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Abstract

This study highlights the importance of coupling the typology of planktonic food webs and their emerging properties to better describe the ecological status of an ecosystem under permanent disturbance mainly caused by phosphate industry. Linear inverse models were built to describe four stations under various levels of nutrient pressure, using the Markov Chain Monte Carlo method to estimate known and unknown carbon flows, later used to calculate food web typology ratios. Ecological network analysis (ENA) was used to describe the structural and functional properties of each food web. Based on the food web typology ratios, three planktonic trophic pathways (PTP) with different functional indices were distinguished according to nutrient stress. The microbial food web dominated in the least nutrient-rich environment. It mainly relied on phytoplankton production (picophytoplankton < 2 µm) that was mainly transferred by the high microbivory of protozooplankton. In contrast, the herbivorous food web developed in the most nutrient-rich environment, where biogenic carbon was mainly produced by large phytoplankton (microphytoplankton > 10 µm) and channeled to higher trophic levels by herbivorous protozooplankton and metazooplankton. In the other two stations – moderately nutrient-rich systems – the PTP acted as a multivorous food web. Phytoplankton (small and large size fractions) and non-living components (detritus and dissolved organic carbon) played a significant role in carbon production, and competed with protozooplankton and metazooplankton for its transport. ENA indices revealed that the herbivorous food web, with the highest total system throughput and lowest relative Ascendency and cycling, was the most active but the least organized and stable system. In contrast, the microbial food web, with the lowest total system flux and highest Ascendency, was least active but more organized than the herbivorous food web. The multivorous food web displayed the most recycling and most organized system, with high values of the detritivory-to-herbivory ratio, cycling and Ascendency. In addition to ENA indices, which are considered effective tools for studying the structural and functional properties of food webs, marine ecosystem management efforts

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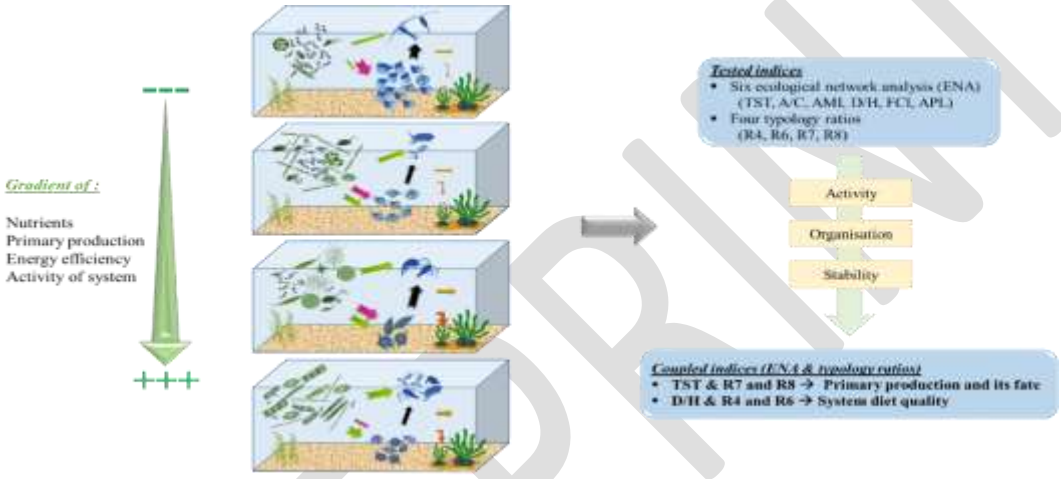
heavily focus on using the "marine food web" as a descriptor of the system's ecological status. However, we suggest that the combination of food web typology and ecological indices could be used as an effective tool for the management and assessment of ecosystem health wherever possible, as well as for the study of anthropogenic pressures.

Keywords: Food-web modeling, ecological network analysis, typology ratios, Mediterranean coastal ecosystem, anthropogenic pressure.

