



Long-term oscillations in the normalized biomass-size spectrum reveal the impact of oligotrophication on zooplankton trophic structure in the North Atlantic Subtropical Gyre

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ABSTRACT

Ocean warming of the North Atlantic Subtropical Gyre (NASG) induced oligotrophication and a decrease in integrated net primary production during the 2010s, potentially affecting higher trophic levels. We analyzed long-term records (1994–2019) of daytime and nighttime zooplankton biomass in five size classes from the NASG. Daytime biomass decreased in the three largest size classes during the 2010s, while decrease in nighttime biomass was less evident due to the relative stability in diel vertical migrator biomass. We used the normalized biomass size spectrum (NBSS) to estimate the relative transfer efficiency between trophic levels. The steepness of the NBSS slope at the end of the time series increased by 14% (daytime) and 24% (nighttime) from the maximum observed annual average values (2011 and 2009, respectively). This suggests oligotrophication during the 2010s led to a significant reduction in the transfer of biomass across trophic levels, with negative impacts on the NASG planktonic food web.

1. Introduction

Subtropical gyres are oligotrophic oceanic regions representing about 40% of Earth's surface (Polovina et al., 2008) and due to their large spatial range contribute significantly to carbon export into the ocean interior (Laws et al., 2000; Polovina et al., 2008). Due to global warming, subtropical gyres are increasing in areal extent, with the North Atlantic Subtropical Gyre (NASG) expanding most rapidly (Polovina et al., 2008; Irwin and Oliver, 2009; Leonelli et al., 2022). In the NASG, satellite observations show a decrease in phytoplankton productivity during the last three decades (Signorini et al., 2015; Leonelli et al., 2022), and earth system models predict further oligotrophication during the 21st century (Kwiatkowski et al., 2018).

In the Sargasso Sea (northwest sector of the NASG), research at the

Bermuda Atlantic Time-series Study (BATS; Steinberg et al., 2001; Lomas et al., 2013) has identified a relationship between ocean warming, oligotrophication, and particulate nutrient stoichiometric changes in the water column (i.e., an increase in the carbon:phosphorus ratio, or C:P) during the 2010s (D'Alelio et al., 2020; Lomas et al., 2022). It is posited that warming enhanced the stratification of the upper water column, resulting in the net drawdown of nutrients in the photic zone and inducing compositional changes in the phytoplankton community. Larger eukaryotic phytoplankton decreased in abundance, while smaller cyanobacterial groups did not (i.e., *Synechococcus* and *Prochlorococcus*), possibly because the latter have a higher nutrient use efficiency (Lomas et al., 2022). Several studies report nutrient induced changes in phytoplankton, which negatively impact higher trophic levels (Malzahn et al., 2007; Dickman et al., 2008; Peace, 2015; Schmidt et al., 2020). In the

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northeast Atlantic Ocean, nutrients co-varied with planktonic diatom (microalgae) and copepod (crustaceans) abundance (Holland et al., 2023). The effects of oligotrophication and changes in phytoplankton abundance and community structure on higher trophic levels remain poorly understood in the NASG.

Prior long-term studies at BATS mostly considered the total biomass of phyto- and zooplankton (e.g., Steinberg et al., 2012; Lomas et al., 2022) or biomass and abundance of specific zooplanktonic groups (e.g., Stone and Steinberg 2014; Ivory et al., 2019). These studies allowed analysis of the responses of specific organisms to environmental parameters (e.g., the positive relationship between calanoid and oncaeid copepods with net primary production, NPP, Ivory et al., 2019), but they provided limited information regarding possible community responses at the trophic-web level. However, a decrease in the abundance of large zooplankton (>5 mm) from 2010 to 2020 (Lomas et al., 2022) suggests that long-term changes in the phytoplankton structure have influenced the overall planktonic trophic structure at BATS.

Trophic structure in this context is the amount of biomass allocated at different trophic levels (Ryckaczewski and Checkley, 2008; Valencia et al., 2018; Décima, 2022), considering the crucial role of body size in driving the trophic hierarchy (Jacob et al., 2011; Riede et al., 2011). Normalized biomass-size spectrum (NBSS; Zhou, 2006) indicates the rate of decrease of biomass towards higher trophic levels by the slope of the linear distribution of biomass in logarithmic intervals of body size, which is indicative of the relative transfer efficiency between trophic levels (Platt and Denman, 1977; Jennings et al., 2002). Ecological theory predicts an NBSS slope value of ca. -1 at equilibrium (Platt and Denman, 1977; Sprules and Barth, 2016), with steeper (more negative) and flatter (less negative) slopes corresponding to lower and higher trophic transfer efficiency (TTE), respectively. Therefore, NBSS can be used to infer TTE, which is the proportion of biomass produced at trophic level n that is converted into biomass at trophic level $n+1$ (Jennings et al., 2002).

