



Global change alters coastal plankton food webs by promoting the microbial loop: An inverse modelling and network analysis approach on a mesocosm experiment

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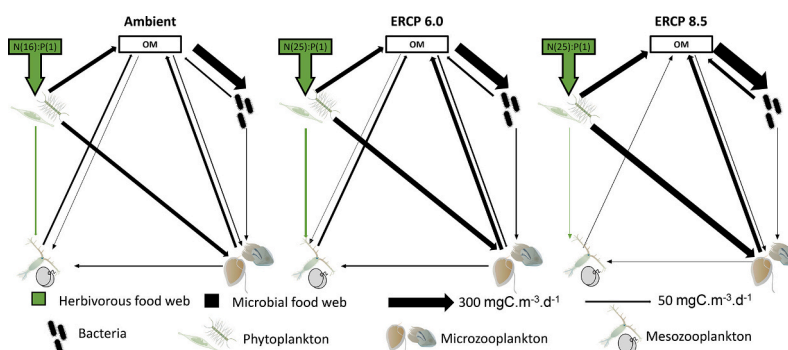
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HIGHLIGHTS

- Global change scenario strengthens the microbial loop.
- Beyond RCP 6.0 scenario, plankton food web was altered.
- We observed reduced energy transfer efficiency to higher trophic levels.
- Food web capacity to recycle carbon was higher under the ERCP 8.5 scenario.
- ERCP 8.5 scenario showed an increased food web stability at the expense of diversity.

GRAPHICAL ABSTRACT



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ABSTRACT

Marine organisms are currently, and will continue to be, exposed to the simultaneous effects of multiple environmental changes. Plankton organisms form the base of pelagic marine food webs and are particularly sensitive to ecosystem changes. Thus, warming, acidification, and changes in dissolved nutrient concentrations have the potential to alter these assemblages, with consequences for the entire ecosystem. Despite the growing number of studies addressing the potential influence of multiple drivers on plankton, global change may also cause less obvious alterations to the networks of interactions among species. Using inverse analyses applied to data collected during a mesocosm experiment, we aimed to compare the ecological functioning of coastal plankton assemblages and the interactions within their food web under different global change scenarios. The experimental treatments were based on the RCP 6.0 and 8.5 scenarios developed by the IPCC, which were extended (ERCP) to integrate the future predicted changes in coastal water nutrient concentrations. Overall, we identified that the functioning of the plankton food web was rather similar in the Ambient and ERCP 6.0 scenarios, but substantially altered in the ERCP 8.5 scenario. Using food web modelling and ecological network analysis, we

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identified that global change strengthens the microbial loop, with a decrease of energy transfer efficiency to higher trophic levels. Microzooplankton responded as well by an increased degree of herbivory in their diet and represented, compared to mesozooplankton, by far the main top-down pressure on primary producers. We also observed that the organisation of the food web and its capacity to recycle carbon was higher under the ERCP 8.5 scenario, but flow diversity and carbon path length were significantly reduced, illustrating an increased food web stability at the expense of diversity. Here, we provide evidence that if global change goes beyond the ERCP 6.0 scenario, coastal ecosystem functioning will be subjected to dramatic changes.

1. Introduction

Human activities and associated increasing greenhouse gas emissions cause simultaneous changes in a range of ocean abiotic parameters. The Intergovernmental Panel on Climate Change (IPCC) has computed different scenarios projecting that, by 2100, ocean's temperature may increase by 1 to 6 °C and pH may decrease by 0.1 to 0.4. In addition, urban, agricultural, and industrial development alter biogeochemical cycles through nutrient runoffs leading to a general increase of dissolved nitrogen:phosphorus (N:P) ratios in European coastal systems (Grizzetti et al., 2012). Consequently, marine organisms are currently, and will continue to be, exposed to the simultaneous effects of multiple anthropogenic-induced environmental changes (Hoegh-Guldberg and Bruno, 2010; Duarte, 2014). Such changes in environmental conditions can have consequences on species assemblages, on interactions between organisms, and therefore on overall ecosystem functioning. Despite the large body of research demonstrating effects of global change on population dynamics and community composition, the challenges associated with quantifying interactions between organisms have led to a paucity of information on the influence of global change on food web functioning (Horn et al., 2021).

Plankton organisms form the base of pelagic marine food webs and are particularly sensitive to ecosystem changes. For instance, warming and changes in dissolved nutrient concentrations in coastal seas observed over the past decades have altered phytoplankton and zooplankton assemblages, marked by shifts in their taxonomic and functional structure, with consequences for the entire ecosystem such as nutrient turnover and fish recruitment (Alvarez-Fernandez et al., 2012; Capuzzo et al., 2018; Di Pane et al., 2022; Di Pane et al., 2023; Marques et al., 2023; Deschamps et al., 2023). However, less is known on how environmental changes could further impact coastal plankton communities, and especially on the combined impact of multiple drivers (Sommer et al., 2015; Garzke et al., 2016; Horn et al., 2020). Moreno et al. (2022) addressed this topic in a mesocosm experiment, and showed that simultaneous warming, acidification, and increased dissolved N:P ratio altered coastal plankton assemblages by favouring smaller phytoplankton and microzooplankton species, and by impairing mesozooplankton abundances. Previous studies also showed a deleterious combined effect of warming and acidification (Peter and Sommer, 2012; Bermúdez et al., 2016), which is further intensified when nutrient availability is low (Peter and Sommer, 2015). These studies provide essential information on the extent to which plankton communities may be restructured as a result of global change, but do not quantify how interactions between organisms may be altered, an information necessary to predict future energy transfer efficiency and food web connectance.

Despite the growing number of studies addressing the potential influence of multiple drivers on plankton organisms (Sala et al., 2000), global change may also cause less obvious alterations to the networks of interactions among species (Tylianakis et al., 2007). Yet, complex biotic interaction networks play an important role in determining the resilience and resistance of ecosystems (Ives and Carpenter, 2007), in maintaining biodiversity (Bascompte et al., 2006), and in mediating ecosystem responses to global change (Suttle et al., 2007). The lack of research on how multiple global change drivers can affect biotic interactions probably stems from difficulties in quantifying changes in

interactions compared to changes in biodiversity (McCann, 2007). Nevertheless, interactions may be particularly susceptible to environmental changes, as they are sensitive to the phenology, behaviour, physiology, and relative abundances of multiple species (Tylianakis et al., 2007). In order to tackle this shortcoming, food web modelling represents a useful tool allowing to estimate energy fluxes between biotic compartments to obtain a representation of the ecosystem functioning from field or experimental studies.

Food web models have been widely used over the past years, aiming to reconstruct a network of components of an ecosystem (i.e. species, taxa or functional units) connected by trophic links (Coll and Libralato, 2012), and to estimate energy transfer and interaction strength between food web components. Despite the importance of energy transfer efficiency within the plankton food web for higher trophic levels, studies on food web processes often display a poor plankton resolution due to the lack of data on energy fluxes at lower trophic levels components (Richardson et al., 2006; Grami et al., 2008). Inverse analyses represent a useful tool to estimate unknown fluxes, which have been used to infer the properties of a system when insufficient data are available (Richardson et al., 2004). Although spatial and temporal variations are neglected in this approach, inverse analyses favour biological complexity of the food web and allow considering a high diversity of components (Tortajada et al., 2012). Since the seminal study of Vézina and Piatt (1988) in which inverse analyses were used to provide a complete description of the plankton food web at steady state, many studies successfully used a similar approach to examine plankton food web dynamics in the field (e.g. Hlaili et al., 2014; Meddeb et al., 2019; Tortajada et al., 2012) and from mesocosm experiments (e.g. Olsen et al., 2006). However, to the best of our knowledge, no study has attended yet to model the potential future functioning of plankton food web under simultaneous changes of multiple global change drivers.

