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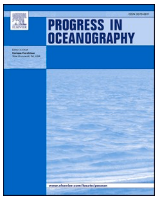

Food web analysis shows an exacerbated dependence of zooplankton on detritus in oligotrophic systems due to ocean warming

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ABSTRACT

Ocean warming can affect plankton both directly, through altered metabolic activities, and indirectly, modifying the physical–chemical properties of the water column, with possible effects on ecosystem functioning. To evaluate the combined action of warming-related physiological responses and environmental changes on plankton functioning, we carried out a long-term analysis (from 1994 to 2019) of the Bermuda Atlantic Time-series Study (BATS) dataset where ocean warming and stratification have driven a decrease in the net primary production over the last decade. Using the time series of plankton observations, we assembled 1000 replicates of a food web model for each year. We observed that the total flow of matter through the model remained constant over time, despite the increased oligotrophication, due to global warming, after 2014. In fact, the plankton food web remained robust through re-modulated trophic interactions with an increased detritivory to herbivory ratio of the food web over time. However, it was problematic to re-establish the trophic connections of the food web broken by ocean warming, as remarked by the increased relative internal ascendency. Thanks to trophic plasticity, the reduced zooplankton dependence on herbivory was compensated by a significant increase in the reliance on carnivory and detritivores, highlighting the crucial role of trophic interactions in buffering significant environmental short-term changes.

1. Introduction

Plankton are aquatic organisms floating in the ocean (Hensen, 1887). They include dimensionally diverse (mean body size) and phylogenetically distant species (Worden et al., 2015) with multiple trophic habits and give rise to tangled food webs (Azam et al., 1983). Plankton play a crucial biogeochemical role, accounting for roughly half of the global net primary production (NPP) and supporting the flow of matter or energy to the highest trophic levels (Glibert and Mitra, 2022; Worden et al., 2015). In light of the importance of plankton and the increase in average global surface ocean temperature of about 1 °C over the last two centuries (Lee et al., 2023), it is of fundamental importance to assess the impact of global warming on these organisms and their ecological interactions.

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Ocean warming can directly influence the metabolic activities of plankton (Brown et al., 2004). Metabolic rates of planktonic heterotrophic consumers are more responsive to temperature compared to autotrophs (Brown et al., 2004; Liu et al., 2019), and thermal changes can result in higher grazing pressure on primary producers (Liu et al., 2019; O'Connor et al., 2009). Among planktonic consumers, mixoplankton, i.e., unicellular plankton behaving as both autotrophs and heterotrophs (Flynn et al., 2019), rely less on photosynthesis and more on predation when temperatures increase (Chu et al., 2023). Increasing ocean temperatures can also indirectly affect plankton modifying the physical–chemical conditions, enhancing water-column stratification, reducing the vertical input of nutrients to phytoplankton (Fischer et al., 2014), and potentially weakening primary production and carbon export (Cael et al., 2017; Fu et al., 2015). Directly and indirectly induced changes at the organisms and plankton population level, however, can further cascade or are damped in the plankton food web as a result of internal adjustments (D'Alelio et al., 2019). The mechanisms of these adjustments involve several processes (e.g., production, consumption, mixotrophy, detritivory) and are difficult to disentangle without a comprehensive analysis of the plankton food web (Glibert and Mitra, 2022).

In this context, multi-decadal oceanographic and plankton data collected in the Bermuda Atlantic Time-series Study (BATS) in the Sargasso Sea (North Atlantic Subtropical Gyre, NASG) represent a promising opportunity to evaluate both direct and indirect effects of ocean warming on planktonic organisms and their interactions. In the highly oligotrophic NASG, an increase of about 0.9 °C in seawater temperature corresponded to a 25–30% nutrient inventory reduction, a NPP decrease of about 30%, and a reduction of 0.286 mg m^{-2} y^{-1} of chlorophyll *a* during the 2010s (D'Alelio et al., 2020; Lomas et al., 2022; Viljoen et al., 2024). Moreover, during the 2010s, there was a decrease in the efficiency of carbon transfer towards higher trophic levels of plankton at BATS (Russo et al., 2023). Over the same period, smaller phytoplankton (i.e., *Synechococcus* spp. and *Prochlorococcus* spp.) became more abundant, but the decrease in NPP was not reflected in a reduction of carbon export to the ocean interior, suggesting that there were meaningful plankton food web adjustments (Lomas et al., 2022). Indeed, planktonic organisms can respond to environmental changes by modifying metabolic activities (Calbet and Saiz, 2022), becoming more efficient in nutrient uptake (Lomas et al., 2022) and changing the trophic dynamics of the community while maintaining similar functioning (D'Alelio et al., 2019; Russo et al., 2022).

In this study, we investigated the impact of the long-term temperature increase and associated decrease in NPP on plankton trophic dynamics in the NASG by developing a plankton food web model for each year of the dataset and by analyzing a suite of whole-system indicators of the obtained plankton food web time series. Since the assessment of plankton response to ocean warming based solely on satellite observations is incomplete because it does not account for the subsurface community (Viljoen et al., 2024), we applied a novel data-driven modeling approach to derive a planktonic food web model representing the BATS water column up to 140 m depth from 1994 to 2019. Using the food web model and whole-system indicators over the years, we were able to infer the redistribution of organic matter flows within the community in response to environmental changes and to gain information on the trophic strategies stabilizing the circulation of organic matter in the food web under the effect of ocean warming.

2. Material and methods

2.1. Study site

The BATS station (31°40′N, 64°10′W) is in the northwestern quadrant of the Sargasso Sea, which is at the center of an ocean gyre, the NASG, a clockwise circulation that extends from the Gulf of Mexico to the Azores (Cushman-Roisin, 1987). This circulation virtually isolates BATS from the east coast of the American continent, allowing oligotrophic conditions (D'Alelio et al., 2020). The bottom depth at BATS is about 4680 m, with a maximum euphotic zone depth of 140 m (Doney et al., 1996). Biological sampling is conducted approximately monthly (biweekly during the spring bloom) (Lomas et al., 2013). Details of the sampling scheme and analysis method can be found in the BATS methods manual (Knap et al., 1997). At BATS, planktonic organisms are collected and analyzed in different size fractions (Madin et al., 2001), which were used herein to develop the plankton food web in the euphotic zone (from 0 to 140 m depth) over 26 years (1994–2019).