The plankton-based NBSS slope is highly sensitive to environmental conditions. Atkinson et al. (2021) reported steeper slopes under nitrate or phosphate limiting conditions, in the presence of massive phytoplankton blooms, and that the NBSS slope was mainly affected by water column stratification and nutrient supply. Similar results were observed in the East China Sea by García-Comas et al. (2014), which found food availability for zooplankton as the main driver for NBSS slope, and by Kwong et al. (2022) that reported flatter NBSS slopes with increasing Chl a for the zooplanktonic community in the subarctic Northeast Pacific. As the planktonic lower trophic levels respond more rapidly to short-term (daily, weekly, seasonal) environmental shifts (e.g., D'Alelio et al., 2019; Trombetta et al., 2020; Russo et al., 2022), snapshots of NBSS slopes may be misleading (Atkinson et al., 2021). Examining NBSS slopes in the same community with a large spatiotemporal coverage can provide valuable information about ecosystem changes (Quinones et al., 2003; Atkinson et al., 2021).

We analyzed zooplankton trophic structure in the NASG using NBSS from the BATS site over 26 years (1994–2019). NBSS were developed using size-fractionated zooplankton biomass data collected during day- and nighttime for body-size intervals (0.2–0.5, 0.5–1, 1–2, 2–5, and >5 mm) (Madin et al., 2001; Steinberg et al., 2012), spanning from meso- to macrozooplankton (Steinberg and Landry, 2017), which are informative for determining zooplankton trophic structure. Finally, we examined zooplankton trophic structure modifications potentially in relation to oligotrophication in the NASG.

2. Methods

2.1. Data

BATS is a time series with a focus on how plankton impact the biogeochemical cycling of carbon and other relevant elements. The BATS station (31°40'N, 64°10'W) is in the western NASG, called the

Sargasso Sea (Steinberg et al., 2001). We downloaded NPP and zooplankton biomass (1994–2019) from the BATS website (<http://bats.bios.edu/bats-data/>). These data were approximately monthly, with biweekly sampling during the phytoplankton spring bloom period. NPP was measured by the uptake of ^{14}C in dawn to dusk in situ incubations (see methods for NPP measurements in Steinberg et al., 2001). We analyzed NPP as integrated values in the photic zone (0–140 m, Doney et al., 1996). We used average monthly values calculated when more than one sampling effort occurred per month. Zooplankton dry-weight biomass at BATS was analyzed from epipelagic net tows of 202 μm mesh collected during each cruise and then fractionated through nested sieves with mesh sizes of 5, 2, 1, 0.5, and 0.2 mm (Madin et al., 2001; Steinberg et al., 2012). Average biomass values from two net tows each for the day- and nighttime, in five different size fractions (0.2–0.5, 0.5–1, 1–2, 2–5, >5 mm), were normalized for a 200-m water sampling depth (see methods for biomass determination in Madin et al., 2001; Steinberg et al., 2012). C biomass (0–200m; mg C m^{-2}) was determined from the following formulas (Madin et al., 2001):

$$C(\text{daytime biomass}) = B_d * 0.36$$

$$C(\text{nighttime biomass}) = B_n * 0.37$$

where B_d and B_n are the day- and nighttime dry weight biomass, respectively.

We also estimated the biomass of zooplankton diel vertical migrators in the three largest size fractions (1–2, 2–5, and >5 mm), which included 84% of the total diel vertical migrators, as the difference between nighttime and daytime biomass, following Madin et al. (2001) and Steinberg et al. (2012).

2.2. Normalized biomass-size spectrum (NBSS)

We estimated the NBSS slope by calculating the least squares regression between the logarithm ($\log_{10}$) of the size-fractionated biomass normalized by the bin width and the midpoint of the $\log_{10}$ -transformed bins of each size fraction based on the following equation (Mehner et al., 2018) (see Table S1 for data input):

$$\log_{10}(B_x/\Delta_x) = b[\log_{10}(m)] + a$$

where B_x is the biomass of each sample, Δ_x is the width of each size fraction (taken here as 300, 500, 1000, 3000, and 15,000 μm), m is the midpoint of the $\log_{10}$ -transformed bins of each size fraction, and a and b are the intercept and the slope of the linear regression, respectively.

