

**DIEL, SEASONAL, AND INTERANNUAL PATTERNS IN
MESOZOOPLANKTON ABUNDANCE IN THE SARGASSO SEA**

A Thesis

Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment

of the Requirements for the Degree of
Master of Science

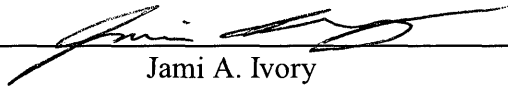
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Jami Alora Ivory

2015

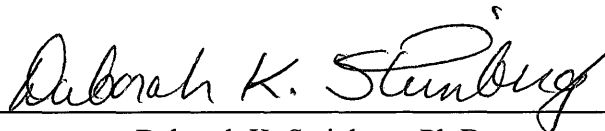
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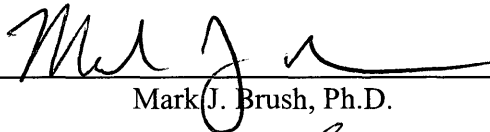


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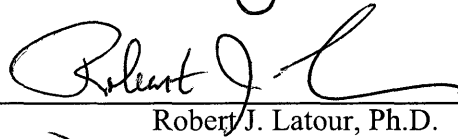
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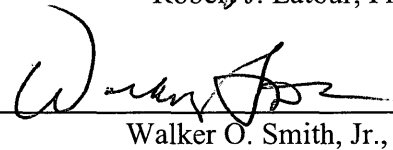
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ABSTRACT

Temporal changes in mesozooplankton community structure are influenced by a combination of environmental factors. Epipelagic mesozooplankton biomass in the Sargasso Sea has increased over the last two decades, with a related increase in zooplankton-mediated carbon export. Unknown, however, are the patterns and variability at different temporal scales (diel, seasonal, and interannual) in abundance of each major zooplankton taxon, and how these patterns relate to physical and other environmental changes. I enumerated major taxa of mesozooplankton collected from monthly day and night net tows in the epipelagic zone at the Bermuda Atlantic Time-series Study (BATS) site in the Sargasso Sea from 1999 to 2010. Abundances of each taxon were determined using a ZooScan optical imaging system and microscopy. Generalized Linear Models (GLMs) were used to determine what environmental parameters best explain abundance of major taxa. I used annual averages to determine broader patterns. Zooplankton taxa with the most pronounced diel vertical migration (i.e., night:day ratio, N:D, $\gg 1$) included euphausiids (N:D=1.9), *Limacina* spp. pteropods (1.5), and other thecosome (shelled) pteropods (1.6). Taxa with a pronounced spring abundance peak included euphausiids, larvaceans, and *Limacina* spp., while harpacticoid copepods peaked in late summer, and calanoid copepods in both spring and summer. There is some evidence of changes in phenology occurring in calanoid copepods and chaetognaths that exhibited spring abundance peaks on average 1-month earlier than reported for the same taxa in the early 1960's. Many taxa, including all copepod taxa, exhibited a period of highest abundance increase in 2003, coinciding with a 2003 April diatom bloom and the largest primary production peak (April 2003) in the time series. There was also indication of a long-term increase in calanoid and oncaeid copepod abundance. Sub-decadal-scale climate oscillations, long term warming, and ocean acidification may be driving decreases in larvaceans, *Limacina* spp., and other shelled pteropod densities. Environmental variables affecting abundance differed among taxa. For example, calanoid copepod density was highly influenced by the abundance of a major predator—chaetognaths. Multi-year densities of calanoid copepods and ostracods both increased with increasing Water Column Stratification Index and the Atlantic Multidecadal Oscillation (AMO) index, indicating warmer sea surface temperatures are favorable for these taxa. These patterns in zooplankton community structure have important implications for energy transfer in pelagic food webs and for biogeochemical cycling.

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**DIEL, SEASONAL, AND INTERANNUAL PATTERNS IN
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1. INTRODUCTION

Climate change and zooplankton in the North Atlantic Ocean

The Earth is experiencing rapid warming due to an increase in CO₂ in the atmosphere (Doney et al., 2009; Hoegh-Guldberg and Bruno, 2010). The oceans have mitigated some of this increase in CO₂ by acting as a sink, having absorbed 30% of anthropogenic atmospheric CO₂ (Sabine et al., 2004; Doney et al., 2009; Hoegh-Guldberg and Bruno, 2010; IPCC, 2014). Ocean sea surface temperatures have increased by 0.09 to 0.13 °C per decade from 1971 to 2010 (IPCC, 2014) with disproportionately more of that warming occurring in the Northern Hemisphere (Hansen et al, 2006; Beaugrand, 2009).

Increasing water temperatures in the North Atlantic Ocean are altering zooplankton assemblage distributions in this region (Beaugrand, 2009; Beaugrand et al., 2009; Beaugrand et al., 2013). For example, the geographic distribution of temperate calanoid copepods has moved northwards as subpolar waters warm (Beaugrand, 2009; Beaugrand et al., 2013). The abundance of cold water and subarctic species in calanoid copepod assemblages has decreased along with euphausiid abundance, while small, temperate calanoid copepods are increasing (Beaugrand et al., 2009). Some copepod species are also showing an earlier seasonal peak in abundance (Beaugrand, 2009). These changes in zooplankton biogeography, abundance, size distribution, and phenology could lead to trophic mismatches (Beaugrand, 2009). Changes in the North Atlantic zooplankton assemblage could also affect biogeochemical cycling and the efficiency by which the ecosystem sequesters atmospheric CO₂. For example, as smaller zooplankton produce smaller fecal pellets which sink more slowly, the system could change to one of

primarily recycling rather than exporting (Beaugrand, 2009; Steinberg, in press). Also, changes in composition and abundance can lead to changes in diel vertical migration, a component of the biological pump whereby zooplankton actively transport carbon from the photic zone to depth via feeding in surface waters and metabolizing at depth (e.g., Longhurst et al., 1990; Dam et al., 1995; Steinberg et al., 2000). Long-term measurements of plankton species composition and abundance, along with potential environmental controls, are important for predicting planktonic food web changes in the North Atlantic Ocean due to global climate change (Steinberg et al., 2001).

The Bermuda Atlantic Time-series Study (BATS)

The Bermuda Atlantic Time-series Study (BATS) was initiated in October, 1988 to better understand biogeochemical processes on seasonal and decadal time scales and improve predictions of how these processes will be affected by climate change (Steinberg et al., 2001; Lomas et al. 2013). The BATS site is located in the oligotrophic western North Atlantic subtropical gyre, 82 km southeast of the island of Bermuda in the Sargasso Sea (Figure 1), and is sampled monthly (bimonthly during the spring bloom period January-April). A broad suite of biogeochemical measurements are taken on BATS cruises, including: temperature, salinity, $p\text{CO}_2$, nutrients, chlorophyll a and other phytoplankton pigments, and zooplankton biomass. Process rates, such as primary production, bacterial production, and particle flux are also measured.

Most of the year nutrients are low or undetectable in the euphotic zone at BATS, although cool winter temperatures and winds deepen the mixed layer introducing some nutrients into the euphotic zone and leading to a spring phytoplankton bloom, usually in

February or March (Steinberg et al., 2001; Lomas et al. 2013). In early summer and fall the mixed layer shoals, reducing nutrient inputs, which typically results in low phytoplankton and zooplankton biomass (Roman et al., 1993). Chlorophyll concentrations peak in the top 120 m usually in March, with total zooplankton biomass peaking around the phytoplankton spring bloom in March/April (Steinberg et al., 2001, 2012). Prokaryotic picoplankton usually dominate the phytoplankton (Steinberg et al., 2001), and diatoms have become increasingly rare over the course of the more than two-decade time series (Lomas et al., 2010). The BATS site has also experienced a significant increase in sea surface temperature from 1994 to 2011 (Stone and Steinberg, 2014); other long-term changes at BATS include an increase in primary production (Saba et al., 2010) and epipelagic zooplankton biomass (Steinberg et al., 2012).

Historical zooplankton studies in the Sargasso Sea

The first comprehensive study of Sargasso Sea zooplankton diel and seasonal abundance took place from 1938-1940 (Moore, 1949). This pioneer study measured the abundance of major zooplankton taxa at four depth intervals between 0-300 m and showed a spring peak in zooplankton abundance, with the most abundant zooplankton, copepods, peaking in mid-March (Moore, 1949). A higher temporal resolution (biweekly) study of zooplankton biomass 0-500 m, at Station “S” (24 km southeast of Bermuda; Figure 1) from 1957-1960, indicated a peak in zooplankton dry weight in mid-March (Menzel and Ryther, 1961). Seasonal sampling from 1959-1960 showed a peak abundance in copepods in July (Grice and Hart, 1962), but this study site was further from the BATS station than earlier studies and may not be representative of BATS

(Madin et al., 2001). From 1961-1962 the major groups of zooplankton between 0-2000 m were quantified from both day and night tows (Deevey, 1971; Deevey and Brooks, 1971). Copepods represented 70-85% of the total zooplankton and peaked with other zooplankton taxa in April, with copepods having a second abundance peak in September (Deevey and Brooks, 1971). Ostracods, pelagic tunicates, cnidarians ('coelenterates' in the original study), and chaetognaths were other abundant taxa (Deevey and Brooks, 1971). Similar trends were found during monthly sampling in Bermuda inshore waters from 1979-1980, but with a maximum peak of zooplankton in July (von Bodungen et al., 1982). Von Bodungen et al. (1982) found that zooplankton peaks followed chlorophyll peaks.

Starting in the late 1980's zooplankton sampling coupled with physical and chemical measurements such as nutrients, oxygen, and sinking particulate organic matter became more common. Roman et al. (1993, 1995) reported highest macrozooplankton biomass in March/April during which zooplankton contributed more to the sinking particle flux than during August. Zooplankton ingestion rates, metabolic rates, and biomass at BATS in March and April of 1990 indicated that ingestion rates and biomass were greatest at night (Dam et al. 1995). These data, compared with sediment trap particle flux, showed that respiratory carbon and dissolved inorganic nitrogen from diel vertical migrators accounted for a significant export of carbon and nitrogen (Dam et al. 1995).

Up to this point zooplankton were either only periodically sampled or sampled for fewer than three consecutive years. Methods (e.g., size of net mesh used) often varied, making it difficult to make long-term comparisons between studies. Due to the

importance of zooplankton as environmental indicators for climate change (Richardson, 2008), and their key role in biogeochemical cycling (Steinberg et al. 2012), regular zooplankton sampling became a component of the BATS program.

The BATS zooplankton time series

In April 1994, monthly (bimonthly January-April), day and night sampling of zooplankton in the epipelagic zone (0-200 m) commenced as part of the BATS program (initiated in 1988) (Madin et al., 2001; Steinberg et al., 2012). Many of the studies since the BATS zooplankton time series began have focused on the role zooplankton play in biogeochemical cycling and in the biological pump. Measurements of the biomass of diel vertical migrators and their metabolism of both C and N at depth (respiration and excretion) indicated diel vertically migrating zooplankton are an important component of dissolved C and N export (Steinberg et al., 2000; Schnetzer and Steinberg, 2002a). These vertical migrators also produce fecal pellets at depth, contributing as much as 18% of the mean sinking POC measured in sediment traps at 150 m (Schnetzer and Steinberg, 2002a). A study of the natural diets of three vertically migrating zooplankton species found differences in feeding preference among the species, suggesting that an individual species approach is necessary when determining the effect of zooplankton feeding habits on the carbon cycle (Schnetzer and Steinberg, 2002b). A multidisciplinary study of mesoscale eddies in the Sargasso Sea showed increased zooplankton abundance, diel vertical migration, and fecal pellet flux inside eddies, making eddies regions of high export flux (Goldthwait and Steinberg, 2008; Eden et al., 2009).

Recent analyses of the BATS zooplankton time series have been used to detect long-term changes in zooplankton biomass. Mesozooplankton biomass increased 61% from 1994-2011, likely due to bottom-up controls such as increasing primary production (Steinberg et al., 2012). The result of this increase in zooplankton biomass was an increase in the magnitude of export flux via active transport (diel vertical migration), and passive flux of zooplankton fecal pellets (Steinberg et al., 2012). Zooplankton biomass over the 17-year period was positively correlated with primary production, sea-surface temperature, and water column stratification, with weak but significant correlations with several multi-decadal climate indices (Steinberg et al., 2012). Salp (gelatinous, pelagic tunicates) abundance and biomass from 1994-2011 was significantly correlated with primary production, the North Pacific Gyre Oscillation, and the Pacific Decadal Oscillation (Stone and Steinberg, 2014).

While significant progress has been made in determining the role of zooplankton in biogeochemical cycling at BATS and in examining long-term changes in zooplankton biomass with some specific taxa (salps) being well described, this thesis is the first analysis of long-term seasonal and interannual patterns in zooplankton at BATS. This information is vital for understanding the effects of a changing climate on zooplankton abundance and phenology, food web interactions, and the role of zooplankton in biogeochemical cycling.

Objectives and significance of this study

The first objective of this thesis was to analyze seasonal, interannual, and longer-term changes in major taxa of mesozooplankton at BATS in the oligotrophic North

Atlantic subtropical gyre. A second objective was to determine environmental drivers of patterns and temporal changes detected in taxonomic composition. The first objective was accomplished by identifying and counting the major groups of mesozooplankton from a 12-year time-series (1999-2010). Timing of peak abundance was noted and compared to historical findings to determine if taxa were peaking earlier in the year during this time-series. Comparisons of the abundance of migrating taxa addressed which taxa contribute to the observed increase in night-time mesozooplankton biomass at BATS (Steinberg et al., 2012). To accomplish the second objective, generalized linear models were used to quantify which environmental variables significantly influenced specific mesozooplankton taxon abundance. This study provides the first detailed analysis of temporal patterns in major mesozooplankton taxonomic composition, and determines what environmental variables drive composition changes at BATS. The location of the BATS study site makes these results applicable to other subtropical gyres around the world, which comprise a large proportion of Earth's oceans. Because the taxonomic composition of zooplankton affect food web interactions and export of organic carbon, this information is key to predicting effects of global climate change on trophic interactions and biogeochemical cycling in the North Atlantic Ocean and other subtropical gyres.

2. MATERIALS AND METHODS

Zooplankton collection

Zooplankton were collected from the Bermuda Atlantic Time-series Study (BATS) site in the oligotrophic North Atlantic subtropical gyre (31°40'N, 64°10'W). Mesozooplankton sampling for BATS began in April 1994 and is ongoing, with sampling methods described previously (Madin et al., 2001, Steinberg et al., 2012). Briefly summarized, mesozooplankton (>200 μm) were collected using a 1-m² rectangular frame net with 202 μm mesh. Two replicate day and night, double-oblique tows were performed on each monthly cruise, and usually on two cruises during each month between January and April. The targeted sampling depth interval was 0-200 m, with the absolute depth recorded by a Vemco Minilog recorder. A General Oceanics mechanical flowmeter measured volume filtered through the net. Samples were split immediately onboard, with half used for biomass measurements and C/N content, and half preserved in 4% buffered formaldehyde for zooplankton taxonomic identification and enumeration (Madin et al., 2001; Steinberg et al. 2012).

Taxonomic analysis

For this study 12 years (1999 –2010) of the time series were analyzed, with mesozooplankton identified to major taxa (Table 1) similar to Eden et al. (2009). Paired t-tests were performed on mesozooplankton counts from tows conducted in 2010 and showed that primary and replicate tows were not significantly different from each other. As a result, major taxa from one randomly selected day and night tow from each cruise

were enumerated. Overall, 305 tows were analyzed from 161 cruises from January 1999 through December 2010. To avoid over estimating vermiform (chaetognaths, polychaetes, and larvaceans) and some other taxa (decapods and euphausiids), only heads were counted. An additional 5 years (1995-1999) of calanoid copepod data were included in preliminary analyses, providing a 16-year time series for this group; however, preliminary modeling showed that the inclusion of chaetognaths, a predator for which we only have data from 1999-2010, produced the model with the most empirical support. As a result the additional calanoid data were not used.

Each preserved sample was first size fractioned through a 2000 μm sieve nested in a 200 μm sieve. All animals in the large ($> 2000 \mu\text{m}$) size fraction were identified to major taxon, counted, and measured using the Zooscan optical imaging system at a resolution of 2400 dpi with identification software (Gorsky et al., 2010). The Zooscan produces high-resolution digitized images of a sample and distinguishes one organism from another by detecting space between each individual to create a ‘vignette’. Zooprocessing and PkID programs are then used to create a learning set that the operator develops to properly identify the vignette. The learning set is created by providing 200+ vignettes of individuals within each group to be identified. Program identified vignettes were thoroughly reviewed and identification corrections were made whenever necessary during a validation process for each sample. A Stempel pipette (5 ml) was used to subsample the smaller (200-2000 μm) size fraction to obtain a minimum of 200 animals (a 1/2 to 1/2240 split); the most abundant taxa in the small size fraction subsample (Table 1) were enumerated using Zooscan. Because the Zooscan subsample was not large enough to adequately account for other rarer taxa in the small size fraction, a 1/4 to 1/256

split was separately enumerated for these taxa (Table 1) using an Olympus SZX12 stereo microscope under dark and light field illumination.

Statistical analysis

Generalized Linear Models (GLMs; Nelder and Wedderburn, 1972) were used to investigate patterns in abundance (i.e., individuals m^{-3}) of taxonomic groups and their relationship to environmental parameters of interest measured synoptically with each tow. Explanatory variables considered included year, month, day/night, Chl *a* concentration, primary production, raw accessory pigment concentrations for prymnesiophytes and diatoms phytoplankton groups (i.e., 19'-hexanoyloxyfucoxanthin and fucoxanthin, respectively), mesopelagic (300-600 m) temperature extracted from the BATS project website (<http://bats.bios.edu/>), and prey/predator density whenever applicable. While fucoxanthin is found in prymnesiophytes, chrysophytes, raphidophytes, as well as diatoms (Ansotegui et al., 2001), fucoxanthin is used to primarily indicate diatoms at BATS (Lomas et al., 2013). The variables year, month, and day/night were treated as categorical while all others were continuous and standardized: $x_{std} = (x - \bar{x})/\sigma_x$. Tows with missing explanatory variable data (n= 38 out of 305) were assigned a value using linear interpolation of two known cruise values surrounding the missing value. For most cruises, only one measurement of an explanatory variable was missing and no cruises were missing measurements of all explanatory variables. Plots of raw taxa densities consistently showed positively skewed patterns suggestive of a lognormal distribution. Therefore, taxa densities of zero were adjusted by adding a small constant and then all data were transformed using the natural logarithm. Delta GLMs

were used when taxa had densities of zero for 25-89% of the samples (cladocera, gymnosome, leptocephali, and brachiolaria). The delta model has two parts; first a binomial model estimated the rate of encounter of the target animal and then a lognormal model estimated the mean density of the animal when it was encountered. One taxon (phylosoma- lobster larvae) had densities of zero for $\geq 90\%$ of the samples and was not analyzed.

The general form of a GLM is as follows:

$$g(\mu_i) = \sum_1^p \mathbf{x}_i \beta_i \quad (1)$$

where g is a differentiable and monotonic link function, $\mu_i = E(y_i)$, which is the expected value of the i^{th} dependent variable (zooplankton density), \mathbf{x}_i are the p explanatory variables (e.g., year, month, Chl a , etc.), and β is the vector of estimated parameters (McCullagh and Nelder, 1989). A suite of 23 models for each taxonomic group were fitted, with each model including year and month (for interpretation of seasonal and interannual patterns), as well as combinations of additional explanatory variables.

Fucoxanthin was not included in most of the models tested because the pigment is rare at BATS (Krause et al., 2009a; Krause et al., 2009b; Lomas et al., 2013) and preliminary models did not show fucoxanthin to be influential. The model with the most empirical support was identified using Akaike's Information Criterion (AIC; Akaike 1973, Burnham and Anderson 2002). From the model receiving the most empirical support, significance of each explanatory variable (or level for the categorical variables) was determined by identifying which β s differ from zero using a χ^2 -test, and directionality of

the effects relative to the intercept (β_0) was given by the sign of the estimated parameter (positive vs. negative).

Comparisons with annualized environmental parameters and climate indices

The most empirically supported GLM for zooplankton density from above for five abundant taxonomic groups that were representative of different major groups (Table 1) was used to evaluate longer-term variables potentially driving interannual temporal changes. The “year” variable in the best fitting GLMs was substituted for 12-month averages of long-term variables of interest including the following: North Atlantic Oscillation (NAO) (www.cpc.noaa.gov/products/precip/CWlink/pna/nao.shtml), average winter months (DJFM) Hurrell NAO (<https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>), Hurrell NAO (<https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>), Atlantic Multidecadal Oscillation (AMO) (<http://www.esrl.noaa.gov/psd/data/correlation/amon.us.data>), Gulfstream North Wall (GSNW) (<http://www.pml-gulfstream.org.uk/data.htm>), Multivariate El Niño Southern Oscillation Index (MEI) (www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/), North Pacific Gyre Oscillation (NPGO) (<http://eros/eas/gatech/edu/npgo/>), Pacific Decadal Oscillation (PDO) (<http://jisao.washington.edu/pdo/>), water column stratification index (WCSI; the density difference between 40 and 160 m averaged over the four months of July-October for each year, as described previously in Steinberg et al., 2001), as well as environmental parameters listed above collected from satellite data (annual mean sea

surface temperature, Chl *a* concentration, and primary production). Again, AIC was used to compare among competing parameterizations within each taxonomic group.