2.2. Conceptual model structure

We constructed food web models that considered both body size and trophic habits in driving trophic interactions. Although body size is a fundamental trait structuring marine food webs (Sommer et al., 2018), trophic habits can be unrelated to size in plankton communities (Stukel et al., 2021). Indeed, body size fails to represent the functional diversity of unicellular plankton when deriving ecological models (Jordán et al., 2018). For instance, unicellular plankton include taxa that can be only prey (phytoplankton, i.e., strictly autotrophic organisms) and both prey and predators (mixoplankton and protozooplankton, i.e., respectively mixotrophic and strictly heterotrophic protists) (Flynn et al., 2019).

Our conceptual model (Fig. 1) included such trophic diversity, aggregated within 15 *functional nodes (FNs)*, including: eight unicellular planktonic FNs (heterotrophic bacteria, pico-, nano- and micro-phytoplankton, nano- and micro-mixoplankton, nano- and micro-protozooplankton); five zooplanktonic FNs corresponding to five measured size fractions (0.2–0.5, 0.5–1, 1–2, 2–5, and > 5 mm); two non-living FNs, i.e., the *dissolved organic carbon* (DOC) as a primary source of carbon for heterotrophic bacteria (Lechtenfeld et al., 2015), and the *particulate detritus*, a component of zooplankton diet (Schnetzer and Steinberg, 2002).

Plausible trophic links between unicellular planktonic FNs, were established by considering general literature information on dietary preferences of the most representative organisms associated with each FN (see Supplementary Material). Trophic links for zooplankton FNs were approximated to those of the most representative taxa of each size fraction: juvenile Copepoda (0.2–0.5 mm), Oithonidae and Oncaeidae (0.5–1 mm), Corycaeidae (1–2 mm), Calanoida (2–5 mm), and Euphausiacea (>5 mm) (Russo et al., 2023) (see Supplementary Material for further information).

2.3. Input data

Raw data, from 1994 to 2019, were downloaded from the BATS website (http://bats.bios.edu/bats-data/). We used average monthly values when more than one sampling occurred per month. Discrete-depth bottle data (e.g., phytoplankton pigments, NPP, particulate organic carbon, and heterotrophic bacterial abundance), using trapezoidal integration, were integrated (from 0 to 140 m depth) for monthly values for each variable to derive model input data. The temperature profile was averaged between 0 and 140 m depth, as already done at BATS (D'Alelio et al., 2020). The masses and C:P, C:N, and N:P stoichiometric ratios of exported elemental material were derived from sediment trap data at 150 m depth. Size-fractionated zooplankton biomass was normalized to the depth interval from 0 to 200 m. As this work concerns the long-term changes of the plankton communities and not the intra-annual variability, all monthly values were then averaged over the year (see Supplementary Material for plankton input parameterization and Supplementary Tables S1–S7 for input data).

The approach used here to produce food webs required as input, for each living FN, the following data:

(I) Carbon (C) biomass (mgC m^{-2});
(II) Growth rate (μ, d^{-1});

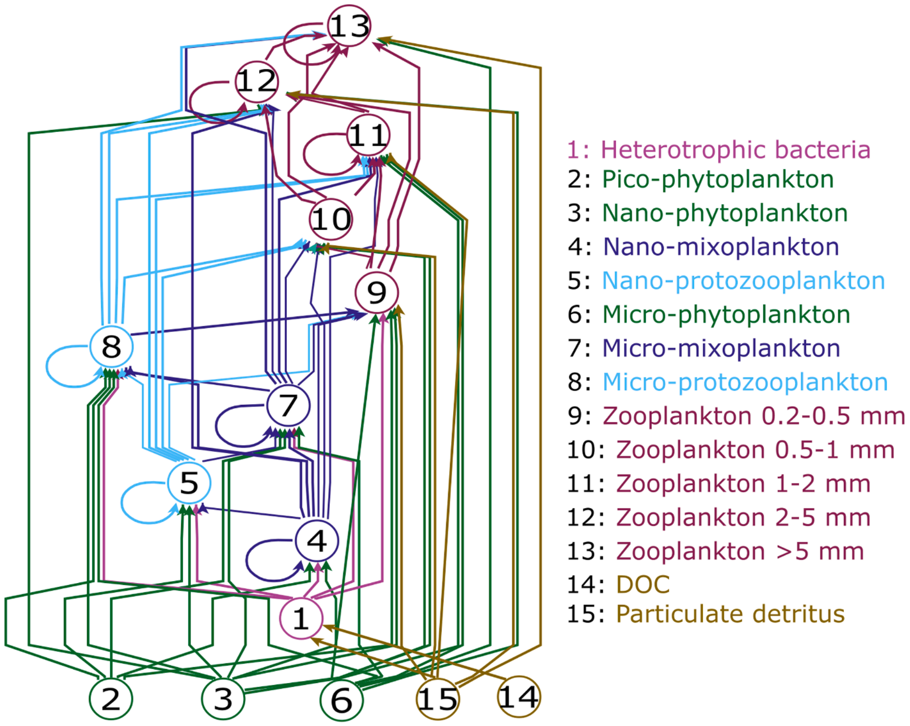

Fig. 1. Conceptual food web model. Numbers refer to FNs (illustrated in the legend). Arrows, directed from sources to sinks, represent trophic interactions between FNs at BATS and are color-coded by the source.

(III) Consumption rate (α, d^{-1});
(IV) The fraction of unassimilated food (ε, dimensionless);
(V) The proportion of phototrophy in individual metabolism (ph, dimensionless);
(VI) The proportion of the flows to detritus (γ, dimensionless);
(VII) Plausible trophic interaction strengths (ordinal qualitative information).

Heterotrophic bacteria C biomass was obtained by multiplying measured bacterial abundances by the conversion factor 15 fgC cell^{-1} (Caron et al., 1995). Total phytoplankton C biomass was derived by multiplying total integrated chlorophyll *a* in the depth interval from 0 to 140 m by the conversion factor 39.74 mgC mg chlorophyll a^{-1} (Lomas et al., 2022). Total phytoplankton C biomass was then partitioned into pico-, nano- and micro-phytoplankton size fractions using diagnostic secondary pigments characteristic of specific phytoplanktonic groups (Uitz et al., 2006).