Using inverse analyses applied to data collected during a mesocosm experiment (Moreno et al., 2022), we aimed to compare the ecological functioning of plankton assemblages and the interactions within the coastal plankton food web under different global change scenarios. Our objectives were to 1) estimate and compare carbon fluxes across compartments, 2) predict ecological properties of the plankton food web, and 3) evaluate how the coastal plankton food web could be impacted in the future by global change. We assessed trophic relationships, including predator-prey and producer-decomposer interactions, to determine whether global change will strengthen or weaken these crucial connections. Therefore, this study provides unique insights into the extent and direction of changes in plankton trophic systems in response to global change.

2. Materials and methods

2.1. Experiment and data acquisition

The data used in the study were obtained during a mesocosm experiment conducted over three weeks in the mesocosm facilities at the Wadden Sea station of the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research on the island of Sylt, Germany, in late summer (August–September) 2018 (Meunier et al., 2022; Moreno et al., 2022). Using a multiple driver approach, Moreno et al. (2022) tested the influence of two global change scenarios, based on predictions by the

Intergovernmental Panel on Climate Change for the end of the 21st century (IPCC), on the structure and dynamics of plankton assemblages. Temperature and $p\text{CO}_2$ levels were chosen to represent (1) ambient conditions (i.e. condition observed in the field in real time; T: 18.4 ± 0.3 °C; pH: 8.3 ± 0.1), (2) a moderate global change scenario based on RCP 6.0 ($+1.5$ °C and -0.2 pH), and (3) a more severe global change scenario based on RCP 8.5 ($+3$ °C and -0.3 pH). Additionally, dissolved inorganic nutrient concentrations were also manipulated to simulate the predicted increase in N:P ratios in coastal European seas (Grizzetti et al., 2012), with the Ambient and the Extended RCP scenarios (ERCP) having an N:P ratio (molar) of 16 (Redfield ratio), and 25, respectively, at the onset of the experiment. More detailed information about the experimental design can be found in Moreno et al. (2022).

During the three weeks of the experiment, plankton (i.e. bacterioplankton, phytoplankton, micro- and meso-zooplankton) was sampled ten times (\sim every two days) in order to determine carbon biomass ($\mu\text{gC}\cdot\text{ind}^{-1}$) and species composition. For the three scenarios, we grouped all plankton organisms reported in Moreno et al. (2022) into 10 compartments according to their morphotype, feeding behaviour, and size class (Tortajada et al., 2012). Pelagic bacteria (bac) represented the lowest non-autotroph trophic level. Phytoplankton was composed of four compartments, namely nano-diatoms (ndi), coccolithophores (coc), phytoflagellates (phf) and micro-phytoplankton (mph). Micro-zooplankton was composed of two groups, heterotrophic dinoflagellates (din) and ciliates (cil). Mesozooplankton was composed of three compartments, copepods (cop), cladocerans (cla) and the species *Noctiluca scintillans* (Nsc). List of taxa included in each group, and their relative contribution, are given in appendix (Appendix 1).

Since plankton organisms are highly cyclic, and in order to obtain one value of biomass per compartment for each scenario, we calculated the median carbon biomass over the experiment for each compartment and scenario (Appendix 2), to reflect the temporal dynamics in the steady state food web model. This approach is preferable when the data display some extreme low and high values (typical for blooming organisms) in their distribution as it provides a good measure of central tendency of the plankton assemblage during its growing period. Executing the model at each sampling time step would have revealed timing variations in carbon flows over the growing period (Haraldsson et al., 2018) which is beyond the scope of this study focusing on general trends.

2.2. Inverse analysis

The main objective of this study was to reconstruct the food web structure of plankton assemblages from controlled environment experiments, to quantify interactions and fluxes within the food web, and to assess how those may be influenced by global change. Food webs are represented by energy fluxes between organisms, which are often difficult to quantify, but can be mathematically estimated (van Oevelen et al., 2010). Here, we used inverse Monte Carlo modelling coupled with Markov chains to determine daily carbon flows in the three scenarios at equilibrium ($\text{mgC}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$) using the *LimSolve* package (Meersche et al., 2009) of the R software (R core Team, 2022). Inverse modelling (LIM; Meersche et al., 2009; van Oevelen et al., 2010) allows to model a food web from in situ or mesocosm measurements and equations, estimating the possible values of the unknown fluxes in the food web at equilibrium. LIM is well suited to describe the eco-physiological processes of plankton food web that are often neglected in other types of models (Niquil et al., 2011). In addition, the Monte Carlo Markov chain approach allows the variability built into the model to be considered via minimum and maximum values assigned to each flow. After compartment creation, the LIM approach follows four main steps, starting by (1) constructing an a priori model considering the topology of the food web, i.e. all possible flows between compartments as well as all different import and export flows, (2) setting mass balance equations between flows as equalities, (3) setting inequalities, from either in situ

measurements or from literature, consisting in a number of biological constraints to reduce the range of possible values for each flow, and (4) calculating a large sample of possible solutions for unknown flows (Meddeb et al., 2019).

2.2.1. Food web topology

Since the experiment was performed in a closed environment (mesocosm bags), gross primary production (GPP) of the four phytoplankton compartments was the only source of carbon import within the biological system. Carbon exports, or losses were driven by respiration of all living compartments. Losses by sinking were not considered since the experimental setup simulated a well-mixed water column by constant stirring. Bacterial and phytoplankton exudation, as well as zooplankton excretion contributed to the dissolved organic carbon (doc) pool, while natural mortality (senescence) contributed to the detrital pool (det). Doc was only consumed by bacteria, while det was used by bacteria, ciliates, dinoflagellates, copepods and *N. scintillans*. The dissolution of det into doc was also considered. The microzooplankton compartment (dinoflagellates and ciliates) grazed on phytoplankton (ndi, phf, coc, mph) and bacteria (bac). In the mesozooplankton compartment, copepods were preying on microzooplankton (din and cil) and grazing on micro-phytoplankton and det (Nakamura and Turner, 1997; Suzuki et al., 1999; Castellani et al., 2005). *Noctiluca scintillans* (Nsc) and cladocerans (cla) can consume a wide variety of prey and have a relatively limited ability to actively select food due to their feeding mode (Turner et al., 1988; Kirchner et al., 1996; Zhang et al., 2016). Both Nsc and cla were feeding on all phytoplankton and microzooplankton compartments, but only Nsc on det (Atienza et al., 2006; Zhang et al., 2015). A total of 66 flows were considered in the a priori model of each scenario (Fig. 1).

2.2.2. Model constraints

The system was considered stable and at equilibrium. In other words, the sum of the inflows was equal to the sum of the outflows. The mass balance equations are given in Appendix 3. In order to make the model consistent with the biological reality of the system, the solutions of the flows estimated by the model were constrained by equations and inequations taken from the literature which have been used in numerous studies (Appendix 4). These inequalities represented the threshold constraining the values of biological processes (e.g. ingestion rate) within realistic limits. In order to be as accurate as possible, and where the literature allowed it, predation and grazing rates on specific prey compartments were also used as upper limits.