We considered the monthly values of the five zooplankton size fractions sampled at BATS (daytime $n = 280$; nighttime $n = 280$), following previous studies (Ryckaczewski and Checkley, 2008; Valencia et al., 2018; Décima, 2022). We normalized size fractions to correct logarithmic bins in the biomass spectrum, which increased in width with body size (Platt and Denman, 1977; Sprules and Barth, 2016). To normalize size fractions, we defined a size range for the larger size class (>5 mm) and set an upper limit of 20 mm after considering a median value of the body sizes of the most abundant zooplankton in this size range found at the BATS site, according to Ivory et al. (2019) and other published literature on zooplankton body size. Linear regression fit was evaluated by the coefficient of determination (r^2), which resulted in a median r^2 value of 0.91 for the whole dataset (range: 0.5–0.99), and only statistically significant regressions (p -value <0.05) (see Table S2 and S3) were included in the analysis.

Body size alone can introduce a potential bias in the application of NBSS due to the presence of large (>5 mm) gelatinous, filter-feeding zooplankton like salps, which can consume small prey (<0.2 mm) (Sutherland et al., 2010; Fender et al., 2023) and sit at a relatively low trophic level despite their size. We tested NBSS consistency against this bias, as the BATS dataset includes documented periods (between 1994 and 2011) with and without salp blooms (Stone and Steinberg, 2014).

We analyzed using the non-parametric Wilcoxon test in R version 4.2.2 (R Core Team, 2022) the differences in NBSS slope values for the time points reported by Stone and Steinberg (2014) between 1994 and 2011 for daytime salp bloom ($n = 81$) vs. non-bloom ($n = 111$), and nighttime salp bloom ($n = 72$) vs. non-bloom ($n = 109$) conditions (see Fig. 2 in Stone and Steinberg 2014 and Table S2).

2.3. Long-term trends

We explored long-term trends (1994–2019) of monthly time series of NPP, day- and nighttime zooplankton size-fractionated biomass, and day- and nighttime NBSS slopes with the Seasonal Kendall test following Cloern (2019) and using the *seaRoll* function in the R package *wql* (Jassby and Cloern, 2016). This package is developed for a minimum window of five years data (Jassby and Cloern, 2016). In order to align and compare our results with others analyses carried out at BATS, we considered a window width of ten years, as previously done at BATS when analyzing NPP for a similar time length (1990–2016, see D'Alelio et al., 2020). The Seasonal Kendall test utilizes monthly time series, moving 1 year at a time within the time-specified window (i.e., ten

years), and allows detection of significant (p -value < 0.05) annual oscillatory variability (Cloern, 2019). Finally, we used information from long-term abundance of copepods at BATS (Ivory et al., 2019) to assign taxa to the zooplankton size fractions considered herein, based on copepod body lengths from an extensive database published by Brun et al. (2017). This choice was based on the observation that about 80% of the zooplankton biomass at BATS was comprised of copepods (Roman et al., 1993, 2001). This information was used to consider long-term trends in zooplankton biomass and trophic transfer efficiency in the context of potential community compositional changes.

3. Results and discussion

3.1. Size-specific trends in zooplankton biomass

We identified 10-year trends in the size-fractionated zooplankton biomass at BATS (Fig. 1). The biomass of the largest zooplankton size classes (2–5 mm and > 5 mm) peaked in 2011 and decreased afterward, except for the nighttime > 5 mm size fraction, which did not significantly change over the time series. Based on available taxonomic records, these

