>
<td>1.86</td>
<td>1.98</td>
<td>3.26</td>
<td>S</td>
</tr>
<tr>
<td>s(SiN):catsecond</td>
<td>1.00</td>
<td>1.00</td>
<td>13.53</td>
<td>**</td>
</tr>
<tr>
<td>s(MXLD):catfirst</td>
<td>1.00</td>
<td>1.00</td>
<td>1.31</td>
<td>S</td>
</tr>
<tr>
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Table 3.12 $\delta^{15}N_{\text{SAA}}$ Coral CSIA-AA models fit vs environmental and coral CSIA-AA parameters. See Table 3.4 for details.

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<td>1.00</td>
<td>17.92</td>
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Figure 3.1 The study region is located in Jordan Basin, Gulf of Maine, and was defined by the EcoMon strata 42. Black points are the locations where the coral colonies were retrieved from an average depth of 219 m. Red points are C. finmarchicus, and blue points are C. typicus and reflect individual station locations where samples were collected across years 1996-2017. Contours fall on the 100m (light grey) and 200m (dark grey) depth.
Figure 3.2 Measured $\delta^{15}N$ of individual amino acids in each CSIA-AA sample presented in this study. Symbols reflect the individual samples measured.
Figure 3.3 Actual Values and Error of the CSIA-AA coral Data, with non-linear GAMs time trends overlaid. a) The higher trophic position trend is the $TP_{44}$ and the lower is the $TP_{GLX}$; error is calculated from the terms in the trophic position equation. b) is the relative microbial contribution to trophic transfers. c) is the $\sum V$ value, and d) is the $\delta^{15}N_{SAA}$. Shading represents the first derivative of the GAMs time smooth, purple is 0.15 units/year and light blue is -0.15 units/year. Black shading behind the GAMs time smooth represents the periods where the first derivatives is measured to be significantly not equal to zero.
Figure 3.4 Decadal trends between coral and copepod data sets. Gray lines are the best linear fit as determined in Table 3.13. See Figure 3.3 for details on line fit and shading.
Figure 3.5 Bulk GAMs model fit vs the environmental data. Points are original values, first time frame shading is red, and second time frame shading is blue. Shading alpha (degree of transparency) is proportional to the RSS value normalized to a RSS value of 0.2. See Table 3.4 for a full description of variable notations.
Figure 3.6 Each environmental relationship with the Bulk $\delta^{15}N$ GAMs additive component fit with a time trend. Continuous line in the background and light gray points reflect the GAM$_{time}$ of the original values, and the foreground broken line represents the additive component of each variable as modeled in Table 3.4. See Table 3.4 for a full description of variable notations and Figure 3.3 for information on line’s and shading.
Figure 3.7 Coral CSIA-AA GAMs mode fit vs environmental Copepod CSIA-AA parameters. Points are original values. Shading alpha (degree of transparency) is proportional to the RSS value normalized to a RSS value of 0.2 to make alpha values compared across figures. See Table 3.4 for a full description of variable notations.
Figure 3.8 Relative contribution of microbial trophic transfers: Coral CSIA-AA GAMs mode fit vs environmental Copepod CSIA-AA parameters. See Figure 3.6 for additional details. See Table 3.4 for a full description of variable notations and Figure 3.3 for information on line’s and shading.
Figure 3.9 Coral CSIA-AA models fit vs environmental and coral CSIA-AA parameters. First time frame is shaded red, second time frame shaded blue. Shading alpha is proportional to the RSS value normalized to a RSS value of 0.2 to make alpha values compared across figures. See Table 3.4 for a full description of variable notations.
Figure 3.10 Relative contribution of microbial trophic transfers: Coral CSIA-AA models fit vs environmental and coral CSIA-AA parameters. See Figure 3.6 for additional details. See Table 3.4 for a full description of variable notations and Figure 3.3 for information on line’s and shading.
Figure 3.11 Sum V: Coral CSIA-AA models fit vs environmental and coral CSIA-AA parameters. See Figure 3.3 for additional details on reading points, lines, and shading. See Table 3.4 for a full description of variable notations.
Figure 3.12 Deep Sea coral centric food web schematic. Arrows depict possible pathways trophic transfers may occur to result in the $TP_{Ala}$ and $TP_{Glu}$ values measured in this study. Black lines are feasible transfers, and grey lines are not likely as determined by the $TP_{Ala}$ and $TP_{Glu}$ values. Labels on the arrows indicate the increase in the trophic transfer index that pathway would incur for both microbial and metazoan-facilitated trophic transfers. Each component of the food web is labeled with the expected trophic position values in the boxes.
Figure 3.13 Anomaly plots for environmental parameters fit with GAM’s time additive fit. Black points are annual anomaly values, and shading represents the first derivative of the GAMs time smooth, purple is 0.15 units/year and light blue is -0.15 units/year. Black shading behind the GAMs time smooth represents the periods where the first derivatives is measured to be significantly not equal to zero. See Table 3.4 for a full description of variable notations. ST: Surface Temperature.
APPENDICES

Table 3.13 Linear, fixed, and mixed effects models to test if the linear trends in the coral and copepod data are significantly different or not. Model is the form used, AIC is the Akaike information criterion value and the AIC_Diff is the difference between the linear model and the other model forms; the lowest value is considered to be the most likely equation form while weighting for the number of parameters used in fitting the model.

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Table 3.14 Test to identify if coral and C. fin have the same linear trend and intercept. See Table 3.13.

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Figure 3.14 *P. resedaeformis* cross sections prior to dissection, imaged under UV light with a GoPro Hero10 camera retro fitted with a C mount to a dissection microscope. Annual dating was done by counting bands from the outer band using the annual light to dart transitions in the calcite and proteinaceous tissue. Each section was cut from portions of the coral with live polyp tissue to ensure the outside band was the most recent growth band associated with the sample collection date.
Figure 3.15  All bulk nitrogen isotope data from Primnoa resedaeformis coral colonies a) Fixed effect model by colony bulk $\delta^{15}N$ values. R2013 are circles, R2114 are triangles, and R2115 are squares. b) is the GAMs time additive component across all bulk $\delta^{15}N$ coral measurements, the black line represents the linear fit across all three colonies which was more significant than fitting separate trends for each colony. Shading represents the first derivative of the GAMs time smooth, purple is 0.15 units/year and light blue is -0.15 units/year. Black shading behind the GAMs time smooth represents the periods where the first derivatives is significantly different from zero.
Figure 3.16 Test to identify if coral and C. fin have the same linear trend and intercept (Table 3.14). See Figure 3.3 for additional details on reading points, lines, and shading.