The maximum specific respiration rate (MSR, Moloney and Field, 1991) represented the maximum respiration boundary for all compartments and was calculated as a function of community weighted mean (CommWM) body mass of the compartment, temperature, and biomass (Richardson et al., 2004; Marquis et al., 2007; Grami et al., 2008). Calculating CommWM body mass for each mesocosm and each sampling day permitted to account for variation in relative abundances of taxa within compartments composed by more than one taxon. To do so, the CommWM body mass, i.e. the mean body mass of a compartment at each sampling day was calculated as follow:

$$\text{CommWM}mc = \sum_{i=1}^n pi^* Bi$$

With *CommWM*mc being the community weighted mean body mass ($\text{pgC}\cdot\text{ind}^{-1}$) of the compartment *c* within the mesocosm (experimental unit + day) *m*, *n* the number of taxa composing the compartment *C*, *pi* the proportion of the taxon *i*, and *Bi* the biomass of the taxon *i* ($\text{pgC}\cdot\text{ind}^{-1}$). Following that, the MSR at 20 °C was calculated for each compartment within each plot:

$$\text{MSR}mc^{@20^\circ\text{C}} = a^* \text{CommWM}mc^{-0.25}$$

With *MSR*mc^{@20°C} being the maximum specific respiration rate (d^{-1}) of the compartment *c* within the mesocosm *m* at 20 °C, and *a* ($\text{pgC}^{0.25}\text{d}^{-1}$) the allometric argument either equal to 1.7 for phytoplankton and

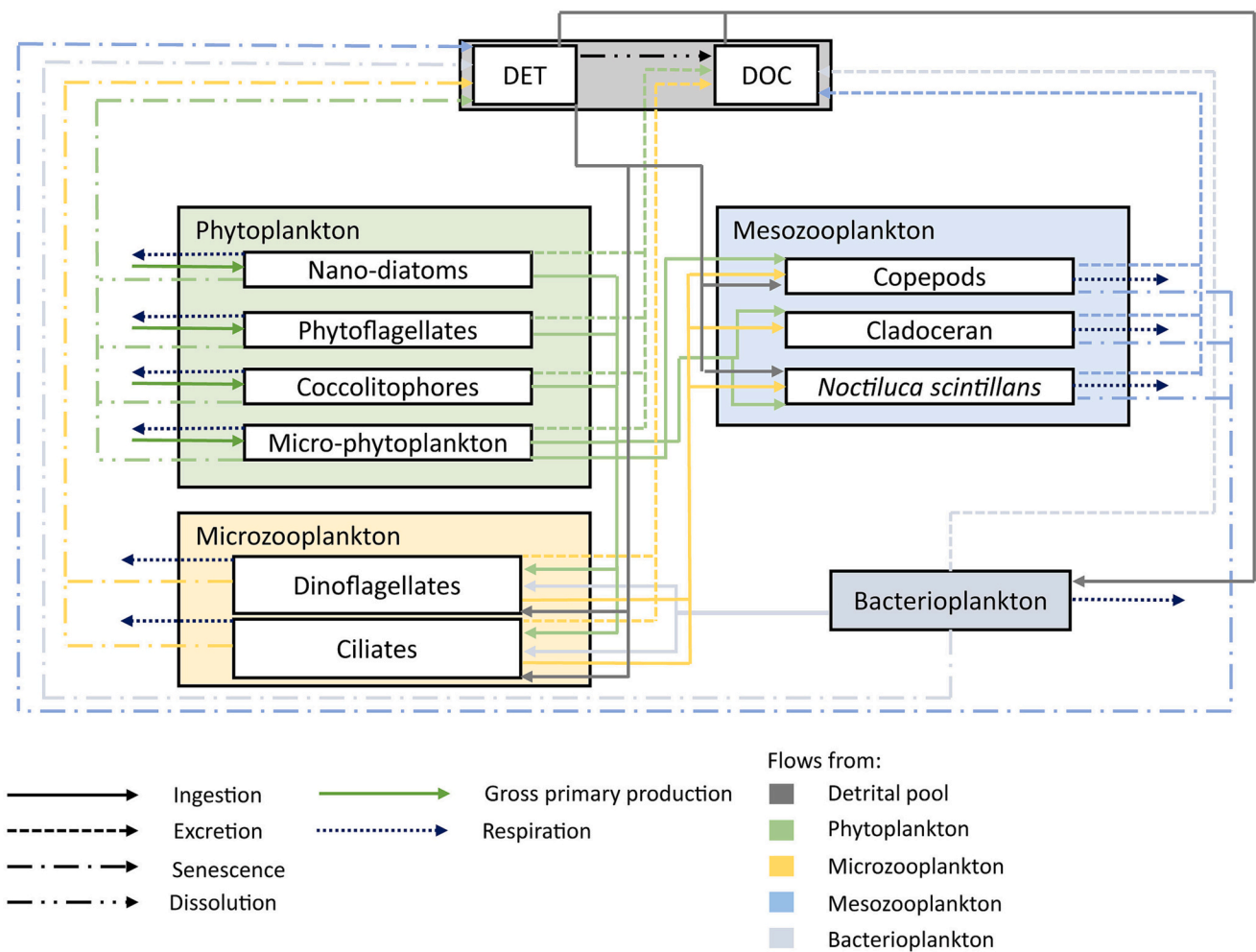


Fig. 1. A priori model structure summarising all compartments and possible flows considered in the food web model.

bacteria, or to 14 for heterotrophs (Moloney and Field, 1991). On the same basis, maximum specific uptake (MSU) and its relative maximum specific senescence (MSS) were calculated for phytoplankton and bacterial compartments respectively. The same formula was applied but the allometric argument (a) was equal to 3.6 (Moloney and Field, 1991). As these values were calculated for a temperature of 20 °C, a Q10 correction, i.e. the factor by which rate changes due to 10 °C increase in temperature, of 2 was applied, as suggested by Moloney and Field (1991). The rates were therefore corrected according to the measured daily temperature of each experimental unit.

Finally, all equations and inequations constrained the model enough to provide estimates of fluxes.

2.2.3. Calculation of LIM solutions

The different equations and constraints were integrated into the LIM-MCMC to calculate the unknown carbon flows between compartments. The vectors of unknown flows were thus sampled through a solutions space of 500,000 iterations with a jump size of 0.5. Model simulations were realised via the *LimSolve* package (Meersche et al., 2009). Visual observations were realised to ensure that the distribution of possible values follows a Gaussian distribution, meaning a good sampling (van Oevelen et al., 2010).

2.3. Indices, trophic pathways and ecological network analysis

The range of values obtained for each flux from the LIM was used to calculate indices allowing to extract ecological tendencies for each

global change scenario. These indices were ratios of fluxes and ecological network analysis.

2.3.1. Ecological network analysis

Ecological network analysis (ENA) allows to summarize information hidden from the different flows of carbon extracted from the model by providing a set of global system indices representing an overview of food web functioning and efficiency (Ulanowicz, 2004; Fath et al., 2019). Following literature (Fath et al., 2019; van der Heijden et al., 2020) and ecological issues specific to this study, we selected six ENA indices in order to compare the organisation and functioning of the plankton food web between the different scenarios.