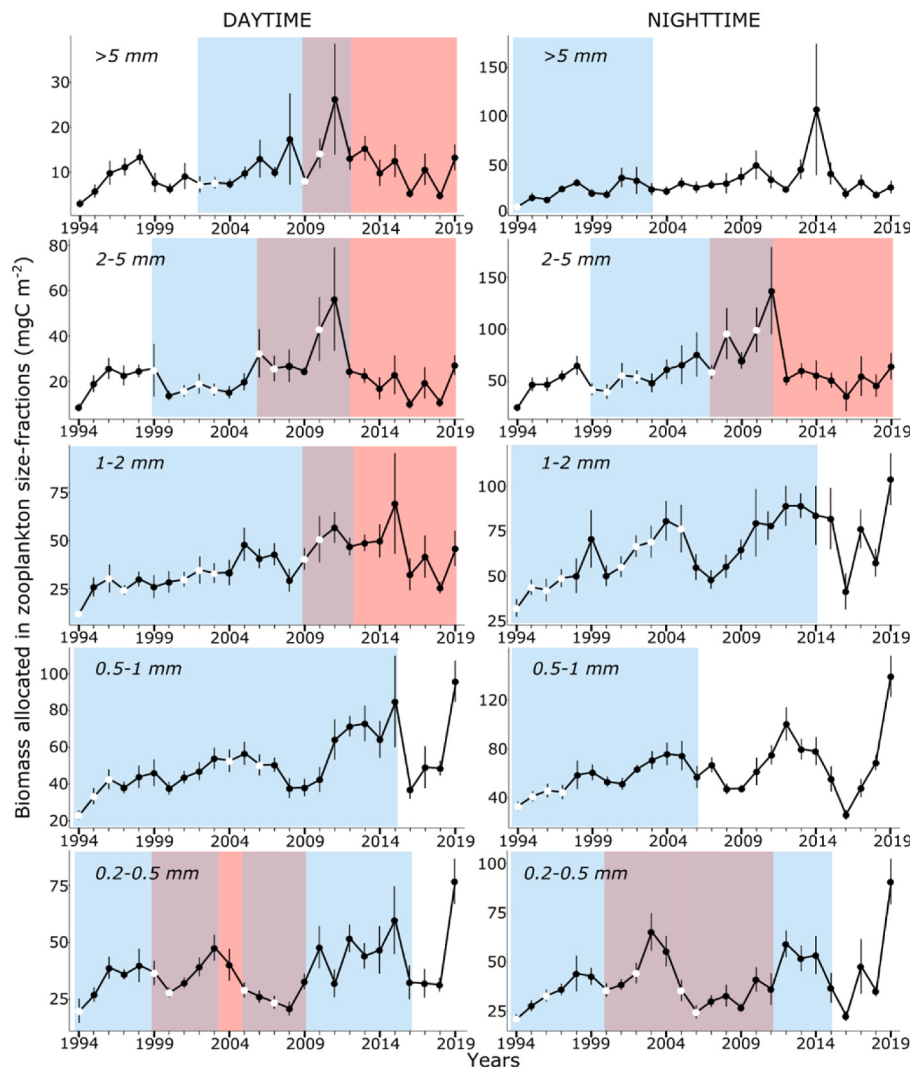


Fig. 1. Long-term trends of day- and nighttime carbon biomass of zooplankton size fractions integrated between 0 and 200 m at BATS. The mean ($\pm$ standard error) annual biomass of zooplankton size-fractions at day- and nighttime are shown, in comparison with the results of the Seasonal Kendall tests (window = 10 years) conducted on the monthly time series. Colored windows represent results of Seasonal Kendall test on monthly data with significant (p -value < 0.05) 10-year periods of positive (light blue) or negative (red) trends. Violet sections indicate transitions between significant positive and negative trends, white windows indicate periods without significant changes. White data points represent the starting year of each 10-year period of significant trend.