Figure 3.17 Test nonlinear time structure between coral and copepod CSIA-AA data using anomaly values. See Figure 3.3 for additional details on reading points, lines, and shading.
Figure 3.18 Test nonlinear time structure between coral and C. finmarchicus CSIA-AA data using anomaly values. See Figure 3.3 for additional details on reading points, lines, and shading.

Figure 3.19 Testing the time structure between the bulk and coral CSIA-AA structure by method with GAMs time model. See Figure 3.3 for additional details on reading points, lines, and shading.
Figure 3.20 Coral CSIA-AA models fit vs environmental and coral CSIA-AA parameters. AIC values plotted vs time from each time change tested as a categorical variable in GAMs predictor models. Horizontal line is the AIC value of a model fit without a time change; vertical line reflects the best fit model with the lowest AIC value. a) Relative microbial contribution to trophic transfers, b) heterotrophic microbial reworking c) $\delta^{15}N_{\text{SAAA}}$ value.

| $\delta^{15}N_{\text{SAAA}}$ | $\Sigma V$ |
Relative microbial contribution to trophic position

Figure 3.21 Residuals from model described in Figure 3.17 Test nonlinear time structure between coral and copepod CSIA-AA data using anomaly values.

$\delta^{15}N_{SA}$

$\Sigma Y$

Relative microbial contribution to trophic position
Figure 3.22 Residuals from model described in Figure 3.18 Test nonlinear time structure between coral and C. finmarchicus CSIA-AA data using anomaly values.

Figure 3.23 Residuals from model described in Table 3.4 Bulk Isotope nitrogen values GAMs model fit vs the environmental data. Estimated parametric and smoothed effects, effective degrees of freedom (edf), standard error (Std.Error) and reference degrees of freedom (Ref.df), test statistic critical values (t-value/F) and p-values are shown by significance (’” ’ < 0.1, “*” <0.05, “**” < 0.01, “***” <0.001) for best fit model of tropic position by species. Terms in all models are as follows: Si:N: Silicate:Nitrate; N2: Stratification Index; MXLD: Mixed layer depth; calanus: C. finmarchicus abundance; centyp: C. typicus abundance; s_mean: δ15N_SAA; sum_v: ΣV; per_micro: relative contribution to microbial trophic transfers. Any CSIA-AA index with “cope” on the end of a term refers to zooplankton values, and with out “cope” refers to coral values.

\[ \delta^{15}N_{SAA} \quad \Sigma V \]
Relative microbial contribution to trophic position

Figure 3.24 Residuals from model described in Table 3.5 Coral CSIA-AA GAMs mode fit vs environmental and Copepod CSIA-AA parameters. See Table 3.4 for a full description of variable notations.

Relative microbial contribution to trophic position
Figure 3.25 Residuals from model described in Table 3.9 Coral CSIA-AA models fit vs environmental and coral CSIA-AA parameters. See Table 3.4 for a full description of variable notations.
Chapter 4 Transdisciplinary data visualization through science, sculpture, and film: A case study of Gulf of Maine food webs and climate.

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KEYWORDS:
Transdisciplinary; Data Visualization; Sculpture; Film; Education; Climate; Ocean; Food web; science communication; Outreach; Earth and Life Sciences.

SHORT ABSTRACT:
The goal of this method is to visualize bio-physical and food web relationship data and concepts through a transdisciplinary process to connect fundamental scientific knowledge with the people it impacts. We hope this work increases accessibility and engagement around how Gulf of Maine food webs change with warming temperatures.

LONG ABSTRACT:
In the face of the climate crisis, finding ways to engage with the public on the impacts of environmental change has become essential to shaping our collective future. To do this effectively, we need to challenge our current baseline for performing and presenting science and reimagine the processes in which we are participating. We need to expand the community engaged in that process beyond traditional western science disciplines to include additional ways of acquiring and valuing knowledge. Doing so will build resilience, accessibility, and equity into our approach to discovering and disseminating knowledge. This study documents the process and methods of building a transdisciplinary collaboration among scientists, artists, journalists, teachers, and public media organizations to visualize scientific data through physical and film arts to enhance research and public engagement around shifting Gulf of Maine ocean food webs.
under a changing climate. Our team brought distinct yet complementary motivations, goals, and toolsets to this shared goal. Our research documents how changing oceanographic conditions revolving around climate warming manifest as changing ocean food webs that influence everything from marine fisheries to the global carbon cycle. Two major outcomes from this work are: 1) a series of sculpture installations that encourage affective interaction with ocean food webs to build an appreciation for how microscopic animals support ecosystems and how changing environmental conditions impact those relationships; and 2) educational videos coupled to curriculum resources that freely and publicly disseminate our science to K-12 students across the US. Through this transdisciplinary collaboration, we aim to increase the collective impact of climate science storytelling through a more holistic, inclusive approach to engaging with our audience.

INTRODUCTION:

Modern climate change is one of the most globally pressing crises facing humanity today\textsuperscript{1}. Accessibility and engagement with scientific data is paramount to effective science communication and resulting effective change\textsuperscript{2}. Traditional science data dissemination through static figures in academic journals brings with it multiple accessibility and engagement barriers, including limited access, required technical knowledge, and assumed fundamental knowledge motivations. Scientists need to develop approaches for effective data visualizations that consider the diverse goals, motivations, and learning styles of people who need access to this information. To do this, transdisciplinary data visualization
involving people across diverse backgrounds and approaches working towards the shared goals of making science data accessible to the public is essential. This process involves identifying a problem or question based in shared actual experience and collaborating with others on new methods that are tailored to the problem and its context through dissolving disciplinary boundaries. This approach challenges the current academic baseline for performing and presenting science and draws on the values of methods outside of the academic realm to further application and delivery. The end goal is to create literacy around environmental and societal topics in order for the public to make informed decisions about civic issues. Transdisciplinary data visualizations are effective tools for creating this needed engagement and literacy by involving the public in underlying science that supports public action through inclusion of more people in the conception process as well as the intended audience for the final product.