Graphical abstract



Highlights

- Food web typology ratios and ENA indices were used to describe the structural and functional properties of three food webs quantified along a gradient of nutrient stress.
- In the most nutrient-rich waters, the herbivorous food web was most active but least organized and stable.
- In the nutrient-poorest waters, the microbial food web was least active but more organized than the herbivorous one.
- In the intermediate-nutrient-level waters, the multivorous food web was the most recycled and organized system.
- Food web typology ratios + ecological ENA indices represent an effective tool for managing and assessing ecosystem health.

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1. Introduction

In marine waters, primary production can reach higher consumers through different types of food webs. The size structure of phytoplankton is the most relevant functional trait driving carbon transfer pathways. Small phytoplankton are mainly involved in microbial food webs, dominated by protozooplankton (PRO) grazing, while large phytoplankton are mainly consumed by metazooplankton (MET) (e.g., copepods) leading to herbivorous food webs. In-between these two contrasting food webs, the trophic continuum includes multivorous pathways in which microbial and herbivorous trophic patterns both play significant roles (Legendre and Rassoulzadegan, 1995, 1996). These food webs channel biogenic carbon to higher consumers with different efficiencies. Consequently, changes in the size structure of phytoplankton in response to any environmental variation leads to a shift in the food web structure that ultimately influences the ability of the ecosystem to export or recycle biogenic carbon (Decembrini et al., 2009; Legendre and Le Fèvre, 1989; Meddeb et al., 2019).

Determining marine food web types is of great ecological and practical interest, since it is the main step toward characterizing ecosystem functioning and understanding the flows of material and energy within marine planktonic communities. For example, in the fisheries sector, identifying the type of food web can provide a clear idea of the capacity of the system to support the fishing activity, and this helps for proper exploitation and management (Hill et al., 2006; Gaichas, 2008; Knights et al., 2013; Subramaniam et al., 2022). In ecosystems subject to natural and anthropogenic disturbances, knowledge of the marine food web is an essential step in assessing ecosystem responses to these disturbances (Gotwals and Songer, 2010; Lewis et al., 2022). Environmental managers who ignore the structure and functioning of food webs face the danger of making choices that might ultimately result in even greater costs. Impacts may include a health decline of the ecosystem, resulting in less services provided and higher expenses for restoration and repair. Food webs are currently in the foreground in marine ecosystem management programs. The European Marine Strategy Framework Directive has

retained the "marine food web" as a descriptor of the ecological status of the system (Cardoso et al., 2010; European Commission, 2010). This means that one of the major criteria for "good environmental status" is based on the typology of food webs, highlighting the usefulness of identifying the structure and functioning of food webs for managing marine ecosystems.

Several modeling approaches have been developed to characterize marine food webs. These models can provide ecological underpinnings for ecosystem services and the management of natural marine systems (Carpenter et al., 2009; Bagstad et al., 2013; Beske-Janssen et al., 2015). Ecopath with Ecosim (EwE) food web modeling is an approach mainly used to study upper trophic levels subject to fishing (Pauly et al., 2000; Christensen et al., 2005; Sreekanth et al., 2021) and to assess the impact of human exploitation and environmental changes on aquatic food webs (Steenbeek et al., 2018). The linear inverse model (LIM), as defined by Vézina and Piatt (1988), is derived from the physical sciences and is considered among the most useful methods in the study of the state of marine ecosystems (Niquil et al., 2011; Pacella et al., 2013; Taffi et al., 2015; Hines et al., 2018). This method has been combined with the Markov Chain Monte Carlo (MCMC) technique to become the innovative LIM Markov Chain Monte Carlo (LIM-MCMC; Meersche et al., 2009). LIM-MCMC estimates uncertainty in flows and indices of structural and functional properties of the food web (De Laender et al., 2010; Grami et al., 2011; Niquil et al., 2011; Saint-Béat et al., 2013; Chaalali et al., 2015; Hines et al., 2018).