Total system throughput (TSTp) is the sum of all flows in the system and is considered as proxy of the total power generated by the system. Average path length (APL) is defined as the sum of all the flows between the compartments and the inputs or the outputs (called total system throughflow or TSTf) divided by the total boundary input into the system (Finn, 1976). This index represents the average number of compartments a unit of energy passes from its entry to the system until it leaves (Finn, 1976). Thus, a higher APL indicates a longer pathway length in the system. The Finn Cycling Index (FCI) calculates the fraction of the TSTf that is cycled in the network, traducing how much of the flow would revisit the same compartment multiple times before exiting the system (Fath et al., 2019). A high FCI is then highlighting a high recycling capacity of the system. The flow diversity is calculated by applying Shannon's diversity index to the flow structure, the higher the value, the more diverse and even are the food web flows. The last index calculated

was the relative internal Ascendency (rASCI) which represents the efficiency and definitiveness by which the carbon is transferred internally. The higher the rASCI value, the greater the internal organisation of the food web (Heymans et al., 2014). These indices were calculated from the 500,000 iterations via the *enaR* package (Borrett and Lau, 2014).

A Lindeman spine was created for each scenario using the function *enaTroAgg* (package *enaR*, Borrett and Lau, 2014) which uses the mean of each carbon flow obtained from the 500,000 iterations. This linear chain represents a food web where each compartment is allocated to a discrete trophic level (Fath et al., 2019). In this representation, autotrophs belong to the trophic group I and represent the discrete level where the energy is entering the food web. The following trophic levels represent the integer trophic levels of the consumers. The losses due to respiration, trophic efficiencies, and output as detritus are also detailed. Ultimately, this enables to extract ecological properties such as the relation between detritivory and herbivory (D:H ratio), the degree of omnivory (Omnivory index), the ratio between autotrophic production and respiration, as well as compartment-specific trophic levels.

2.3.2. Proportion of different food sources in zooplankton diet

In addition to ENA, we calculated a series of ecological trophic pathway ratios following (Legendre and Rassoulzadegan, 1995). These ratios of carbon flows are useful tools to summarize and compare processes such as grazing or detritivory between ecological systems and allow the identification of the trophic pathway that dominates a given plankton assemblage (Hlaili et al., 2014). Concretely, they permitted to see whether the proportion of the different food sources changed between global change scenarios. All ratios were ranged from 0 to 1. We used the flow values obtained from the LIM to compute six ratios (Table 1) for each scenario before comparing them (see Section 2.3.3 for the method used). The ratio 1 to 3 allow the calculation of the feeding proportion of microzooplankton on its different food source (i.e. phytoplankton, bacteria, detritus), while ratio 4 and 5 refer to the

Table 1

Ratios of carbon fluxes used in the study, adapted from Hlaili et al. (2014) and Legendre and Rassoulzadegan (1995). det = detrital organic carbon, bac = bacteria, pht = phytoplankton, mic = microzooplankton, mes = mesozooplankton. foodTOMIC = phtTOMIC + bacTOMIC + detTOMIC. foodTOMES = phtTOMES + micTOMES + detTOMES.

Ratio	Formula	Description	Ecological meaning
Ratio 1	$\frac{\text{phtTOMIC}}{\text{foodTOMIC}}$	Consumption rate of total phytoplankton by microzooplankton divided by total consumption rate by microzooplankton	Proportion of pht in mic diet
Ratio 2	$\frac{\text{bacTOMIC}}{\text{foodTOMIC}}$	Consumption rate of bacteria by microzooplankton divided by total consumption rate by microzooplankton	Proportion of bac in mic diet
Ratio 3	$\frac{\text{detTOMIC}}{\text{foodTOMIC}}$	Consumption rate of detritus by microzooplankton divided by total consumption rate by microzooplankton	Proportion of det in mic diet
Ratio 4	$\frac{\text{phtTOMES}}{\text{foodTOMES}}$	Consumption rate of total phytoplankton by mesozooplankton divided by total consumption rate by mesozooplankton	Proportion of pht in mes diet
Ratio 5	$\frac{\text{micTOMES}}{\text{foodTOMES}}$	Consumption rate of mic by mesozooplankton divided by total consumption rate by mesozooplankton	Proportion of mic in mes diet
Ratio 6	$\frac{\text{phtTOMIC}}{(\text{phtTOMIC} + \text{phtTOMES})}$	Consumption rate of total phytoplankton by microzooplankton divided by the consumption rate of total phytoplankton by micro- and mesozooplankton	Grazing pressure exerted by mic versus mes

proportion of herbivory and carnivory in mesozooplankton diet, respectively. Finally, ratio 6 illustrates the grazing pressure of microzooplankton versus mesozooplankton, a value of 1 defining a grazing pressure exclusively exerted by microzooplankton.

2.3.3. Statistical analyses

ENA indices and carbon flow ratios were compared pairwise between scenarios using the Cliff's delta statistic (*effsize* package; Torchiano and Torchiano, 2020). This non-parametric effect size statistic quantifies the amount of differences between groups of observations beyond *p*-values interpretation (Macbeth et al., 2011). In other words, it estimates the probability that a randomly selected value in one group is higher than a randomly selected value from another group, minus reverse probability. Threshold values are then used to determine significance or magnitude. Low threshold values, <0.15 considered as negligible and <0.33 as small, mean no statistical difference. Delta values ranged between 0.33 and 0.47 are considered medium and equal or superior to 0.47, means large difference, both highlighting a statistically difference between groups.

3. Results

3.1. Ecological network indices

The food web structure and functioning, summarized by ENA indices, shows differences between the scenarios (Fig. 2, Appendix 5). Overall, the structure and functioning of the plankton food web were rather similar in the Ambient and ERCP 6.0 scenarios, whereas the ERCP 8.5 scenario substantially altered ENA indices. The sum of energy flows (i.e. TSTp) was significantly different among all scenarios. The lowest TSTp was observed in the Ambient scenario (1603 mgC·m⁻³·d⁻¹), and the highest in the ERCP 6.0 (1986 mgC·m⁻³·d⁻¹). Relative internal ascendancy (rASCI) did not significantly differ between the ambient (31.8 %) and ERCP 6.0 (31.5 %) scenarios but was statistically higher in the ERCP 8.5 (34 %) compared to the other two scenarios. Flow diversity was higher in the Ambient and ERCP 6.0 scenarios (3.20 and 3.24, respectively) than in the ERCP 8.5 scenario (3.02). Finn cycling index showed the opposite pattern, with the highest value in the ERCP 8.5 scenario (14.2 %), and lower ones in the Ambient (12.7 %) and ERCP 6.0 (12 %) scenarios. Despite relatively similar average path length (APL) values in the three scenarios, we observed statistically significant differences between the Ambient and ERCP 8.5 scenarios, with the lowest APL values in the ERCP 8.5 scenario (3.33).

Structural network calculations were performed based on the interaction of the living and non-living compartments in order to determine the mean trophic structure in each scenario (Table 2; Fig. 3).

The highest degree of herbivory (i.e., from trophic level I to II) was observed in the ERCP 6.0 scenario (234 mgC·m⁻³·d⁻¹), while the highest detritivory level (i.e., from D to II) was in the ERCP 8.5 scenario (405 mgC·m⁻³·d⁻¹). The Detritivory:Herbivory ratio was similar in the Ambient and ERCP 6.0 scenarios (1.88 and 1.63, respectively), and was higher in the ERCP 8.5 scenario (2.22). While the mean trophic level did not change between the Ambient and ERCP 6.0 scenarios, it dropped to 2.09 in the ERCP 8.5 scenario, showing a general decrease in trophic level performed by all compartments, especially dinoflagellates and copepods (Table 2). Efficiency of energy transfer to the trophic level III (i.e., predation on trophic level II) was more than twice lower in the ERCP 8.5 compared to the two other scenarios.