Filtered particulate organic carbon (POC) includes particulate detritus, phytoplankton, heterotrophic bacteria, and all the other mixo- and protozooplankton (Andersson and Rudehall, 1993; Ribes et al., 1999). Mixo- and protozooplankton C biomasses were derived by subtracting the C biomass of phytoplankton, heterotrophic bacteria and particulate detritus from the integrated POC in the depth interval from 0 to 140 m. A similar approach was already previously used to derive the particulate detritus by subtracting from the POC all other constituents (i.e., phytoplankton, heterotrophic bacteria, mixoplankton, and protozooplankton) (Scotti et al., 2022). The mixo- and protozooplankton biomass obtained in the present study was then divided into nano- (FNs 4 and 5) and micro-plankton (FNs 7 and 8) by assuming the same proportions observed for the nano- and micro-phytoplankton, based on previous observations at BATS (Caron et al., 1995; Roman et al., 1995). Metazoans were included in the model as the zooplankton size fractions collected at BATS (0.2–0.5, 0.5–1, 1–2, 2–5, and > 5 mm). Their C biomass was obtained by converting the dry weight using the conversion factor of 0.36 dry weight to mgC (Madin et al., 2001) (see Supplementary Material for plankton input parameterization and Supplementary Tables S3–S7 for input data).

Lacking specific taxonomic identification of the planktonic groups, we derived their growth and consumption rates from representative organisms of each model FNs and considering the effect of temperature on metabolic rates (Brown et al., 2004). While mixoplankton can include organisms that are almost completely photoautotrophic, heterotrophic or photoheterotrophic (Jeong et al., 2021), we assumed that nano- and micro-mixoplankton performed 50% of their metabolic activities as photoautotrophs and 50% as heterotrophs (see Supplementary Material for plankton input parameterization and Supplementary Tables S3–S7 for input data).

Finally, interaction strengths among plankton FNs (Fig. 1) were given ordinal qualitative values (null, weak, medium, or strong interaction strength) to indicate their relative intensity in the diet of plankton consumers (Loschi et al., 2023) (see Supplementary Material for plankton input parameterization and Supplementary Tables S3–S7 for input data).

2.4. Food web model

We employed an iterative approach for developing the food web model for each year based on the conceptual model structure (Fig. 1) with random sampling of parameters and a posteriori check for ecological realism (Loschi et al., 2023). To provide the algorithm a range for each input for each year, we used minimum and maximum values that were either calculated from the data input, as in the case of grow rates of phyto-, mixo-, and protozooplankton, or estimated by assuming specific ranges of variability for FN's parameters based on the uncertainty of the input data: 5% for the average biomasses of heterotrophic bacteria and zooplankton of each year directly measured at the BATS site and the zooplankton grow rates, based on equations applied for the local community (Roman et al., 2001); 10% for the proportion of flows to detritus, particulate detritus and phyto-, mixo-, and protozooplankton biomasses, which were derived indirectly but using data measured directly at the BATS location such as pigments and NPP; and 20% for bacterial μ and α where we found little information from the literature (see Supplementary Material for the plankton input parameterization and Supplementary Tables S3–S7 for the inputs). The values of each parameter of the food web model were sampled from its defined range using a uniform distribution (Loschi et al., 2023).

Strengths of trophic interactions were transformed from ordinal qualitative to quantitative values. Initially, two random values were sampled between 0 and 1 to establish the boundaries of the ordinal qualitative values for each FN. Then, each ordinal qualitative value equal to weak, medium, or strong was substituted sampling random values between 0 and the lower boundary, between the two boundaries, and between the greater boundary and 1, respectively. All samplings were from a uniform distribution. In the end, the values obtained were normalized to have the sum equal to 1 for each consumer, obtaining the matrix of the proportion of the diet DC.

The entire approach is based on two main equations (Christensen and Pauly, 1992):

$$\mu_k \cdot B_k - \sum_{j=1}^{n} \left(\alpha_j \cdot B_j \cdot DC_{k,j}\right) - m_k = 0 \tag{1}$$

where, for each living node k, the production (as product of biomass B and the growth rate μ) was balanced by the sum of consumption by various predators (as product of biomass B, consumption rate α, and the proportion DC of a prey k in the predator j diet), and the natural mortality m; and

$$\sum_{i=1}^{n} \left[\gamma_{i,d} \cdot (\varepsilon_i \cdot \alpha_i \cdot B_i + m_i)\right] - \sum_{j=1}^{n} \left(\alpha_j \cdot B_j \cdot DC_{d,j}\right) - ex_d + im_d = 0 \tag{2}$$

where for each non-living node d, the sum of flows to detritus was the product of the proportion γ of flow of node i to non-living node d times the sum of natural mortality and the unassimilated food (as product of biomass B, consumption rate α, and the fraction of unassimilated food ε) and was balanced by the sum of consumption of the detritivores (as product of biomass B, consumption rate α, and the proportion DC of a source d in the consumer j diet), the vertically integrated export, ex, and import, im, in the 140 m water column. Export is here the amount of flows to detritus that leaves the system because it is not consumed by detritivores, however it can become an import for an adjacent and comparable system (Ulanowicz, 1980). Import is here the organic matter that flows from an adjacent system and allows to sustain detritivores (Ulanowicz, 1980). We decided to introduce export and import for non-living FNs because these flows are difficult to measure experimentally (Crossman et al., 2001), but we can have their estimates thanks to our model (Christensen and Walters, 2004). In this way, we can consider the effects of ocean circulation, which was reported to convey organic matter within the NASG through lateral transport from eddies' boundaries (Gupta et al., 2022; Letscher et al., 2016).

The food web representation obtained by iterative random sampling of parameters was subjected to a posteriori check for realism in order to keep only realistic food webs (Loschi et al., 2023) identified on the basis of: (I) positive or null respirations (in mgC m^{-2} d^{-1}), namely the amount of carbon that leaves the community and no longer can serve as an import to any comparable system (Ulanowicz, 1980), obtained for each FN i as:

$$R_i = B_i \cdot \alpha_i - B_i \cdot \mu_i \cdot (1 - ph_i) - B_i \cdot \varepsilon_i \cdot \alpha_i \tag{3}$$

(II) positive or null natural mortalities; (III) for each consumer j, the ratio between $\mu_j \cdot (1 - ph_j)$ and α_j greater than 0.1 for all consumers, and smaller than 0.5 for protists and heterotrophic bacteria and 0.3 for zooplankton size fractions (Christensen and Walters, 2004). Given a range for each parameter, infinite solutions are able to satisfy these conditions: the approach is iterated in order to obtain the first 1000 valid food webs for each year. In this way, we were able to build an ensemble of quantitative and realistic replicates starting from qualitative information for some of the input parameters (interactions) and randomly exploring the input ranges of the other parameters (Loschi et al., 2023).