Food web determination and modeling requires knowledge of carbon flows, which cannot always be measured in the field. Therefore, several researchers have provided operational criteria to identify and describe food web types, based on ratios calculated from carbon stocks or fluxes easy to estimate in the field (Legendre and Rassoulzadegan, 1995; Mousseau et al., 2001; Sakka Hlaili et al., 2014). Based on a list of numerous LIM models of plankton food webs, Sakka Hlaili et al. (2014) proposed seven food web typology ratios, which can be used as indicators of the type of trophic pathways in natural planktonic systems.

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Food web modeling is often coupled with ecological network analysis (ENA). ENA provides ecological indicators that characterize ecosystem functioning in terms of activity, retention capacity, organization and food web maturity (Ulanowicz, 1986; Christensen, 1995; Christian et al., 2009; Bodini et al., 2012a; Pezy et al., 2017; de Jonge and Schückel, 2021). ENA indicators are frequently used to assess the impact of natural and anthropogenic pressures on coastal marine ecosystems (Belgrano et al., 2005; Niquil et al., 2014a; Piroddi et al., 2015; Chaalali et al., 2016). They also provide useful information on the degree of stress and stability of food webs (Grami et al., 2008; Heymans et al., 2014; Saint-Béat et al., 2015). In addition, recent studies have presented a set of ENA indices that are most appropriate for studying the health status of ecosystems and could be applied by ecosystem managers (Fath et al., 2019a; Safi et al., 2019). ENA indices were recently applied in the context of the assessment of the quality of four marine ecosystems in the Oslo-Paris (OSPAR) Quality Status Report 2023 (Schückel et al., 2022). The report showed that ENA indices could be used to support the assessment of the structure and functioning of food webs.

Although much effort has been undertaken to assess the ecological state of Mediterranean ecosystems (Méndez et al., 2008; Liquete et al., 2016; Meddeb et al., 2019; Danovaro et al., 2020; Decembrini et al., 2021), studies on the food web structure and function and on ecosystem health remain scarce. For example, MerMex group reported that common indicators of ecological degradation of Mediterranean marine ecosystems are biomass depletion at high trophic levels, simplification of food webs, and shifts in biomass and productivity to lower trophic levels (Durrieu de Madron et al., 2011). Meddeb et al. (2018) showed that LIM-MCMC food web models combined with ENA indicators are a powerful approach to detect changes in the environmental status and anthropogenic impacts in southwestern Mediterranean ecosystems. Several Mediterranean ecosystems, particularly coastal waters, are under strong anthropogenic pressure that causes an imbalance in their communities and biodiversity, with a serious threat on their ecosystem services (Templado, 2014; Danovaro, 2003; Bevilacqua et al., 2021). Therefore, predicting the consequences of anthropogenic disturbances on ecosystem

functioning by a holistic approach is very relevant. The present study aims to investigate the structure of the trophic food web and its emerging properties in a Mediterranean site under permanent anthropogenic pressure (the Gulf of Gabès). It also aims to provide useful ecological indicators for assessing the health status of the ecosystem, to be considered by environmental managers. The Gulf is highly impacted by the Tunisian Chemical Group (TCG), which discharges high quantities of phosphogypsum into the sea that bring high inputs of nutrients and metals and lead to chronic disruption of the ecosystem (Ayadi et al., 2015; El Zrelli et al., 2015). Our previous study in the Gulf (Chkili et al., 2023) was conducted in four stations located at different distances from the TCG complex (Fig. 1). It showed a spatial nutrient gradient causing significant spatial variations in the size structure and production of phytoplankton. This was determined with a spatial change in the community composition of PRO and MET, zooplankton grazing and particle sinking.