3. RESULTS

3.1 Diel vertical migration

Of the 24 major taxa of zooplankton examined, model selection using AIC supported inclusion of the day/night explanatory variable for 14 taxonomic groups (Appendix 6-13). Of those taxa, 11 exhibited diel vertical migration with a significant ($p < 0.05$) higher mean density in the epipelagic zone at night than during the day (Figure 2). The strongest migrators were euphausiids, with a doubling in density at night (mean N:D=1.9), thecosome pteropods other than *Limacina* (N:D=1.6), both amphipod taxa (N:D=1.5), and *Limacina* spp. pteropods (N:D=1.5). Other migrators included cnidarians (N:D = 1.4), ostracods (N:D = 1.4), calanoid copepods (N:D=1.3), and other crustacea such as decapods and mysids (N:D=1.3). For the remaining three groups (oncaeid and corycaeid copepods, and doliolids), the day/night variable explained enough additional variation in the data to improve overall model fit and reduce AIC, however, the estimated standard errors of the day/night parameters were large such that statistical significance could not be inferred ($p > 0.05$).

3.2 Seasonal and interannual trends

Arithmetic means were included in all seasonal and interannual figures for comparative purposes with early studies (Figures 3-7). However, all results for seasonal and interannual trends presented and interpreted are based on the GLMs. This is because empirical means were positively skewed and presented a biased estimate of the true mean. The GLMs accounted for lack of normality.

3.21 Copepods

All groups of copepods exhibited significant ($p < 0.05$) seasonal trends except the oithonids (Figure 3A, Appendix 9). Calanoid and oncaeid copepod densities peaked in both spring (Feb-Mar) and summer (Aug) with both peaks similar in magnitude for calanoids but considerably higher in summer than spring for oncaeids. Sapphirinid copepod abundance peaked in spring (Mar-May) with an additional but less pronounced peak in fall (Oct). Harpacticoid copepod density had a distinct seasonal maximum in October. Bootstrapped CVs for the month effects for all copepod groups were low (< 0.4) and suggestive of generally good precision, with the exception of harpacticoids during the first half of the year when densities were extremely low.

Interannual variability over the 12-year time-series was statistically significant for all copepods except the sapphirinids (Appendix 9). There was a distinct two-year low density across all copepod groups in 2000 and 2001 transitioning in 2002 to a two-year maximum from 2003-2004 for calanoid, oithonid, and oncaeid copepods and a one-year maximum in 2003 for harpacticoid copepods (Figure 3B). There was also indication of a long-term increase in calanoid and oncaeid copepod density over the 12-year time period. Bootstrapped CVs for the year effects were all generally low (most < 0.3 for all taxa) and indicative of good precision.

3.22 Non-copepod crustacea

Non-copepod crustacea such as euphausiids, decapods/mysids, hyperiid and gammarid amphipods, and cladocera exhibited statistically strong seasonal trends (Figure

4A, Appendix 10). Peaks in the spring occurred for euphausiids (Mar), and hyperiid (Mar-May) and gammarid (Apr) amphipods, with a secondary fall peak lower in magnitude for both amphipod groups. Decapod/mysid density peaked in summer (Jun-Sept) and cladocera abundance peaked in mid-summer (Aug). Ostracods, which were the most abundant non-copepod crustaceans, exhibited no statistically-supported seasonal variation ($p > 0.05$), although small peaks in abundance did occur (Figure 4A, Appendix 1). CVs for the month effects were low (< 0.3) for all groups except cladocerans during non-peak seasons when densities were very low.

There was a similar interannual trend amongst ostracods, euphausiids, and decapods/mysids which peaked in 2003 or 2004 followed by a significant ($p < 0.05$) decrease in abundance in the following years (Figure 4B, Appendix 10). While no group exhibited a long-term directional increase or decrease, euphausiid density has remained at a level consistently lower than the peak realized in 2004. Similar to the seasonal results, estimated CVs for the year effects were low (near 0.25) indicating good precision for all groups except cladocerans.

3.23 Gelatinous zooplankton

Gelatinous zooplankton with significant ($p > 0.05$) seasonal peak densities in spring and a secondary peak in the fall included chaetognaths (May-Oct), larvaceans (Mar-Sep/Oct), and doliolids (Mar-May, Oct) (Figure 5A, Appendix 11). Cnidarians and polychaetes had multiple peaks throughout the year resulting in no significant seasonality. Bootstrapped CVs were low (< 0.3) for all groups except larvaceans during months of very low density.

Once again for some taxa (larvaceans and polychaetes) peak abundances occurred in 2002-2003 followed by a decline that, in the case of larvaceans, continued throughout the remainder of the time period (Figure 5B, Appendix 11). Doliolids and cnidarians also exhibited significant interannual variability, with a doliolid density minimum in 2008. Chaetognath densities remained relatively stable compared to the other gelatinous taxa (Figure 5B). Estimated year effect CVs were again low (< 0.3) for all groups except larvaceans during the latter few years, and doliolids during middle years (~ 0.5) of the time period.

3.24 Pelagic snails (pteropods and heteropods)

The thecosome pteropod *Limacina* spp. and the heteropods exhibited two significant ($p < 0.05$) seasonal abundance peaks (May, Aug) (Figure 6A, Appendix 12). Gymnosome pteropod densities peaked in fall (Oct). Thecosome pteropods other than *Limacina* spp. showed a winter (Dec) abundance peak. Estimated month effect CVs were low (< 0.4) for *Limacina* spp. and other thecosomes except for a period of low density (Apr) for other thecosomes. Bootstrapped CVs for heteropods were low (< 0.4) from Mar-Nov when densities were highest, and CVs for gymnosomes were generally high (> 0.5) due to very low densities.

Limacina spp. and other thecosome pteropods notably decreased in abundance after 2003 and 2004, respectively (Figure 6B, Appendix 12). Heteropods generally increase over the time series with progressively larger abundance peaks in 2004/2005 and in 2008 (Figure 6B, Appendix 12). Estimated year CVs were low (< 0.4) and suggestive

of good precision for all pelagic snail taxa, with the exception of gymnosomes (~ 0.5) due to very low densities.

3.25 Selected benthic invertebrate and fish larvae

Barnacle nauplii densities were high in late winter/early spring—peaking in February, but near zero during most of the latter half of the year (Jun-Nov) (Figure 7A, Appendix 13). Brachiolaria (sea star larvae) density was near zero from late spring into summer (Apr-Aug) and completely absent during late winter (Feb-Mar). Leptocephali (eel larvae) density increased in winter (Sept-Dec). However, due to the low densities of both brachiolaria and leptocaphali, no seasonal trend was statistically supported. CVs for the month effects were generally high (> 0.5) for all groups due to generally very low densities.

Barnacle nauplii abundance increased slightly later in the time series, with maximum abundance in 2008 (Figure 7B, Appendix 13). Brachiolaria mean annual density peaked in 2001 over the 7-year time-series (1999-2005) analyzed for this taxon. Again, leptocaphali were too rare to statistically support any interannual variability. Barnacle nauplii CVs for the year effects were low (< 0.4) and suggestive of good precision; however brachiolaria and leptocephali year effect CVs (> 0.6) indicate high variability for these taxa.

3.3 Environmental influences

Mesozooplankton density changes were most notably influenced by primary production, as AIC statistics supported the inclusion of the explanatory variable primary

production in GLMs for 16 of 24 taxa analyzed (Appendix 6-13). All 16 taxa had a positive relationship with primary production (of which 8 were statistically significant). These included herbivorous or omnivorous taxa such as calanoid and oncaeid copepods, and ostracods (Figure 8A). Primary production did not explain abundance patterns of 8 groups: harpacticoid and corycaeid copepods, chaetognaths, decapods/mysids, cladocera, gymnosome pteropods, and sea star and eel larvae. Another variable with prevalent (AIC supported inclusion for 9 of 24 taxa) and positive influence on zooplankton abundances was the prymnesiophyte accessory pigment 19'-hexanoyloxyfucoxanthin (19'-hex) (Appendix 6-13). Taxa that significantly increased in abundance with increasing 19'-hex included: oncaeid, oithonid, and sapphirinid copepods; euphausiids; decapods/mysids; hyperiid amphipods; chaetognaths; larvaceans; and doliolids. The shape of the response varied by taxa, with larvaceans increasing exponentially and oncaeid copepods increasing linearly with increasing 19'-hex (Figure 8B).

A potential predator-prey relationship between chaetognaths and copepods was hypothesized and, as a result, calanoid copepod densities were included in chaetognath GLMs and chaetognath densities included in calanoid GLMs. We recognized that a trophic interaction cannot be detected due to structure of these data (i.e., no time-lags in the respective series). However, chaetognaths did have a significant ($p > 0.05$) positive exponential response to increasing copepod prey density, with rapid chaetognath increase as calanoid densities approach 300 ind m^{-3} (Figure 8C). The inclusion of chaetognaths in calanoid copepod GLMs also greatly improved the model fit, explaining 56% of deviance, as opposed to 32% or 37% of deviance seen with a longer time-series (1995-

2010) or the same time-series (1999-2010), respectively, excluding the chaetognath predator (Appendix 7 and 8).

Of the remaining variables used in the GLMs, mesopelagic temperature was another common variable found across multiple zooplankton taxa, occurring in 11 of the 24 taxa models (Appendix 6-13). When influential, mesopelagic temperature was positively related to zooplankton mean density. Some important diel vertically migrating zooplankton like ostracods and calanoid copepods had a strong positive relationship to mesopelagic temperature (Figure 8D). Other taxa that significantly increased in abundance with mesopelagic temperature included: oithonid and oncaeid copepods, gammarid amphipods, and larvaceans.

The remaining environmental variables tested for inclusion in GLMs were chlorophyll *a* and fucoxanthin. Chlorophyll *a* was present in GLMs of 6 taxa and fucoxanthin was not included in any best fitting model (Appendix 6-13). All models with the most empirical support explained anywhere between 15-66% of the deviance, with the cnidaria GLM explaining 15%, and barnacle nauplii GLM explaining 66% of the deviance.

3.4 Annualized environmental and climate indices

The three top models with ΔAIC values less than 4.1 (Appendix 14) for both crustacean taxa tested (calanoid copepods and ostracods) indicate mean density is positively related to AMO and WCSI, and negatively related to GSNW (Figure 9A,B). Chaetognath mean density was also strongly related to WCSI (Appendix 14), but the relationship was negative (Figure 9C). Best fitting models for the remaining groups,

larvaceans and *Limacina* spp., with ΔAIC values less than 4.1 included different predictor variables with mean density of larvaceans negatively related to chlorophyll *a* and positively related to NAO (Figure 9D), and mean density of *Limacina* spp. negatively related to MEI and positively related to NPGO (Figure 9E). All models with the most empirical support explained anywhere between 13-49% of the deviance, with the ostracod GLM using WCSI explaining 13%, and the calanoid copepod GLM using WCSI explaining 49%, of the deviance.

4. Discussion

4.1 Diel vertical migration

Nearly half of the major mesozooplankton taxa we examined exhibited diel vertical migration. Mean epipelagic night:day (N:D) ratios for migrating taxa ranged from 1.3 to 1.9, similar to N:D ratios previously reported for mesozooplankton inside mesoscale eddies near BATS (Eden et al., 2009) and to the overall mean mesozooplankton biomass N:D ratio at BATS of 1.9 for the 1994-2010 time series (Steinberg et al., 2012). The most abundant migrators in our analysis, copepods and ostracods, accounted for 94% of the total diel vertical migrator abundance, and are thus likely key components of the long-term increase in migrator biomass (73% from 1994 to 2010) reported in Steinberg et al. (2012).

4.2 Seasonal trends

4.21 Copepods and other crustacea

There were distinct seasonal patterns in nearly all major copepod taxa. Calanoid and oncaeid copepod densities peaked in spring, following the seasonal increase in primary production and chl *a* biomass (Steinberg et al., 2001; Lomas et al., 2013), with a second abundance maximum in the summer coinciding with the secondary summer primary production increase usually dominated by picoplankton (Steinberg et al., 2001). This pattern mirrors that for total mesozooplankton biomass at BATS from 1994 to 2010 (Steinberg et al., 2012). The spring maximum in calanoid copepods occurred on average earlier (Feb) in the 12-year time period of our study compared to March as reported in

Deevey (1971), a 14-month study which took place near BATS from March 1961 through April 1962. However, in our study 4 out of 12 years also had March calanoid copepod peaks, and given the short time period of the 1961-62 study, we cautiously infer a long-term change in phenology. Mesozooplankton biomass peaks at BATS from 1994-2010 shifted to March later in the time-series from April/March (Steinberg et al., 2012), and phenology shifts have been reported in copepod species in the North Atlantic (Richardson, 2008). As sea surface temperatures continue to warm, progression through zooplankton life history stages, which is often temperature dependent (Richardson, 2008) may be starting earlier in the season at BATS.

The remaining copepod taxa exhibiting seasonality at BATS did not as clearly follow spring phytoplankton blooms, but rather seasonal changes in their prey. Sapphirinid copepod abundance, which peaked in spring/summer and again in the fall, may be partially tied to seasonal cycles of pelagic tunicates. Sapphirinid copepods are often associated with and regarded as predators of pelagic tunicates (Harbison, 1998; Boxshall and Halsay, 2004; Takahashi et al., 2013), and seasonal peaks of Sapphirinids co-occurred with those of doliolids in our analysis, and immediately followed seasonal salp peaks observed at BATS from 1994-2011 (Stone and Steinberg, 2014). Carnivorous corycaeid copepods peaked in abundance in August, during the secondary peak of copepods. As corycaeid copepods prey on nauplii of copepods (Turner et al. 1984, Landry et al. 1985; Turner, 2004), the August peak may be timed with high prey availability. Harpacticoid copepod abundance, which peaked in September, is likely tied to the summer maximum in the warm-water adapted colonial cyanobacteria *Trichodesmium* spp. (Orcutt et al., 2001; Breitbarth et al., 2007; Zhang et al., 2014).

Abundant harpacticoid copepods in the Sargasso Sea, such as *Macrosetella gracilis* (Anderson et al., 2011), are often found associated with colonies of *Trichodesmium* which serve as a substrate and food source for the copepods (O'Neil et al., 1996; Uye et al., 2001).

Similar to the calanoid and oncaeid copepods, spring peaks in other crustacea such as euphausiids and amphipods follow the seasonal increase in primary production and chl *a* biomass (Steinberg et al., 2001; Lomas et al., 2013). There are relatively few species of cladocera in the Sargasso Sea (e.g., *Evadne spinifera*), but those that occur are known to favor warm temperatures and vertical stability (Gülsahin & Tarkan, 2012), which likely explains the very distinct August cladocera peak. Abundant decapods included many species of larvae and *Lucifer* spp.; a large, diverse grouping which may account for the broad summer/fall seasonal increase. Decapods, mysids, and amphipods likely contribute to the smaller secondary fall mesozooplankton biomass peak observed at BATS from 1994-2010 (Steinberg et al., 2012).

4.23 Gelatinous zooplankton, including pelagic snails

Gelatinous zooplankton generally peaked in the spring with a secondary fall peak. As reported for other gelatinous filter feeders such as salps (Stone and Steinberg, 2014), larvaceans and doliolids have early spring maxima following the spring phytoplankton bloom at BATS. Deevey (1971) showed a large secondary peak in larvacean abundance in June that was absent in our time series. Carnivorous chaetognaths peaked late spring (May) and fall (Oct.), following copepod (their primary prey) maxima. Deevey (1971) also reported spring and fall chaetognath density peaks, however, the seasonal peaks

observed in our time series occurred on average 1-month earlier in the year than in 1961-1962 (May/June, Nov) (Deevey, 1971). As noted for calanoid copepods, this suggests that on average chaetognaths are blooming earlier in the year, however, there were occasional years when seasonal maximums were during the same months as reported in Deevey (1971).

Another taxon with peak densities occurring on average earlier in the year (May) compared to previous records in the early 1960's (July) (Deevey, 1971) is the pelagic snail *Limacina* spp., although over the 12 years peaks varied throughout spring/summer months making changes in phenology unclear for this taxon. For the remaining pelagic snail taxa, compared to prior observation from the early 1960's, gymnosome pteropods had a shorter (Sept-Oct), and heteropods a longer (May-Sept), season of high abundance in our time-series analysis than reported in Deevey et al. (1971; gymnosomes- Sept, Nov, Jan; heteropods- Jun/Jul & Oct-Apr). The summer heteropod maximum coincided with peaks in their common prey, *Limacina* spp. and "other shelled" pteropods.

4.24 Benthic invertebrate and fish larvae

Barnacle nauplii had a seasonal maximum beginning in the winter and peaking in February following the spring phytoplankton bloom (Steinberg et al., 2001; Lomas et al., 2013). While presence/absence of barnacle nauplii (Deevey, 1971) and depth profiles of barnacle cypriids (Eden et al., 2009) have been previously reported, little was known about barnacle nauplii seasonal trends in this region. Although seasonality in leptocephali and brachiolaria was not statistically supported due to their low densities, these taxa did have periods of high density compared to periods during the year of near zero abundance

or complete absence. Both the American eel *Anguilla rostrate* and the critically endangered European eel *A. anguilla* (Jacoby and Gollock, 2014) spawn in the southern Sargasso Sea (Andersen et al., 2011). Leptocephali were present 15% of BATS samples, with the highest densities occurring in December following fall peaks of their hypothesized food sources- gelatinous zooplankton, larvacean houses, and copepods (Mochioka and Iwamizu, 1996; Riemann et al., 2010; Andersen et al., 2011), and following the spawning season (Mar-Jul) (Jacoby and Gollock, 2014). Some brachiolaria in the BATS samples were identified as in the Oreasteridae family, which are capable of asexual reproduction, an adaptation hypothesized to allow this short-lived larva the opportunity to drift to a location suitable for settlement and increase densities to counteract high mortality rates (Jaeckle, 1994). Thus the high density in December in the BATS time series may indicate a period of asexual reproduction for brachiolaria.

4.3 Interannual trends

The highest density increase over the 12-year time series occurred during 2003 for all 6 copepod taxa, 3 crustacean taxa (ostracods, euphausiids, decapods/mysids), and 2 gelatinous zooplankton (larvaceans, polychaetes). Consistently high positive annual anomalies of total mesozooplankton biomass also occurred from 2002-2004, although the highest annual biomass anomaly was in 2006 (Steinberg et al., 2012). In the winter of 2003, NO₃ concentrations were at a detectable level over multiple cruises, a rare occurrence that only happened 2 other times (1995 and 2001) over 24 years of monitoring at BATS (Lomas et al., 2013). This nutrient influx likely supported the highest rate of primary production in the time series which was observed in April, 2003, and

additionally one of 3 distinct diatom blooms (as indicated by high fucoxanthin concentrations) also occurred in April, 2003. Thus we posit that the majority of BATS zooplankton (~half of the taxa in this study, constituting a large percentage of total zooplankton abundance) were responding to not only increased phytoplankton production, but an increase in diatoms. While 2004 was not an equally productive year for phytoplankton, in 2003 and 2004 calanoid copepod and larvacean density peaks occurred in March (as in the 1960's; Deevey, 1971), one-month later than the mean for the time series which was February which would be timed to take advantage of the seasonal spring primary production increase. This may explain why 2004 was also a high density year for many zooplankton taxa.

Another year of significant abundance change across multiple taxa was 2008. During this year heteropods and barnacle nauplii both exhibited density maxima for the time series. Interestingly, doliolids experienced a density minimum in 2008, which was also the only negative annual mesozooplankton biomass anomaly in the latter half of the time series (Steinberg et al., 20012). The year 2008 had one of the lowest mean annual rates of primary production which may explain lower abundance of other taxa and low overall biomass in 2008.

There was evidence of a long-term increase in calanoid and onceaid copepod abundance over time which may partially account for the long-term increase of total mesozooplankton biomass at BATS (Steinberg et al., 2001) given copepods make up the majority of the biomass. Longer-term decreases in abundance across the time series occurred in larvaceans, *Limacina* spp. pteropods, and other thecosome pteropods. GLMs determined that long-term larvacean abundance was positively related to the North

Atlantic Oscillation index (NAO). The decrease in larvacean density might indicate that frequent mixing conditions at BATS, which are associated with an increasingly negative NAO since 1996 (Steinberg et al., 2012) might not be favorable conditions for this taxa. Dissolved inorganic carbon (DIC) concentrations have increased 2% and pH levels in the euphotic zone have decreased ~ 0.05 over the last 3 decades at BATS (Bates et al., 2012). Ocean acidification has been shown to reduce calcification ability of shelled pteropods (Fabry et al., 2008). Direct effects of increasing DIC and decreasing pH on pteropods at BATS has not been investigated, but this apparent decrease in *Limacina* spp. and other thecosome pteropod densities over this 12-year period suggests that further studies of these and other environmental controls on pteropods is warranted.

4.4 Environmental influences

Mesozooplankton at BATS are regulated by a variety of environmental parameters, the most significant of which in our analyses was primary production. Deep advective mixing in winter provides nutrients for a spring phytoplankton bloom at BATS typically in February or March (Steinberg et al., 2001; Lomas et al. 2013). More than half of the 24 mesozooplankton taxa analyzed responded with increased abundance with increasing primary production, including three of the most abundant zooplankton at BATS, calanoid and oncaeid copepods, and ostracods. Oncaeid copepods are active predators (Go et al., 1998) or detritivores (Alldredge, 1972; Ohtsuka and Kubo, 1991; Turner, 2004), but exhibited a similar positive relationship to primary production as ostracods, suggesting that energy transfer up the food chain at BATS may occur rapidly. Other omnivorous or carnivorous zooplankton, such as decapods/mysids (mostly *Lucifer*

spp.) and chaetognaths (Lee et al., 1992; Venetia and Hans 1991), respectively, did not respond as strongly to primary production increases. Chaetognaths, for example, increased exponentially as calanoid copepod prey increased. Harpacticoid copepod abundance also was not significantly correlated with community primary production which is dominated by picoplankton and prymnesiophytes (Lomas et al., 2013), presumably due to dependence of at least some harpacticoid species on *Trichodesmium* (O'Neil et al., 1998).