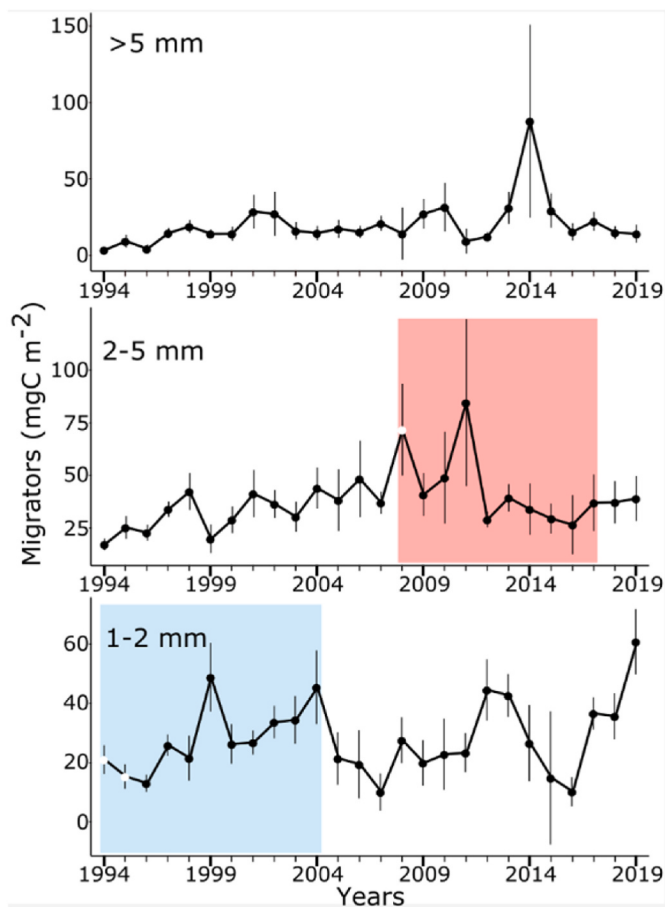


Fig. 2. Long-term trend in zooplankton carbon biomass (integrated between 0 and 200 m) attributed to zooplankton diel vertical migrators (nighttime minus daytime) at BATS. The mean ($\pm$ standard error) annual biomass of migrators in large size fractions (1–2, 2–5, and >5 mm) are shown, in comparison with the results of the Seasonal Kendall tests (window = 10 years) conducted on the monthly time series. Colored windows represent results of Seasonal Kendall test on monthly data with significant (p -value <0.05) 10-year periods of positive (light blue) or negative (red) trends. White windows indicate periods without significant changes. White data points represent the starting year of each 10-year period of significant trend.

size fractions include mainly larger calanoid copepods, euphausiids, amphipods, and salps (Steinberg et al., 2000; Stone and Steinberg, 2014; Ivory et al., 2019). After the period of increase, the 2–5 mm size class started a transitional phase in both day- and nighttime (2006–2012 and 2007–2011, respectively), followed by significant decreases until 2019. A significant decrease was also observed from 2008 to 2017 in the vertical migrators of the 2–5 mm size fraction (Fig. 2), and may be due to the reduced food available to largely omnivorous calanoid copepods (Schnetzer and Steinberg, 2002; Calbet et al., 2007). At BATS these copepods are positively related to NPP (Ivory et al., 2019), which significantly decreased during the 2010s (D'Alelio et al., 2020). The stability of nighttime biomass >5 mm throughout the study period (excluding 2014, which included months with very high biomass values causing large standard errors) may be due to stability of vertical migrator biomass in that size fraction (Madin et al., 2001; Steinberg et al., 2012). This is supported by the difference between night- and daytime zooplankton biomass (a proxy for vertical migrator biomass) of the >5 mm size-fraction that was relatively stable, with no significant trends observed (Fig. 2).

In the intermediate size fraction (1–2 mm), daytime biomass significantly increased up to 2009, then entered in a transitional phase until 2012, after which it entered a period of decrease (Fig. 1). Nighttime

biomass and diel vertical migrators in the 1–2 mm size fraction showed significant increases in the first part of the time series (1994–2014 and 1994–2004), and no trend after 2014 (Figs. 1 and 2). The dominant copepod taxa within the 1–2 mm size class include the orders cyclopoida and harpacticoida (Brun et al., 2017; Ivory et al., 2019), which feed on juvenile copepods and detritus, but also on unicellular plankton (Turner, 2004; Jagadeesan et al., 2017). Differences between the time series of day- and nighttime biomass in the 1–2 mm size fraction could stem from reduced grazing during the nighttime due to the decrease in the diel vertical migrators in the 2–5 mm size fraction. The smaller zooplankton size fractions (0.2–0.5 mm and 0.5–1 mm) showed contrasting trends. The 0.2–0.5 mm animals increased between 1994 and 1999 during daytime and 1994–2000 during nighttime, were in a transitional period until 2009 (daytime) and 2011 (nighttime), and increased thereafter until 2016 (daytime) and 2015 (nighttime) (Fig. 1). In contrast, the 0.5–1 mm size fraction increased over the time series, with significant increases from 1994 to 2015 during daytime and between 1994 and 2006 during nighttime (Fig. 1).