In this paper, we used the planktonic carbon stock and flux data determined in our previous study (Chkili et al., 2023), and measured dissolved organic carbon (DOC) and particulate organic carbon (POC) stocks. Then, the LIM-MCMC approach was applied to characterize planktonic food webs and find out what this implied in terms of overall changes in the food web. We used models calculated from LIM-MCMC to explore the planktonic community, highlighting the role played by nutrients in determining phytoplankton size structure. This overview of the planktonic food web allowed us to test the performance of indices commonly used in food web theory to identify the most appropriate ones for practical management. We used a multivariate analysis to achieve a correlative approach of nutrient gradients and indicators of proposed planktonic food web functioning by combining two types of functional indicators: ENAs that apply to all food webs (Niquil et al., 2012; Meddeb et al., 2018; 2019), and R_n ratios that distinguish planktonic food web types (Sakka Hlaili et al., 2014). Our objective was to provide useful and user-friendly indicators for specialists and non-specialists alike.

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2. Materials and Methods

2.1. Study Site

The Gulf of Gabès is located on the south-eastern coast of Tunisia (Fig. 1). It represents more than half of the Tunisian coastline with about 700 km and has the largest continental shelf in the Mediterranean Sea. Its outline measured only on the 20-metre isobath is 110 nautical miles. The 50-metre depth extends to more than 70 nautical miles off Kerkennah Islands (Hattour et al., 2010). The Gulf is characterized by a complex water circulation resulting from the combination of general currents, tidal currents, wind-driven currents and/or swell or littoral currents, and tides reach the highest range in the Mediterranean sea (~ 2 m) (Hattour et al., 2010; Othmani et al., 2017). The Gulf hosts nutrient-rich waters as a result of inputs from anthropogenic activities (Bel Hassen et al., 2009; Drira et al., 2009; Khammeri et al., 2018), in contrast with the well-known oligotrophy of the Eastern Mediterranean Basin (D'Ortenzio and Ribera d'Alcalà, 2009; Ben Brahim et al., 2010). The Gulf is a highly productive ecosystem supporting a high marine biodiversity and contributing up to ~50% of the national fish production (DGPA 2015; Béjaoui et al., 2019). It also constitutes a crucial nursery ecosystem for the Mediterranean sea (Enajjar et al., 2015; Koched et al., 2015). This ecosystem was recently considered as one out of eleven consensus eco-regions in the Mediterranean Sea and is classified as a shallow-water region characterized by phytoplankton blooms (Ayata et al., 2018). Nevertheless, the Gulf is identified as a hotspot of anthropogenic pressures (Reygondeau et al., 2017) because it is strongly impacted by industrialization, notably discharges from phosphate production plants, mainly the TCG (Boudaya et al., 2019; Kmiha-Megdiche et al., 2021). Overfishing is also an increasing problem in the Gulf, leading to an imbalance of the ecosystem and the decline of fisheries resources (Béjaoui et al., 2019).