Prymnesiophyte abundance (19'-hex) also had a significant and positive affect on more than 1/3 of the mezooplankton taxa, including larvaceans and oncaeid copepods. Prymnesiophytes, such as coccolithophorids, are the most abundant nanophytoplankton at BATS (Steinberg et al., 2001). Diatom abundance was not influential in any of the models, likely because diatoms are overall rare at BATS (Krause et al., 2009a; Krause et al., 2009b; Lomas et al., 2013) and it was only in conjunction with peaks in primary production that we saw diatoms possibly influencing zooplankton densities. Larvacean abundance increased slowly with increasing prymnesiophyte concentration until a threshold was reached after which larvacean abundance increased rapidly. This relationship may illustrate the ability of larvaceans to rapidly respond to favorable conditions, as also seen in coastal regions (Nakamura et al., 1997). Oncaeid copepods also increased in density with increased prymnesiophyte abundance. Although oncaids may not feed on prymnesiophytes directly, *Oncaea* spp. use larvacean mucous houses as a habitat and food source (e.g., Ohtsuka et al., 1993). Interestingly, the inclusion of larvacean abundance in the most empirically supported GLM for oncaids increased the deviance explained from 37% to 43%.

Increases in mesopelagic temperature, at daytime residence depths for vertically migrating zooplankton, could lead to increased calanoid copepod and ostracod abundance. One identified ecological advantage of diel vertical migration is to slow metabolism of food consumed in surface waters at night while residing in colder, deeper waters during the day, as an energy saving adaptation (Lampert, 1989). It is thus counterintuitive that warmer mesopelagic temperatures corresponded with increases in abundance of some migrators. Perhaps production of some of these species increases with warmer temperatures up to a point, and continued increases in mesopelagic temperatures may eventually negatively affect their abundance. If warming mesopelagic temperatures remains a positive influence on calanoid and ostracod abundance, however, then this combined with potential increased metabolic rate at depth due to higher temperatures could result in greater active flux of carbon and nutrients by migrators below the mixed layer (Steinberg et al., 2000).

4.5 Annualized environmental and climate indices

Calanoid copepod and ostracod long-term (12-year) density trends were significantly influenced by the Atlantic Multidecadal Oscillation (AMO), Gulf Stream North Wall (GSNW), and Water Column Stratification Index (WCSI). The phase of AMO denotes long-term sea surface temperature variability and is linked to hurricane frequency in the North Atlantic (Goldenberg et al., 2001; Knight et al., 2006). The AMO, which is on an ~ 20-year cycle, has been in a warm phase since 1996 (Goldenberg et al., 2001), which causes warm sea surface temperatures and increased episodic mixing events due to increased hurricane occurrence in the North Atlantic (Goldenberg et al., 2001).

Thus the positive AMO may support increased calanoid and ostracod densities because episodic mixing allows greater nutrient mixing which allows for increased primary production (Saba et al., 2010).

The GSNW is used to track the movement of the Gulf Stream north wall and is known to correlate with the NAO with a lag of 2 years (Taylor and Stephens, 1998). A high NAO index results in a more northerly path of the Gulf Stream (Taylor and Stephens 1998). GSNW movement is related to sea surface temperature, winds, atmospheric pressure, and salinity in the North Atlantic (Taylor and Stephens, 1998). Zooplankton, especially copepods, are reported to increase in abundance as GSNW moves north across the North Atlantic (Taylor et al., 1992). In our study the opposite was observed, as both calanoid copepods and ostracods from the more southerly BATS region decreased in abundance as the GSNW moved north. This suggests that zooplankton position, north or south of the GSNW, may change the directional response of the relationship zooplankton have with the GSNW index. This is likely due to local changes in mixing as a result of changes in wind speeds and directions (Taylor and Stephens, 1980).

Calanoid copepods, ostracods, and chaetognath densities were influenced by the WCSI, which has been increasing over the time series and suggests a decrease in mixing and nutrient input (Steinberg et al., 2001, 2012). Calanoid copepods and ostracods increased in abundance with increasing water column stability, as did total zooplankton biomass (Steinberg et al., 2012) and two species of salps (Stone and Steinberg, 2014) at BATS. Increased net primary production observed at BATS from 1989 to 2007 (Saba et al., 2010) suggests that stronger summer stratification over time does not affect winter mixing which is crucial for supplying nutrients to support spring phytoplankton blooms

(Lomas et al., 2010; Lomas et al., 2013). Chaetognath density decreased with increasing stratification, however, which is surprising given the strong positive relationship with their copepod prey.

Larvaceans were most strongly influenced by long-term chl *a* concentrations and secondly by the North Atlantic Oscillation (NAO). The NAO became negative in 1996 and has continued to increase negatively, which leads to increased mixing (Lomas et al., 2010) from higher storm activity (Dickson et al., 1996). This resulted in increased primary production (Lomas et al., 2010), chl *a* (Saba et al., 2010), mesozooplankton biomass (Steinberg et al., 2012), and abundance and biomass of *cyclosalpa polae* (Stone and Steinberg, 2014) over the course of the time series. The relationship of larvacean density to chl *a* and the NAO was the opposite, which may explain the decrease in abundance observed later in the time series. A negative relationship with NAO was also seen in three of the major salp species at BATS (Stone and Steinberg, 2014).

Long-term *Limacina* spp. abundance was most closely linked to Pacific climate indices including the North Pacific Gyre Oscillation (NPGO) and Multivariate El Niño Southern Oscillation Index (MEI). Although the mechanism is still not fully understood, Pacific climate oscillations do appear to affect the BATS planktonic food web— as primary production (Saba et al., 2010), mesozooplankton biomass (Steinberg et al., 2012), salp biomass and abundance (Stone and Steinberg, 2014), and *Limacina* spp. abundance increased with increased NPGO index. *Limacina* spp. abundance also increased as MEI decreased, a relationship also noted for salps at BATS (Stone and Steinberg, 2014).

5. CONCLUSION

Mesozooplankton seasonal and interannual cycles at BATS are driven by changes in local environmental conditions that are tied to larger-scale, longer-term climate control. Primary production was found to be a leading driver of zooplankton abundance, with a high primary production season coupled with a diatom bloom potentially increasing abundance of zooplankton across multiple taxa and trophic levels. Over the BATS time series primary production and total mesozooplankton biomass from 1994-2010 increased (Steinberg et al., 2012). The possible long-term increase in calanoid and oncaeid copepod abundance may partially account for this increase, despite that the time period of this analysis (1999-2010) excluded several early years of low biomass (1994-1998) reported in Steinberg et al. (2012). Decreases in abundance over the time series were observed in three taxa, which may be related to increased sea surface temperatures and ocean acidification, however, further study is required to fully understand the mechanisms driving abundance decreases.

Phenology changes have been observed in the North Atlantic zooplankton (Richardson, 2008), and we found some evidence of earlier peaks in abundance for two taxa. While the historical data for comparison is limited to a 14-month time series, it is compelling that on average a 1-month earlier peak in abundance compared to the early 1960's occurred in different taxa.

Zooplankton also play a key role in biogeochemical cycling through their feeding, metabolism, and diel vertical migration (Steinberg, 2012). We detected a significant relationship between the most abundant zooplankton migrators and mesopelagic

temperatures suggesting that warming of these waters may increase efficiency of active transport of carbon below the mixed layer.

Future analyses of this data set will be useful to further test hypothesized changes in zooplankton communities with continued warming, such as predicted size changes (shift to smaller, more tropical species). In addition, while much of this analysis was aimed at detecting bottom-up controls of zooplankton abundance, we did find evidence of top-down control that warrants further investigation. While the mechanisms by which environmental drivers affected patterns in abundance of some of the mesozooplankton taxa in our study require further exploration, it is evident that future changes to the zooplankton community could affect the pelagic food web and biogeochemical cycling in the North Atlantic and other subtropical gyres.

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Table 1. Major taxa identified from BATS from 1999-2010, based on categories used in Eden et al. (2009). Additional data from 1995-1998 were available and included in preliminary analyses for calanoid copepods. * marks smaller size fraction (200-2000 μ m) identified and enumerated using Zooscan and \diamond indicates taxa for which additional GLMs were used to evaluate longer-term variables potentially driving interannual changes.

| Taxonomic Categories | Sub Categories |
|-----------------------------|---------------------------------|
| Amphipods | Gammarid |
| | Hyperiid |
| Barnacle nauplii | |
| Brachiolaria | |
| Chaetognath* \diamond | |
| Cladocera | |
| Copepods | Calanoid* \diamond |
| | Corycaeidae* |
| | Harpacticoid |
| | Oithonidae* |
| | Oncaeidae* |
| | Sapphirinidae |
| Decapod and Mysid | |
| Doliolid | |
| Euphausiid | |
| Heteropod | |
| Larvacean* \diamond | |
| Leptocephali | |
| Ostracod* \diamond | |
| Cnidaria | |
| Polychaete | |
| Pteropods | <i>Limacina</i> spp. \diamond |
| | Other Thecosome |
| | Gymnosome |

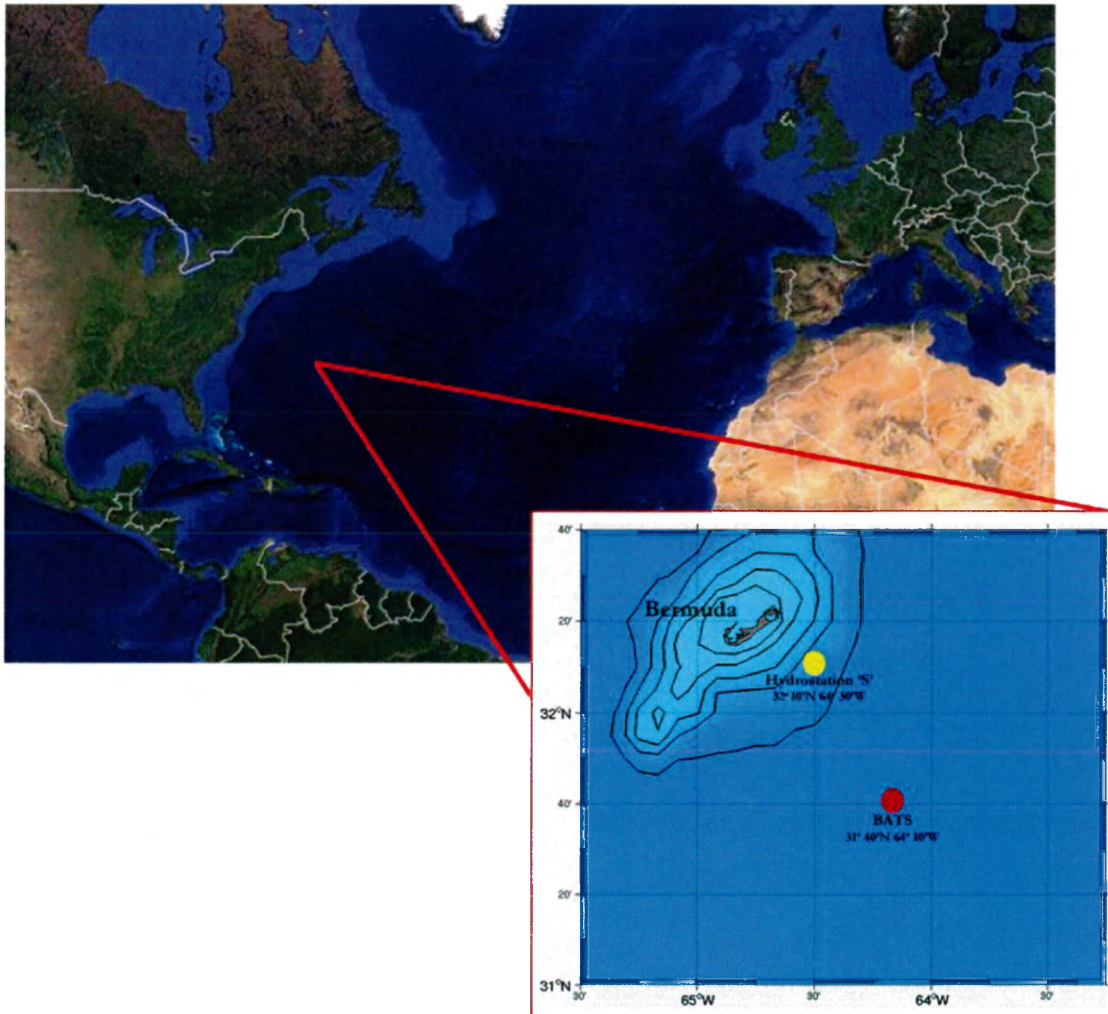


Figure 1. Location of BATS, 82 km southeast of the island of Bermuda ($31^{\circ}40'N$, $64^{\circ}10'W$) in the North Atlantic Ocean (red circle). Noted also is the location of Hydrostation “S” 25 km southeast of Bermuda ($32^{\circ}10'N$, $64^{\circ}30'W$) (yellow circle). This is the site of some of the early zooplankton studies in the Sargasso Sea, and is still sampled today. (Google Maps and http://bats.bios.edu/bats_location.html).

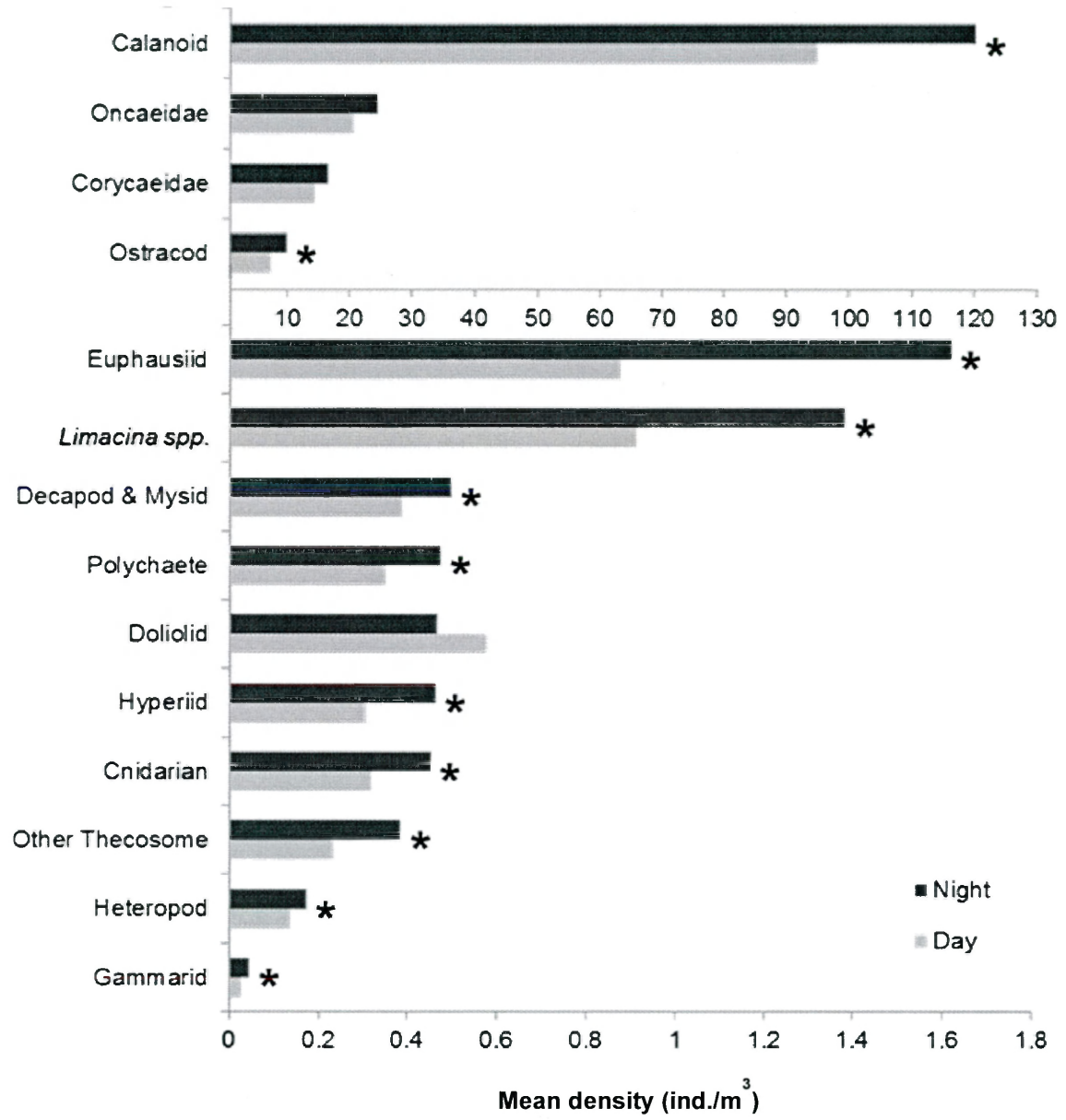


Figure 2. Mesozooplankton diel vertical migration. Day and night mean density of epipelagic zooplankton taxa at the Bermuda Atlantic Time-series Study (BATS) site, calculated across the time series (January 1999 to December 2010). Taxa are listed in order of decreasing mean night density. Night/day parameter was included in the most empirically supported models of all 14 taxa. Taxa exhibiting diel vertical migration (significantly higher night density than day) are marked with an asterisk. The coefficient of variation (SE/model-based mean) for day densities ranged from 0.04-0.15 and for night densities ranged from 0.13-0.4, suggestive of good precision.

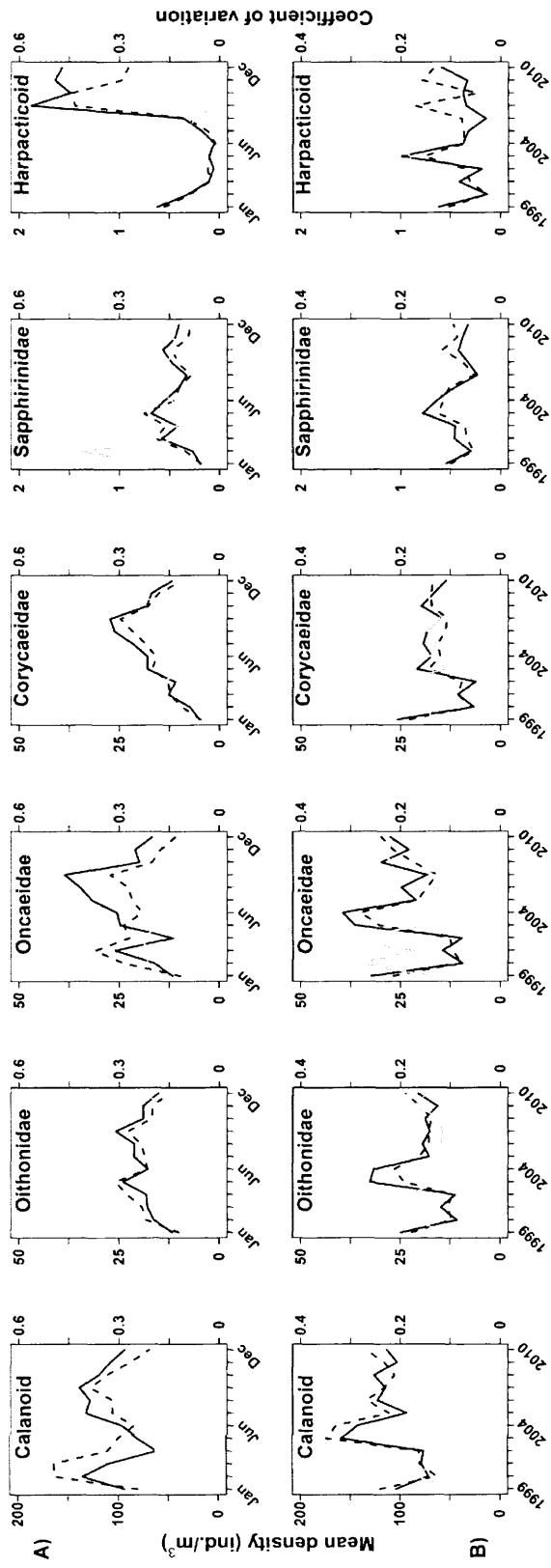


Figure 3. Mean monthly densities across all years (A) and mean annual densities across all 12 months in a given year (B) of the six major groups of copepods at BATS. Solid black line represents the model-based mean, dashed line represents the raw data mean, and gray line represents the coefficient of variation (SE/model-based mean). Note that in some cases the coefficient of variation was too large for the scale to be graphed.