This study documents the process and methods of building a transdisciplinary collaboration among scientists, artists, journalists, teachers, and public media organizations to visualize scientific data through physical and film arts to enhance both research and public engagement in a way that promotes an accessible, resilient, sustainable, and equitable approach. Here, we apply this transdisciplinary approach to scientific research on how changing oceanographic conditions due to climate warming manifest in changing ocean food webs, which influence everything from marine fisheries to the global carbon cycle. This work takes place in the Gulf of Maine, located at the intersection of
major ocean currents linked to global climate: the warm, salty, high nutrient Warm Slope Water (WSW) and the fresh, cold, low nutrient Labrador Slope Water (LSW). This system is an ideal location to investigate the interactions among climate, ocean physics, and ocean food webs. Gulf of Maine copepods are key conduits of energy within ocean food webs fueling biogeochemical cycles through their trophic interactions and community dynamics\textsuperscript{6-8}. Changes in their abundance and species composition align with decadal hydrographic-nutrient-phytoplankton shifts\textsuperscript{6,9,10} and, in turn, have major impacts on the production and biodiversity of animals higher in the food web\textsuperscript{11}. As a result, copepods are excellent ecosystem indicators for processes that link climate to ocean structure, function, and health. For example, abrupt warming on the Northwest Atlantic Shelf was identified in 2009-2010\textsuperscript{12} and has been connected to shifts in copepod population dynamics from large-bodied copepod community composition (e.g., *Calanus finmarchicus*) to a smaller bodied plankton community (e.g., *Centr科普les typicus*)\textsuperscript{14}. These changes have been implicated in shifting Gulf of Maine ecosystem structure and function, propagating through ocean food webs to influence commercially important fisheries species like Atlantic cod\textsuperscript{13} and even the endangered North Atlantic Right Whale\textsuperscript{14}. Delivering scientifically rigorous information to the general public about the complex relationships among climate, oceanography, and ocean food webs in a way that is accessible and engaging requires a process that considers a diverse audience and their unique goals, motivations, and learned experiences.

A major challenge in effective science communication around climate
change and ocean health is presenting rigorous scientific data in a way that is accessible beyond the scientific community targeted through scientific figures in traditional academic journals. Here, we developed a transdisciplinary approach to visualizing scientific data through multi-media art (sculpture and film) to communicate a message about how warming ocean conditions connected to modern climate change impact commercially important fisheries species like Atlantic Cod through the population dynamics of microscopic copepods in the Gulf of Maine food web. This approach converts challenging, often abstract scientific concepts in conventional scientific figures into emotionally and viscerally accessible formats to bring fundamental scientific knowledge to the public in a way that increases accessibility, engagement, and inclusivity. Our team included scientists, artists, journalists, teachers, and public media organizations, all of whom share the need to effectively communicate science information around climate change, but who often have different audiences, scopes, final products, materials, and processes. Two major outcomes from this work are: 1) a series of art sculpture visualizations modeled to real climatic and oceanographic scientific data that encourage affective interaction with ocean food webs to build an appreciation for how microscopic animals support ecosystems and how changing environmental conditions impact those relationships; and 2) educational videos coupled to curriculum resources that freely and publicly disseminate science to K-12 students across the US through a partnership with the PBS LearningMedia online platform.

To do this work, we conducted a scientific study on copepod abundance
over the last 40 years and related it to changes in climate/oceanographic condition visualized in classic scientific figures. Results from that study showed that rising ocean temperature through recent climate warming is driving a copepod community shift from larger to smaller-bodied copepods in the Gulf of Maine\textsuperscript{16}. The ratio of the abundance of these two sentinel species was used to generate an upper trophic level energy index (Fig. 1.d) that translates these relationships to impacts on commercially important fisheries species like Atlantic Cod. From these scientific data, two sculptures were created with a local artist to increase accessibility and engagement around the relationships among climate, oceanography, and society. The sculptures depict the changing Gulf of Maine food web over time, with stained glass pendulums shifting color from blue to red scaled to changing ocean temperatures through time. The height and width of the sculpture were scaled to the upper trophic level energy index to intuitively illustrate changing energy supplies through the food web. The sculptures and associated scientific data were then used to create educational videos that are rooted in Next Generation Science Curricula for use in PreK-12 schools in partnership with Rhode Island PBS and local educators. These educational products are part of PBS LearningMedia, which is an online PreK-12 content library that provides free access to media-based instructional resources for educators, students, and parents, available nationally, and distributed locally by public media stations across the country. Together, these coupled data visualizations aim to increase the collective impact of climate science storytelling through a more holistic, inclusive approach to engaging with our audience.
PROTOCOL:

A goal of transdisciplinary research is to develop and extend methodology that is tailored to the problem and its context though dissolving disciplinary boundaries. While the actualized methods for each individual transdisciplinary project will be unique, the overarching approach shares common themes and challenges that we illustrate here through our case study on Gulf of Maine food dynamics and climate change visualized through scientific figures, art sculptures, and education video production. This section lays out the process and key steps that this team identified as essential to executing this project and is informed by frameworks in transdisciplinary research. While the protocol is presented in a linear format, the steps to develop a transdisciplinary visualization are iterative and therefore non-chronological.

1. **Identifying the problem:** The problem being addressed by the transdisciplinary collaboration needs to be originated and developed in the context of the “world” and actual experienced problems and not just in theory or conception.