Uncoupling between lower and higher zooplanktonic trophic levels at BATS is suggested collectively by the increase in the 0.2–0.5 mm and 0.5–1 mm size classes from 2009 to 2014 during the daytime and the 0.2–0.5 mm size class during the nighttime, and the decrease in the larger size classes during the last 8 years of the time series. We speculate that this uncoupling was determined by the mid-size zooplankton (1–2 mm), which decreased most in the latter part of the BATS time series when NPP and larger phytoplankton also decreased (Lomas et al., 2022). A decrease in this intermediate size fraction could reduce food availability to the larger and more carnivorous zooplankton size fractions (2–5 and >5 mm), leading to a decrease in the larger size fractions and a relaxation of grazing pressure exerted by the intermediate size animals on the smaller size fractions (0.2–0.5 mm and 0.5–1 mm) (top-down effect). This could lead to an increase in small copepods (<1 mm) such as oithonidae and oncaeidae at BATS (Ivory et al., 2019), which are able to exploit detritus and unicellular plankton <20 μ m (Gonzalez and Smetacek, 1994; Roff et al., 1995; Paffenhöfer and Mazzocchi, 2002). Similar results were also observed by Zhou et al. (2009), who found the mid-size zooplankton of the Norwegian Coastal Sea exerted the highest influence over the whole zooplankton community.

3.2. Long-term changes in the plankton trophic structure

Ocean warming, accounting for $+1.09$ $^{\circ}\text{C}$ in the global surface temperature since the pre-industrial era (Pörtner et al., 2022), can substantially affect marine communities (Bates et al., 2018) by modifying plankton productivity and trophic processes (Chust et al., 2014; Fu et al., 2016; Kwiatkowski et al., 2019). Previous analyses of the BATS dataset show a general warming for different averaged depth layers and time periods, i.e., 0–120 m (1990–2016) (D'Alelio et al., 2020), and 0–10 m (1983–2019, in Bates and Johnson, 2020; and 1988–2019 in Lomas et al., 2022).

At BATS, ocean warming paralleled a weakening of vertical mixing, increase in stratification, and oligotrophication of the photic zone, negatively affecting NPP during the 2010s (D'Alelio et al., 2020; Lomas et al., 2022). By extending the time series, we also found a significant positive trend in NPP (1994–2003), followed by a short period with no trend (2003–2007), and lastly a significant negative trend (2007–2018) (Fig. 3). As observed by D'Alelio et al. (2020), the fastest temperature increase occurred from 1994 to 2004 during which there was also a significant NPP increase. However, the highest temperatures observed during the 2010s were associated with a significant decrease in NPP. D'Alelio et al. (2020) proposed that the observed warming during the first part of the time series induced a physiological response in phytoplankton (e.g., changing C:P ratios in cells) that maintained high NPP, whereas the following further temperature increase led to conditions outside the cells' physiological range that decreased NPP. This explanation is supported by an increase in phytoplankton C:P ratio during the