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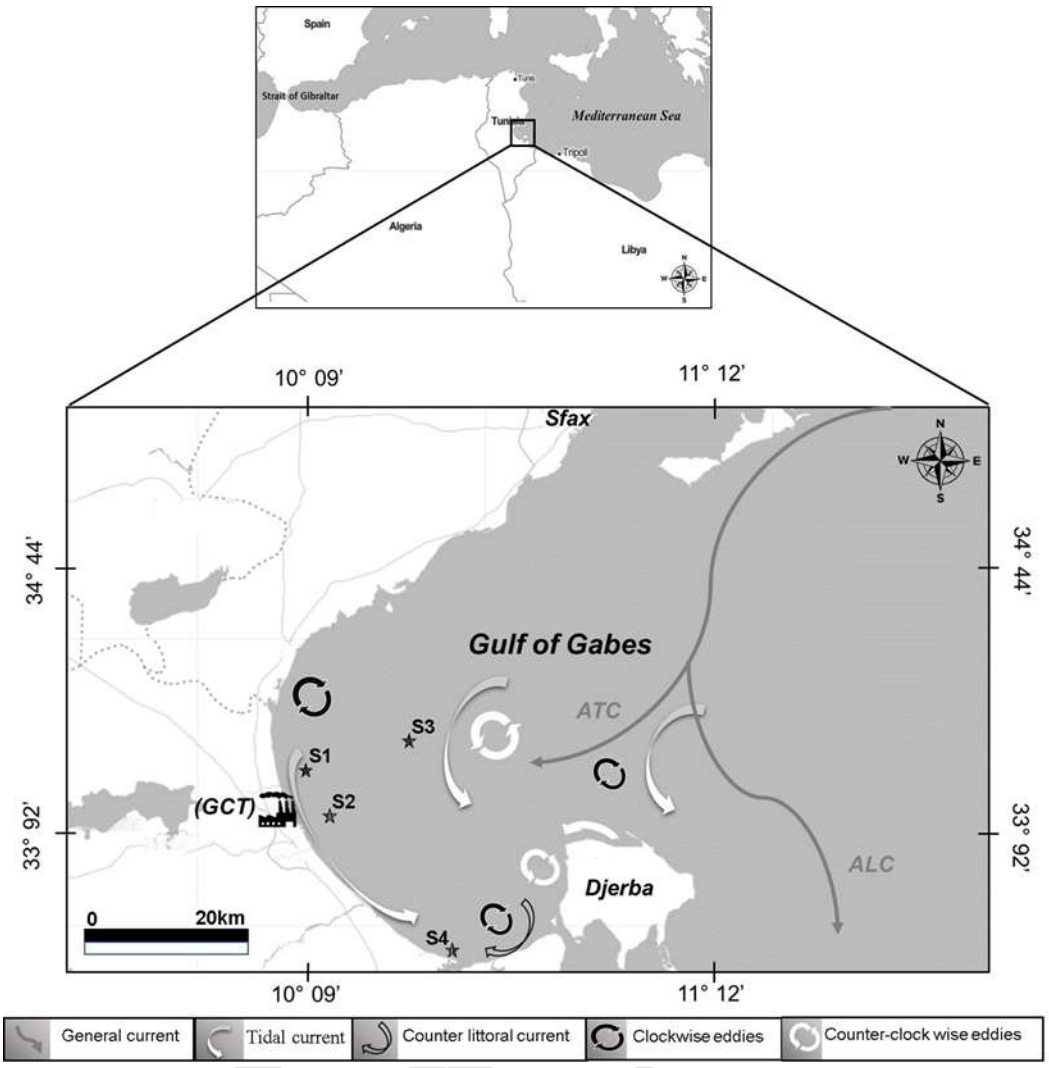

Fig .1. Location of the sampling stations and hydrodynamic circulation in the Gulf of Gabès, southeastern Mediterranean Sea. (From Chkili et al., 2023)

2.2. Sampling and water analyses

Sampling was conducted in the fall of 2017 at four stations selected on either side of the main source of contamination (TCG) (Fig. 1). Station S2 was located in front of the phosphoric acid facility and was suspected to be most affected by phosphogypsum loading; stations S1 and S4 were also located in the marine coastal zone, north and south of S2, respectively, and S3 was an offshore station in front of S1. Chkili et al. (2023) showed that anthropogenic nutrient loading coupled with the complex hydrodynamic circulation within the Gulf create north-south (from S1 to S4) and coast-offshore (from S1 to S3) ascending gradients of nutrients.

Water was collected at three depths at each station (between 0.5 and 14 m depending on the maximum water depth of the station) using an acid-washed water sampler (HydroBios). Subsamples