3.2. Zooplankton diet and grazing pressure

Using the previously calculated carbon fluxes, we computed trophic pathways to determine the proportion of each food source in the diet of microzooplankton and mesozooplankton. We identified that microzooplankton trophic pathways were overall similar in the Ambient and ERCP 6.0 scenarios, but significantly changed in the ERCP 8.5 scenario

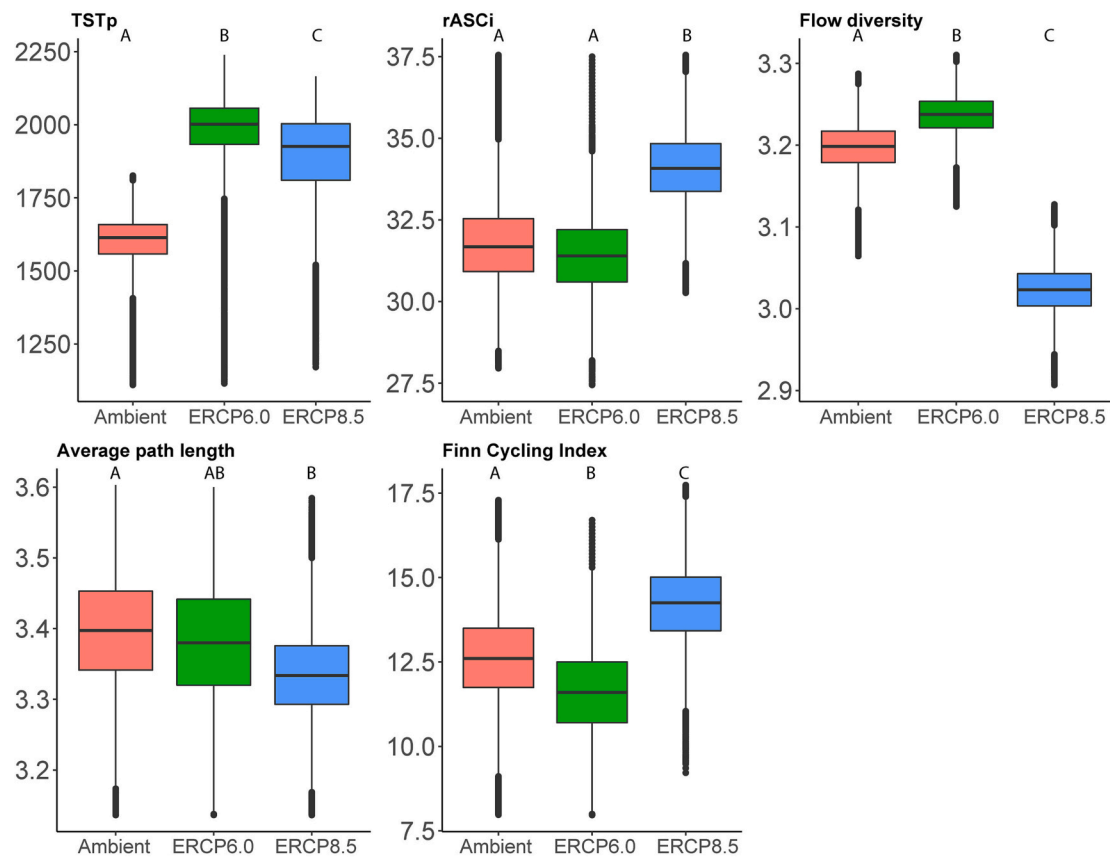


Fig. 2. ENA indices calculated for each scenario. TSTp unit is in $\text{mgC}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$. Flow diversity and Average path length are unitless values. Finn Cycling Index and rASci are percentage values. Letters highlight significant differences resulting from a Cliff's delta superior to 0.33. Two boxplots with a common letter illustrate no statistical difference at this threshold. Cliff's delta values for each pair of comparison are given in Appendix 5.

Table 2

Food web indices referring to the mean trophic level (MTL), detritivory to herbivory (D:H) ratio, and gross primary production (GPP) to autotroph respiration (RI) for each scenario. The trophic level specific to each consumer was also added.

Scenario	MTL	D:H	GPP:RI	Trophic level
Ambient	2.25	1.88	5.21	din
				cil
				cop
				Nsc
				cla
ERCP 6.0	2.25	1.63	5.20	din
				cil
				cop
				Nsc
				cla
ERCP 8.5	2.09	2.22	5.08	din
				cil
				cop
				Nsc
				cla

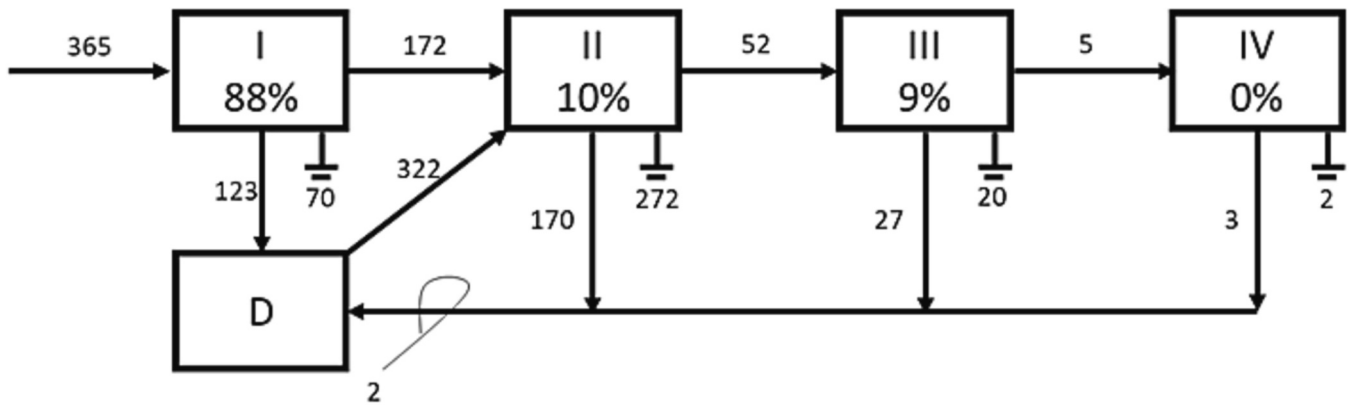
(Fig. 4, Appendix 5). For instance, the proportion of phytoplankton (i.e. ratio 1), bacteria (i.e. ratio 2), and detritus (i.e. ratio 3) in microzooplankton diet, were not statistically different between the Ambient and ERCP 6.0 scenarios. In contrast, the proportion of phytoplankton in microzooplankton diet was significantly higher, and the proportion of bacteria and detritus in microzooplankton diet were significantly lower in the ERCP 8.5 scenario than in the other two scenarios. Similarly, the proportion of phytoplankton in the diet of mesozooplankton (i.e. ratio 4) was significantly higher in the ERCP 8.5 than in the Ambient scenario.