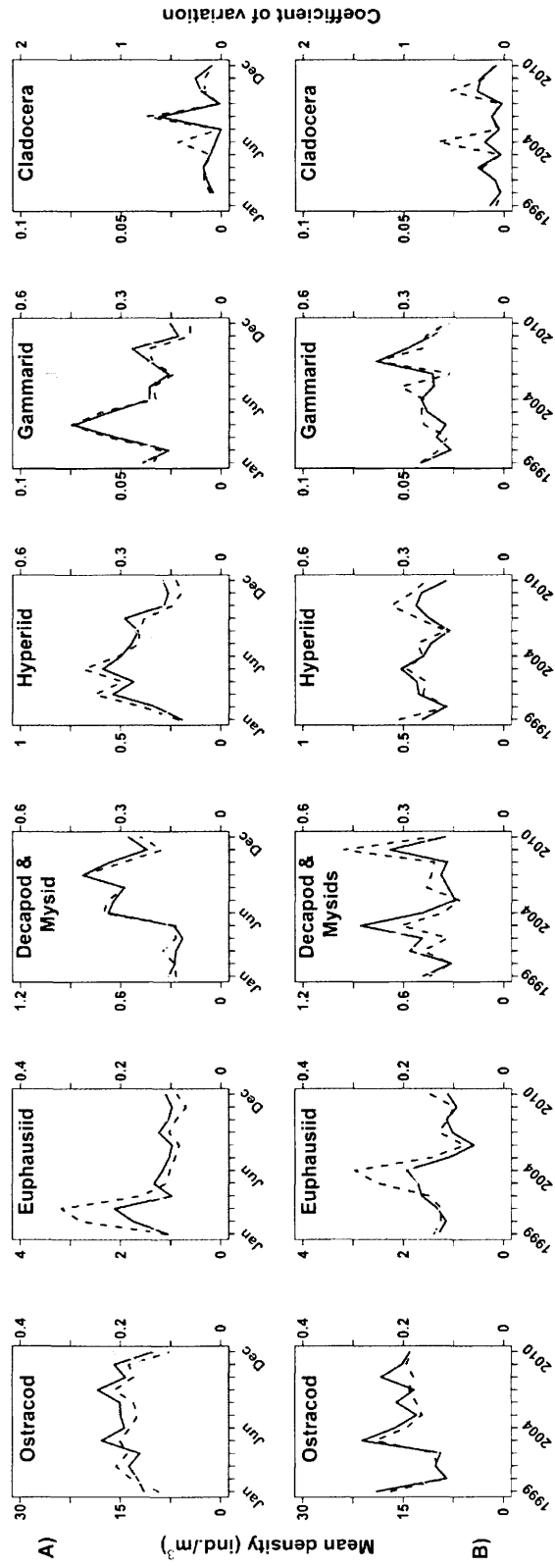


Figure 4. Mean monthly densities across all 12 years (A) and mean annual densities across all 12 months in a given year (B) of the major taxa of crustacean zooplankton (other than copepods) at BATS. Solid black line represents the model-based mean, dashed line represents the raw data mean, and gray line represents the coefficient of variation (SE/model-based mean). Note that in some cases the coefficient of variation was too large for the scale to be graphed.

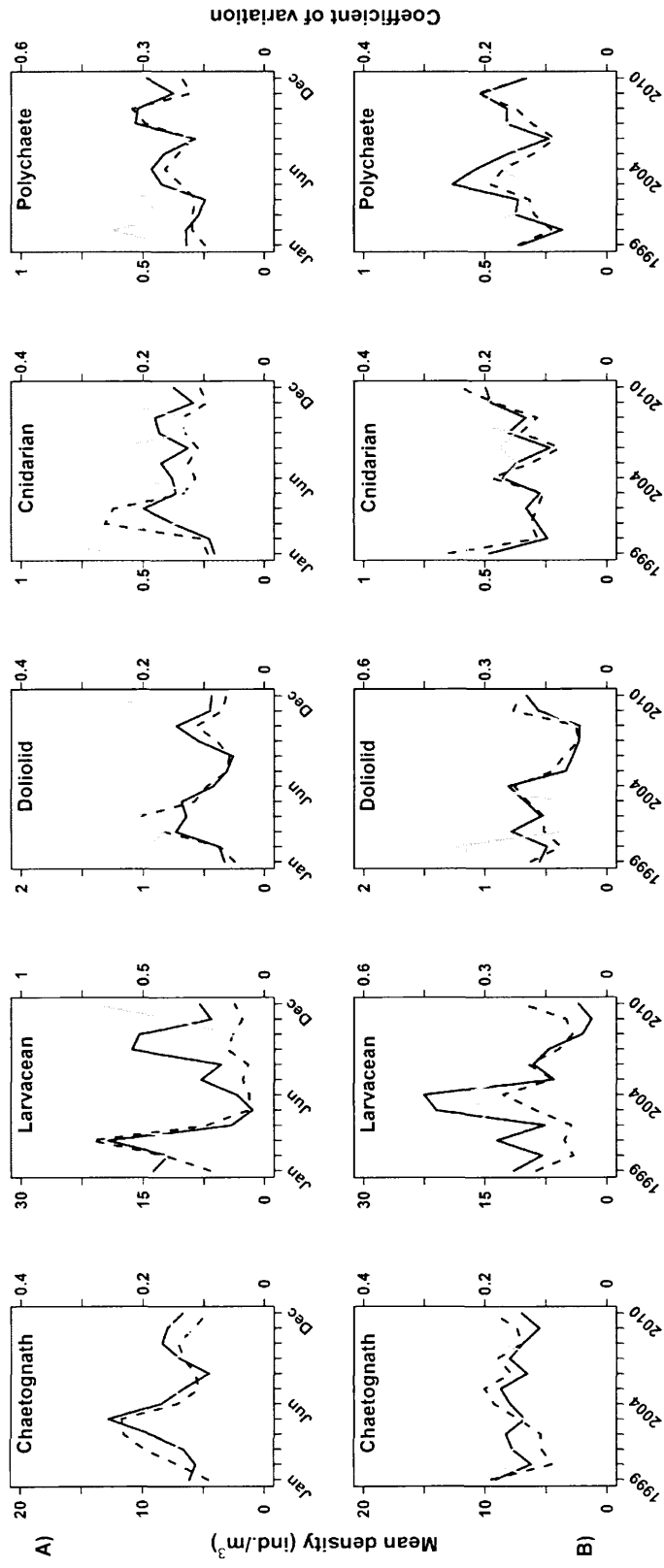


Figure 5. Mean monthly densities across all 12 years (A) and mean annual densities across all 12 months in a given year (B) of gelatinous zooplankton (chaetognaths, larvaceans, doliolids, cnidarians, and polychaetes) at BATS. Solid black line represents the model-based mean, dashed line represents the raw data mean, and gray line represents the coefficient of variation (SE/model based mean). Note: raw mean larvacean data do not indicate a secondary summer/fall density maximum in (A), as the data were positively skewed and that bias was not accounted for in the raw means as it was in model-based means. Also, in some cases the coefficient of variation was too large for the scale to be graphed.

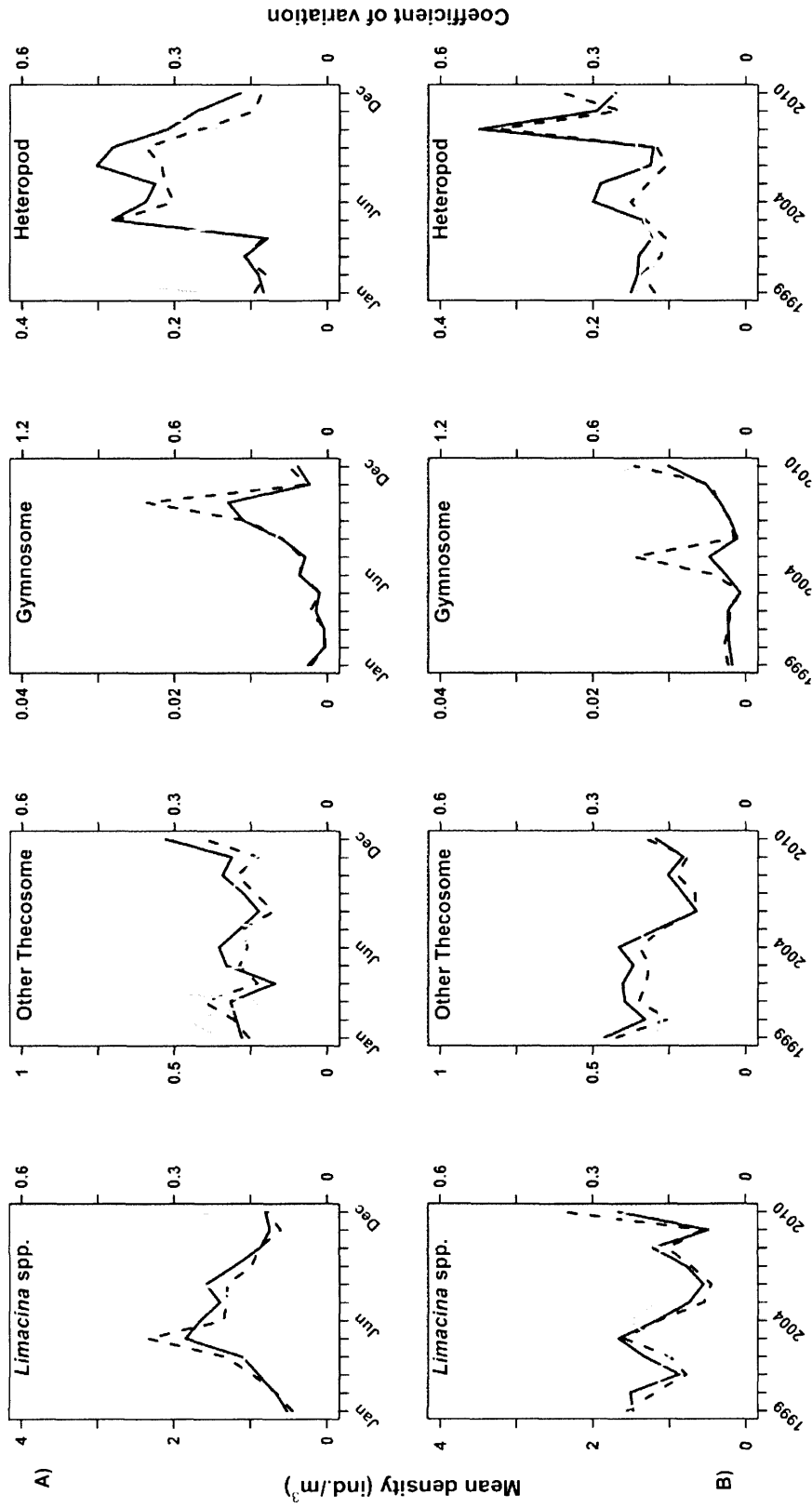


Figure 6. Mean monthly densities across all 12 years (A) and mean annual densities across all 12 months in a given year (B) of pelagic snails (pteropods and heteropods) at BATS. Solid black line represents the model-based mean, dashed line represents the raw data mean, and gray line represents the coefficient of variation (SE/model-based mean). Note that in some cases the coefficient of variation was too large for the scale to be graphed.

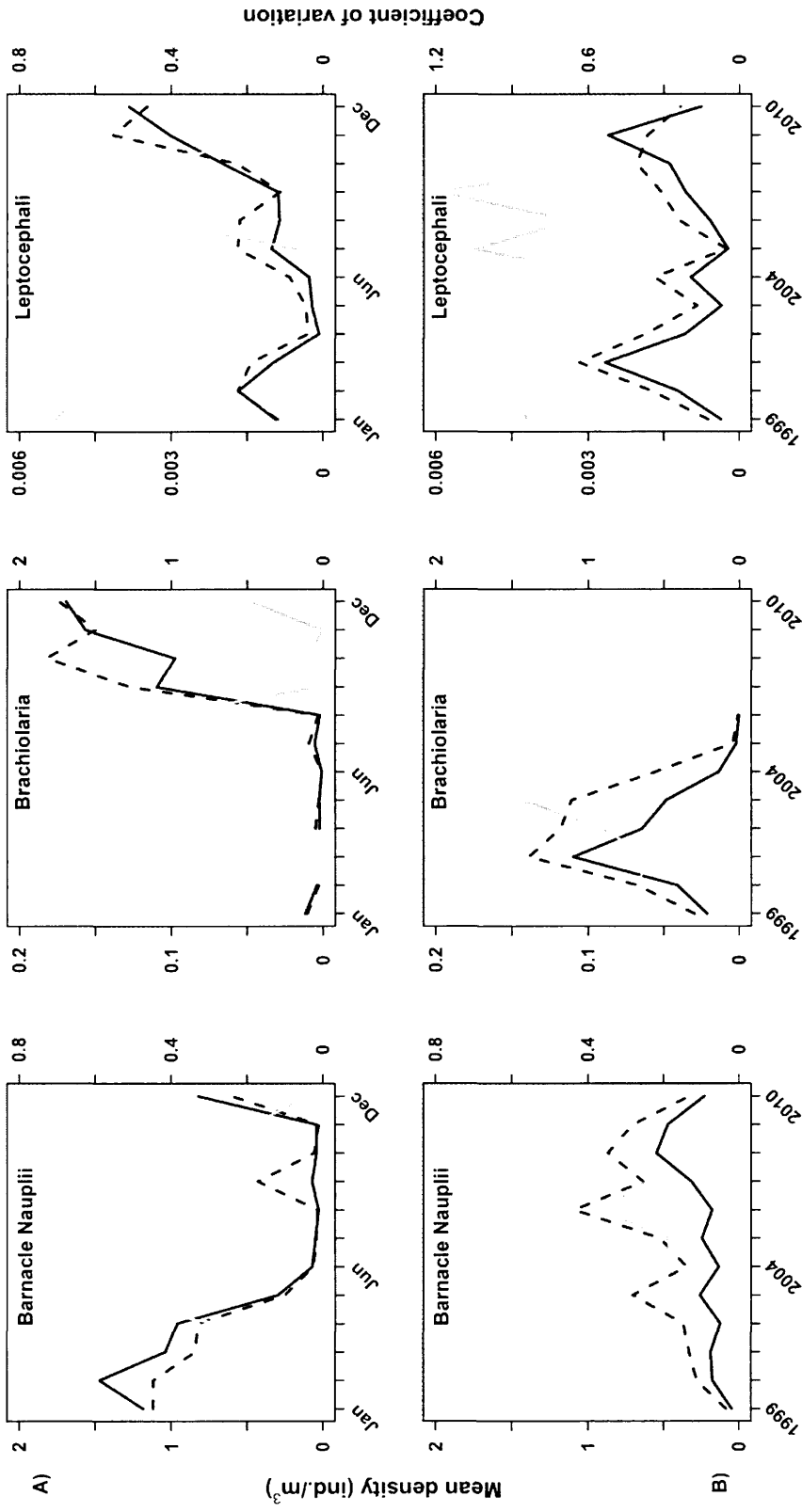


Figure 7. Mean monthly densities across all 12 years (A) and mean annual densities across all 12 months in a given year (B) of selected larval benthic invertebrates (barnacle nauplii, brachiolaria-sea star larvae) and fish (leptocephali-eel larvae) at BATS. Solid black line represents the model-based mean, dashed line represents the raw data mean, and gray line represents the coefficient of variation (SE/model-based mean). Note average annual density of brachiolaria is not included for years 2007-2010 (see text). Also, in some cases the coefficient of variation was too large for the scale to be graphed.

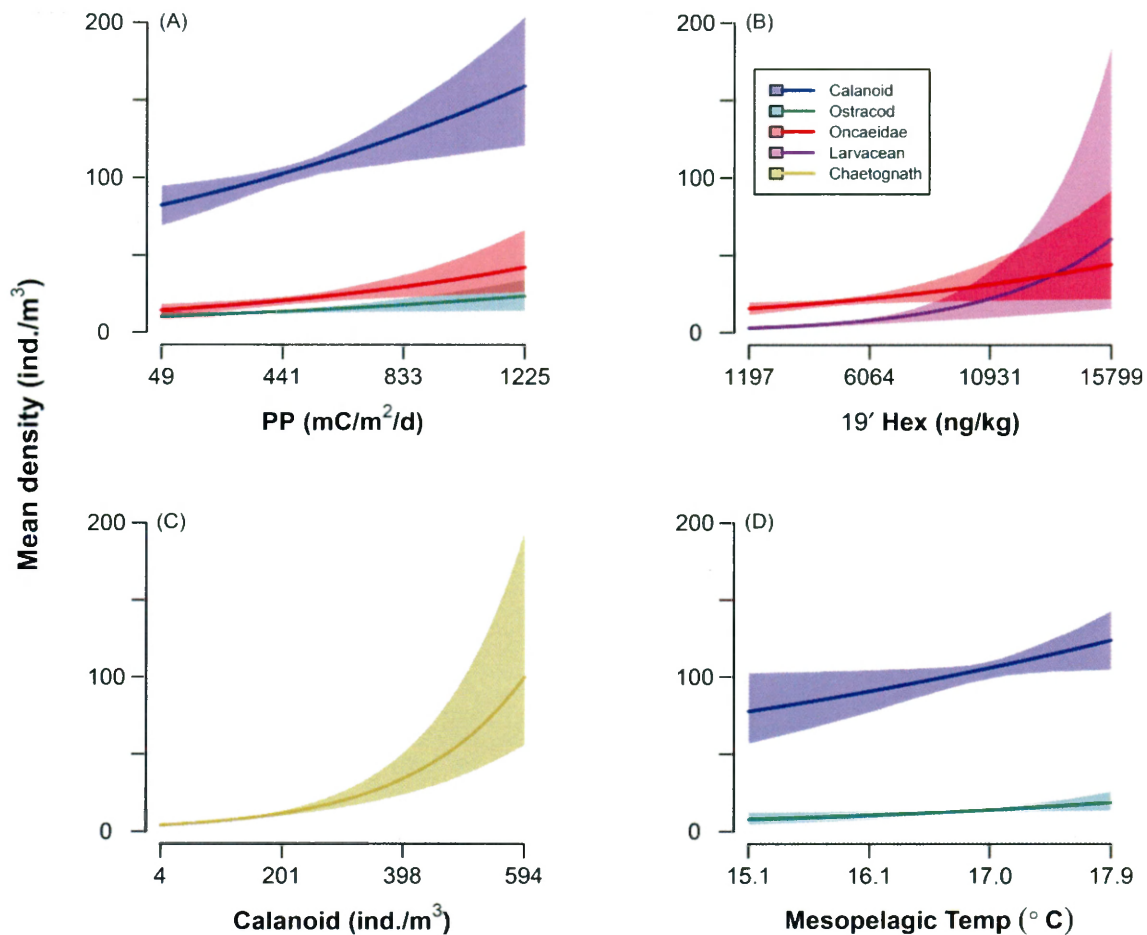


Figure 8. Short-term environmental and biological influences on mesozooplankton abundance. (A) Primary production ($\text{mC}/\text{m}^2/\text{d}$) integrated 0-140 m vs. abundance of calanoid and oncaeid copepods, and ostracods ($\text{ind.}/\text{m}^3$), (B) Prymnesiophytes (19'-hexanoyloxyfucoxanthin concentration) (ng/kg) integrated 0-140 m vs. calanoid copepods and larvaceans ($\text{ind.}/\text{m}^3$), (C) calanoid copepod ($\text{ind.}/\text{m}^3$) vs. chaetognath abundance ($\text{ind.}/\text{m}^3$), and (D) mesopelagic temperature ($^{\circ}\text{C}$) vs. density of two diel vertical migrating taxa- calanoid copepods and ostracods ($\text{ind.}/\text{m}^3$). Shaded regions represent 95% confidence intervals and x-axes are labeled from the observed minimum to the observed maximum in the time series.

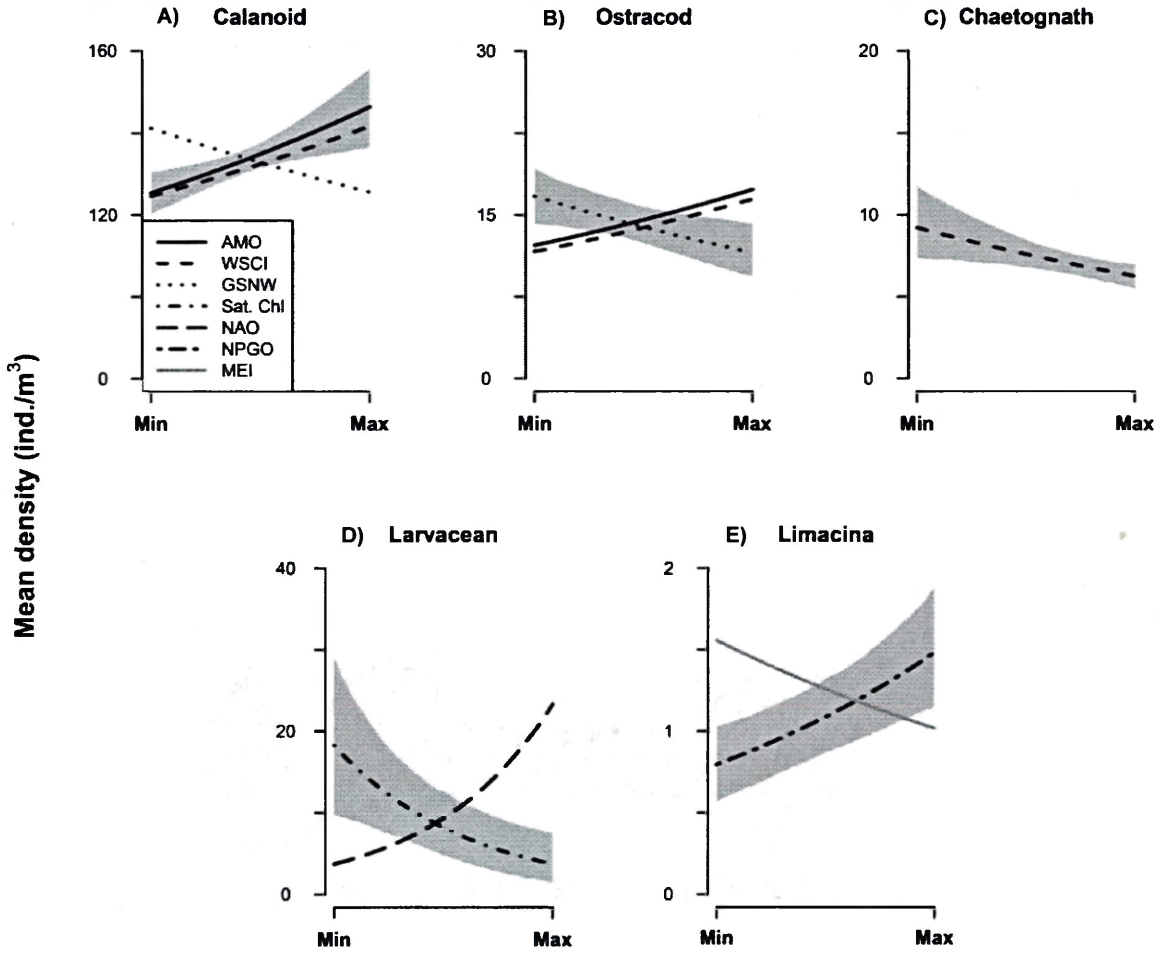


Figure 9. Mean density of abundant mesozooplankton and long-term environmental and climate indices. Note that because environmental and climate indices have different scales the data were standardized $x_{std} = (x - \bar{x})/\sigma_x$ with minimum to maximum values listed below. Black solid lines represent Atlantic Multidecadal Oscillation (AMO) (0.3 to 0.35), gray solid lines Water Column Stratification Index (WCSI) (0.97 to 1.44), black dashed lines Gulf Stream North Wall Index (GSNW) (0.44 to 1.72), blank dotted line Satellite Chlorophyll *a* (0.08 to 0.12 mg/m³), gray dashed line North Atlantic Oscillation (NAO) (-1.15 to 0.39), black dot dashed line Multivariate El Niño Southern Oscillation (MEI) (-0.93 to 0.58), and gray dotted line represents North Pacific Gyre Oscillation (NPGO) (-0.88 to 2.08). Shaded regions represent 95% confidence intervals of the most empirically supported longer-term variable potentially driving internal temporal changes (calanoid copepods-AMO, ostracods-GSNW, chaetognaths-WCSI, larvaceans-Chl *a*, and *Limacina* spp. pteropods-NPGO).