   1.1. **Summarize the problem.**

   1.1.1. The core problem our data visualization aims to address is how to share scientific data and associated knowledge to a general audience who may not have a strong background in earth and life sciences to enhance their understanding of how increasing temperature affects ocean food webs. In developing a transdisciplinary data visualization approach through a
science, art, and education lens, we seek to foster a recognition of interconnectedness and appreciation for microscopic animals in the function of major ecosystem processes like fisheries production and global climate and how they connect with human life. This is information with which our audience may not have an active connection, so in creating a connection with the audience, we raise awareness for how humans influence and are connected to these complex environmental relationships.

1.2. **Identify the disciplines who experience the problem and their goals for approaching it.**

1.2.1. **Academic:** When the academic community approaches visualizing climate and environmental data, the goal is usually to create something that communicates accuracy and precision and allows for reproducible results that can be built upon in future research by other trained scientists. This is typically done through two- and three-dimensional scientific figures that illustrate patterns and variance in data.

1.2.2. **Artist:** When an artist approaches a visualization, they provide a medium to make intangible things tangible. When approaching a visualization around climate data, an artist’s goal is often to make the abstract emotions and the global impact of the climate crisis tangible and relatable to the audience. This is done through creative expression and physical and emotional engagement by breaking down the preconceived notions of a shared background. “Art belongs to everybody and nobody. Art does not
exist for art’s sake: it exists for people’s sake.”

1.2.3. **Education:** When teachers and education professionals at public media organizations create and apply data visualizations through use of digital media, and in particular video, it is done with the goal to expand the reach of available information for teachers and students, as well as the general public. In this study, the Public Broadcasting Service (PBS) acts as a connector for the information coming from multiple types of sources (e.g., scientific, and artistic) and offers a platform for synthesizing shared knowledge across these sources to create and deliver new content to a global audience. This results in quality educational materials for educators to use in their classrooms to build on essential cross-cutting concepts in Next Generation Science Standards.

1.3. **Identify common threads or themes among collaborators behind how they frame their motives, language, and process.**

1.3.1. The team shares an altruistic motive behind creating a climate and ocean-based data visualization. The members of the team all share core values around working to improve the health and sustainability of our world and the communities that rely on it; whether that is creating the scientific knowledge, transforming it in accessible ways for the general public, or bringing it to the classroom for enhanced learning, sharing it with other members of the community is a common thread among collaborators seeking to enhance science communication.
1.3.2. Each discipline is united in a visual storytelling process that is rooted in identifying the elements behind the climate and ocean food web data that are appropriate for their audience to understand the key take home messages.

1.3.2.1. For example: The story from the scientific data is that increasing temperature through recent climate change has changed microscopic animal community composition towards smaller animals. These recent climatic, oceanographic, and ecosystem shifts do not fit patterns of past decades in this system, suggesting both a loss of large copepods and a loss of energy transfer to fishes higher in the food chain. The artist involved in this work shared a similar theme of loss. She has a focus on sculpture, performance, and installation inspired by things that are fragile, not permanent, and constantly changing. Creating a sculpture around the theme of loss in the ecosystem was an important connection between the artist's motives and the scientists' results.

2. **Personal and Communal Reflection.** In doing transdisciplinary research, it is important that the researcher(s) reflect on how their frames of reference/values/beliefs/assumptions shape the problem and how they approach investigating and solving it. It is also important to reflect on how each discipline’s body of knowledge deconstructs and reshapes one another to develop new collaborative, transdisciplinary research methods specific to the problem.
2.1. **Who is the target audience that each team member addresses?**

2.1.1. **Academic:** The target audience in our scientific data visualization is trained scientists with shared knowledge and expertise in earth and life sciences. This audience typically engages in data visualization through scientific figures in peer reviewed academic journals. This context requires that all of the information and scientific tests behind the figure be available and clearly explained for interpretation and reproducibility.

2.1.2. **Artist:** While scientists aim to share their findings and methods with other adept scientists, artists target broader, more diverse audiences with the mission to evoke emotion, discussion, and personal connection.

2.1.3. **Education:** PBS LearningMedia’s audience generally has a shared goal of learning and includes PreK-12 educators and their students and families. This content is delivered in classrooms, after school programs, and other educational organizations. This specific video content visualization and supplemental instructional resources of this case study are geared towards the middle school and high school levels with the intent that they could be adapted by teachers to both lower and higher grades.

2.2. **How does each team member work to define the scope of the question and visualization?**

2.2.1. **Academic:** Defining scope in relation to the development of a scientific
data visualization for a peer reviewed journal involves carefully considering how much information is presented in each figure - the more complexity added, the more information shared and the better representation of true system variance. However, too much complexity can obscure the overarching patterns and in turn cloud the interpretations of the key take home points. Similarly, simplicity can help emphasize overarching patterns, but oversimplification can underreport details of variance in data.

2.2.2. **Artist:** Defining the scope of an art piece is a balance between intention and instability. Like science, a clear message is conveyed when each component is purposefully designed, but this alone limits the audience’s ability to connect. An artist is concerned with invoking a reaction or curiosity in the audience and introducing elements that destabilize preconceived notions by introducing uncertainty and unpredictability into interpreting the work.

2.2.3. **Education:** When defining the scope from the PBS and educational implementation viewpoint, identifying the aspects that would be useful in a classroom to bring the academic research to curriculum-aligned resources is important. Current school science curricula in Rhode Island are set by the Next Generation Science Standards (NGSS)\textsuperscript{22}. This can look like using a short video or story line or data to capture students’ attention around a subject and make the content relatable. Then the instructional units and supplemental resources are designed around the questions students generate - inevitably their questions generally line up
with lessons teachers have planned, but those lesson plans can now be
framed in a context that the students have created.

2.2.3.1. Locally here in Rhode Island, in the classroom or when creating a PBS
LearningMedia instructional resource, making connections for the audi-
ence often looks like asking what does this information mean for the peo-
ple in the classroom here in Rhode Island and how does it affect their
lives. Do they go to the beach? Is a family member involved in the blue
economy? If that connection is missing, the goal is to build it. This can
include using videos, field trips, and experiments to simulate the relation-
ships among climate, oceans, and society.

2.3. What does the final product need to look like and embody to accom-
plish the project goals?

2.3.1. Academic: The final product in an academic setting is a series of scien-
tific figures that present an accurate representation of the patterns ob-
served in data to ensure that the viewers walk away with the proper in-
terpretation. People who have experience with academic figures will be
able to interpret and follow the content from tangential subdisciplines
within science.