Interestingly, we did not see significant change in the proportion of microzooplankton in mesozooplankton diet (i.e. ratio 5) between the different scenarios, the proportion of carnivory in mesozooplankton diet being around 35 % in all scenarios. The grazing pressure exerted by mesozooplankton on phytoplankton compared to that exerted by microzooplankton (i.e. ratio 6) was significantly lower in the ERCP 8.5 than in the other two scenarios.

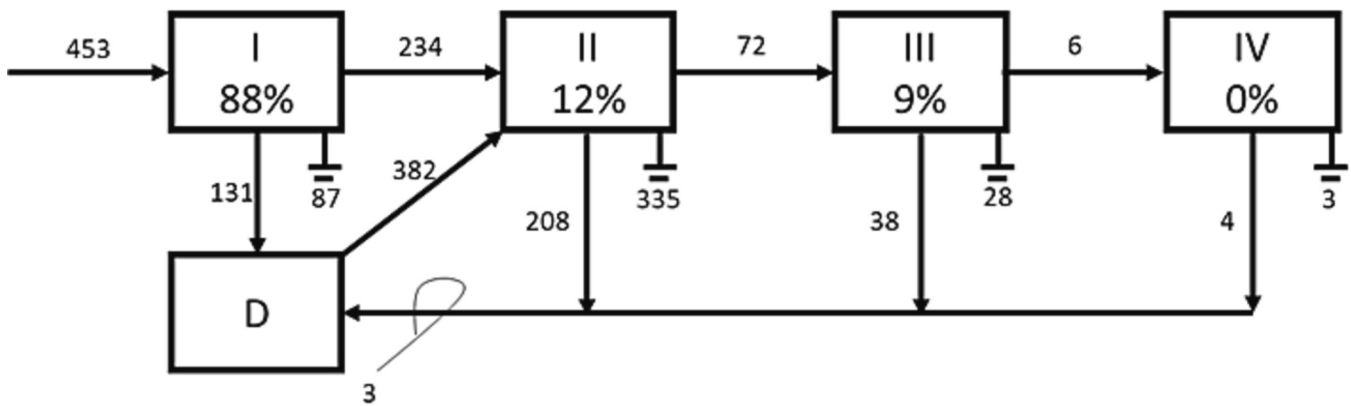
4. Discussion

Overall, we identified that the functioning of the coastal plankton food web was rather similar in the Ambient and ERCP 6.0 scenarios, but substantially altered in the ERCP 8.5 scenario, highlighting a tipping point between the ERCP 6.0 and 8.5 beyond which considerable changes occur. Using food web modelling and ecological network analysis, we identified that simultaneous warming, acidification, and increased dissolved N:P ratio favoured the microbial loop, and decreased energy transfer to higher trophic levels. At the organismal level, autotrophs displayed a lower metabolic balance, respiration rate increasing faster than GPP, while omnivorous organisms increased the degree of herbivory in their diet. Regarding functioning, we also observed that the organisation of the food web and its capacity to recycle carbon were higher under the ERCP 8.5 scenario, but flow diversity and carbon path length were significantly reduced. We provide evidence that if global change goes beyond the ERCP 6.0 scenario, dramatic changes in coastal ecosystem functioning may occur.

Ambient



ERCp 6.0



ERCp 8.5

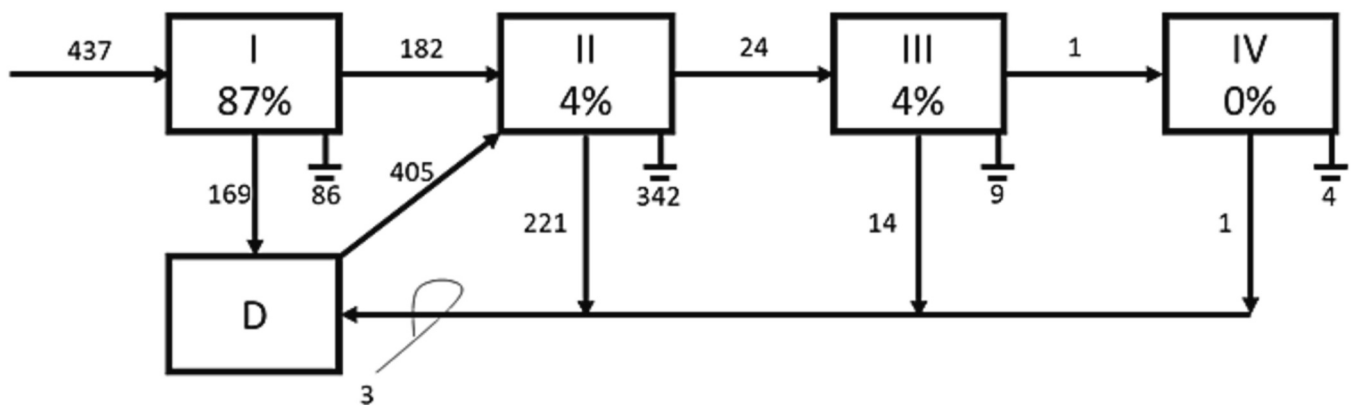


Fig. 3. Lindeman spine of the three scenarios. Flows are in mgC·m⁻³·d⁻¹. Boxes refer to the integer or discrete trophic levels (I, II, III and IV) and detrital pool (D). Percent values refer to the efficiency of energy transfer between the integer trophic levels, i.e. the ratio of input to a trophic level to the amount of flow that is passed on the next level from it. Dashed arrows represent the vector of canonical respirations. Black arrows refer to the vector of the input flow to a trophic level from the preceding trophic level, i.e. the Grazing Chain for the network, and the vector of the returns to detrital pool from each trophic level. The loop refers to the detrital circle, i.e. the flow circulation within the detrital pool.

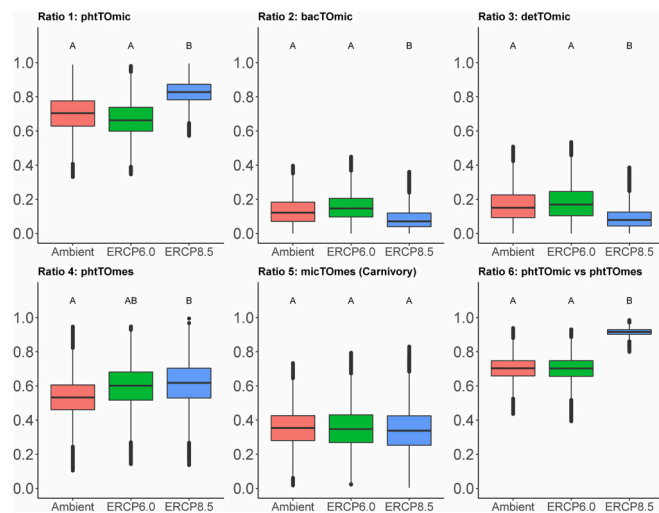


Fig. 4. Distribution of carbon flow ratios for each scenario. Ratios from 1 to 3 refer to realised proportion of phytoplankton, bacteria and detritus in microzooplankton diet. Ratio 4 refers to herbivory proportion in mesozooplankton diet and ratio 5 to its proportion of carnivory. The ratio 6 refers to the grazing pressure exerted by microzooplankton over mesozooplankton. See Table 1 for more descriptions. Letters highlight significant differences resulting from a Cliff's delta superior to 0.33. Cliff's delta values for each pair of comparison are given in Appendix 5. det = detrital organic carbon, bac = bacteria, pht = phytoplankton, mic = microzooplankton, mes = mesozooplankton.