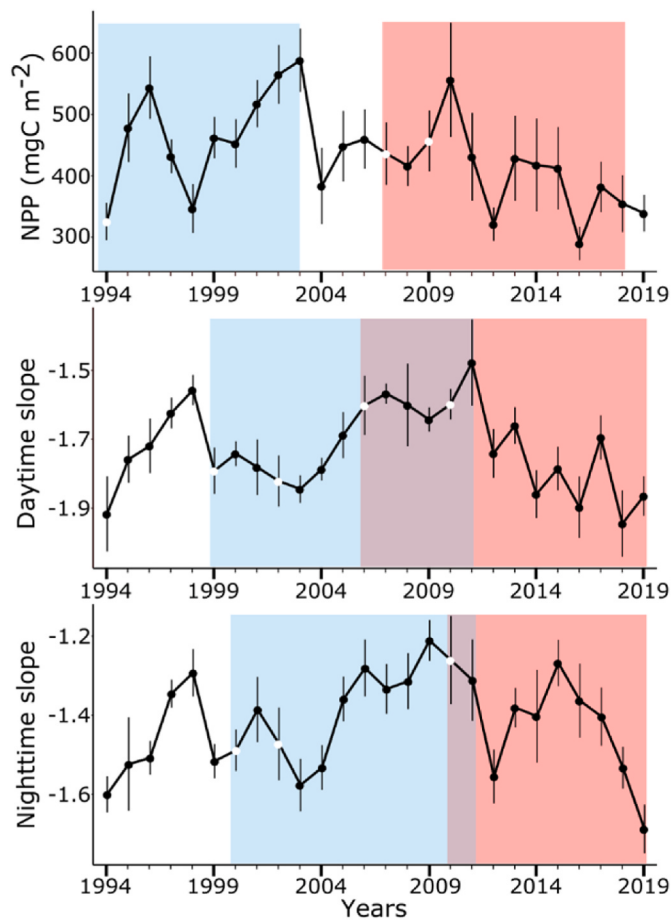


Fig. 3. Long-term trends in temperature, NPP and NBSS slopes. The mean ($\pm$ standard error) NPP (integrated 0–140 m and averaged by month) and day- and nighttime zooplankton slopes are shown, in comparison with the results of the Seasonal Kendall tests (window = 10 years) conducted on the monthly time series. Colored windows represent results of Seasonal Kendall test with significant ($p < 0.05$) 10-year periods of positive (light blue) or negative (red) trends. Violet sections indicate transitions between significant positive and negative trends, white windows indicate periods without significant changes. White data points represent the starting year of each 10-year period of significant trend.

2010s (Lomas et al., 2022).

In addition, we observed changes in the zooplankton trophic structure: significant ($p < 0.05$) NBSS slopes from the day- ($n = 279$) and nighttime ($n = 265$) became flatter in the 2000s (relative slope increase of about 16% and 24% in the day- and nighttime slopes, respectively), and steeper during the 2010s (relative slope reduction of 14% and 24% in the day- and nighttime slopes, respectively), following the sequential increase and decrease in NPP in these two decades, with an offset from the changes in NPP by roughly 5 years (Fig. 3). Flatter NBSS slopes suggest that the biomass was more efficiently transferred within the zooplankton community towards the top consumers at BATS before 2010, as evidenced by the increase over time in the >5 mm size fraction. In contrast, the steeper NBSS slopes observed after 2010 suggest that less organic matter was transferred to higher trophic levels (Zhou, 2006; Zhou et al., 2009). Overall, NBSS slope values in the NASG at BATS (annual range -1.9 to -1.5 and -1.7 to -1.2 during day- and nighttime, respectively) were in similar range as those found in other studies focused on zooplankton (Ryckaczewski and Checkley, 2008; Valencia et al., 2018; Ryckaczewski, 2019). In an analogous system in the North Pacific Subtropical Gyre, interannual variability in zooplankton NBSS slope was less evident than at BATS but with overlapping slope values (annual range -1.1 to -1.6) (Valencia et al., 2018).

3.3. Oligotrophication affects trophic efficiency via biogeochemical changes

At BATS, planktonic trophic structure changes occurred in parallel with oligotrophication during the last decade, as evidenced from the overlap between 10-year trend windows of NPP and NBSS slopes. Oligotrophic and less productive (low NPP) systems are often characterized by steeper NBSS slopes, although NBSS slope is not always sensitive to increasing productivity (Sprules and Barth, 2016). NPP and NBSS slopes were not directly related in a 23-year (1994–2016) study in the North Pacific Subtropical Gyre, where peaks in NPP were not followed by increases in NBSS slope (Valencia et al., 2018). Despite this, steeper NBSS slopes were found at more productive coastal stations compared to the more oligotrophic offshore, along a trophic gradient in the California Current Ecosystem (from coastal to offshore) (Ryckaczewski and Checkley, 2008; Ryckaczewski, 2019). Furthermore, Kwong et al. (2022) reported flatter NBSS slopes with increasing phytoplankton biomass when analyzing the zooplanktonic community in the subarctic Northeast Pacific Ocean.

Moreover, an analysis from the East China Sea found that food availability for zooplankton exerted the most important effect on NBSS slope (García-Comas et al., 2014). In this respect, the sestonic carbon:phosphorus ratio (C:P) increased at BATS during the 2010s (Lomas et al., 2022). Several studies report that nutrient limitation and a subsequent increase in the C:P ratio are associated with a decrease in trophic efficiency (Malzahn et al., 2007; Dickman et al., 2008; Peace, 2015). In a six-year NBSS analysis of the plankton community in the northwest English Channel, higher NBSS steepness (lower trophic efficiency) occurred under nitrate or phosphate limiting conditions (Atkinson et al., 2021). A meta-analysis of available aquatic literature on planktonic NBSS slopes showed a dome-shaped relationship between NBSS slope and surface chlorophyll a , with steeper slopes both under highly eutrophic (e.g., harmful algal blooms) and oligotrophic (e.g., subtropical gyres) conditions (Atkinson et al., 2021).