2.3.2. Art: The final artistic product strips away the complexity of the data to
distill the concepts behind the scientific work down to its essence. It then
combines these simplified relationships into one place to make a very
powerful message that can be perceived very quickly and intuitively.
2.3.3. **Education:** Students are often only exposed to careers with the people that they know and see every day. The final multi-media product of this transdisciplinary data visualization approach offers an opportunity to expose young students to scientific information in a way that is engaging and informative. This approach can help break down the compartmentalization of academic knowledge and lived experience, to enhance connection building across disciplines and their own lives. One way we did this in our case study was to infuse the local perspectives from scientists, artists, and community members into locally relevant information in the resources created.

2.4. **What are the tools used in each discipline’s process?**

2.4.1. **Academic:** We used generalized additive models to visualize complex climatic, environmental, and biological data into interpretable patterns of changing relationships over time. Here, we were able to quantify how key variables like ocean temperature, major water mass mixing, and water column stratification influenced the population dynamics of two key copepod species with juxtaposed long-term abundance patterns in the Gulf of Maine (Fig. 2 and 3).

2.4.2. **Artist:** Artists can use the physical elements: color, shape, light, rhythm, form, and structure to alter the meaning a physical form can convey. This visualization used color to define temperature, shape as a proxy for an animal (abstractly in Sculpture One, literally in Sculpture Two), light to
show loss and energy flow (with both transparency in resin (Sculpture One) and glass (Sculpture Two)), rhythm was created through repetition of shapes and structures to show temporal change within the system, and form was used to identify animals and their interactions.

2.4.2.1. A specific example of the use of form in Sculpture Two is how the amount of glass was distributed. Phytoplankton have more glass around their form at the bottom to show that that is where the most biomass in the food web is located. As energy decreases in each trophic level step and from the past to the present, so does animal biomass and therefore the amount of glass and metal that is used.

2.4.3. **Education:** Our partnership with Rhode Island PBS provides expertise in structural media and a platform for sharing educational material on a national scale through the PBS LearningMedia library. It is an effective and efficient way to communicate information to a large educator and student audience and to inform the community. PBS’s work has both a large educational and media focus as well as a national audience that makes their content free to access within the United States.

2.4.3.1. As part of the PBS LearningMedia product, we collaborated with a high school teacher to turn our coupled science and art data visualization approach into educational lesson plans that meet National Standard Benchmarks for Science Literacy. Each education lesson plan was designed to make connections for the students with concepts from their own lives that
are familiar in order to take something that is abstract like ocean sea surface temperature and make it relatable and more likely to be retained. For instance, in the sculptures blue and red gradients in the stained glass were used to illustrate changing temperature over time. Students can make connections to similar color schemes in their homes, such as a kitchen faucet where red is used to indicate hot and blue cold.

2.5. What are the materials used in each discipline's process?

2.5.1. Academic: In the academic context of producing a data visualization, materials are often constrained to two- or three-dimensional images with different combinations of points, lines, and shadings due to the traditional delivery mechanism of print and online papers in an academic journal format.

2.5.2. Artist: The materials in Sculpture One consisted primarily of resin and ink to capture the concept of energy flow and the ocean currents. The resin also enabled the creation of cylindrical shapes with ranging diameters to be used in repetition as a proxy for animals in a food web. The materials in Sculpture Two were changed to increase the literal, and thus more intuitive, interpretation of the changing conditions in the final visualization. Metal was used instead of resin to provide a form that could be cut into the shape of our target organisms. This material also invokes an emotional connection with the audience. As the temperature rises, so
does the amount of rust in each piece, conveying a familiar sense of aging and loss. Sculpture Two also used glass to show the transition in temperature and energy transfer while maintaining the use of light and transparency in the first iteration.

2.5.3. Education: So much information is communicated through video today beyond simple entertainment. Most everyone has access to videos in their pocket all of the time. The formal education environment can make use of this familiarity and comfort level with media to benefit instruction, which is a key strategy applied by PBS in creation and distribution of its resources. This approach has been shown to have significant positive impacts on students’ understanding of concepts and performance on assessments\textsuperscript{28}. With this current project, we are applying this proven strategy for communicating data visualization as a powerful educational tool to generate student engagement, understanding, and knowledge retention. It increases both availability and accessibility by giving the students the option to watch, rewatch, pause, and go slower when needed. As our consulting educator offered: if a video is talking to the students at their level (or even a little higher than their level) the students will be more receptive to the message.

2.5.3.1. The resulting videos are then applied as tools in lesson plans written by educators with expertise in the relevant curriculum area, standards-aligned, and contextualized with supporting instructional strategies, including where possible, identifying activities that engage the students in
a hands-on manner to deepen comprehension. The more students are hands-on (doing or making something), the more the content is made real to the students. From the videos, students will be able to create their own data visualizations in in-class, hands-on activities to enrich the instructional process.

2.6. What is the process to get to the final product?

2.6.1. Academic: To make the final scientific data visualization product clear and impactful takes an iterative approach. Often the first time a figure is made, it either has too much detail and complexity or not enough. The initial questions must then be reassessed to guide the figure towards the right level of complexity to accurately represent the patterns and their variance in a way that is easily interpretable. This process involves showing those visualizations to experts in the field that share key demographics with your target audience, getting feedback and revising the presentation of information to make it clear, accurate, and engaging while simultaneously illustrating the key take home points.

2.6.2. Artist: One of the most important parts of the art process is creating a multi-directional conversation with the viewer (in contrast to a science figure where the information is moving from the author to the audience). This is done in art by removing elements of accuracy and detail to prevent the piece from becoming didactic and to move closer to the essence of the concept as possible. This makes the piece more effective
and interesting because it makes space for the audience to fill in and connect to the story with their own personal narrative.