This approach was entirely developed in R version 4.2.2 (R Core Team, 2022) through RStudio version 2022.07.2 + 576 (RStudio Team, 2022) with the help of `rtri` function from `EnvStats` package version 2.7.0 (Millard, 2013).

2.5. Whole-system indicators

Changes in structure and functioning of the food webs were evaluated using a set of whole-system indicators that are widely used to disentangle the ecological differences among food webs (Fath et al., 2019; Heymans et al., 2014). Whole-system indicators were calculated for the 1000 valid food webs for each of the 26 years in R version 4.2.2 (R Core Team, 2022) via RStudio version 2022.07.2 + 576 (RStudio Team, 2022), using the `AscInd` and `GenInd` functions of the `NetIndices` package version 1.4.4.1 (Kones et al., 2009) for some of them. The calculated whole-system indicators are as follows.

Total system throughput (TST) is the total amount of energy or matter circulating in a system and is an overall measure of its "ecological size" (Finn, 1976):

$$TST = \sum_{i=0}^{n} \sum_{j=1}^{n+2} T_{ij} \tag{4}$$

where T_{ij} is the flow matrix with the flows which move from prey i to predator j, n is the number of FNs, n + 2 is the number of FNs to which respiration and export are added and i = 0 represents the import row (Hirata and Ulanowicz, 1984).

The detritivory to herbivory ratio (D/H) is the ratio of the sum of all consumption flows on detritus and the sum of all consumption flows on primary producers and measures the relative importance of the recycled matter or energy in the community (Ulanowicz and Kay, 1991):

$$D/H = \frac{\sum_{j=1}^{k} \sum_{i=k+1}^{n} T_{ij}}{\sum_{j=1}^{k} \sum_{i=1}^{n} \left(T_{ij} \cdot ph_i\right)} \tag{5}$$

where k is the number of living nodes, so that numbers from k + 1 to n represent non-living nodes. Values of D/H greater than 1 indicate that the system maintains its activities primarily using detritus rather than relying solely on primary producers (Safi et al., 2019), underscoring the maturity of the community (Odum, 1969).

The relative internal ascendency (A_i/C_i) is a measure of the internal organization of the system and is therefore only calculated for internal flows (prey-predator interactions and flows to detritus), so excluding export, respiration and import (Hirata and Ulanowicz, 1984; Ulanowicz and Norden, 1990):

$$A_i/C_i = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} \left(T_{ij} \cdot \log_2 \frac{T_{ij} \cdot TST}{\sum_{j=1}^{n} T_{ij} \cdot \sum_{i=1}^{n} T_{ij}}\right)}{-\sum_{i=1}^{n} \sum_{j=1}^{n} \left(T_{ij} \cdot \log_2 \frac{T_{ij}}{TST}\right)} \tag{6}$$

It is represented by values between 0 and 1, with higher values associated with an organized system with high internal stability that is less dependent by exogenous connections to adjacent ecological systems (Baird et al., 1991). However, if a perturbation is able to interrupt flows between FNs it is more difficult for the system to reestablish them (Baird et al., 1991).

Relative redundancy (R/C) (Ulanowicz and Norden, 1990) provides an indication of the proportion of parallel pathways through which energy or matter can be exchanged within the community, so it is a measure of the inefficiency of the system (Ulanowicz, 1980):

$$R/C = \frac{-\sum_{i=1}^{n} \sum_{j=1}^{n} \left(T_{ij} \cdot \log_2 \frac{T_{ij}^2}{\sum_{j=1}^{n} T_{ij} \cdot \sum_{i=1}^{n} T_{ij}}\right)}{-\sum_{i=0}^{n} \sum_{j=1}^{n+2} \left(T_{ij} \cdot \log_2 \frac{T_{ij}}{TST}\right)} \tag{7}$$

R/C values range between 0 and 1, with larger values of R/C indicating that there are more redundant pathways for the movement of energy or matter between FNs, so a system subjected to perturbation can continue its activity because the impacted pathway can be easily replaced by other ones (Ulanowicz, 1980).

Robustness (Ro) is the balance between organization and reserve capacity (Ulanowicz et al., 2009) and it is calculated as:

$$\mathrm{Ro} = -e\cdot \ln e\cdot \frac{\sum_{i=0}^{n}\sum_{j=1}^{n+2}\left(T_{ij}\cdot \log_2\frac{T_{ij}\cdot \mathrm{TST}}{\sum_{j=1}^{n+2}T_{ij}\cdot \sum_{i=0}^{n}T_{ij}}\right)}{-\sum_{i=1}^{n}\sum_{j=1}^{n}\left(T_{ij}\cdot \log_2\frac{T_{ij}}{\mathrm{TST}}\right)}\cdot \ln \frac{\sum_{i=0}^{n}\sum_{j=1}^{n+2}\left(T_{ij}\cdot \log_2\frac{T_{ij}\cdot \mathrm{TST}}{\sum_{j=1}^{n+2}T_{ij}\cdot \sum_{i=0}^{n}T_{ij}}\right)}{-\sum_{i=1}^{n}\sum_{j=1}^{n}\left(T_{ij}\cdot \log_2\frac{T_{ij}}{\mathrm{TST}}\right)} \tag{8}$$

This indicator is based on the observation that the organization of flows in food webs consist of different types of pathways that can be either organized or redundant (Ulanowicz, 2009). Values range between 0 and 1, and food webs with a value of Ro close to 1 have a balance between efficient and redundant pathways and are considered optimal, because they are both resistant and resilient (Ulanowicz, 2009; Ulanowicz et al., 2009).

2.6. *Statistical analysis*

We applied a non-parametric analysis of the annual means of temperature, NPP, C:N, N:P, and C:P measured at BATS to detect change points in the multivariate time series independently from food webs. Specifically, the `e.divisive` function of the `ecp` package version 3.1.3 (James and Matteson, 2013) was used, given 1000 as the maximum number of permutations for each iteration and the minimum number of observations between change points (i.e., 2). The statistical significance of the estimated change point is determined by a permutation test of the iteration results (James and Matteson, 2013).