(5 mL) were immediately filtered on sterilized 0.2-µm polycarbonate filters and frozen in acid-washed vials at -20 °C until DOC analysis using a Shimadzu TOC-5000A autoanalyser (Sharp et al., 1993). The remaining water was pre-filtered through a 200-µm mesh screen to remove MET, and several subsamples were taken to analyze nutrients, POC, bacterioplankton (BAC), size-fractioned phytoplankton (picophytoplankton, PIC: < 2 µm; nanophytoplankton, NAN: 2-10 µm; microphytoplankton, MIC: 10-200 µm) and protozooplankton (PRO). Most of these analyses are described in Chkili et al. (2023). Briefly, inorganic nutrients (N_{inorg}: NO_2^- + NO_3^- + NH_4^+; P_{inorg}: PO_4^{3-}; $Si(OH)_4$) and organic nitrogen (N_{org}) and phosphorus (P_{org}) were measured using a BRAN & LUEBBE type 3 autoanalyzer (Bran + Luebbe Co., Germany). Subsamples for POC determination were filtered on pre-combusted (450 °C, 24 h) GF/F filters (21 mm) and analyzed by the high combustion method and mass spectrometry (Raimbault et al., 2008). The subsamples were fixed with 20% paraformaldehyde solution, placed at 4 °C in the dark for 15 min, and finally frozen at -80 °C in liquid nitrogen until analysis with a CyFlow® Space flow cytometer (Partec) to determine BAC and PIC abundances, according to Khammeri et al. (2020, 2018). The samples for NAN and MIC analyses were fixed with acid Lugol solution (4% final concentration), while the samples for PRO analysis were fixed with alkaline Lugol solution at 5% final concentration (Parsons et al., 1984; Sherr and Sherr, 1993). The cell abundances and species compositions of these planktonic groups were determined under an inverted microscope (Motic AE31E, 100×objective) (Utermöhl, 1931). To determine MET abundance and composition, a WP2 200-µm mesh net, with ring diameter of 28 cm, was used. The net was pulled vertically at a speed of 1 m s^{-1} from depths 10m at S1, 11m at S2 and S4 and 12m at S3 to the surface. A flow meter was used to determine the volume of water filtered during the towing of the net.

2.3. Plankton data

Data about planktonic carbon stocks and carbon fluxes were sourced from Chkili et al. (2023). Biovolumes of BAC, PIC, NAN, MIC and PRO were converted into carbon contents using specific conversion factors or formulae (Table 1 in Meddeb et al., 2018). The length and width of MET

organisms were measured and converted to carbon contents using conversion factors or formulae corresponding to each taxonomic group (Table 1 in Meddeb et al., 2018). The cell carbon of each plankton community was multiplied by its abundance to get its carbon concentration. DOC concentrations were obtained considering that 1 µM of DOC was equal to 12 mg C m^{-3} (Grami et al., 2008). Detrital organic carbon (DET) was estimated as POC minus the carbon biomasses of all organisms. Finally, for each planktonic compartment, carbon concentrations (mg C m^{-3}) from the three depths were vertically integrated over the maximum depth of each station to get carbon stocks (mg C m^{-2}).

Production rates (mg C m^{-2} d^{-1}) of BAC and size-fractioned phytoplankton (PIC, NAN and MIC) as well as their grazing rates by PRO (mg C m^{-2} d^{-1}) were estimated using the dilution technique (Landry and Hassett, 1982; Dokulil and Qian, 2021). The experimental procedure, the analysis and the rate estimation are detailed in Chkili et al. (2023). The relative contribution of PIC, NAN and MIC to primary production was calculated as the production rate of each size fraction divided by the total phytoplankton production rate multiplied by 100.

Grazing of phytoplankton (NAN and MIC) by MET (mg C m^{-2} d^{-1}) was assessed by the gut fluorescence method (Meddeb et al., 2018; Tseng et al., 2008) The experimental procedure and the calculations are detailed in Chkili et al. (2023). Sinking fluxes were estimated by collecting organic particles (NAN, MIC, DET and MET fecal pellets) that settle down along the water column in sediment traps moored at two meters from the bottom of each station. The deployment of sediment traps, the analyses of their contents and the calculation of the vertical fluxes of each type of particle are described in Chkili et al. (2023).

2.4. Model development

Field data provide a limited number of known fluxes. To have a complete model of planktonic food webs, the LIM-MCMC method (Meersche et al., 2009) was used to construct carbon fluxes between planktonic compartments at the four stations. This approach is based on four steps: (i) constructing an *a priori* model, (ii) setting the equalities, (iii) setting the inequalities, and (iv) calculating possible solutions for each flux.