APPENDICES

Appendix 1. Summary of the most empirically supported Generalized Linear Model (GLM) results for the major taxa of copepods at BATS from 1999-2010. Included are predictors, estimate, and standard error (SE). Blank spaces indicate that the predictor was not included in the most empirically supported GLM. Year and Month predictors were used in all GLMs in order to determine seasonal and internal variability even though Year and Month predictors may not have resulted in the best model.

Note chaetognath density was only included in calanoid GLMs.

Diel= day/night explanatory variable
MesoT= mesopelagic temperature (°C)
PP= primary production (mgC/m²/d) integrated 0-140 m
Chl= chlorophyll *a* (ng/m²) integrated 0-140 m
Hex= 19'-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0-140 m
Chaeto= chaetognath, a zooplankton predator, density (ind./m³)

| Predictors | Calanoid | | Oncaeidae | | Oithonidae | | Corycaeidae | | Sapphirinidae | | Harpacticoid | |
|-------------|----------|------|-----------|------|------------|------|-------------|------|---------------|------|--------------|------|
| | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE |
| (Intercept) | 4.27 | 0.16 | 2.36 | 0.27 | 2.53 | 0.20 | 1.80 | 0.24 | -1.71 | 0.25 | -1.71 | 0.25 |
| 2000 | -0.37 | 0.16 | -1.24 | 0.26 | -0.83 | 0.19 | -1.36 | 0.23 | -0.63 | 0.25 | -0.69 | 0.24 |
| 2001 | -0.28 | 0.14 | -0.81 | 0.25 | -0.52 | 0.19 | -0.90 | 0.21 | -0.18 | 0.25 | -0.32 | 0.23 |
| 2002 | -0.31 | 0.15 | -1.22 | 0.26 | -0.79 | 0.19 | -1.44 | 0.21 | -0.24 | 0.25 | -0.38 | 0.23 |
| 2003 | 0.42 | 0.15 | 0.12 | 0.26 | 0.27 | 0.20 | -0.21 | 0.22 | 0.31 | 0.26 | 0.22 | 0.23 |
| 2004 | 0.32 | 0.14 | 0.20 | 0.25 | 0.24 | 0.19 | -0.40 | 0.22 | 0.19 | 0.24 | 0.06 | 0.23 |
| 2005 | -0.10 | 0.14 | -0.43 | 0.25 | -0.33 | 0.19 | -0.29 | 0.22 | -0.16 | 0.24 | -0.07 | 0.23 |
| 2006 | 0.17 | 0.15 | -0.26 | 0.27 | -0.25 | 0.20 | -0.34 | 0.23 | -0.94 | 0.26 | -0.73 | 0.25 |
| 2007 | 0.10 | 0.14 | -0.56 | 0.26 | -0.34 | 0.19 | -0.57 | 0.22 | -0.49 | 0.25 | -0.36 | 0.23 |
| 2008 | 0.19 | 0.16 | -0.08 | 0.26 | -0.28 | 0.20 | -0.26 | 0.23 | -0.25 | 0.26 | -0.14 | 0.25 |
| 2009 | -0.01 | 0.16 | -0.34 | 0.27 | -0.47 | 0.20 | -0.44 | 0.24 | -0.34 | 0.26 | -0.28 | 0.25 |
| 2010 | 0.09 | 0.15 | -0.16 | 0.26 | -0.19 | 0.19 | -0.64 | 0.22 | -0.52 | 0.25 | -0.40 | 0.24 |
| Feb | 0.37 | 0.16 | 0.33 | 0.27 | 0.34 | 0.20 | 0.37 | 0.23 | 0.25 | 0.26 | 0.33 | 0.25 |
| March | 0.16 | 0.16 | 0.81 | 0.27 | 0.43 | 0.20 | 0.94 | 0.23 | 1.06 | 0.26 | 1.15 | 0.25 |
| April | -0.42 | 0.17 | -0.01 | 0.27 | 0.45 | 0.21 | 0.80 | 0.24 | 0.72 | 0.27 | 0.84 | 0.26 |
| May | -0.14 | 0.19 | 0.76 | 0.30 | 0.72 | 0.23 | 1.29 | 0.26 | 1.27 | 0.30 | 1.23 | 0.28 |
| June | 0.04 | 0.18 | 0.79 | 0.30 | 0.42 | 0.23 | 1.29 | 0.26 | 1.02 | 0.30 | 1.01 | 0.28 |
| July | 0.35 | 0.17 | 1.01 | 0.29 | 0.61 | 0.22 | 1.47 | 0.25 | 0.73 | 0.29 | 0.73 | 0.27 |
| Aug | 0.32 | 0.19 | 1.10 | 0.31 | 0.60 | 0.24 | 1.67 | 0.26 | 0.50 | 0.31 | 0.45 | 0.28 |
| Sept | 0.40 | 0.18 | 1.20 | 0.30 | 0.80 | 0.23 | 1.71 | 0.26 | 0.88 | 0.30 | 0.80 | 0.27 |
| Oct | 0.25 | 0.18 | 0.54 | 0.30 | 0.49 | 0.23 | 1.30 | 0.26 | 1.08 | 0.29 | 0.96 | 0.27 |
| Nov | 0.15 | 0.18 | 0.60 | 0.31 | 0.49 | 0.23 | 1.23 | 0.26 | 0.85 | 0.30 | 0.70 | 0.28 |
| Dec | 0.01 | 0.19 | 0.36 | 0.32 | 0.26 | 0.24 | 0.88 | 0.27 | 0.79 | 0.31 | 0.66 | 0.29 |
| Diel | 0.24 | 0.06 | 0.18 | 0.10 | | | 0.14 | 0.09 | | | | |
| MesoT | 0.08 | 0.04 | 0.23 | 0.06 | 0.11 | 0.05 | 0.08 | 0.05 | | | 0.06 | 0.06 |
| PP | 0.12 | 0.04 | 0.20 | 0.07 | 0.07 | 0.05 | | | 0.09 | 0.06 | | |
| Chl | 0.07 | 0.05 | | | -0.14 | 0.07 | | | -0.14 | 0.09 | | |
| Hex | | | 0.19 | 0.09 | 0.19 | 0.08 | | | 0.20 | 0.10 | | |
| Chaeto | 0.38 | 0.03 | | | | | | | | | | |

Appendix 2. Summary of the most empirically supported Generalized Linear Model (GLM) results for the major taxa of crustacean zooplankton (other than copepods) at BATS from 1999-2010. Cladocera required using Delta GLMs to first account for estimating the chance of encountering the animal, using a binomial GLM, and then estimating the mean density given the animal was encountered, using a lognormal GLM. Included are predictors, estimate, standard error (SE), and in the case of cladocera binomial estimate (Bino estimate) and binomial standard error (Bino SE). Blank spaces indicate that the predictor was not included in the most empirically supported GLM. Year and Month predictors were used in all GLMs in order to determine seasonal and internal variability even though Year and Month predictors may not have resulted in the best model.

Diel= day/night explanatory variable

Meso T= mesopelagic temperature (°C)

PP= primary production (mgC/m²/d) integrated 0-140 m

Chl= chlorophyll *a* (ng/m²) integrated 0-140 m

Hex= 19'-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0-140 m

| Predictors | Ostracod | | Euphausiids | | Decapoda | | Hyperiid | | Gammarids | | Cladocera | | | |
|-------------|----------|------|-------------|------|----------|------|----------|------|-----------|------|---------------|---------|----------|------|
| | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE | Bino Estimate | Bino SE | Estimate | SE |
| (Intercept) | 2.29 | 0.22 | -0.45 | 0.22 | -1.48 | 0.23 | -2.05 | 0.22 | -3.73 | 0.23 | -1.89 | 0.83 | -3.47 | 0.44 |
| 2000 | -0.81 | 0.21 | -0.13 | 0.22 | -0.43 | 0.22 | -0.33 | 0.21 | -0.32 | 0.22 | -1.40 | 1.25 | -0.01 | 0.87 |
| 2001 | -0.62 | 0.20 | 0.02 | 0.21 | 0.15 | 0.22 | 0.05 | 0.20 | -0.18 | 0.21 | 0.86 | 0.88 | -1.21 | 0.61 |
| 2002 | -0.70 | 0.20 | 0.23 | 0.21 | 0.01 | 0.22 | 0.07 | 0.21 | -0.29 | 0.21 | 1.43 | 0.82 | -0.55 | 0.52 |
| 2003 | 0.11 | 0.21 | 0.28 | 0.21 | 0.57 | 0.23 | 0.24 | 0.21 | 0.02 | 0.22 | -0.43 | 1.05 | -1.16 | 0.70 |
| 2004 | -0.16 | 0.20 | 0.40 | 0.21 | 0.00 | 0.22 | -0.01 | 0.20 | 0.05 | 0.21 | 0.75 | 0.85 | -0.32 | 0.62 |
| 2005 | -0.38 | 0.20 | -0.16 | 0.21 | -0.50 | 0.22 | -0.11 | 0.20 | -0.04 | 0.21 | -0.46 | 0.91 | -0.62 | 0.58 |
| 2006 | -0.17 | 0.22 | -0.79 | 0.23 | -0.37 | 0.23 | -0.40 | 0.22 | -0.19 | 0.23 | 0.88 | 0.85 | -0.87 | 0.58 |
| 2007 | -0.35 | 0.20 | -0.24 | 0.21 | -0.25 | 0.22 | -0.08 | 0.21 | 0.37 | 0.21 | -0.62 | 0.94 | -1.25 | 0.65 |
| 2008 | -0.04 | 0.22 | -0.13 | 0.22 | -0.36 | 0.23 | 0.08 | 0.21 | 0.11 | 0.23 | 0.90 | 0.89 | -0.11 | 0.60 |
| 2009 | -0.22 | 0.22 | -0.33 | 0.22 | 0.34 | 0.23 | 0.02 | 0.22 | -0.11 | 0.23 | 0.75 | 0.85 | -0.13 | 0.54 |
| 2010 | -0.30 | 0.21 | -0.16 | 0.22 | -0.32 | 0.22 | -0.37 | 0.21 | -0.30 | 0.22 | -0.22 | 0.91 | -0.41 | 0.67 |
| Feb | 0.08 | 0.22 | 0.50 | 0.22 | -0.13 | 0.23 | 0.52 | 0.22 | -0.23 | 0.23 | | | | |
| March | 0.18 | 0.22 | 0.69 | 0.22 | -0.15 | 0.23 | 1.03 | 0.22 | 0.26 | 0.23 | 0.52 | 0.64 | 0.18 | 0.38 |
| April | 0.06 | 0.22 | -0.08 | 0.23 | -0.33 | 0.24 | 0.81 | 0.22 | 0.62 | 0.23 | 0.74 | 0.68 | 0.26 | 0.42 |
| May | 0.44 | 0.25 | 0.24 | 0.25 | -0.12 | 0.26 | 1.12 | 0.24 | 0.40 | 0.26 | -0.64 | 0.88 | 0.88 | 0.62 |
| June | 0.23 | 0.24 | 0.10 | 0.25 | 0.76 | 0.27 | 0.95 | 0.24 | 0.00 | 0.25 | -1.12 | 0.99 | 0.73 | 0.59 |
| July | 0.27 | 0.23 | -0.02 | 0.24 | 0.71 | 0.26 | 0.84 | 0.23 | -0.04 | 0.24 | -1.89 | 1.20 | -0.82 | 0.78 |
| Aug | 0.27 | 0.25 | -0.08 | 0.25 | 0.61 | 0.27 | 0.76 | 0.25 | -0.35 | 0.26 | -1.68 | 1.24 | 3.63 | 0.82 |
| Sept | 0.47 | 0.24 | 0.16 | 0.25 | 0.96 | 0.26 | 0.91 | 0.24 | -0.07 | 0.25 | -1.69 | 1.22 | -0.01 | 0.82 |
| Oct | 0.22 | 0.25 | -0.01 | 0.25 | 0.75 | 0.26 | 0.40 | 0.24 | 0.13 | 0.26 | 0.63 | 0.79 | 0.45 | 0.47 |
| Nov | 0.33 | 0.25 | -0.08 | 0.25 | 0.34 | 0.26 | 0.31 | 0.25 | -0.45 | 0.26 | 0.45 | 0.82 | 0.83 | 0.50 |
| Dec | -0.11 | 0.26 | 0.04 | 0.26 | 0.56 | 0.27 | 0.41 | 0.26 | -0.41 | 0.28 | 0.40 | 0.85 | -0.15 | 0.60 |
| Diel | 0.35 | 0.08 | 0.62 | 0.09 | 0.25 | 0.09 | 0.42 | 0.08 | 0.40 | 0.09 | | | 0.29 | 0.22 |
| MesoT | 0.15 | 0.05 | | | | | | | 0.13 | 0.05 | | | -0.31 | 0.13 |
| PP | 0.13 | 0.05 | 0.12 | 0.05 | | | 0.01 | 0.05 | 0.14 | 0.05 | | | 0.20 | 0.13 |
| Chl | | | | | -0.22 | 0.08 | | | | | -0.57 | 0.30 | | |
| Hex | | | 0.18 | 0.07 | 0.39 | 0.09 | 0.16 | 0.07 | | | 0.53 | 0.31 | | |

Appendix 3. Summary of the most empirically supported Generalized Linear Model (GLM) results of the major taxa for

gelatinous zooplankton (chaetognaths, larvaceans, doliolids, cnidarians, and polychaetes) at BATS from 1999-2010. Included are predictors, estimate, and standard error (SE). Blank spaces indicate that that predictor was not included in most empirically supported GLM. Year and Month predictors were used in all GLMs in order to determine seasonal and internal variability even though Year and Month predictors may not have resulted in the best model. Note calanoid density was only included in chaetognath GLMs.

Diel= day/night explanatory variable

MesoT= mesopelagic temperature (°C)

PP= primary production (mgC/m²/d) integrated 0-140 m

Chl= chlorophyll *a* (ng/m²) integrated 0-140 m

Hex= 19'-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0-140 m

Cal= calanoid, know prey to chaetognths, density (ind./m³)

| | Chaetognath | | Larvacean | | Doliolid | | Cnidarian | | Polychaete | |
|---------------------------|-------------|------|-----------|------|----------|------|-----------|------|------------|------|
| | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE |
| Predictors (Intercept) | 1.80 | 0.20 | 1.74 | 0.56 | -1.29 | 0.34 | -1.76 | 0.31 | -1.71 | 0.30 |
| 2000 | -0.38 | 0.20 | -0.40 | 0.56 | -0.11 | 0.33 | -0.74 | 0.30 | -0.74 | 0.29 |
| 2001 | -0.16 | 0.20 | 0.15 | 0.53 | 0.36 | 0.32 | -0.59 | 0.29 | 0.07 | 0.27 |
| 2002 | -0.09 | 0.19 | -0.43 | 0.54 | -0.03 | 0.32 | -0.49 | 0.28 | 0.03 | 0.27 |
| 2003 | -0.31 | 0.20 | 0.70 | 0.55 | 0.19 | 0.33 | -0.53 | 0.29 | 0.60 | 0.28 |
| 2004 | -0.14 | 0.20 | 0.78 | 0.53 | 0.32 | 0.32 | -0.07 | 0.29 | 0.39 | 0.27 |
| 2005 | -0.05 | 0.19 | -0.57 | 0.54 | -0.51 | 0.32 | -0.24 | 0.29 | 0.16 | 0.27 |
| 2006 | -0.33 | 0.21 | -0.20 | 0.58 | -0.80 | 0.34 | -0.81 | 0.31 | -0.37 | 0.29 |
| 2007 | -0.13 | 0.20 | -0.49 | 0.54 | -0.98 | 0.32 | -0.15 | 0.29 | 0.18 | 0.27 |
| 2008 | -0.28 | 0.21 | -1.55 | 0.56 | -1.03 | 0.34 | -0.43 | 0.31 | 0.07 | 0.29 |
| 2009 | -0.50 | 0.21 | -2.00 | 0.58 | 0.01 | 0.34 | 0.01 | 0.31 | 0.40 | 0.29 |
| 2010 | -0.27 | 0.20 | -1.48 | 0.56 | 0.16 | 0.33 | 0.10 | 0.30 | -0.10 | 0.28 |
| Feb | -0.08 | 0.21 | -0.25 | 0.57 | 0.05 | 0.33 | 0.05 | 0.31 | 0.02 | 0.29 |
| March | 0.07 | 0.21 | 0.23 | 0.57 | 0.71 | 0.34 | 0.56 | 0.31 | -0.26 | 0.29 |
| April | 0.42 | 0.22 | -1.39 | 0.58 | 0.64 | 0.35 | 0.77 | 0.32 | -0.34 | 0.30 |
| May | 0.74 | 0.24 | -2.72 | 0.64 | 0.73 | 0.38 | 0.43 | 0.35 | 0.26 | 0.34 |
| June | 0.32 | 0.24 | -1.51 | 0.64 | 0.26 | 0.39 | 0.29 | 0.34 | 0.34 | 0.34 |
| July | 0.08 | 0.23 | -0.59 | 0.61 | -0.06 | 0.37 | 0.57 | 0.33 | 0.23 | 0.32 |
| Aug | -0.29 | 0.25 | -0.99 | 0.66 | -0.25 | 0.40 | 0.09 | 0.35 | -0.14 | 0.35 |
| Sept | 0.13 | 0.24 | 0.21 | 0.64 | 0.50 | 0.38 | 0.58 | 0.34 | 0.48 | 0.34 |
| Oct | 0.31 | 0.24 | 0.14 | 0.65 | 0.71 | 0.38 | 0.62 | 0.34 | 0.40 | 0.34 |
| Nov | 0.26 | 0.24 | -0.74 | 0.66 | 0.21 | 0.38 | 0.24 | 0.35 | 0.14 | 0.34 |
| Dec | 0.09 | 0.25 | -0.64 | 0.69 | 0.30 | 0.40 | 0.48 | 0.37 | 0.41 | 0.36 |
| Diel | | | | | -0.21 | 0.13 | 0.36 | 0.12 | 0.31 | 0.11 |
| MesoT | | | 0.57 | 0.13 | | | | | 0.09 | 0.07 |
| PP | | | 0.20 | 0.14 | 0.15 | 0.08 | 0.08 | 0.07 | 0.17 | 0.07 |
| Chl | -0.15 | 0.07 | | | -0.24 | 0.12 | | | -0.15 | 0.09 |
| Hex | 0.21 | 0.08 | 0.61 | 0.18 | 0.27 | 0.13 | | | | |
| Cal | 0.45 | 0.05 | | | | | | | | |

Appendix 4. Summary of the most empirically supported Generalized Linear Model (GLM) results for pelagic snails

(pteropods and heteropods) at BATS from 1999-2010. Gymnosomes required using Delta GLMs to first account for estimating the chance of encountering the animal, using a binomial GLM, and then estimating the mean density given the animal was encountered, using a lognormal GLM. Predictors, estimate, standard error (SE), and in the case of cladocera binomial estimate (Bino estimate) and binomial standard error (Bino SE) are noted. Blank spaces indicate that the predictor was not included in the most empirically supported GLM. Year and Month predictors were used in all GLMs in order to determine seasonal and internal variability even though Year and Month predictors may not have resulted in the best model.