2.6.3. **Education:** The process of creating resources for publication on PBS LearningMedia is very different for each project. In this case, where PBS is creating video specifically for use in PreK-12 lesson plans, they meet with the team to create a strong understanding of the content that is being included, the work that is being done, and the message that is being communicated. They then make sure to include all of the voices on the team and work to understand the team’s perspective as well as the needs of students in the target classrooms to direct the type of content that will be the most effective. Then there is the process of creating the video segments, getting/giving feedback, revising content, and creating the educational resources to go along with the videos.

2.6.3.1. In the classroom the short and dynamic videos from PBS LearningMedia are included in instruction with a range of supporting materials written by educators with expertise in the relevant curriculum area, grade level, and standards. These supplemental resources may include full-length lesson plans, more specific discussion questions, activities, assignments, handouts, and assessments all built around the core video content and lesson objectives. The research-based model employed by PBS LearningMedia in its content development utilizes shorter video segments (generally 2-10 minutes) that are directly aligned with a spe-
pecific lesson objective, rather than longer form video, which may not pro-
vide enough instructional focus to achieve the desired instructional goal
for the lesson. Being able to apply shorter videos quickly in a classroom
is a huge advantage over longer ones because it reduces the likelihood
of losing the students’ attention.

3. **Engaging in the process.** The dissolution of disciplinary boundaries oc-
curs throughout the project from conception to final reflections. The peo-
ples executing the work should not only focus on theory and practice – but
also on engaging in the context of the problem as an embedded re-
searcher⁴; this means the work being done by each person is not only
furthering scientific and theoretical understanding, it is also being tied
back into society through the perspective of impacted stakeholders (the
researchers).

3.1. **What did it look like to compromise in the process of developing
this visualization?**

3.1.1. Compromise in this data visualization process often looked like losing
some of the complexity that is captured within the actual scientific data
to gain a more accessible and readily interpretable product for a general
audience. For example, to focus on a key message about the emerging
relationship between climate and ocean food webs in the past decade,
the high-resolution 40-year ocean dataset was truncated into five time
points from the last decade at an annual resolution to emphasize the key
transition point in this dataset.

3.1.2. The design for Sculpture One evolved from the common depiction of food webs and energy transfer: a standard triangle where producers form the wide base and consumers form subsequently higher trophic levels. The triangle was inverted to dramatize how much the whole food web depends on the small animals located at the base. Despite this visualization aligning closely with graphical depictions of the data, the resultant sculpture was too abstract for broad audiences to interpret the central message. As a compromise, the team leaned into a more literal depiction with Sculpture Two and added more complexity to the visualization by repeating physical forms of representative animals. With Sculpture Two a broader audience can perceive the patterns and interpret the message intended by the team.

3.1.3. Another compromise that came with working across a large number of collaborators was unifying each discipline’s way of understanding, disseminating, and valuing data and information to achieve balanced language and representation in the shared message. For example, the process of weaving together the individual perspectives, goals, and values to synthesize one holistic narrative in a video interview style challenged the artist, educators, and scientists to express their thoughts and methods in a short conversational format, while emphasizing the inherent value and purpose of their contribution.
3.1.4. Showing art through video representation is itself a compromise. The dynamic, three-dimensional art sculpture was designed for maximum effectiveness through in person engagement. In doing so, this realistically limits engagement to a subset of the local audience with adequate time and resources to visit the installation. While capturing the art installation through video loses some of the effectiveness that comes with in person engagement, this format enables the project to have a much broader national reach.

3.2. What were the common patterns identified between each process?

3.2.1. A common pattern among science and art visualizations as well as education content creation is considering what elements will be familiar and can prime the audience with information to interpret the piece. For instance, this project applies the common congruence that red reflects hot temperatures and blue cold in both Figure 4.1 as well as Sculptures One and Two.

3.2.2. Though each discipline is unique, they share similar approaches in identifying what the specific audience needs, and how to best deliver that need. This means each discipline is engaging in a similar process of tailoring the final product to an intended audience, despite the fact that their traditional final products are all different mediums (figure/manuscript, art piece, video or lesson plan).

3.2.3. Another common pattern behind the different discipline processes is the
approach to condensing complex data and interpretations into simplified visualizations. Whether in science figures, art sculpture, or video interviews, we found that they all distill complex ideas through summarizing patterns that balanced accuracy/complexity with accessibility and interpretability.

**REPRESENTATIVE RESULTS:**

Data applied in this study are from the NOAA-Northeast Fisheries Science Center Ecomon survey and have been subset to focus on Jordan Basin strata 42 according to methods from Nowakowski et al. 2020. For each panel in Fig. 1, data are represented by a Generalized Additive Model (GAM) time smooth. Figure 1a shows surface temperature monthly anomalies from the years 1977 to 2017 and highlights the time frame from 2004-2017, the duration for which the Gulf of Maine has been warming faster than 99.9% of the rest of the world's oceans\(^{25}\). Figure 1b shows monthly abundance anomaly data for *Calanus finmarchicus*, a large bodied copepod, and Figure 1c shows monthly abundance anomaly data for *Centropages typicus*, a small bodied copepod; these two species reflect the decadal scale inverse community composition trends in the Gulf of Maine that oscillates between large and small copepods\(^{6,9,10}\). The ratio of their two abundance values can be used as a proxy for available biomass to upper trophic levels, termed the “Upper trophic level energy index” (Fig. 1d). Theoretical ecological food web principles\(^{26}\) suggest that under conditions where large copepods are abundant, energy transfers up the
food web are more efficient due to shorter food chain lengths, and under conditions with higher small copepod abundance, energy transformations would be less efficient due to longer food chain lengths. This relationship dictates key ecological population dynamics of commercially important fisheries species\textsuperscript{27}.

Figures 2 and 3 depict results from Nowakowski et al. 2020, which demonstrate the relationship between small and large sized copepod abundance and surface temperature across the years 1977 to 2017 in Jordans Basin during the winter. \textit{C. finmarchicus} abundance anomalies have a negative relationship with surface temperature that has a steeper slope during the second period of decreasing abundance and \textit{C. typicus} has a positive relationship with surface temperature during the second half of the timeseries. From these models, an emerging relationship with winter sea surface temperature was identified as significant and prevailing during the time frame from 2004-2017. Warming temperatures are driving a significant decrease in large bodied \textit{C. finmarchicus} while increasing the abundance of small bodied \textit{C. typicus}.