Next, the Fligner-Pollicello robust rank-order distributional test was performed using the `rrod.test` function of the `trend` package version 1.1.4 (Pohlert, 2020) to detect differences in food web properties between the periods before and after any eventually identified change point. The test was applied to the whole-system indicators, to the total detritus export, to the detritivory and the herbivory, to the total flows to detritus, to the grow rates of all living FNs, and to the consumption rates of all consumers. It was performed 1000 times using the replicates of the estimated food webs, i.e., one value for each variable from each year was used each time to maintain independence among observations. Finally, for each variable, statistical differences between periods before and after the change point were considered significant if almost 550 results with medians that increased or decreased in the same way had p-values less than 0.05.

All statistical analyses were performed in R version 4.2.2 (R Core Team, 2022) using RStudio version 2022.07.2 + 576 (RStudio Team, 2022).

3. Results and discussion

3.1. *Plankton response to ocean warming*

By applying a non-parametric multiple change point analysis of multivariate BATS data (temperature, NPP, C:N, N:P, and C:P) we found, within the time series, a single statistically significant change point between 2014 and 2015 (p-value of 0.004), which divided the time series into two periods, 1994–2014 and 2015–2019. This change point corresponds to an abrupt ecosystem shift in the northern hemisphere after 2014 due to an El Niño event (Beaugrand et al., 2019). Moreover, recent observations at BATS reported significant changes within the zooplanktonic community during the last 8 years with a general decrease among the larger size fractions from 2011 to 2019 (Russo et al., 2023).

Comparing environmental variables with model outputs in the first period of the time series, we found a good concordance between the total amount of matter circulating in the planktonic food web (i.e., TST, or total system throughput) and NPP, both peaked in 2010 in parallel with an anomalous wintertime NAO index (Osborn, 2010) reflected by increased availability of nutrients (Lomas et al., 2022). In contrast, during the last years of the time series, NPP and TST were not concordant. The total matter circulating within the plankton community remained almost constant at BATS despite the increase of ocean water temperature and the associated decrease in NPP (Fig. 2 and Table 1).

The decrease in chlorophyll *a*, NPP and nutrient availability reported during the last decade at BATS is associated with an increase of the relative internal ascendency (A_i/C_i) after 2014. In the second period (from 2015 to 2019), the system internal flows became more organized, as highlighted by an increase in A_i/C_i that evidenced a higher internal stability of the system (Baird et al., 1991). Internal flows became more organized because the flow of matter became more channeled into a few trophic interactions at the expense of others. As shown in the simplified food webs in Fig. 3, following the decrease in NPP and increased oligotrophication, flows from phyto- to mixo- and proto-zooplankton became less intense and flows to detritus and from zooplankton to zooplankton became more intense. However, the relative redundancy (R/C) always had high median values and did not significantly change between the two periods (Fig. 2 and Table 1). This suggests that redundancy – multiple trophic pathways replacing impacted ones (Ulanowicz, 1980) – determined the resilience of the plankton community to warming and the NPP decrease at BATS. Moreover, food web robustness (Ro) did not change significantly (Fig. 2 and Table 1), being always near the maximum value of sustainability for the food webs, highlighting a balance between the overall organization and the reserve capacity that is indicative of global resistance and resilience (Ulanowicz, 2009; Ulanowicz et al., 2009).

3.2. *The importance of detritus*

Model results show that zooplankton at BATS have become more dependent on detritus as a food source after 2014 (Fig. 3). Detritus is a fundamental component of energy flows within aquatic food webs, and it has a strong influence on trophic dynamics, supporting greater food web complexity (Moore et al., 2004). Greater detritivory than herbivory allows for the system to have secondary production greater than primary production thanks to the import of organic matter (Fig. 4), although how long a system can function on allochthonous supply of detritus is unknown. Usually, the D/H increases as NPP and nutrient availability decrease (Luong et al., 2014).

The inverse relationship between the D/H and NPP observed at BATS after 2014 (Fig. 4) was guided by a significant herbivory decrease, indicating that detrital matter did not originate only from local autotrophs (de Jonge and Schückel, 2019), but also from allochthonous sources introduced through the influence of vertical and horizontal ocean circulation (Letscher et al., 2016; Liu et al., 2022). Concerning the