4.1. Impacts of multiple drivers on size structure through changes in metabolic balance

We observed that in the ERCP 8.5 scenario, the simultaneous influence of warming, acidification and increased N:P ratio lowered the metabolic balance (GPP versus respiration) for autotrophs, showing a relatively higher respiration rate per unit of primary production. As summarized by the Metabolic Theory of Ecology (Brown et al., 2004), both phytoplankton respiration and photosynthetic rates should increase with increasing temperature (Gillooly et al., 2001). The temperature-size rule suggests that increased metabolism due to warming may favour smaller organisms (Atkinson, 1995; Angilletta Jr. et al., 2004). While acidification generally shows limited negative effects on phytoplankton and microbes (Joint et al., 2011; Maugendre et al., 2017), it may benefit certain microorganisms, particularly under low nutrient conditions (Riebesell et al., 2013; Sala et al., 2016). In conditions of low nutrient availability, the temperature-size rule may be reinforced for phytoplankton, where small cells with a low surface-to-volume ratio exhibit improved nutrient uptake efficiency, making them more competitive (Marañón, 2015). The observed lower metabolic balance in response to global change could explain the positive selection for smaller plankton organisms reported in our study (Moreno et al., 2022) and other relevant works (Moore and Folt, 1993; Daufresne et al., 2009; Sheridan and Bickford, 2011; Peter and Sommer, 2012; Bermúdez et al., 2016).

A shift in plankton size structure through metabolic balance has the potential to dramatically impact plankton assemblages and therefore food web functioning. Indeed, microzooplankton is particularly well suited to consume small phytoplankton cells, and a reduction in phytoplankton size may redirect energy flows to the microbial food web, instead of efficiently fuelling higher trophic levels (Azam et al., 1983; Legendre and Le Fèvre, 1995).

4.2. Global change strengthens the microbial loop

Microzooplankton play a key role in plankton food web, impacting carbon cycling by consuming a significant portion of primary and

bacterial production (Fenchel, 2008). They contribute to structuring phytoplankton spring blooms, often surpassing copepods in their effects (Löder et al., 2011). Together with their food sources, microzooplankton form the 'microbial food web' (Azam et al., 1983). Mesozooplankton, larger organisms, connect this microbial web to upper trophic levels through predation, serving as a crucial top-down regulator of microzooplankton (Löder et al., 2011). Omnivorous mesozooplankton also directly impact the 'herbivorous food web' by feeding on phytoplankton. (Pomeroy, 1974). The dominance of one food web over another has been shown to be largely influenced by the size structure of primary producers (Azam et al., 1983; Thingstad and Rassoulzadegan, 1999). Legendre and Rassoulzadegan (1995) showed that phytoplankton blooms of large species lead to a dominance of the herbivorous over the microbial food web. Conversely, microzooplankton predominantly feed on smaller phytoplankton species. Blooms of nanophytoplankton (Burkill et al., 1987) or reductions in phytoplankton size structure, as discussed in our findings, may benefit the microbial food web. The low edibility of small phytoplankton for mesozooplankton, stemming from their size class (Paul et al., 2021), results in these microorganisms being less effective in supporting the herbivorous food web.

The strength of carbon flows in the microbial food web appeared to be highly influenced by the different scenarios (Fig. 5). We identified a tipping point between ERCP 6.0 and 8.5, with significantly more carbon going to microzooplankton and bacteria, and much less carbon going to the mesozooplankton compartment. Thus, simultaneously increasing temperature, acidification, and N:P ratios in the ERCP 8.5 scenario, shifted the food web structure to a more pronounced flux of carbon through the microbial loop, while Ambient and ERCP 6.0 scenarios were displaying a more balanced multivorous food web (association between microbial and herbivorous food webs; Tortajada et al., 2012).

In addition to increased carbon flows through microzooplankton, we also observed a higher detrital (both particulate and dissolved organic matter) and bacterial production in the ERCP 8.5 scenario. Due to the gap left by mesozooplankton, large phytoplankton cells were not consumed, which led to higher amount of organic matter going from phytoplankton to the detrital pool (Fig. 5). Moreover, senescence is not the only source of organic matter since phytoplankton exude a significant proportion of dissolved carbon (Fogg, 1983), and exudation has been shown to increase under higher pCO₂ and temperature conditions (Thornton, 2014). Higher metabolism under warming also leads to a higher excretion rate for secondary producers (Vézina and Pace, 1994). The combination of unconsumed phytoplankton and increased excretion/exudation rates likely strengthened detrital production, which in turn enhanced bacterial activity (Aristegui et al., 2014) and fuelled the microbial food web (Ory et al., 2010).

4.3. Global change enhances herbivory in zooplankton diet

The enhanced bacterial production in the ERCP 8.5 led to an overall higher detritivory at the entire food web level. Our study also shows that the proportion of phytoplankton in the diet of microzooplankton and mesozooplankton was the highest in the ERCP 8.5 scenario. Conversely, the proportion of bacteria and detritus in microzooplankton diet was the lowest in this scenario. Two of the ways through which trophic interactions can be affected by higher temperatures are either by an increase in food intake, as metabolic rates and energetic demands increase with temperature, but also by a qualitative change in diet composition (Zhang et al., 2020). For instance, an increased level of herbivory in response to warming has been observed for many omnivorous taxa (Zhang et al., 2020), including zooplankton. This has been linked to the need for ectotherms to consume food with a higher carbon:nutrient ratio at higher temperatures (Croll and Watts, 2004; Laspoumaderes et al., 2022; Malzahn et al., 2016) to fulfil increased carbon metabolic demands in response to warming (Karl and Fischer, 2008; Forster et al., 2011). As primary producers have higher relative carbon content compared to consumers (Sterner and Elser, 2017), omnivores may