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2.4.1. *A priori model*

The *a priori* model included planktonic compartments and all possible known and unknown carbon fluxes between them. In each station, the model included eight compartments: BAC, PIC, NAN, MIC, PRO (mainly protozoans < 200 µm: heterotrophic nanoflagellates, dinoflagellates and ciliates), MET (mainly metazoans > 200 µm), DOC and DET. The model encompassed thirty-five fluxes between the compartments and their outside (Fig. 2). Gross primary production (GPP) of the three phytoplankton size fractions (PIC, NAN and MIC) was the only source of carbon input to the network. Some of this carbon was lost by respiration (RES) by all living compartments, sinking (SINK) of most compartments (except BAC, PIC and PRO), and DOC export (EXP). It was assumed that the very small size of PIC and BAC did not allow them to generate a sinking flux. Dissolution of detritus, exudation by phytoplankton and excretion by zooplankton (PRO and MET) contribute to DOC formation. BAC were the only users of DOC since other potential DOC consumers such as choanoflagellates were absent in our samples (Chkili et al., 2023). All living compartments but PIC and BAC contributed to generate DET through mortality, production of faecal pellets by MET and sloppy feeding by zooplankton. Concerning trophic interactions, BAC and all phytoplankton size fractions were consumed by PRO, while MET only consumed NAN and MIC because smaller cells (BAC and PIC) are inefficiently captured by MET (Fortier et al., 1994). PRO and DET also contributed to a food source for MET.

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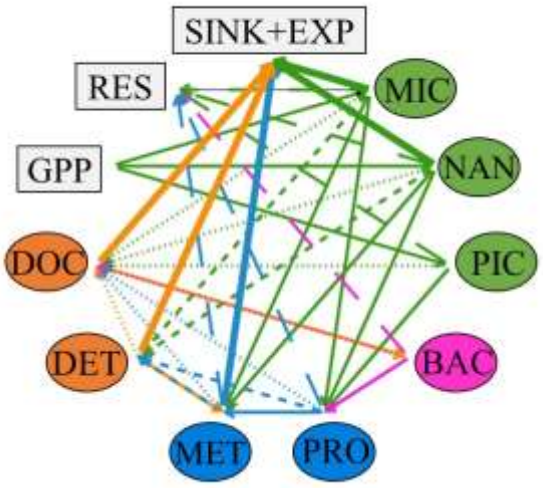

Fig. 2. *A priori* food web model for the four stations. Colored circles represent internal compartments. Green, primary producers (PIC = picophytoplankton < 2 µm, NAN = nanophytoplankton 2-10 µm, MIC = microphytoplankton 20-200 µm); pink, bacterioplankton (BAC); blue, consumers (PRO = protozooplankton, MET = metazooplankton); orange, non-living carbon (DET = detritus, DOC = dissolved organic carbon). Gray boxes correspond to external connections: carbon inputs (gross primary production, GPP) and outputs (respiration, RES; particle vertical sinking, SINK; DOC export, EXP). The arrow color of each flow refers to its source.

2.4.2. Equalities and inequalities

The setting up of the equalities is an essential phase for establishing the mass balances of the network. If the mass of the compartment is constant during the period under consideration, the sum of the ingoing fluxes should be equal to the sum of the outgoing fluxes. However, the daily variations in biomass with respect to the daily flux values were neglected. A mass balance equation was written for each compartment (Table A.1).

The subsequent step was to impose ecological limits (maximum and/or minimum) for each unknown flux to reduce the range of possible solutions. The inequalities represented two types of ranges. The first range considered the average values of the fluxes measured in the field (i.e., production rates of BAC, PIC, NAN and MIC; grazing rates by PRO and MET, and

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316 vertical sinking of particles). These average values did not allow the model to estimate flows
317 with certainty. Therefore, we proposed to define the minimum and maximum values for each
318 flux by calculating a confidence interval around the field data, i.e., by using the minimum and
319 maximum of the mean value of each flux. In doing so, we followed the method recently
320 developed in the LIM-MCMC applications, that considers all local data as ranges, with two
321 inequalities for minimum and maximum values instead of equations, in order to consider the
322 confidence of the estimation (e.g. Nogues et al., 2021).