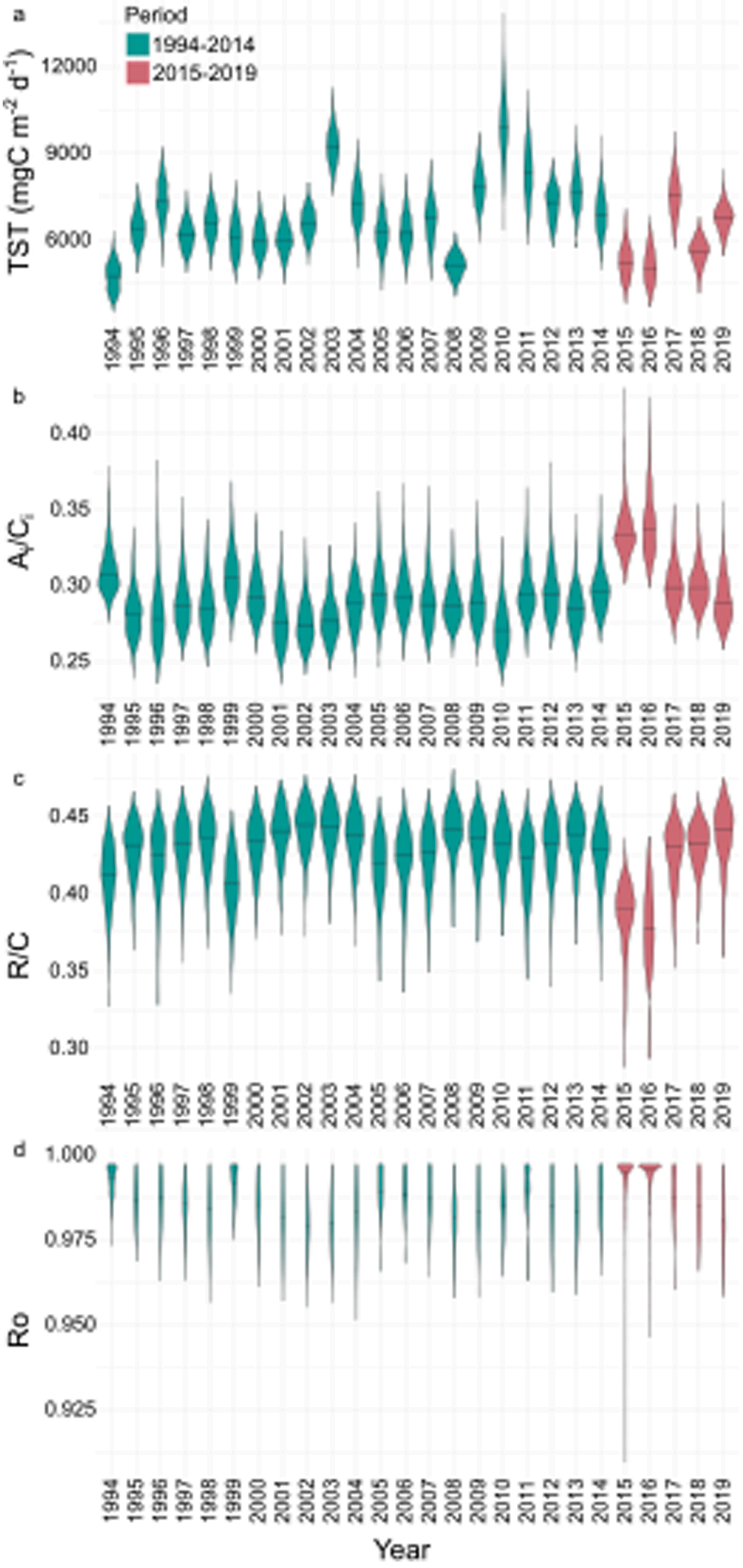

Fig. 2. Violin plots for whole-system indicators. a) Total system throughput (TST), b) relative internal ascendency (A_i/C_i), c) relative redundancy (R/C), and d) robustness (Ro) of the time-series of plankton food web models. Colors highlight periods identified through change point analysis, as illustrated in the legend. Bars represent median values. These plots were obtained with the `ggplot2` (Wickham, 2016) packages versions 3.4.0 for R (R Core Team, 2022).

Table 1
Differences between the two periods identified (1994–2014 and 2015–2019) for all variables. For each variable, the percentage of the 1000 replicates that showed statistically significant differences is reported, as well as the direction of change between the two periods. Variables that increase or decrease showed more than 55% of p-values lower than 0.05, while "-" indicates no significant change. TST is the total system throughput, D/H is the detritivory to herbivory ratio, A_i/C_i is the relative internal ascendency, R/C is the relative redundancy, Ro is the robustness, μ is the growth rate, and α is consumption rate. "Phyto", "mixo", "protozoo", and "zoo" are abbreviations for phytoplankton, mixoplankton, protozooplankton, and zooplankton, respectively.

Variable	Significant differences (%)	Type of change	Variable	Significant differences (%)	Type of change
μ of heterotrophic bacteria	4.0	–	α of micro-mixo	3.9	–
μ of pico-phyto	83.4	Decrease	α of micro-protozoo	4.6	–
μ of nano-phyto	89.7	Decrease	α of zoo 0.2–0.5 mm	84.5	Increase
μ of nano-mixo	66.0	Decrease	α of zoo 0.5–1 mm	78.1	Increase
μ of nano-protozoo	25.8	–	α of zoo 1–2 mm	77.9	Increase
μ of micro-phyto	52.8	–	α of zoo 2–5 mm	78.0	Increase
μ of micro-mixo	26.5	–	α of zoo > 5 mm	77.8	Increase
μ of micro-protozoo	17.2	–	TST	16.7	–
μ of zoo 0.2–0.5 mm	88.9	Increase	A_i/C_i	57.2	Increase
μ of zoo 0.5–1 mm	89.0	Increase	R/C	17.0	–
μ of zoo 1–2 mm	87.9	Increase	Ro	12.2	–
μ of zoo 2–5 mm	88.5	Increase	D/H	91.7	Increase
μ of zoo > 5 mm	89.3	Increase	Detritivory (D)	15.4	–
α of heterotrophic bacteria	7.2	–	Herbivory (H)	79.1	Decrease
α of nano-mixo	29.1	–	Detritus exports	30.0	–
α of nano-protozoo	1.3	–	Flows to detritus	23.2	–

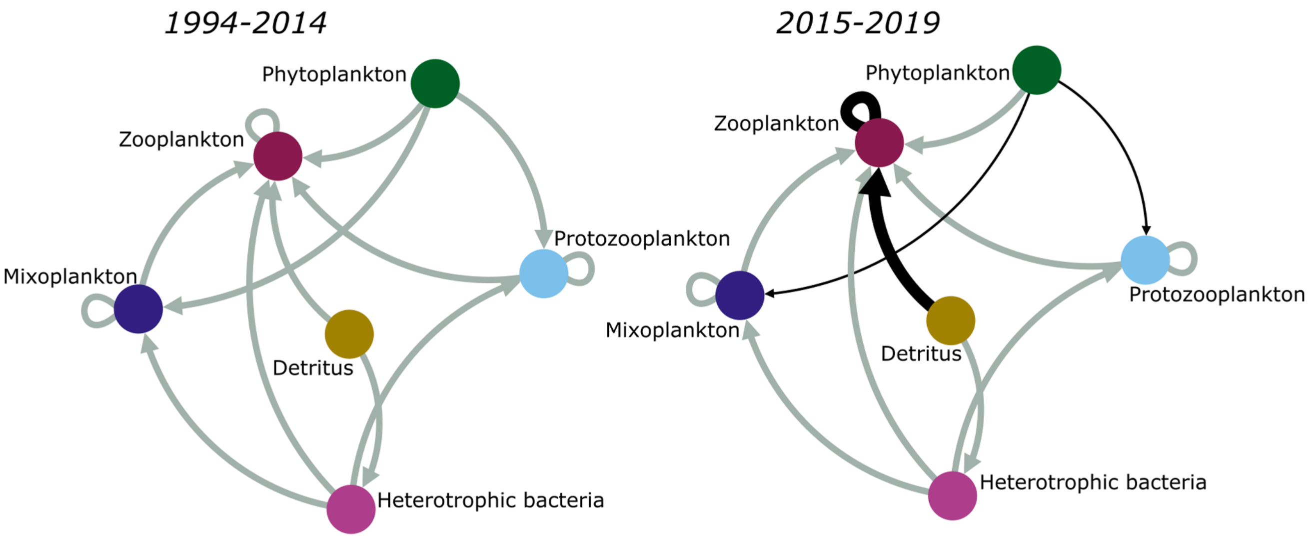

Fig. 3. Simplified plankton food web showing main changes in the trophic pathways at BATS. FNs are colored as in Fig. 1. Arrows, directed from source to consumer, represent trophic interactions between FNs (grey color highlights no changes, black color shows significant changes between the two analyzed periods). Arrows having the same source and consumer represent self-predation. Thickness of black links represents changes (thick and thin arrows indicate increases or decreases, respectively) of consumption flows.