3.4. Methodological considerations

While our results provide compelling indication of ecosystem change, there are methodological considerations. First, in this study we calculated NBSS with only five size fractions and more robust estimations can be made by increasing the number of size intervals (Atkinson et al., 2021). However, NBSS analysis of coastal to offshore zooplankton in the California Current Ecosystem showed that using ZooScan data (providing a high resolution of size categories of zooplankton) and size-fractionated biomass data similar to ours (relatively few size fractions coming from integrated net sampling) gave comparable results, with NBSS slopes showing similar decline with distance offshore (Ryckaczewski and Checkley, 2008; Ryckaczewski, 2019).

Second, diel vertical migrators can flatten NBSS slopes for the nighttime compared to the daytime samples (Décima, 2022). That is why we analyzed NBSS for both the daytime and nighttime data records (Fig. 3). Among the largest zooplankton size-fractions (1–2, 2–5, and >5 mm), only the sizes 1–2 and >5 mm showed differences in the day- and nighttime biomass dynamics plausibly related with diel vertical migrators (Fig. 2). Notwithstanding these differences between single size-fractions, the NBSS slope showed the same trend during both daytime and nighttime (Fig. 3), supporting our interpretation of a systemic shift in zooplankton trophic structure in this ecosystem.

Third, zooplankton include some large gelatinous taxa like salps, which feed on small particles and can occupy a relatively low trophic level, despite their large body size, introducing a potential bias in the application of NBSS which relies on the linear influence of body size on trophic processes. Lack of uniformity emerged from other NBSS analyses with gelatinous zooplankton: for example, Marcolin et al. (2013) and Kwong et al. (2022) observed flatter and steeper NBSS slopes, respectively, associated with gelatinous zooplankton. We compared NBSS

slopes estimated during salp bloom and non-bloom periods at BATS between 1994 and 2011 and found no significant differences for nighttime (Wilcoxon test, $W = 3768$, $p > 0.05$) but there was a significant difference for the daytime (Wilcoxon test, $W = 3731.5$, $p = 0.045$). Flatter slopes were associated with daytime salp blooms (mean slope of -1.65) compared to the non-bloom periods (mean slope of -1.73). Although no data for salp abundance are yet available for BATS after 2011, Lomas et al. (2022) examined the zooplankton dry-to-wet weight ratio as a proxy for relative importance of gelatinous zooplankton such as salps and found no significant changes in the time series up through 2020. Thus, the decrease of NBSS slopes during the 2010s observed herein was unlikely associated with a salp increase at BATS.

Finally, another potential limit of our analyses is the window width considered in the application of the Seasonal Kendall test, which may influence the analytical output. We used a 10-year window that corresponds to about a third of the analyzed time series herein, allowing a sufficient length to look for significant trends over periods shorter than the whole analyzed record when using the Seasonal Kendall test, according to previous studies (e.g., Schertz et al., 1991; Cloern, 2019; D'Alelio et al., 2020; Beck et al., 2022).

4. Conclusion

Globally, ocean warming can decrease NPP (Fu et al., 2016) and secondary productivity (Chust et al., 2014; Kwiatkowski et al., 2019), but models indicate that the impact of these changes on planktonic consumers is highly site-specific (Chust et al., 2014; Kwiatkowski et al., 2019). We show that oligotrophication caused by ocean warming in the NASG can negatively affect the functioning of food webs, starting from their planktonic base. In the NASG, we observed a decrease in NPP and the biomass of the largest zooplankton from 2010 to 2019, with a consequent overall reduction in the TTE. In this respect, the NBSS is suitable for detecting ecosystem shifts and providing early warning for trophic changes. As the NASG and other subtropical gyres are expanding and are expected to become more oligotrophic by the end of the century (Kwiatkowski et al., 2018; Leonelli et al., 2022), this work provides the basis to develop complementary predictive models or manipulative trophic experiments to understand the biological mechanisms behind the trends observed in the NASG.

CRedit authorship contribution statement

Luca Russo: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **Daniele Bellardini:** Data curation, Formal analysis, Methodology, Validation. **Deborah K. Steinberg:** Supervision, Visualization, Writing – original draft, Writing – review & editing. **Roberta Congestri:** Conceptualization, Supervision, Writing – original draft, Writing – review & editing. **Michael W. Lomas:** Conceptualization, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Domenico D'Alelio:** Conceptualization, Methodology, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Raw data are available from BATS website (<http://bats.bios.edu/bats-data/>), Biological and Chemical Oceanographic-Data website (<https://www.bco-dmo.org/dataset/881861> for BATS zooplankton biomass)

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Appendix A. Supplementary data

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