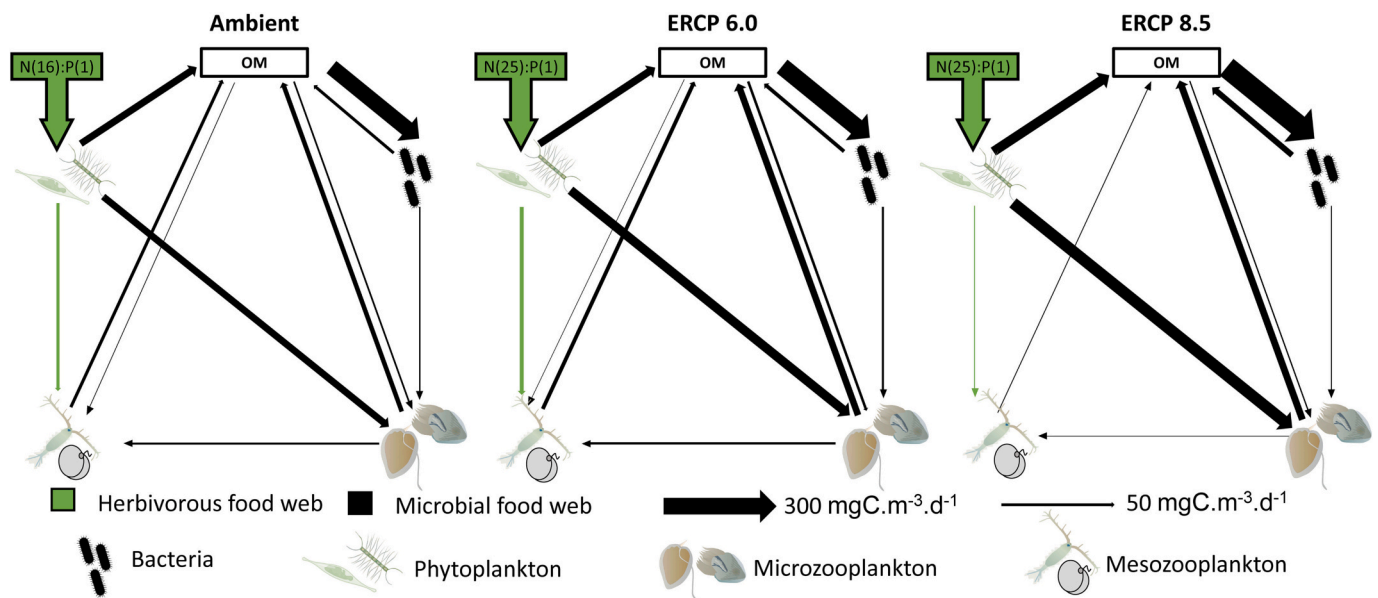


Fig. 5. Simplified food web diagram of carbon flows for each scenario. The height of the arrows is scaled (except for nutrients) according to the amount of carbon (See Appendix 6 for values). The herbivorous and microbial food webs are differentiated by colour code. Under global change scenario, the herbivorous food web is weakening due to small cell size phytoplankton selection. In addition to increased grazing availability for microzooplankton, a substantial part of primary producers, being not consumed, goes to the detrital pool, fuelling the microbial food web. OM = dissolved and particulate organic matter.

increase the degree of herbivory in their diet in order to sustain their increased metabolic demands for carbon. However, there is still no clear consensus, as warming has also been shown to drive a decrease or a non-linear cubic thermal response of consumers nutrient requirements (Laspoumaderes et al., 2022; Ruiz et al., 2020). Additionally, increased feeding rate under warmer conditions may offset higher metabolic demand, resulting in an unchanged carbon demand relative to nutrients (Anderson et al., 2017). While the specific physiological processes remain to be clarified, our study indicates that global change is likely to alter plankton food web by increasing the top-down control of omnivores on primary producers.

In brief, our results are showing a higher bacterial and detrital production in addition to an increased top-down pressure of microzooplankton on primary producers, altogether reinforcing the carbon flows through the microbial loop. This is in line with previous studies stating that, despite a low effect of acidification on microzooplankton (Aberle et al., 2013; Horn et al., 2016), the combination of warming and elevated pCO₂ could enhance the interaction strength between the microbial loop's compartments (Chen et al., 2012; Lara et al., 2013; Olson et al., 2018). Such changes on diet preference and food web structure can alter ecosystem processes, by impacting both carbon cycling and upper trophic levels.

4.4. Implications for ecosystem functioning

ENA indices have been defined and used in order to quantify key properties of food web functioning and stability (Fath et al., 2019). Indices related to cycling, resilience, and organisation such as FCI or rASCI inform on stability properties of the food web (Finn, 1976; Tortajada et al., 2012), and we identified that stability was highest in the ERCP 8.5 scenario. Increased carbon flows through the microbial food web are likely responsible for this, since lower energy transfer efficiency to higher trophic levels reduces overall food chain lengths which is known to increase food web stability (McCann, 2011; Dettner et al., 2012). This is supported by flow diversity, which was the lowest in the ERCP 8.5 scenario, indicating that the energy flows between different compartments were concentrated on few pathways, leading consequently to the lowest amount of system activity generated by each compartment (APL), and lowest system complexity. In addition, the

ERCP 8.5 scenario was characterized by a particularly high TSTp and a low trophic efficiency. Similar results were found in a simulation with increased temperature (Baird et al., 2019), which resulted in an increased detrital production and consumption, a substantial increase in TSTp, and a decline of the herbivorous food web, overall illustrating a shift towards detritus-based food web under warming conditions. In our study, the simultaneous effects of warming, acidification, and elevated N:P ratios produced a more stable and less diverse food web, characterized by few dominant and specialized pathways (low flow diversity and high rASCI) and by low transfer efficiency to higher trophic levels (low trophic efficiency, low APL, high FCI).

The direction of the diversity-stability relationship in food webs has been the topic of numerous debates among ecologists (Rooney and McCann, 2012). Historically, poorly diverse systems have been considered as less stable than richer ones, with a higher diversity of links positively correlated with an increased stability (MacArthur, 1955). However, laboratory experiments on food web structure have shown the stabilizing properties of poor interaction diversity (Rip et al., 2010), and that the relationship diversity-stability should be altered depending on predation pressure in the system; i.e. negative without predators and positive with predators (Jiang et al., 2009). Following this hypothesis, the sharp decrease in predation pressure experienced by the microbial loop in the ERCP 8.5 scenario could have increased stability over diversity. Although our experimental design, limited to plankton, limits our ability to extend our findings to higher trophic levels, we can reasonably expect bottom-up cascading effects on upper planktivorous trophic levels.

Within marine food web, the response of plankton to climate change is crucial for fish. Shifts in plankton assemblages have already shown major effects on fish recruitment over the past decades (Beaugrand et al., 2003; van Deurs et al., 2009; Reid et al., 2016). An increasing dominance of the microbial food web, to the detriment of a more multivorous food web, as reported here, could impact the upper trophic levels. Indeed, the reduction of food web trophic efficiency may create a 'trophic sink' for many planktivorous species which will cascade to higher trophic levels.

Furthermore, an enhanced microbial food web can also have major effects on carbon cycling. Although it has long been debated whether the microbial food web leads to losses of fixed carbon to the system or

whether it primarily channels fixed carbon to higher levels, it is now generally accepted that the microbial food web is a carbon sink (Fenchel, 2008). In addition, the microbial food web plays an important role in the mineralisation of nutrients. Hence, the result presented here of an enhanced microbial food web under future environmental conditions suggests that both carbon losses from the pelagic system, as well as nutrient cycling rates in the water column, are likely to increase.

5. Conclusion

We explored the impact that multiple global change drivers may have simultaneously on the coastal plankton food web. We identified a tipping point between the ERCP 6.0 and 8.5 scenarios, beyond which plankton food web structure and functioning are substantially altered. We identified that the microbial food web gained in prominence, which impaired upper trophic levels, and ultimately the carbon flow diversity. These results, and the shift towards smaller plankton organisms, may be attributed to direct influences of warming, elevated pCO₂ and N:P ratio on metabolism as well as to their indirect effects on prey availability. Moreover, we identified shifts in interaction strengths, with, for instance, higher degrees of herbivory in the diet of microzooplankton and mesozooplankton. These changes are not anodyne, and may have important consequences for ecosystem services, such as nutrient biomineralization, carbon cycling, and fish recruitment.

CRedit authorship contribution statement

Julien Di Pane: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Pierre Bourdau:** Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Sabine Horn:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Hugo Duarte Moreno:** Writing – original draft, Resources, Investigation, Data curation. **Cédric Léo Meunier:** Writing – original draft, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

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

Data used in this paper will be made available on request. Original data from mesocosm experiments can be found at <https://doi.org/10.1594/PANGAEA.940529>.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.171272>.

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