The sculptures (Figure 4 and 5) visualize the emerging relationships among ocean temperature, copepod abundance, and upper trophic level fisheries dynamics by focusing on the recent time period where the relationship is the strongest and most divergent from long term patterns. The color transition from blue to red, which capitalizes on the commonly shared association with cold and hot, is scaled to ocean temperature data from our study and highlights the shift to persistent, above average sea surface temperatures over the course of this time series in the Gulf of Maine. Both the width of each animal and height of
each sculpture column are scaled to the Upper trophic level energy index using time points from years: 2004, 2007, 2010, 2013 and 2016 (vertical lines in Figure 4.1a). As the upper trophic level energy index decreases, the size of expected copepods within the community decreases, and in turn the expected energy transfer to the top of the food web decreases. In addition to capturing these data features, the sculptures also capture an affective, emotional representation of the data as well as put the copepod temperature relationships into the broader context of the ecosystem. The first form (Figure 4) was rooted stronger in the artist's knowledge base and took an abstract approach to visualizing the food web connections. However, this form required significant additional context to produce the desired level of interpretation. To restructure the approach to enhance intuitive interpretability and audience connection, we integrated more literal information and context into the visualization in the Sculpture Two (Figure 5). This sculpture used repeating visuals of specific organisms to add redundancy in how the food web connections are presented to the audience. The final visualization translates the important take-home points from complex and nuanced modeled results into an accessible format for a larger group of ages and demographics by incorporating easily recognizable images and the ecosystem background context for which the results can be interpreted into the final visualization.

Finally, by incorporating this data visualization into a PBS LearningMedia product, we increase the accessibility, availability, and impact of our data and
results. PBS LearningMedia, as a free resource developed and distributed nationally by PBS in close collaboration with public media stations across the country, has seen tremendous growth in usage in recent years, especially as educators, students, and families sought out digital resources due to virtual settings brought about by the onset of the 2020 pandemic. PBS LearningMedia has maintained a 35% increase in usage over pre-pandemic levels, with annual totals of 15.3M total users; 51.7M total pageviews; 1.56M avg. users per month; 4.7M avg. pageviews per month over the 2021-22 school year. PBS LearningMedia resources cover the full range of subject areas and grade levels and include video from PBS broadcast content and original interactives, supplemented by standards-aligned lesson plans, teaching tips, activities, handouts, and assessments to facilitate classroom use. Currently there are over 30,000 media-based instructional resources on the site, generating over 50 million annual user visits nationally, including over 100,000 visits annually by RI users. Rhode Island PBS Education Services has developed and published 18 locally produced resource collections on PBS LearningMedia since 2018. These resources have generated over 125,000 page views by educators and students nationally as of September 2022 (note—a page view may represent use by educators with multiple students, so it is reasonable to factor in an even larger number of total students reached with this content). Specific comparable resources that would be similar to the resources created for this project include: Ocean Exploration: Inner Space (378 page views since March 5, 2020) Oysters & Genetics (123 page views since February 23, 2022) Inside the Work (461 page
views since February 18, 222). Over time, it can reasonably be expected that the distribution of resources from this project will generate comparable results.

An important success metric of these results from the academic point of view is whether this work is reproducible. Scientific data visualizations are often approached with a critical lens of validity; can other scientists identify the key patterns, independently reproduce them, and build on them to ask future questions to advance the field? But when interpreting through a Fine Art lens, the artist has put the work into a social, political, and cultural context that is designed for the viewer to bring their personal experience into the experience\textsuperscript{23}, and this information is very different from what is available to the audience in an academic science context. The fine art process enables the audience to make personal connections and reactions to the social, political, and cultural context of the topic at hand and results in a more memorable experience that may lead to further engagement in the concept. Another metric of success from an artist point of view is the balance between how planned and controlled the work should be and how open or unstable it should be (protocol 2.2.2). When everything is planned, the intention of the work is clearly conveyed, but the instability that comes from derailment, uncertainty, or unpredictability is what brings the artwork to life. It is important to have unconscious and intuitive parts of the artwork that are not clearly understood and not clearly explainable because they arouse curiosity in the audience. Many elements of this visualization were controllable and explainable, but if Sculpture One (Fig. 4) or two (Fig. 5) are still able to spark curiosity and change in just one person then this work is a success.
Figuring out how to capture the audience’s curiosity is a driving force for many artists, scientists, and educators alike.

**Figure 4.1:** Environmental and ecological data in the Gulf of Maine over the past 40-ys a) surface ocean temperature, b) large copepod (Calanus finmarchicus) abundance, c) small copepod (Centropages typicus) abundance, and d) Upper trophic level energy index as an indicator of energy transfer from copepods to upper trophic level predators like Atlantic cod. Color and line reflect the same values, and vertical lines indicate the five time periods reflected in the sculptures (Figure 4.4; Figure 4.5).
Figure 4.2: Relationship between surface temperature and C. finmarchicus abundance. Shading for all lines represents the first derivative for GAMs time smooths (dark blue -0.5 to dark red 0.5) and black shading behind the lines represents periods of statistically significant change. a) Monthly anomaly copepod abundance values are plotted in light gray points, the copepod abundance anomaly time smooth is depicted by the thinner line that spans the entire time series, and thicker lines and black points represent the GAMs surface temperature additive component. b and c) represent the GAMs surface temperature additive component relationship with copepod abundance.
Figure 4.3: Relationship between surface temperature and *C. typicus* abundance. As follows from Figure 2.
Figure 4.4: Sculpture One: Far left of sculpture are resin casts of animals to represent different trophic levels, from phytoplankton (bottom tier), to copepods, to feeder fish, to cod fish (top tier). Right of resin animal casts are resin calendars, where width and diameter are scaled to the upper trophic level energy index as well as the assumed trophic position in the food web. Lower trophic levels are smaller in size and transfer energy the most efficiently up the food web and therefore have a small radius to reflect their actual size and a taller height to reflect the amount of energy they transfer. Upper trophic levels are larger in individual size, but transfer energy less efficiently and therefore have a larger radius but shorter height. Color is created using blue, red and white ink to reflect a change from lower to higher temperature through time. Five time points are reflected in the five different conceptual iterations from left (oldest) to right (most recent).
Figure 4.5: Sculpture Two is as follows from Figure 4.4, Sculpture One, but instead of resin galvanized steel and glass are used and the animal shapes are repeated throughout the five conceptual iterations.