Diel= day/night explanatory variable

MesoT= mesopelagic temperature (°C)

PP= primary production (mgC/m²/d) integrated 0-140 m

Chl= chlorophyll *a* (ng/m²) integrated 0-140 m

Hex= 19'-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0-140 m

| Predictors | Limacina | | Other Thecosome | | Gymnosome | | | | Heteropoda | |
|-------------|----------|------|-----------------|------|---------------|---------|----------|------|------------|------|
| | Estimate | SE | Estimate | SE | Bino Estimate | Bino SE | Estimate | SE | Estimate | SE |
| (Intercept) | -1.05 | 0.32 | -1.56 | 0.29 | -1.53 | 0.76 | -5.13 | 0.51 | -3.20 | 0.29 |
| 2000 | 0.08 | 0.31 | -0.34 | 0.28 | 0.73 | 0.82 | -0.42 | 0.54 | -0.05 | 0.28 |
| 2001 | -0.46 | 0.30 | -0.16 | 0.26 | 0.07 | 0.81 | 0.18 | 0.62 | -0.09 | 0.26 |
| 2002 | -0.04 | 0.30 | -0.14 | 0.26 | 0.22 | 0.84 | 0.07 | 0.58 | -0.20 | 0.26 |
| 2003 | 0.18 | 0.31 | -0.23 | 0.27 | -0.74 | 0.96 | 0.55 | 0.88 | -0.09 | 0.27 |
| 2004 | -0.24 | 0.30 | -0.11 | 0.27 | 0.02 | 0.83 | 0.38 | 0.59 | 0.28 | 0.26 |
| 2005 | -0.62 | 0.30 | -0.48 | 0.27 | 0.95 | 0.79 | 0.19 | 0.50 | 0.21 | 0.26 |
| 2006 | -0.93 | 0.32 | -1.05 | 0.28 | -0.10 | 0.88 | -0.40 | 0.58 | -0.17 | 0.28 |
| 2007 | -0.58 | 0.30 | -0.81 | 0.27 | 0.79 | 0.77 | -0.50 | 0.54 | -0.24 | 0.26 |
| 2008 | -0.14 | 0.32 | -0.60 | 0.29 | 0.25 | 0.84 | 0.45 | 0.57 | 0.80 | 0.28 |
| 2009 | -1.12 | 0.32 | -0.81 | 0.28 | 0.64 | 0.88 | 0.54 | 0.60 | 0.23 | 0.28 |
| 2010 | 0.18 | 0.31 | -0.45 | 0.28 | 1.42 | 0.76 | 0.61 | 0.49 | 0.14 | 0.27 |
| Feb | 0.25 | 0.32 | 0.06 | 0.29 | -1.71 | 0.95 | -0.37 | 0.67 | 0.10 | 0.29 |
| March | 0.50 | 0.32 | 0.12 | 0.29 | -2.72 | 1.19 | 0.76 | 0.95 | 0.25 | 0.29 |
| April | 0.71 | 0.33 | -0.50 | 0.30 | -0.77 | 0.79 | 0.37 | 0.55 | 0.00 | 0.29 |
| May | 1.27 | 0.36 | 0.16 | 0.32 | -1.22 | 0.98 | 0.16 | 0.70 | 1.18 | 0.32 |
| June | 1.16 | 0.36 | 0.23 | 0.32 | -0.52 | 0.83 | 0.82 | 0.57 | 1.04 | 0.32 |
| July | 0.99 | 0.35 | 0.02 | 0.31 | -0.60 | 0.83 | 0.62 | 0.56 | 0.98 | 0.31 |
| Aug | 1.11 | 0.36 | -0.22 | 0.33 | 0.42 | 0.79 | 0.55 | 0.53 | 1.25 | 0.32 |
| Sept | 0.85 | 0.35 | -0.02 | 0.32 | 1.11 | 0.75 | 0.74 | 0.52 | 1.18 | 0.31 |
| Oct | 0.45 | 0.35 | 0.20 | 0.32 | 0.49 | 0.77 | 1.29 | 0.48 | 0.93 | 0.31 |
| Nov | 0.36 | 0.37 | 0.11 | 0.33 | -0.29 | 0.85 | 0.16 | 0.58 | 0.67 | 0.32 |
| Dec | 0.42 | 0.38 | 0.64 | 0.34 | -0.44 | 0.91 | 0.78 | 0.64 | 0.37 | 0.34 |
| Diel | 0.41 | 0.13 | 0.49 | 0.11 | | | 0.40 | 0.23 | 0.25 | 0.11 |
| MesoT | | | | | -0.21 | 0.18 | | | | |
| PP | 0.10 | 0.08 | 0.12 | 0.07 | | | -0.22 | 0.19 | 0.23 | 0.07 |
| Chl | | | | | | | | | | |
| Hex | | | | | | | | | | |

Appendix 5. Summary of the most empirically supported Generalized Linear Model (GLM) results for larval benthic

invertebrates (barnacle nauplii, brachiolaria-sea star larvae) and fish (leptocephali- eel larvae) at BATS from 1999-2010.

Brachiolaria and leptocephali required using Delta GLMs to first account for estimating the chance of encountering the animal, using a binomial GLM, and then estimating the mean density given the animal was encountered, using a lognormal GLM.

Predictors, estimate, standard error (SE), and in the case of cladocera binomial estimate (Bino estimate) and binomial standard error (Bino SE) are noted. Blank spaces indicate that that predictor was not included in the lowest AIC ranked GLM. Year and

Month predictors were used in all GLMs in order to determine seasonal and internal variability even though Year and Month predictors may not have resulted in the best model.

Diel= day/night explanatory variable

MesoT= mesopelagic temperature (°C)

PP= primary production (mgC/m²/d) integrated 0-140 m

Chl= chlorophyll *a* (ng/m²) integrated 0-140 m

Hex= 19'-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0-140 m

| Predictors | Barnacle Nauplii | | | Brachiolaria | | | Leptocephali | | | |
|-------------|------------------|------|---------------|--------------|----------|------|---------------|---------|----------|------|
| | Estimate | SE | Bino Estimate | Bino SE | Estimate | SE | Bino Estimate | Bino SE | Estimate | SE |
| (Intercept) | -2.08 | 0.36 | -18.98 | 2511.87 | -4.67 | 0.52 | -3.50 | 0.94 | -5.49 | 0.53 |
| 2000 | 1.32 | 0.36 | -0.40 | 0.90 | 0.07 | 0.69 | 0.47 | 0.97 | 0.78 | 0.70 |
| 2001 | 1.38 | 0.34 | -1.69 | 1.22 | 0.45 | 0.44 | 1.13 | 0.85 | 0.99 | 0.63 |
| 2002 | 0.98 | 0.34 | -0.07 | 0.87 | -0.13 | 0.32 | 0.36 | 0.95 | 0.77 | 0.68 |
| 2003 | 1.71 | 0.35 | -0.50 | 0.90 | 0.18 | 0.53 | 0.43 | 0.89 | -0.42 | 0.60 |
| 2004 | 1.05 | 0.34 | -1.02 | 1.00 | -0.14 | 0.45 | 0.77 | 0.87 | 0.28 | 0.61 |
| 2005 | 1.66 | 0.34 | -0.18 | 0.90 | -0.11 | 0.35 | -0.74 | 1.25 | 0.23 | 0.96 |
| 2006 | 1.33 | 0.36 | -0.83 | 0.99 | -0.44 | 0.35 | 0.61 | 0.90 | -0.08 | 0.56 |
| 2007 | 1.91 | 0.34 | -17.86 | 1877.09 | | | 0.16 | 0.94 | 0.93 | 0.72 |
| 2008 | 2.46 | 0.37 | -1.49 | 1.24 | -0.53 | 0.37 | 1.13 | 0.88 | 0.34 | 0.59 |
| 2009 | 2.31 | 0.36 | -0.74 | 1.00 | -1.03 | 0.34 | 1.78 | 0.93 | 0.45 | 0.70 |
| 2010 | 1.58 | 0.35 | 0.02 | 0.86 | -0.39 | 0.33 | 0.77 | 0.91 | 0.03 | 0.60 |
| Feb | 0.22 | 0.37 | 17.23 | 2511.87 | | | 0.34 | 0.84 | 0.29 | 0.54 |
| March | -0.13 | 0.37 | 15.98 | 2511.87 | 1.37 | 0.83 | -0.16 | 0.86 | 0.18 | 0.58 |
| April | -0.21 | 0.38 | 16.06 | 2511.87 | 1.07 | 0.79 | -1.32 | 1.05 | -1.19 | 0.88 |
| May | -1.38 | 0.41 | 0.05 | 3344.91 | | | -1.45 | 1.28 | -0.07 | 1.01 |
| June | -2.82 | 0.41 | 0.06 | 3341.70 | | | -1.04 | 1.08 | -0.27 | 0.77 |
| July | -3.18 | 0.39 | 17.09 | 2511.87 | 0.02 | 0.74 | -0.24 | 0.91 | 0.30 | 0.56 |
| Aug | -3.72 | 0.42 | 17.34 | 2511.87 | -0.23 | 1.09 | -0.70 | 1.06 | 0.55 | 0.70 |
| Sept | -2.81 | 0.40 | 18.86 | 2511.87 | 0.16 | 0.67 | -0.05 | 0.94 | 0.00 | 0.61 |
| Oct | -3.35 | 0.40 | 18.74 | 2511.87 | 0.08 | 0.62 | 0.37 | 0.91 | 0.43 | 0.58 |
| Nov | -3.37 | 0.42 | 17.74 | 2511.87 | 0.12 | 0.65 | 0.98 | 0.91 | 0.37 | 0.61 |
| Dec | -0.37 | 0.44 | 17.82 | 2511.87 | 0.06 | 0.64 | 0.64 | 0.95 | 0.87 | 0.59 |
| Diel | | | | | | | 1.88 | 0.41 | | |
| MesoT | | | | | | | -0.39 | 0.19 | -0.18 | 0.15 |
| PP | 0.09 | 0.09 | -0.08 | 0.35 | | | | | | |
| Chl | | | | | -0.26 | 0.40 | | | | |
| Hex | | | | | 0.32 | 0.40 | | | | |

Appendix 6. Summary of Generalized Linear Models (GLMs) for the five major copepod taxa at BATS. Included are model number (m), predictors, number of parameters (p), AIC values, Δ AIC values, and $-2 \cdot \log \text{Lik}$ ($-2 \log L$). Year and Month predictors were used in all GLMs in order to determine seasonal and internal variability even though Year and Month predictors may not have resulted in the best model.

Y= year
M= month
D= day/night explanatory variable
MT= mesopelagic temperature ($^{\circ}\text{C}$)
P= primary production ($\text{mgC}/\text{m}^2/\text{d}$) integrated 0-140 m
C= chlorophyll *a* (ng/m^2) integrated 0-140 m
H= 19'-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0-140 m
F= fucoxanthin (ng/kg) integrated 0-140 m

| TAXA | | | | | | | | | | | | | | | | | |
|------|----------------------|----|------------|--------------|--------|-----------|--------------|--------|-------------|--------------|--------|---------------|--------------|--------|--------------|--------------|--------|
| m | Predictors | p | Oithonidae | | | Oncaeidae | | | Corycaeidae | | | Sapphirinidae | | | Harpacticoid | | |
| | | | AIC | Δ AIC | -2logL | AIC | Δ AIC | -2logL | AIC | Δ AIC | -2logL | AIC | Δ AIC | -2logL | AIC | Δ AIC | -2logL |
| 1 | Y+M+D+MT+ P+C+H+F | 30 | 644.8 | 2.9 | 584.8 | 828.2 | 3.5 | 768.2 | 749.4 | 2.9 | 689.4 | 806.4 | 2.7 | 746.4 | 1047.5 | 5.3 | 987.5 |
| 2 | Y+M+D+MT+ P+C+H | 29 | 642.9 | 1.0 | 584.9 | 826.3 | 1.5 | 768.3 | 748.9 | 2.4 | 690.9 | 806.2 | 2.5 | 748.2 | 1045.7 | 3.6 | 987.7 |
| 3 | Y+M+D+MT+ P+C | 28 | 647.3 | 5.4 | 591.3 | 829.4 | 4.6 | 773.4 | 750.4 | 3.9 | 694.4 | 808.5 | 4.9 | 752.5 | 1044.5 | 2.4 | 988.5 |
| 4 | Y+M+D+MT+ P | 27 | 645.8 | 3.9 | 591.8 | 828.0 | 3.3 | 774.0 | 748.4 | 1.9 | 694.4 | 806.7 | 3.0 | 752.7 | 1046.0 | 3.9 | 992.0 |
| 5 | Y+M+D+MT+ P+H | 28 | 645.2 | 3.3 | 589.2 | 824.7 | 0.0 | 768.7 | 748.2 | 1.7 | 692.2 | 806.5 | 2.9 | 750.5 | 1044.7 | 2.6 | 988.7 |
| 6 | Y+M+D+MT+ C+H | 28 | 643.3 | 1.4 | 587.3 | 834.3 | 9.6 | 778.3 | 746.9 | 0.4 | 690.9 | 806.0 | 2.4 | 750.0 | 1044.4 | 2.3 | 988.4 |
| 7 | Y+M+D+MT | 26 | 646.7 | 4.8 | 594.7 | 841.0 | 16.2 | 789.0 | 746.5 | 0.0 | 694.5 | 807.1 | 3.4 | 755.1 | 1044.0 | 1.9 | 992.0 |
| 8 | Y+M+MT | 25 | 645.3 | 3.4 | 595.3 | 841.7 | 16.9 | 791.7 | 746.9 | 0.5 | 696.9 | 805.7 | 2.1 | 755.7 | 1042.1 | 0.0 | 992.1 |
| 9 | Y+M+MT+P | 26 | 644.5 | 2.6 | 592.5 | 829.1 | 4.4 | 777.1 | 748.9 | 2.4 | 696.9 | 805.3 | 1.7 | 753.3 | 1044.1 | 2.0 | 992.1 |
| 10 | Y+M+MT+P+ C | 27 | 646.0 | 4.1 | 592.0 | 830.5 | 5.7 | 776.5 | 750.9 | 4.4 | 696.9 | 807.2 | 3.6 | 753.2 | 1042.6 | 0.5 | 988.6 |
| 11 | Y+M+MT+P+ C+H | 28 | 641.9 | 0.0 | 585.9 | 827.8 | 3.1 | 771.8 | 749.7 | 3.2 | 693.7 | 805.0 | 1.4 | 749.0 | 1043.8 | 1.7 | 987.8 |
| 12 | Y+M+MT+P+ H | 27 | 644.0 | 2.1 | 590.0 | 826.2 | 1.5 | 772.2 | 748.8 | 2.4 | 694.8 | 805.3 | 1.7 | 751.3 | 1042.8 | 0.7 | 988.8 |
| 13 | Y+M+MT+C+ H | 27 | 642.2 | 0.3 | 588.2 | 835.5 | 10.8 | 781.5 | 747.7 | 1.2 | 693.7 | 804.8 | 1.2 | 750.8 | 1042.5 | 0.4 | 988.5 |
| 14 | Y+M+P | 25 | 649.3 | 7.4 | 599.3 | 842.5 | 17.8 | 792.5 | 749.0 | 2.5 | 699.0 | 804.0 | 0.4 | 754.0 | 1045.5 | 3.4 | 995.5 |
| 15 | Y+M+P+C | 26 | 650.8 | 8.9 | 598.8 | 843.9 | 19.1 | 791.9 | 751.0 | 4.5 | 699.0 | 805.9 | 2.2 | 753.9 | 1044.1 | 1.9 | 992.1 |
| 16 | Y+M+P+C+H | 27 | 646.4 | 4.5 | 592.4 | 840.9 | 16.1 | 786.9 | 749.6 | 3.2 | 695.6 | 803.6 | 0.0 | 749.6 | 1045.4 | 3.3 | 991.4 |
| 17 | Y+M+P+H | 26 | 648.5 | 6.6 | 596.5 | 839.3 | 14.5 | 787.3 | 748.8 | 2.3 | 696.8 | 803.9 | 0.3 | 751.9 | 1044.5 | 2.3 | 992.5 |
| 18 | Y+M+C+H | 26 | 648.3 | 6.4 | 596.3 | 853.1 | 28.3 | 801.1 | 747.7 | 1.2 | 695.7 | 803.9 | 0.2 | 751.9 | 1044.8 | 2.7 | 992.8 |
| 19 | Y+M+D+P | 26 | 650.4 | 8.5 | 598.4 | 841.2 | 16.4 | 789.2 | 748.4 | 1.9 | 696.4 | 805.3 | 1.7 | 753.3 | 1047.4 | 5.3 | 995.4 |
| 20 | Y+M+D+P+C | 27 | 652.0 | 10.1 | 598.0 | 842.5 | 17.8 | 788.5 | 750.4 | 3.9 | 696.4 | 807.2 | 3.5 | 753.2 | 1046.0 | 3.9 | 992.0 |
| 21 | Y+M+D+P+C +H | 28 | 647.3 | 5.4 | 591.3 | 839.1 | 14.3 | 783.1 | 748.7 | 2.2 | 692.7 | 804.7 | 1.1 | 748.7 | 1047.3 | 5.2 | 991.3 |
| 22 | Y+M+D+P+H | 27 | 649.6 | 7.7 | 595.6 | 837.6 | 12.8 | 783.6 | 748.0 | 1.6 | 694.0 | 805.1 | 1.5 | 751.1 | 1046.4 | 4.3 | 992.4 |
| 23 | Y+M+D+C+H | 27 | 649.3 | 7.4 | 595.3 | 851.6 | 26.9 | 797.6 | 746.8 | 0.3 | 692.8 | 805.0 | 1.3 | 751.0 | 1046.7 | 4.6 | 992.7 |

Appendix 7. Summary of Generalized Linear Models (GLMs) for calanoid copepods and chaetognaths at BATS. Included are model number (m), predictors, number of parameters (p), AIC values, Δ AIC values, and $-2 \cdot \log \text{Lik}$ ($-2 \log \text{Lik}$). Predator and prey densities were included in all models because preliminary results indicated that the inclusion of chaetognath densities in calanoid GLMs and calanoid densities in chaetognath GLMs resulted in a much lower AIC and greater deviance was explained. Year and Month predictors were used in all GLMs in order to determine seasonal and internal variability even though Year and Month predictors may not have resulted in the best model.

Y= year
M= month
D= day/night explanatory variable
MT= mesopelagic temperature ($^{\circ}\text{C}$)
P= primary production ($\text{mgC}/\text{m}^2/\text{d}$) integrated 0-140 m
C= chlorophyll *a* (ng/m^2) integrated 0-140 m
H= 19'-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0-140 m
F= fucoxanthin (ng/kg) integrated 0-140 m
P/P= predator or prey density ($\text{ind.}/\text{m}^3$)

| TAXA | | | | | | | | | |
|------|----------------------|----|----------|--------------|--------|-------------|--------------|--------|--|
| m | Predictors | P | Calanoid | | | Chaetognath | | | |
| | | | AIC | Δ AIC | -2logL | AIC | Δ AIC | -2logL | |
| 1 | Y+M+D+MT+P+C+H+F+P/P | 31 | 498.0 | 3.5 | 436.0 | 669.5 | 3.5 | 607.5 | |
| 2 | Y+M+D+MT+P+C+H+P/P | 30 | 496.4 | 2.0 | 436.4 | 668.5 | 2.5 | 608.5 | |
| 3 | Y+M+D+MT+P+C+P/P | 29 | 494.5 | 0.0 | 436.5 | 674.2 | 8.2 | 616.2 | |
| 4 | Y+M+D+MT+P+P/P | 28 | 494.8 | 0.4 | 438.8 | 672.3 | 6.3 | 616.3 | |
| 5 | Y+M+D+MT+P+H+P/P | 29 | 495.8 | 1.3 | 437.8 | 669.9 | 3.9 | 611.9 | |
| 6 | Y+M+D+MT+C+H+P/P | 29 | 504.5 | 10.1 | 446.5 | 667.4 | 1.4 | 609.4 | |
| 7 | Y+M+D+MT+P/P | 27 | 508.0 | 13.5 | 454.0 | 670.8 | 4.9 | 616.8 | |
| 8 | Y+M+MT+P/P | 26 | 521.4 | 27.0 | 469.4 | 671.0 | 5.0 | 619.0 | |
| 9 | Y+M+MT+P+P/P | 27 | 509.8 | 15.3 | 455.8 | 672.6 | 6.6 | 618.6 | |
| 10 | Y+M+MT+P+C+P/P | 28 | 509.5 | 15.0 | 453.5 | 674.5 | 8.5 | 618.5 | |
| 11 | Y+M+MT+P+C+H+P/P | 29 | 511.4 | 17.0 | 453.4 | 668.5 | 2.5 | 610.5 | |
| 12 | Y+M+MT+P+H+P/P | 28 | 511.1 | 16.7 | 455.1 | 669.8 | 3.9 | 613.8 | |
| 13 | Y+M+MT+C+H+P/P | 28 | 518.6 | 24.2 | 462.6 | 667.3 | 1.3 | 611.3 | |
| 14 | Y+M+P+P/P | 26 | 513.6 | 19.1 | 461.6 | 670.9 | 4.9 | 618.9 | |
| 15 | Y+M+P+C+P/P | 27 | 513.3 | 18.8 | 459.3 | 672.9 | 6.9 | 618.9 | |
| 16 | Y+M+P+C+H+P/P | 28 | 515.3 | 20.8 | 459.3 | 666.9 | 0.9 | 610.9 | |
| 17 | Y+M+P+H+P/P | 27 | 514.9 | 20.4 | 460.9 | 668.3 | 2.3 | 614.3 | |
| 18 | Y+M+C+H+P/P | 27 | 525.5 | 31.0 | 471.5 | 666.0 | 0.0 | 612.0 | |
| 19 | Y+M+D+P+P/P | 27 | 498.5 | 4.1 | 444.5 | 670.7 | 4.7 | 616.7 | |
| 20 | Y+M+D+P+C+P/P | 28 | 498.2 | 3.7 | 442.2 | 672.6 | 6.6 | 616.6 | |
| 21 | Y+M+D+P+C+H+P/P | 29 | 500.1 | 5.7 | 442.1 | 667.0 | 1.0 | 609.0 | |
| 22 | Y+M+D+P+H+P/P | 28 | 499.4 | 4.9 | 443.4 | 668.3 | 2.3 | 612.3 | |
| 23 | Y+M+D+C+H+P/P | 28 | 511.3 | 16.8 | 455.3 | 666.2 | 0.2 | 610.2 | |

Appendix 8. Summary of Generalized Linear Models (GLMs) for calanoid copepods at BATS for 16 year time-series (1995-2010) and 12 year time-series (1999-2010). Included are model number (m), predictors, number of parameters (p), AIC values, Δ AIC values, and $-2 \cdot \log \text{Lik}$ ($-2 \log L$). Year and Month predictors were used in all GLMs in order to determine seasonal and internal variability even though Year and Month predictors may not have resulted in the best model.