last point, the lateral transport from eddies occurring during the summer to fall stratified period is estimated to supply the BATS site with organic matter and nutrients (Gupta et al., 2022; Letscher et al., 2016). This phenomenon is quantified by our model applied over the BATS data because it requires an import into non-living FNs to sustain consumption. Our results, therefore, concur with the fact that lateral advection of organic material supports net heterotrophy in oligotrophic ocean regions and is the result of net autotrophy in a neighboring region (Duarte et al., 2013).

Decreases in NPP can reduce the total carbon flows occurring within a community (Luong et al., 2014), yet at BATS despite the decrease in NPP, the TST of the plankton food web remained statistically constant over time (Fig. 1) (Luong et al., 2014). However, decreases in TST due to decreases in NPP can be balanced by increased activity of the microbial loop or higher importance of detritus to the total carbon flows of a community (Luong et al., 2014). In our food web model, non-living FNs were mainly eaten by heterotrophic bacteria, which, being efficient in nutrient uptake (Lomas et al., 2022), are the most abundant FN of the community in each year of the time series, as already observed at the highly oligotrophic site of BATS (Caron et al., 1995; Roman et al., 1995). This feature explains the high D/H values found for the plankton food web developed along the BATS time series and the lack of significant decrease of the TST in the second part of the time series, despite the increased oligotrophication and decrease of NPP.

Detritus flows to bacteria are fundamental but often neglected (Ducklow, 1994; Pomeroy and Wiebe, 1988) and can determine increases in the D/H and secondary production of plankton communities (Blight et al., 1995; Serret et al., 1999; Loschi et al., 2023), as it was observed from our models (Fig. 4) and from previous modeling exercises at BATS (Ducklow, 1994). The response of the D/H to the change point in the system led to short-lived, on 2015 and 2016, dramatic increases in the reliance on detritus, which then recovered but with higher values than the first period, and the secondary to primary production ratio increased (Fig. 4). These values in 2015 and 2016 are high but not unreasonable. For example, in the Venice Lagoon (Italy) for the years 2005 and 2007 D/H median values were 34.78 and 25.56, respectively

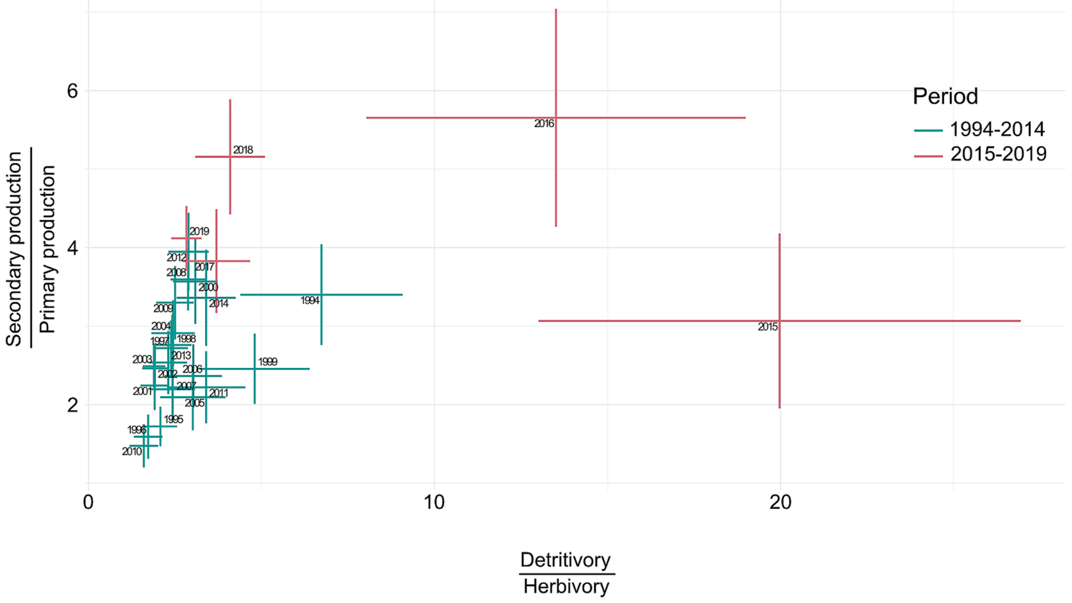

Fig. 4. The plot shows how the detritivory higher than herbivory allow to obtain secondary production much greater than primary production. Segments represent the absolute median deviation and their point of intersection are the medians of the detritivory to herbivory ratio (D/H) and the ratio of the total heterotrophic production to the total autotrophic production. Colors highlight periods identified through change point analysis, as illustrated in the legend. This plot was obtained with the `ggplot2` (Wickham, 2016) and `ggrepel` (Slowikowski, 2022) packages, versions 3.4.0 and 0.9.2 respectively, for R (R Core Team, 2022).

(Loschi et al., 2023), mainly due to Manila clam (*Ruditapes philippinarum*) harvesting (Pranovi et al., 2004; Sfriso et al., 2005) that caused the sediment resuspension in the water column making more organic matter available to consumers. Similarly, in BATS the allochthonous source of organic matter permits high D/H values and high secondary to primary production ratio (Fig. 4).

Our finding also highlights the stability of the unicellular mixo- and proto-zooplankton, whose growth rates, except for nano-mixoplankton, did not change after 2014 (Table 1). Indeed, unicellular plankton can provide alternative trophic pathways to channel detrital matter through heterotrophic bacteria to higher trophic levels (Baird et al., 2019; Stock et al., 2014). The increased influence of detritus within the zooplankton consumption flows at BATS could explain the previous estimated decrease in the trophic transfer efficiency towards the higher planktonic trophic levels during the 2010s (Russo et al., 2023). Moreover, our results (Table 1) are in general agreement with previous observations at BATS reporting no decrease in carbon exports despite the decrease of phytoplankton biomass and NPP (Lomas et al., 2022; Viljoen et al., 2024).