DISCUSSION:

By coupling the accuracy and reproducibility of scientific data with the emotional and intuitive engagement of art through a free, open access education platform to create an immersive data visualization, our team was able to: 1) identify a major problem shared by many disciplines engaged in science communication: sharing complex scientific data and associated knowledge to a general audience in a way that promotes engagement and literacy, 2) reflect on both personal and communal processes to address that problem, and 3) engage in the process of building a transdisciplinary data visualization approach to science communication as embedded researchers. This study has expanded each member of the team’s ability to work across and apply different bodies of knowledge to develop a dynamic method for visualizing complex climate and ocean food web relationships for a diverse audience.

One of the most critical steps during our transdisciplinary data visualization process was making sure that everyone’s goals were acknowledged, recognized as shared goals, and worked on as a team; this was essential to framing Section 1 of the protocol: Identifying the Problem and executing Section 2 of the protocol: Personal and Communal Reflection. Here, trust was critical to uncovering our shared underlying values of information dissemination, which allowed
us to deconstruct the traditional singular disciplinary science communication approaches in favor of building a collaborative, transdisciplinary approach. We created a setting where it was okay to ask the same question multiple times, and we took time to talk through fundamental discipline specific knowledge explanations. This was very important to keep the whole team on the same page and communicating with compatible languages. Together, these efforts enabled the team to exchange perspectives and approaches more honestly and integratively. In doing so, we were able to step past viewing each discipline as a subsidiary tool for understanding the other and to valuing each other's methods as our own.

Identifying limitations and troubleshooting the method behind our collaborative, transdisciplinary data visualization required recognizing the aspects of the visualization where the balance between one body of knowledge was tipped too far in one direction or the other. An example of this (Protocol 3.1.1) can be seen in the effort to discern the appropriate amount of information to translate from the academic figures to the sculpture. A compromise was struck to maintain the accuracy of the scientific data but scale back the length of the time series shown to allow the details of the art sculpture to be accentuated. This is what directed the choice to focus on the most recent decade of dramatic climatic change represented in the five annual panels (vertical lines Fig. 1). Another limitation was in the colors of the visualization. Compromise was struck to limit the artistic color palette to portray temperature change in an intuitive format using red and blue with preconceived connotations of hot and cold (Protocol 3.2.1).
This approach allowed educators to help students build familiar connections with the visualization and increase information processing and retention (Protocol 2.4.3). Another of disciplinary strengths informing transdisciplinary decisions can be seen in the reframing of the overall form between Sculpture One and Sculpture Two. Through applying the artist process described in protocol 2.6.2, the Sculpture One captured the essence of the concepts and science relationships behind a food web transition and warming water to make a provoking figure that was effective in capturing curiosity. However, in the end the product was too abstract to be literally interpreted, which made it challenging to effectively incorporate into PreK-12 educational resources shared with educators, students, and families across the country through the PBS Learning Media online portal. We redesigned the materials and application of more literal animal imagery in Sculpture Two to make the final product more identifiable and emotionally engaging for diverse student audiences.

Delivering this coupled science and art data visualization approach through PBS LearningMedia is expected to have a significant positive impact across several metrics related to student engagement, academic performance, and teaching strategies\textsuperscript{24,28}. Teachers found PBS LearningMedia resources to be high quality and easy to integrate into their instruction and appreciated that the resources were standards-aligned and curated, and virtually all teachers in the study thought that the collections had positive effects on their students, promoted and deeper understanding of the content\textsuperscript{24,28}. In particular, they appreciate the ability of PBS LearningMedia to engage students through interactives,
visuals, and connections to real-world applications. Most participating teachers strongly agree that they wanted to continue using the collections and would recommend them to others\textsuperscript{24,28}. Importantly, recent studies have shown that access to free, standards-aligned, online educational content can significantly increase participation in STEM across historically minoritized groups\textsuperscript{30}. With our current project applying these same strategies to the development and distribution of educational resources, we can anticipate comparable results with teachers and students who will utilize them.

Our data visualization method reshapes approaches to science communication across multiple methods and disciplines to construct a new transdisciplinary method of sharing environmental science with major societal significance\textsuperscript{4,19,23}. One of the challenges with science communication in a classic science figure is that it is often not designed to elicit emotional or visceral responses\textsuperscript{19}. Scientists do not typically get the opportunity to express vulnerability and to highlight the human interaction within the questions and resulting data visualizations, yet that is often exactly what we need to engage a wider audience and enact social change and policy change\textsuperscript{19,23}. Conversely, the final products of art are often abstract and intended to leave space for people to fill in their own personal narrative, which makes it challenging to keep the interpretation centered on the facts of a global climate crisis. Art creates tremendous synergies when it is combined with science\textsuperscript{29} and it conveys emotions and provides a firm narrative base that makes learning more memorable\textsuperscript{23}. It also provides a way to more actively engage the public in the scientific process through shared
educational resources. This data visualization approach seeks to find central ground capitalizing on scientific approaches that advance our fundamental understanding of the mechanisms that influence the structure and function of the world while also creating content that provides the necessary context and background for a general audience. It is imperative that we build on the knowledge and approaches of multiple complementary disciplines in the context of their shared challenges in effective science communication to engage and uplift diverse audiences. Our data visualization approach is a primary example of why science technology engineering art and math (STEAM) education is so important - real life is not compartmentalized into different subjects and topic areas. It is messy, and it is collaborative. We hope that our work at the intersection of science, art, and education can ripple in people's perception and inspire new ideas for how to approach and develop data visualizations by sparking curiosity about ocean sciences that will build engagement and literacy around environmental and societal topics to create a much needed wave of social and policy action.

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