Y= year
M= month
D= day/night explanatory variable
MT= mesopelagic temperature ($^{\circ}\text{C}$)
P= primary production ($\text{mgC}/\text{m}^2/\text{d}$) integrated 0-140 m
C= chlorophyll a (ng/m^2) integrated 0-140 m
H= 19'-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0-140 m
F= fucoxanthin (ng/kg) integrated 0-140 m

| TAXA | | | | | | | | | | | |
|------|------------------|--------------------|-------|--------------|--------|----|--------------------|--------------|--------|--|--|
| m | Predictors | Calanoid 1995-2010 | | | | | Calanoid 1999-2010 | | | | |
| | | P | AIC | Δ AIC | -2logL | P | AIC | Δ AIC | -2logL | | |
| 1 | Y+M+D+MT+P+C+H+F | 34 | 801.0 | 1.7 | 733.0 | 30 | 602.7 | 2.5 | 542.7 | | |
| 2 | Y+M+D+MT+P+C+H | 33 | 800.0 | 0.8 | 734.0 | 29 | 601.4 | 1.2 | 543.4 | | |
| 3 | Y+M+D+MT+P+C | 32 | 799.2 | 0.0 | 735.2 | 28 | 602.4 | 2.3 | 546.4 | | |
| 4 | Y+M+D+MT+P | 31 | 804.8 | 5.6 | 742.8 | 27 | 605.9 | 5.7 | 551.9 | | |
| 5 | Y+M+D+MT+P+H | 32 | 800.4 | 1.2 | 736.4 | 28 | 600.2 | 0.0 | 544.2 | | |
| 6 | Y+M+D+MT+C+H | 32 | 806.1 | 6.8 | 742.1 | 28 | 604.6 | 4.4 | 548.6 | | |
| 7 | Y+M+D+MT | 30 | 820.8 | 21.5 | 760.8 | 26 | 615.4 | 15.2 | 563.4 | | |
| 8 | Y+M+MT | 29 | 833.4 | 34.1 | 775.4 | 25 | 629.1 | 28.9 | 579.1 | | |
| 9 | Y+M+MT+P | 30 | 818.4 | 19.2 | 758.4 | 26 | 620.8 | 20.7 | 568.8 | | |
| 10 | Y+M+MT+P+C | 31 | 812.9 | 13.6 | 750.9 | 27 | 617.4 | 17.3 | 563.4 | | |
| 11 | Y+M+MT+P+C+H | 32 | 813.9 | 14.7 | 749.9 | 28 | 617.2 | 17.0 | 561.2 | | |
| 12 | Y+M+MT+P+H | 31 | 814.6 | 15.4 | 752.6 | 27 | 616.3 | 16.1 | 562.3 | | |
| 13 | Y+M+MT+C+H | 31 | 819.5 | 20.2 | 757.5 | 27 | 619.8 | 19.6 | 565.8 | | |
| 14 | Y+M+P | 29 | 823.8 | 24.6 | 765.8 | 25 | 625.3 | 25.2 | 575.3 | | |
| 15 | Y+M+P+C | 30 | 817.5 | 18.3 | 757.5 | 26 | 621.9 | 21.8 | 569.9 | | |
| 16 | Y+M+P+C+H | 31 | 818.7 | 19.5 | 756.7 | 27 | 621.5 | 21.3 | 567.5 | | |
| 17 | Y+M+P+H | 30 | 819.9 | 20.7 | 759.9 | 26 | 620.5 | 20.3 | 568.5 | | |
| 18 | Y+M+C+H | 30 | 826.5 | 27.2 | 766.5 | 26 | 626.3 | 26.1 | 574.3 | | |
| 19 | Y+M+D+P | 30 | 810.0 | 10.8 | 750.0 | 26 | 610.2 | 10.0 | 558.2 | | |
| 20 | Y+M+D+P+C | 31 | 803.7 | 4.5 | 741.7 | 27 | 606.7 | 6.6 | 552.7 | | |
| 21 | Y+M+D+P+C+H | 32 | 804.6 | 5.4 | 740.6 | 28 | 605.4 | 5.2 | 549.4 | | |
| 22 | Y+M+D+P+H | 31 | 805.6 | 6.3 | 743.6 | 27 | 604.1 | 4.0 | 550.1 | | |
| 23 | Y+M+D+C+H | 31 | 812.9 | 13.7 | 750.9 | 27 | 610.9 | 10.7 | 556.9 | | |

Appendix 9. Summary of Generalized Linear Models (GLMs) for the major five taxa of crustacean zooplankton (other than copepods and cladocera) at BATS. Included are model number (m), predictors, number of parameters (p), AIC values, Δ AIC values, and $-2 \cdot \log \text{Lik}$ ($-2 \log L$). Year and Month predictors were used in all GLMs in order to determine seasonal and internal variability even though Year and Month predictors may not have resulted in the best model.

Y= year

M= month

D= day/night explanatory variable

MT= mesopelagic temperature ($^{\circ}\text{C}$)

P= primary production ($\text{mgC}/\text{m}^2/\text{d}$) integrated 0-140 m

C= chlorophyll *a* (ng/m^2) integrated 0-140 m

H= 19'-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0-140 m

F= fucoxanthin (ng/kg) integrated 0-140 m

| TAXA | | | | | | | | | | | | | | | | | |
|------|------------------|----|----------|--------------|--------|------------|--------------|--------|----------|--------------|--------|----------|--------------|--------|----------|--------------|--------|
| m | Predictors | p | Ostracod | | | Euphausiid | | | Decapoda | | | Hyperiid | | | Gammarid | | |
| | | | AIC | Δ AIC | -2logL | AIC | Δ AIC | -2logL | AIC | Δ AIC | -2logL | AIC | Δ AIC | -2logL | AIC | Δ AIC | -2logL |
| 1 | Y+M+D+MT+P+C+H+H | 30 | 711.5 | 3.1 | 658.4 | 718.1 | 4.4 | 658.1 | 739.3 | 5.3 | 679.3 | 703.5 | 4.1 | 643.5 | 738.2 | 4.5 | 678.2 |
| 2 | Y+M+D+MT+P+C+H | 29 | 710.8 | 2.4 | 653.6 | 716.6 | 2.9 | 658.6 | 737.3 | 3.3 | 679.3 | 703.1 | 3.7 | 645.1 | 737.7 | 3.9 | 679.7 |
| 3 | Y+M+D+MT+P+C | 28 | 710.3 | 1.9 | 654.4 | 717.0 | 3.3 | 661.0 | 753.7 | 19.7 | 697.7 | 704.2 | 4.8 | 648.2 | 735.7 | 1.9 | 679.7 |
| 4 | Y+M+D+MT+P | 27 | 708.4 | 0.0 | 651.5 | 720.6 | 6.9 | 666.6 | 751.8 | 17.8 | 697.8 | 704.5 | 5.1 | 650.5 | 733.8 | 0.0 | 679.8 |
| 5 | Y+M+D+MT+P+H | 28 | 709.6 | 1.2 | 652.8 | 715.7 | 2.0 | 659.7 | 743.2 | 9.2 | 687.2 | 701.2 | 1.7 | 645.2 | 735.7 | 1.9 | 679.7 |
| 6 | Y+M+D+MT+C+H | 28 | 714.4 | 6.0 | 654.3 | 718.9 | 5.2 | 662.9 | 735.9 | 1.9 | 679.9 | 701.2 | 1.8 | 645.2 | 742.3 | 8.6 | 686.3 |
| 7 | Y+M+D+MT | 26 | 713.0 | 4.7 | 661.0 | 728.5 | 14.8 | 676.5 | 751.3 | 17.3 | 699.3 | 703.7 | 4.3 | 651.7 | 738.7 | 5.0 | 686.7 |
| 8 | Y+M+MT | 25 | 728.3 | 19.9 | 678.3 | 773.7 | 60.0 | 723.7 | 756.3 | 22.3 | 706.3 | 726.5 | 27.0 | 676.5 | 756.9 | 23.1 | 706.9 |
| 9 | Y+M+MT+P | 26 | 724.5 | 16.1 | 672.5 | 768.1 | 54.3 | 716.1 | 757.0 | 23.0 | 705.0 | 727.6 | 28.1 | 675.6 | 752.9 | 19.1 | 700.9 |
| 10 | Y+M+MT+P+C | 27 | 726.5 | 18.1 | 672.5 | 765.0 | 51.2 | 711.0 | 758.9 | 24.9 | 704.9 | 727.3 | 27.8 | 673.3 | 754.8 | 21.1 | 700.8 |
| 11 | Y+M+MT+P+C+H | 28 | 727.5 | 19.1 | 671.5 | 765.8 | 52.1 | 709.8 | 744.2 | 10.2 | 688.2 | 727.2 | 27.8 | 671.2 | 756.7 | 23.0 | 700.7 |
| 12 | Y+M+MT+P+H | 27 | 726.0 | 17.6 | 672.0 | 765.3 | 51.6 | 711.3 | 749.2 | 15.2 | 695.2 | 725.4 | 26.0 | 671.4 | 754.7 | 21.0 | 700.7 |
| 13 | Y+M+MT+C+H | 27 | 730.4 | 22.0 | 676.4 | 767.0 | 53.2 | 713.0 | 742.7 | 8.7 | 688.7 | 725.3 | 25.8 | 671.3 | 760.5 | 26.7 | 706.5 |
| 14 | Y+M+P | 25 | 732.5 | 24.1 | 682.5 | 766.2 | 52.5 | 716.2 | 755.1 | 21.1 | 705.1 | 725.7 | 26.2 | 675.7 | 757.4 | 23.7 | 707.4 |
| 15 | Y+M+P+C | 26 | 734.5 | 26.1 | 682.5 | 763.1 | 49.4 | 711.1 | 757.0 | 23.0 | 705.0 | 725.3 | 25.9 | 673.3 | 759.4 | 25.6 | 707.4 |
| 16 | Y+M+P+C+H | 27 | 735.3 | 27.0 | 681.3 | 763.9 | 50.2 | 709.9 | 742.3 | 8.3 | 688.3 | 725.4 | 25.9 | 671.4 | 761.3 | 27.6 | 707.3 |
| 17 | Y+M+P+H | 26 | 733.9 | 25.5 | 681.9 | 763.4 | 49.7 | 711.4 | 747.3 | 13.3 | 695.3 | 723.5 | 24.1 | 671.5 | 759.3 | 25.6 | 707.3 |
| 18 | Y+M+C+H | 26 | 741.0 | 32.6 | 689.0 | 765.4 | 51.7 | 713.4 | 740.8 | 6.8 | 688.8 | 723.4 | 23.9 | 671.4 | 767.6 | 33.9 | 715.6 |
| 19 | Y+M+D+P | 26 | 716.2 | 7.9 | 664.2 | 718.6 | 4.9 | 666.6 | 749.9 | 15.9 | 697.9 | 702.7 | 3.3 | 650.7 | 738.1 | 4.4 | 686.1 |
| 20 | Y+M+D+P+C | 27 | 718.2 | 9.8 | 664.2 | 715.1 | 1.3 | 661.1 | 751.8 | 17.8 | 697.8 | 702.4 | 2.9 | 648.4 | 740.1 | 6.3 | 686.1 |
| 21 | Y+M+D+P+C+H | 28 | 718.5 | 10.1 | 662.5 | 714.7 | 0.9 | 658.7 | 735.5 | 1.5 | 679.5 | 701.4 | 1.9 | 645.4 | 742.1 | 8.3 | 686.1 |
| 22 | Y+M+D+P+H | 27 | 717.3 | 8.9 | 663.3 | 713.7 | 0.0 | 659.7 | 741.3 | 7.3 | 687.3 | 699.4 | 0.0 | 645.4 | 740.1 | 6.4 | 686.1 |
| 23 | Y+M+D+C+H | 27 | 725.0 | 16.6 | 671.0 | 717.2 | 3.5 | 663.2 | 734.0 | 0.0 | 680.0 | 699.4 | 0.0 | 645.4 | 749.4 | 15.6 | 695.4 |

Appendix 10. Summary of Generalized Linear Models (GLMs) for two rare zooplankton taxa, cladocera and gymnosomes at

BATS. Included are model number (m), predictors, number of parameters (p), binomial AIC values (Bino AIC), binomial

Δ AIC values (Bino Δ AIC), lognormal AIC (AIC) values, lognormal Δ AIC values (Δ AIC), and $-2 * \log \text{Lik}$ ($-2 \log L$). Year and

Month predictors were used in all GLMs in order to determine seasonal and internal variability even though Year and Month

predictors may not have resulted in the best model.

Y= year

M= month

D= day/night explanatory variable

MT= mesopelagic temperature ($^{\circ}\text{C}$)

P= primary production ($\text{mgC}/\text{m}^2/\text{d}$) integrated 0-140 m

C= chlorophyll *a* (ng/m^2) integrated 0-140 m

H= 19'-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0-140 m

F= fucoxanthin (ng/kg) integrated 0-140 m

| TAXA | | | | | | | | | | | | |
|-----------|------------------|----|-----------|-----------|-------|------|--------|-----------|-----------|-------|------|--------|
| Cladocera | | | | | | | | | | | | |
| m | Predictors | P | Cladocera | | | | | Gymnosome | | | | |
| | | | Bino AIC | Bino ΔAIC | AIC | ΔAIC | -2logL | Bino AIC | Bino ΔAIC | AIC | ΔAIC | -2logL |
| 1 | Y+M+D+MT+P+C+H+F | 30 | 274.9 | 3.5 | 120.4 | 5.3 | 62.4 | 287.1 | 3.9 | 137.1 | 5.8 | 77.1 |
| 2 | Y+M+D+MT+P+C+H | 29 | 277.3 | 5.9 | 118.4 | 3.3 | 62.4 | 287.7 | 4.6 | 135.1 | 3.8 | 77.1 |
| 3 | Y+M+D+MT+P+C | 28 | 278.3 | 6.8 | 117.0 | 1.9 | 63.0 | 286.7 | 3.5 | 133.5 | 2.2 | 77.5 |
| 4 | Y+M+D+MT+P | 27 | 277.6 | 6.1 | 115.1 | 0.0 | 63.1 | 284.8 | 1.6 | 132.5 | 1.2 | 78.5 |
| 5 | Y+M+D+MT+P+H | 28 | 278.9 | 7.5 | 116.8 | 1.7 | 62.8 | 286.4 | 3.2 | 133.2 | 1.9 | 77.2 |
| 6 | Y+M+D+MT+C+H | 28 | 275.4 | 3.9 | 120.4 | 5.3 | 66.4 | 287.2 | 4.0 | 136.4 | 5.1 | 80.4 |
| 7 | Y+M+D+MT | 26 | 275.6 | 4.1 | 117.9 | 2.8 | 67.9 | 284.5 | 1.3 | 132.7 | 1.4 | 80.7 |
| 8 | Y+M+MT | 25 | 273.6 | 2.2 | 119.7 | 4.6 | 71.7 | 283.2 | 0.0 | 134.9 | 3.6 | 84.9 |
| 9 | Y+M+MT+P | 26 | 275.6 | 4.1 | 116.5 | 1.4 | 66.5 | 283.4 | 0.2 | 135.6 | 4.3 | 83.6 |
| 10 | Y+M+MT+P+C | 27 | 276.3 | 4.8 | 118.2 | 3.1 | 66.2 | 285.4 | 2.2 | 136.8 | 5.5 | 82.8 |
| 11 | Y+M+MT+P+C+H | 28 | 275.4 | 4.0 | 119.0 | 3.9 | 65.0 | 286.5 | 3.3 | 138.2 | 6.9 | 82.2 |
| 12 | Y+M+MT+P+H | 27 | 277.0 | 5.5 | 117.8 | 2.7 | 65.8 | 285.1 | 1.9 | 136.2 | 4.9 | 82.2 |
| 13 | Y+M+MT+C+H | 27 | 273.5 | 2.0 | 121.6 | 6.5 | 69.6 | 285.9 | 2.7 | 138.8 | 7.5 | 84.8 |
| 14 | Y+M+P | 25 | 273.6 | 2.1 | 123.2 | 8.1 | 75.2 | 283.5 | 0.3 | 134.7 | 3.4 | 84.7 |
| 15 | Y+M+P+C | 26 | 274.3 | 2.9 | 125.1 | 10.0 | 75.1 | 285.4 | 2.3 | 136.1 | 4.8 | 84.1 |
| 16 | Y+M+P+C+H | 27 | 273.4 | 2.0 | 124.9 | 9.8 | 72.9 | 286.8 | 3.6 | 137.8 | 6.5 | 83.8 |
| 17 | Y+M+P+H | 26 | 275.0 | 3.5 | 123.7 | 8.6 | 73.7 | 285.3 | 2.1 | 135.8 | 4.5 | 83.8 |
| 18 | Y+M+C+H | 26 | 271.5 | 0.0 | 127.2 | 12.1 | 77.2 | 285.7 | 2.5 | 137.9 | 6.6 | 85.9 |
| 19 | Y+M+D+P | 26 | 275.6 | 4.1 | 123.3 | 8.2 | 73.3 | 284.9 | 1.7 | 131.3 | 0.0 | 79.3 |
| 20 | Y+M+D+P+C | 27 | 276.3 | 4.8 | 125.3 | 10.1 | 73.3 | 286.8 | 3.6 | 132.4 | 1.1 | 78.4 |
| 21 | Y+M+D+P+C+H | 28 | 275.3 | 3.9 | 125.7 | 10.5 | 71.7 | 288.1 | 5.0 | 134.3 | 3.0 | 78.3 |
| 22 | Y+M+D+P+H | 27 | 276.9 | 5.5 | 124.2 | 9.1 | 72.2 | 286.6 | 3.5 | 132.5 | 1.2 | 78.5 |
| 23 | Y+M+D+C+H | 27 | 273.4 | 1.9 | 127.5 | 12.4 | 75.5 | 287.1 | 3.9 | 135.1 | 3.8 | 81.1 |

Appendix 11. Summary of Generalized Linear Models (GLMs) for gelatinous zooplankton (larvaceans, doliolids, cnidarians, and polychaetes) at BATS. Included are model number (m), predictors, number of parameters (p), AIC values, Δ AIC values, and $-2 \cdot \log \text{Lik}$ ($-2 \log L$). Year and Month predictors were used in all GLMs in order to determine seasonal and internal variability even though Year and Month predictors may not have resulted in the best model.

Y= year
M= month
D= day/night explanatory variable
MT= mesopelagic temperature ($^{\circ}\text{C}$)
P= primary production ($\text{mgC}/\text{m}^2/\text{d}$) integrated 0-140 m
C= chlorophyll *a* (ng/m^2) integrated 0-140 m
H= 19'-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0-140 m
F= fucoxanthin (ng/kg) integrated 0-140 m

TAXA

| m | Predictors | p | Larvacean | | | Dololid | | | Cnidarian | | | Polychaete | | |
|----|------------------|----|-----------|--------------|--------|---------|--------------|--------|-----------|--------------|--------|------------|--------------|--------|
| | | | AIC | Δ AIC | -2logL | AIC | Δ AIC | -2logL | AIC | Δ AIC | -2logL | AIC | Δ AIC | -2logL |
| 1 | Y+M+D+MT+P+C+H+F | 30 | 1290.6 | 4.5 | 1230.6 | 964.3 | 2.7 | 904.3 | 925.7 | 4.9 | 865.7 | 881.8 | 2.9 | 821.8 |
| 2 | Y+M+D+MT+P+C+H | 29 | 1289.6 | 3.5 | 1231.6 | 963.1 | 1.5 | 905.1 | 925.3 | 4.5 | 867.3 | 880.9 | 2.0 | 822.9 |
| 3 | Y+M+D+MT+P+C | 28 | 1297.5 | 11.4 | 1241.5 | 965.6 | 3.9 | 909.6 | 923.5 | 2.6 | 867.5 | 879.0 | 0.0 | 823.0 |
| 4 | Y+M+D+MT+P | 27 | 1297.6 | 11.5 | 1243.6 | 964.6 | 3.0 | 910.6 | 922.8 | 2.0 | 868.8 | 880.3 | 1.4 | 826.3 |
| 5 | Y+M+D+MT+P+H | 28 | 1288.0 | 1.9 | 1232.0 | 965.4 | 3.8 | 909.4 | 924.7 | 3.9 | 868.7 | 880.9 | 1.9 | 824.9 |
| 6 | Y+M+D+MT+C+H | 28 | 1290.1 | 4.0 | 1234.1 | 964.2 | 2.5 | 908.2 | 923.8 | 3.0 | 867.8 | 885.1 | 6.1 | 829.1 |
| 7 | Y+M+D+MT | 26 | 1302.0 | 15.9 | 1250.0 | 965.7 | 4.1 | 913.7 | 922.1 | 1.3 | 870.1 | 882.3 | 3.3 | 830.3 |
| 8 | Y+M+MT | 25 | 1300.2 | 14.1 | 1250.2 | 967.2 | 5.6 | 917.2 | 929.2 | 8.4 | 879.2 | 887.7 | 8.8 | 837.7 |
| 9 | Y+M+MT+P | 26 | 1295.7 | 9.6 | 1243.7 | 966.1 | 4.4 | 914.1 | 930.2 | 9.3 | 878.2 | 886.1 | 7.2 | 834.1 |
| 10 | Y+M+MT+P+C | 27 | 1295.6 | 9.5 | 1241.6 | 967.0 | 5.3 | 913.0 | 930.8 | 9.9 | 876.8 | 885.0 | 6.0 | 831.0 |
| 11 | Y+M+MT+P+C+H | 28 | 1287.7 | 1.6 | 1231.7 | 964.2 | 2.6 | 908.2 | 932.5 | 11.6 | 876.5 | 886.9 | 7.9 | 830.9 |
| 12 | Y+M+MT+P+H | 27 | 1286.1 | 0.0 | 1232.1 | 966.7 | 5.1 | 912.7 | 932.1 | 11.3 | 878.1 | 886.5 | 7.5 | 832.5 |
| 13 | Y+M+MT+C+H | 27 | 1288.2 | 2.1 | 1234.2 | 965.3 | 3.7 | 911.3 | 930.9 | 10.1 | 876.9 | 890.6 | 11.6 | 836.6 |
| 14 | Y+M+P | 25 | 1314.7 | 28.6 | 1264.7 | 964.6 | 2.9 | 914.6 | 928.2 | 7.3 | 878.2 | 886.4 | 7.4 | 836.4 |
| 15 | Y+M+P+C | 26 | 1314.6 | 28.5 | 1262.6 | 965.5 | 3.8 | 913.5 | 928.8 | 7.9 | 876.8 | 885.3 | 6.3 | 833.3 |
| 16 | Y+M+P+C+H | 27 | 1306.3 | 20.2 | 1252.3 | 962.6 | 1.0 | 908.6 | 930.5 | 9.6 | 876.5 | 887.2 | 8.3 | 833.2 |
| 17 | Y+M+P+H | 26 | 1304.8 | 18.7 | 1252.8 | 965.2 | 3.5 | 913.2 | 930.1 | 9.3 | 878.1 | 886.9 | 7.9 | 834.9 |
| 18 | Y+M+C+H | 26 | 1310.0 | 23.9 | 1258.0 | 964.3 | 2.6 | 912.3 | 928.9 | 8.1 | 876.9 | 892.5 | 13.6 | 840.5 |
| 19 | Y+M+D+P | 26 | 1316.6 | 30.5 | 1264.6 | 963.2 | 1.6 | 911.2 | 920.8 | 0.0 | 868.8 | 880.4 | 1.5 | 828.4 |
| 20 | Y+M+D+P+C | 27 | 1316.5 | 30.5 | 1262.5 | 964.2 | 2.5 | 910.2 | 921.5 | 0.6 | 867.5 | 879.1 | 0.2 | 825.1 |
| 21 | Y+M+D+P+C+H | 28 | 1308.3 | 22.2 | 1252.3 | 961.6 | 0.0 | 905.6 | 923.3 | 2.5 | 867.3 | 881.1 | 2.1 | 825.1 |
| 22 | Y+M+D+P+H | 27 | 1306.8 | 20.7 | 1252.8 | 963.9 | 2.3 | 909.9 | 922.7 | 1.9 | 868.7 | 881.1 | 2.1 | 827.1 |
| 23 | Y+M+D+C+H | 27 | 1311.9 | 25.9 | 1257.9 | 963.2 | 1.6 | 909.2 | 921.8 | 1.0 | 867.8 | 886.8 | 7.9 | 832.8 |

Appendix 12. Summary of Generalized Linear Models (GLMs) for pelagic snails (pteropods and heteropods) at BATS.