We also found a significant decrease in pico- and nano-phytoplankton growth rates in the second period of the time series (Table 1), corroborating the view that nutrient stress modulates the temperature dependence of phytoplankton metabolic rates (Marañón et al., 2018). The same was not the case for zooplankton, whose growth and consumption rates significantly increased (Table 1). We also found a significant decrease of nano-mixoplankton growth rates after 2014, while growth rates of micro-mixoplankton, growth and consumption rates of nano- and micro-protozooplankton, and consumption rates of nano- and micro-mixoplankton remained almost constant (Table 1). These results, combined with the NPP decrease, suggested that mixoplankton at BATS relied less on photosynthesis and more on heterotrophy with warming (Chu et al., 2023; Wilken et al., 2013).

The general understanding of mixotrophic plankton is still scarce, and ecological models may not fully capture the complexity of mixoplankton physiology and behavior (Gonzalez et al., 2022; Mitra et al., 2023). However, our results are in accordance with previous studies on mixoplankton, which reported an increased heterotrophy within mixotrophic protists during warming (Chu et al., 2023; Wilken et al., 2013), and our data also align with metabarcoding results of environmental DNA conducted on the protists' community at BATS between 2016 and 2018, which highlighted the importance of the mixo- and protozooplankton in this oligotrophic site (Blanco-Bercial et al., 2022).

3.3. *From herbivory to detritivory and carnivory*

Increasing temperature, through modifying the phytoplankton community composition to favor pico-phytoplankton, could increase the reliance on the detrital pool (Ullah et al., 2018), with the DOC consumed by heterotrophic bacteria (Baird et al., 2019) and the particulate detritus eaten by the zooplankton (Perhar and Arhonditsis, 2012).

Zooplankton include different trophic behaviors, spanning from herbivorous to carnivorous or detritivores feeding (Bellardini et al., 2024; Benedetti et al., 2015). Growth and feeding experiments in culture evidenced that zooplankton survival and growth based on mixed diets of living and non-living matter is significantly greater than those based only on living matter, highlighting the fundamental role of detritus in sustaining planktonic communities (Harfmann et al., 2019; Roman, 1984). Indeed, although detritus alone is not the most nutritive source of food, it does provide zooplankton non-protein nitrogen like amino-sugars and phenol–protein, and, by acting as substrate, mucopolysaccharides produced by bacteria (Harfmann et al., 2019; Roman, 1984).

Changes in the phytoplanktonic community affected the carbon flows occurring within the plankton food web at BATS, with the decrease in the herbivory of mixo- and protozooplankton, and the increased carnivory and detritivory of zooplankton (Fig. 3). While large phytoplankton might be eaten directly by zooplankton, heterotrophic bacteria and pico-phytoplankton make up only a small portion of the diet of those animals (Roff et al., 1995; Sutherland et al., 2010). Thus, at lower phytoplankton availability, the zooplankton modified their diet moving towards other available sources of food, by increasing detritivory and carnivory (Fig. 3). The crucial role of detritus in the diet of the zooplanktonic community at BATS highlighted from our models was already reported in previous analyses of zooplankton gut content, which reported detritus as the main component of the copepods' diet at BATS (Ducklow, 1994; Schnetzer and Steinberg, 2002). Moreover, from the same analyses it was also found that carnivory was a widespread trophic strategy among copepods at BATS (Ducklow, 1994; Schnetzer and Steinberg, 2002).

3.4. Limitations and future directions

Food web modelling assumptions introduce limitations and the current approach can be improved in the future. For instance, the use of representative species to parameterize the corresponding FNs cannot capture the full metabolic and trophic plasticity of the species embedded in the FNs. Although employing an iterative random search of parameters in quite wide ranges in the 1000 independent replicates could address some of this variability, further improvements could be made in the future as more species-specific information becomes available.

The modelling approach successfully addresses the uncertainties determined by the peculiar location of the studied system by allowing import and export for non-living FNs. However, immigration and emigration for living nodes were not implemented to avoid indeterminate outcomes, which could limit the model's applicability in open ocean systems such as BATS, where lateral advection could affect the input for all functional groups. Resolving this limitation would require several spatiotemporal measures that are rarely available, making the current solution appropriate with the data currently available.

Finally, the steady-state assumption used in our modelling approach, while consistent with the sampling assumption, may be less realistic for highly dynamic systems such as the planktonic community. Nevertheless, the results of our approach could serve as valuable initial conditions for future dynamic models (Christensen and Walters, 2004).

4. Conclusion

During the last decade, ocean warming rapidly occurred in the North Atlantic Subtropical Gyre, leading to a progressive increase of water column stratification, a reduction of nutrient availability, a decrease of NPP, and a shift in the phytoplankton community towards smaller organisms (Bates and Johnson, 2020; Lomas et al., 2022).

Our modeling results show that despite ocean warming and decreased NPP following a significant climatic event, i.e., the 2014 El Niño, the redundancy of the overall planktonic food web remained stable. This resulted from the trophic plasticity of planktonic consumers. Although detritivory was always greater than herbivory (D/H is always greater than 1), after 2014 the system showed a decreased importance of grazing on phytoplankton, with the zooplankton community relying more on carnivory and detritivory probably associated with changes in its taxonomical composition, and therefore trophic features. These results can provide new insights in the interpretation of forecasting models, from which it is expected on a global average a general decrease of NPP (Fu et al., 2015) and secondary production by the end of the century (Chust et al., 2014; Kwiatkowski et al., 2019).

Studying the past over a long term helps us to understand present and future events. In this paper, we defined a procedure to study long-term changes of marine planktonic food webs, optimizing the balance between the detail of the ecological description of the system under investigation and the workload required, in terms of data analyses (i.e., food model derivation and ecological indicators calculations). From this perspective, food web models would help to understand the future effects of climate change on the plankton community of the North Atlantic Subtropical Gyre. This issue is of high importance considering that subtropical gyres are the largest biomes of the planet, covering about 40% of the planetary surface, are expanding in size (Leonelli et al., 2022), and are experiencing a general decrease in phytoplankton biomass and NPP (Signorini et al., 2015).

CRediT authorship contribution statement

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

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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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2024.103389.

Data availability

Raw data are available from the BATS website (http://bats.bios.edu/bats-data/). Data input used to carry out statistical analyses and derive food web models are provided as Supplementary material.

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