Included are model number (m), predictors, number of parameters (p), AIC values, Δ AIC values, and $-2 \cdot \log \text{Lik}$ ($-2 \log L$). Year and Month predictors were used in all GLMs in order to determine seasonal and internal variability even though Year and

Month predictors may not have resulted in the best model.

- Y= year
- M= month
- D= day/night explanatory variable
- MT= mesopelagic temperature ($^{\circ}\text{C}$)
- P= primary production ($\text{mgC}/\text{m}^2/\text{d}$) integrated 0-140 m
- C= chlorophyll a (ng/m^2) integrated 0-140 m
- H= 19'-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0-140 m
- F= fucoxanthin (ng/kg) integrated 0-140 m

| TAXA | | | | | | | | | | | | | |
|------|------------------|----|----------------------|--------------|--------|-------|-----------------|--------------|--------|------|-----------|--------------|--------|
| m | Predictors | p | <i>Limacina</i> spp. | | | | Other Thecosome | | | | Heteropod | | |
| | | | AIC | Δ AIC | -2logL | | AIC | Δ AIC | -2logL | | AIC | Δ AIC | -2logL |
| 1 | Y+M+D+MT+P+C+H+F | 30 | 951.4 | 6.7 | 891.4 | 882.0 | 6.1 | 822.0 | 870.6 | 1.6 | 810.6 | | |
| 2 | Y+M+D+MT+P+C+H | 29 | 949.4 | 4.7 | 891.4 | 880.1 | 4.2 | 822.1 | 872.3 | 3.2 | 814.3 | | |
| 3 | Y+M+D+MT+P+C | 28 | 947.7 | 3.1 | 891.7 | 879.2 | 3.3 | 823.2 | 870.5 | 1.5 | 814.5 | | |
| 4 | Y+M+D+MT+P | 27 | 945.7 | 1.1 | 891.7 | 877.3 | 1.4 | 823.3 | 869.6 | 0.5 | 815.6 | | |
| 5 | Y+M+D+MT+P+H | 28 | 947.4 | 2.8 | 891.4 | 878.3 | 2.4 | 822.3 | 871.5 | 2.5 | 815.5 | | |
| 6 | Y+M+D+MT+C+H | 28 | 948.3 | 3.7 | 892.3 | 881.0 | 5.1 | 825.0 | 881.0 | 12.0 | 825.0 | | |
| 7 | Y+M+D+MT | 26 | 945.1 | 0.5 | 893.1 | 879.3 | 3.4 | 827.3 | 877.8 | 8.8 | 825.8 | | |
| 8 | Y+M+MT | 25 | 954.4 | 9.8 | 904.4 | 897.4 | 21.5 | 847.4 | 880.6 | 11.6 | 830.6 | | |
| 9 | Y+M+MT+P | 26 | 955.2 | 10.6 | 903.2 | 896.0 | 20.1 | 844.0 | 872.8 | 3.8 | 820.8 | | |
| 10 | Y+M+MT+P+C | 27 | 957.2 | 12.5 | 903.2 | 897.9 | 22.1 | 843.9 | 873.9 | 4.8 | 819.9 | | |
| 11 | Y+M+MT+P+C+H | 28 | 959.0 | 14.4 | 903.0 | 899.3 | 23.4 | 843.3 | 875.7 | 6.7 | 819.7 | | |
| 12 | Y+M+MT+P+H | 27 | 957.0 | 12.4 | 903.0 | 897.4 | 21.5 | 843.4 | 874.8 | 5.7 | 820.8 | | |
| 13 | Y+M+MT+C+H | 27 | 957.8 | 13.2 | 903.8 | 899.7 | 23.8 | 845.7 | 884.0 | 15.0 | 830.0 | | |
| 14 | Y+M+P | 25 | 954.3 | 9.6 | 904.3 | 894.4 | 18.5 | 844.4 | 872.4 | 3.4 | 822.4 | | |
| 15 | Y+M+P+C | 26 | 956.2 | 11.6 | 904.2 | 896.3 | 20.5 | 844.3 | 873.5 | 4.5 | 821.5 | | |
| 16 | Y+M+P+C+H | 27 | 958.0 | 13.4 | 904.0 | 897.7 | 21.9 | 843.7 | 875.3 | 6.3 | 821.3 | | |
| 17 | Y+M+P+H | 26 | 956.0 | 11.4 | 904.0 | 895.8 | 19.9 | 843.8 | 874.4 | 5.4 | 822.4 | | |
| 18 | Y+M+C+H | 26 | 957.2 | 12.6 | 905.2 | 897.9 | 22.0 | 845.9 | 885.4 | 16.4 | 833.4 | | |
| 19 | Y+M+D+P | 26 | 944.6 | 0.0 | 892.6 | 875.9 | 0.0 | 823.9 | 869.0 | 0.0 | 817.0 | | |
| 20 | Y+M+D+P+C | 27 | 946.6 | 2.0 | 892.6 | 877.8 | 1.9 | 823.8 | 870.0 | 1.0 | 816.0 | | |
| 21 | Y+M+D+P+C+H | 28 | 948.2 | 3.6 | 892.2 | 878.8 | 2.9 | 822.8 | 871.7 | 2.7 | 815.7 | | |
| 22 | Y+M+D+P+H | 27 | 946.2 | 1.6 | 892.2 | 876.9 | 1.0 | 822.9 | 871.0 | 2.0 | 817.0 | | |
| 23 | Y+M+D+C+H | 27 | 947.6 | 2.9 | 893.6 | 879.2 | 3.3 | 825.2 | 882.3 | 13.2 | 828.3 | | |

Appendix 13. Summary of Generalized Linear Models (GLMs) for larval benthic invertebrates (barnacle nauplii, brachiolaria-sea star larvae) and fish (leptocephali-eel larvae) at BATS. Brachiolaria and leptocephali required using Delta GLMs to first account for estimating the chance of encountering the animal, using a binomial GLM, and then estimating the mean density given the animal was encountered, using a lognormal GLM. Included are model number (m), predictors, number of parameters (p), binomial AIC values (Bino AIC), binomial Δ AIC values (Bino Δ AIC), lognormal AIC (AIC) values, lognormal Δ AIC values (Δ AIC), and $-2 * \log \text{Lik} (-2 \log L)$. Year and Month predictors were used in all GLMs in order to determine seasonal and internal variability even though Year and Month predictors may not have resulted in the best model.

Y= year

M= month

D= day/night explanatory variable

MT= mesopelagic temperature ($^{\circ}\text{C}$)

P= primary production ($\text{mgC}/\text{m}^2/\text{d}$) integrated 0-140 m

C= chlorophyll a (ng/m^2) integrated 0-140 m

H= 19'-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0-140 m

F= fucoxanthin (ng/kg) integrated 0-140 m

| TAXA | | | | | | | | | | | | | | | |
|------|------------------|----|------------------|--------------|--------|----------|-------------------|-------|--------------|--------|--------------|-------------------|-------|--------------|--------|
| | | | Barnacle Nauplii | | | | Brachiolaria | | | | Leptocephali | | | | |
| m | Predictors | p | AIC | Δ AIC | -2logL | Bino AIC | Bino Δ AIC | AIC | Δ AIC | -2logL | Bino AIC | Bino Δ AIC | AIC | Δ AIC | -2logL |
| 1 | Y+M+D+MT+P+C+H+F | 30 | 1028.8 | 4.7 | 968.8 | 225.3 | 6.8 | 763.8 | 5.7 | 703.8 | 262.8 | 2.5 | 113.5 | 1.8 | 53.5 |
| 2 | Y+M+D+MT+P+C+H | 29 | 1030.3 | 6.3 | 972.3 | 223.9 | 5.4 | 763.3 | 5.2 | 705.3 | 264.2 | 3.9 | 114.7 | 3.0 | 56.7 |
| 3 | Y+M+D+MT+P+C | 28 | 1028.9 | 4.8 | 972.9 | 221.9 | 3.4 | 761.8 | 3.7 | 705.8 | 263.3 | 2.9 | 113.8 | 2.1 | 57.8 |
| 4 | Y+M+D+MT+P | 27 | 1027.5 | 3.5 | 973.5 | 220.1 | 1.6 | 760.0 | 1.9 | 706.0 | 261.9 | 1.5 | 113.0 | 1.3 | 59.0 |
| 5 | Y+M+D+MT+P+H | 28 | 1029.5 | 5.4 | 973.5 | 222.0 | 3.5 | 761.9 | 3.8 | 705.9 | 263.8 | 3.4 | 112.8 | 1.1 | 56.8 |
| 6 | Y+M+D+MT+C+H | 28 | 1029.6 | 5.5 | 973.6 | 224.9 | 6.4 | 761.5 | 3.5 | 705.5 | 262.8 | 2.5 | 115.9 | 4.2 | 59.9 |
| 7 | Y+M+D+MT | 26 | 1026.5 | 2.4 | 974.5 | 221.4 | 2.9 | 758.2 | 0.1 | 706.2 | 260.3 | 0.0 | 113.4 | 1.7 | 61.4 |
| 8 | Y+M+MT | 25 | 1024.5 | 0.5 | 974.5 | 220.5 | 2.0 | 758.1 | 0.0 | 708.1 | 284.0 | 23.7 | 111.7 | 0.0 | 61.7 |
| 9 | Y+M+MT+P | 26 | 1025.6 | 1.5 | 973.6 | 219.2 | 0.7 | 759.9 | 1.8 | 707.9 | 285.3 | 25.0 | 112.2 | 0.5 | 60.2 |
| 10 | Y+M+MT+P+C | 27 | 1026.9 | 2.9 | 972.9 | 221.0 | 2.5 | 761.7 | 3.6 | 707.7 | 286.8 | 26.5 | 113.3 | 1.6 | 59.3 |
| 11 | Y+M+MT+P+C+H | 28 | 1028.4 | 4.3 | 972.4 | 223.0 | 4.5 | 763.3 | 5.2 | 707.3 | 287.1 | 26.8 | 113.7 | 2.0 | 57.7 |
| 12 | Y+M+MT+P+H | 27 | 1027.6 | 3.5 | 973.6 | 221.1 | 2.6 | 761.8 | 3.8 | 707.8 | 287.0 | 26.6 | 112.0 | 0.3 | 58.0 |
| 13 | Y+M+MT+C+H | 27 | 1027.6 | 3.5 | 973.6 | 224.0 | 5.5 | 761.5 | 3.4 | 707.5 | 285.9 | 25.6 | 114.2 | 2.5 | 60.2 |
| 14 | Y+M+P | 25 | 1024.1 | 0.0 | 974.1 | 218.5 | 0.0 | 759.4 | 1.3 | 709.4 | 285.7 | 25.4 | 112.9 | 1.2 | 62.9 |
| 15 | Y+M+P+C | 26 | 1025.4 | 1.4 | 973.4 | 220.4 | 1.9 | 761.2 | 3.1 | 709.2 | 287.3 | 27.0 | 113.6 | 1.9 | 61.6 |
| 16 | Y+M+P+C+H | 27 | 1026.9 | 2.8 | 972.9 | 222.4 | 3.9 | 762.8 | 4.7 | 708.8 | 287.3 | 27.0 | 114.1 | 2.4 | 60.1 |
| 17 | Y+M+P+H | 26 | 1026.0 | 2.0 | 974.0 | 220.4 | 1.9 | 761.3 | 3.2 | 709.3 | 287.2 | 26.9 | 112.2 | 0.5 | 60.2 |
| 18 | Y+M+C+H | 26 | 1026.4 | 2.4 | 974.4 | 223.6 | 5.1 | 761.3 | 3.2 | 709.3 | 286.8 | 26.5 | 114.6 | 2.9 | 62.6 |
| 19 | Y+M+D+P | 26 | 1026.0 | 1.9 | 974.0 | 219.4 | 0.9 | 759.4 | 1.3 | 707.4 | 263.2 | 2.9 | 113.7 | 2.0 | 61.7 |
| 20 | Y+M+D+P+C | 27 | 1027.4 | 3.3 | 973.4 | 221.3 | 2.8 | 761.2 | 3.1 | 707.2 | 264.7 | 4.4 | 113.9 | 2.2 | 59.9 |
| 21 | Y+M+D+P+C+H | 28 | 1028.8 | 4.7 | 972.8 | 223.2 | 4.7 | 762.7 | 4.6 | 706.7 | 265.4 | 5.1 | 115.0 | 3.3 | 59.0 |
| 22 | Y+M+D+P+H | 27 | 1028.0 | 3.9 | 974.0 | 221.3 | 2.8 | 761.3 | 3.2 | 707.3 | 265.0 | 4.6 | 113.0 | 1.3 | 59.0 |
| 23 | Y+M+D+C+H | 27 | 1028.3 | 4.3 | 974.3 | 224.4 | 5.9 | 761.2 | 3.1 | 707.2 | 264.8 | 4.4 | 116.3 | 4.5 | 62.3 |

Appendix 14. Summary of Generalized Linear Models (GLMs) evaluating longer-term variables potentially driving interannual temporal changes of abundant mesozooplankton (calanoid copepods, chaetognaths, larvaceans, *Limacina* spp., and ostracods) at BATS. Taxa, desired GLM explaining zooplankton density and their relationship to environmental parameters of interest measured synoptically with each tow (Model), annualized environmental parameters and climate indices tested (X), number of parameters (p), AIC, Δ AIC, and $-2*\log\text{Lik}$ ($-2\log L$). Month predictors were used in all GLMs in order to determine seasonal variability.

X= annualized environmental parameters and climate indices used in place of year parameter

M= month

D= day/night explanatory variable

MT= mesopelagic temperature ($^{\circ}\text{C}$)

P= primary production ($\text{mgC}/\text{m}^2/\text{d}$) integrated 0-140 m

C= chlorophyll *a* (ng/m^2) integrated 0-140 m

H= 19'-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0-140 m

Chaeto= chaetognath density ($\text{ind.}/\text{m}^3$)

Cal= calanoid copepod density ($\text{ind.}/\text{m}^3$)

| Taxa | Model | X | p | AIC | Δ AIC | -2logL |
|-------------------------|---------------------|---------|-------|---------|--------------|---------|
| Calanoid | X+M+D+MT+P+C+Chaeto | P | 19 | 531.11 | 11.16 | 493.11 |
| | | C | 19 | 531.24 | 11.28 | 493.24 |
| | | SST | 19 | 530.04 | 10.09 | 492.04 |
| | | WCSI | 19 | 522.53 | 2.57 | 484.53 |
| | | AMO | 19 | 519.96 | 0.00 | 481.96 |
| | | GSNW | 19 | 524.04 | 4.08 | 486.04 |
| | | MEI | 19 | 529.80 | 9.85 | 491.80 |
| | | NAO | 19 | 531.64 | 11.68 | 493.64 |
| | | NPGO | 19 | 525.95 | 6.00 | 487.95 |
| | | PDO | 19 | 525.07 | 5.11 | 487.07 |
| | | hwNAO | 19 | 531.59 | 11.63 | 493.59 |
| hNAO | 19 | 531.40 | 11.44 | 493.40 | | |
| Chaetognath | X+M+C+Hex+Cal | P | 17 | 657.76 | 7.32 | 623.76 |
| | | C | 17 | 656.44 | 5.99 | 622.44 |
| | | SST | 17 | 658.63 | 8.18 | 624.63 |
| | | WCSI | 17 | 650.45 | 0.00 | 616.45 |
| | | AMO | 17 | 658.39 | 7.94 | 624.39 |
| | | GSNW | 17 | 656.90 | 6.45 | 622.90 |
| | | MEI | 17 | 658.47 | 8.02 | 624.47 |
| | | NAO | 17 | 657.80 | 7.35 | 623.80 |
| | | NPGO | 17 | 658.00 | 7.55 | 624.00 |
| | | PDO | 17 | 658.79 | 8.34 | 624.79 |
| | | hwNAO | 17 | 658.44 | 7.99 | 624.44 |
| hNAO | 17 | 658.67 | 8.22 | 624.67 | | |
| Larvacean | X+M+MT+P+H | P | 17 | 1308.42 | 14.98 | 1274.42 |
| | | C | 17 | 1293.44 | 0.00 | 1259.44 |
| | | SST | 17 | 1307.47 | 14.03 | 1273.47 |
| | | WCSI | 17 | 1302.05 | 8.62 | 1268.05 |
| | | AMO | 17 | 1308.43 | 14.99 | 1274.43 |
| | | GSNW | 17 | 1309.88 | 16.44 | 1274.04 |
| | | MEI | 17 | 1308.04 | 14.60 | 1260.75 |
| | | NAO | 17 | 1294.75 | 1.31 | 1269.82 |
| | | NPGO | 17 | 1303.82 | 10.38 | 1264.34 |
| | | PDO | 17 | 1298.34 | 4.90 | 1275.54 |
| | | hwNAO | 17 | 1309.54 | 16.10 | 1274.83 |
| hNAO | 17 | 1308.83 | 15.39 | 892.64 | | |
| <i>Limacina</i> spp. | X+M+D+P | P | 16 | 964.40 | 7.08 | 932.40 |
| | | C | 16 | 961.59 | 4.26 | 929.59 |
| | | SST | 16 | 963.69 | 6.37 | 931.69 |
| | | WCSI | 16 | 965.39 | 8.07 | 933.29 |

| | | | | | | |
|--------------------------------------|------------|--------|------|--------|------|--------|
| <i>Limacina</i> spp. continued | X+M+D+P | AMO | 16 | 965.29 | 7.97 | 933.23 |
| | | GSNW | 16 | 965.23 | 7.91 | 928.69 |
| | | MEI | 16 | 960.69 | 3.36 | 933.39 |
| | | NAO | 16 | 965.39 | 8.06 | 925.33 |
| | | NPGO | 16 | 957.33 | 0.00 | 933.43 |
| | | PDO | 16 | 965.43 | 8.10 | 933.34 |
| | | hwNAO | 16 | 965.34 | 8.02 | 933.34 |
| | | HNAO | 16 | 965.11 | 7.79 | 933.11 |
| Ostracod | X+M+D+MT+P | P | 17 | 725.55 | 3.98 | 691.55 |
| | | C | 17 | 728.20 | 6.63 | 694.20 |
| | | SST | 17 | 726.18 | 4.61 | 692.18 |
| | | WCSI | 17 | 722.94 | 1.37 | 688.94 |
| | | AMO | 17 | 722.63 | 1.06 | 688.63 |
| | | GSNW | 17 | 721.57 | 0.00 | 687.57 |
| | | MEI | 17 | 728.22 | 6.64 | 694.22 |
| | | NAO | 17 | 728.18 | 6.61 | 694.18 |
| | | NPGO | 17 | 725.35 | 3.77 | 691.35 |
| | | PDO | 17 | 727.88 | 6.31 | 693.88 |
| | | hwNAO | 17 | 728.22 | 6.64 | 694.22 |
| hNAO | 17 | 727.54 | 5.97 | 693.54 | | |

VITA

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Born in Sidman, PA on January 28, 1990. Graduated from Forest Hills High School in 2008. Earned a Bachelor's of Science in Biology with an emphasis in Marine Biology and a minor in Scientific Diving from Humboldt State University in 2012. Entered the Master's of Science program at the Virginia Institute of Marine Science, College of William and Mary in 2012 under Dr. Kam Tang, and completed the program under Dr. Deborah Steinberg.