323 Thirteen inequalities derived from field measurements were considered for every station
324 (Table A.2). A second group of constraints was adopted from the literature to constrain the
325 unknown fluxes (Vézina and Piatt, 1988; Steinberg et al., 2000; Vézina and Pahlow, 2003).
326 These inequalities included the lower and/or upper limits of several processes such as
327 respiration of all living compartments; DOC production by phytoplankton, PRO, MET and
328 BAC; production and dissolution of DET; growth efficiency of BAC, PRO and MET, and
329 assimilation efficiency of PRO and MET. For preferential ingestion by MET, we used diet
330 constraints, which are based on the assumption that MET feeding depends on the availability
331 of their prey, i.e., the abundance of a prey relative to other prey (Haraldsson et al., 2018). The
332 availability (A, as a fraction) of prey compartment *i* to consumer compartment *j* was calculated
333 based on the specific diet data about each species *k* in the consumer compartment:

334 $$A_{ij} = \sum_{k=0}^{n} \left(\frac{prey_{ijk} \times SC}{\sum prey_{ijk}} \times \frac{consum_{jk}}{\sum consum_{jk}} \right)$$

335

336 where prey and consum are the biomasses of the prey and consumer, respectively, SC is the
337 selection coefficient (= 1 when there was no selection, = 1.4 when there was assumed positive
338 selection, and = 0.6 when there was negative selection) (Table A.3). Twenty-six inequalities
339 from this second group were applied in the model to the four stations (Table A.3).

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2.4.3. Solutions

The calculation of the unknown fluxes was the last step of the inverse analysis. The LIM-MCMC method based on the mirror technique defined by Meersche et al. (2009) estimates each unknown flux. Two parameters must be specified to use this technique: the number of iterations to be used to maximize the exploration (or coverage) of the polytope of solutions, and the jump value – the average distance between two successive solutions in a randomly chosen direction. For the present study, a jump value of 10 mg C m^{-2} d^{-1} and 300,000 iterations were adopted to run the models and optimize the coverage of all possible solutions.

2.5. Food web typology ratios

To describe the different interactions between compartments and identify the type of trophic pathway, Sakka Hlaili et al. (2014) provided seven operational criteria based on carbon flux ratios that can be easily estimated in the field. In our study, four food web typology ratios were calculated from the flux data yielded by the models (Table 1). Ratio R4 (total net phytoplankton production divided by the net production of potential food for PRO) determined the relative importance of phytoplankton production, while ratio R6 (net production of DOC and DET divided by the net production of potential food for PRO) expressed the significance of production by non-living compartments. Ratio R7 (picophytoplankton net production divided by total phytoplankton net production) discriminated between herbivorous ($R7 \leq 0.1$), multivorous ($0.1 < R7 < 0.6$) and microbial food webs ($R7: \geq 0.6$). Ratio R8 (consumption rate of total phytoplankton by PRO divided by the consumption rate of total phytoplankton by PRO and MET) identified the main phytoplankton grazers (i.e., PRO when $R8 > 0.5$ or MET when $R8 < 0.5$).

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Table 1. Carbon flow ratios for the determination of planktonic food web types (Sakka Hlaili et al., 2014). PIC, Picophytoplankton; PRO, Protozooplankton; MET, Metazooplankton; DOC, Dissolved Organic Carbon; DET, Detritus.

Ratio	Formula	Description	Trophic interpretation
Ratio 4 (R4)	Pnetpht*/D2**	Total net phytoplankton production divided by net production of potential (PRO) feed	Phytoplankton contribution to production of potential protozooplankton feed
Ratio 6 (R6)	(PnetDET + PnetDOC)/D2	Net production of DOC and DET divided by net production of potential PRO food	Contribution of non-living organic matter to production of potential PRO feed
Ratio 7 (R7)	PnetPIC/Pnetpht	Net PIC production divided by total net phytoplankton production	PIC contribution to total net phy production
Ratio 8 (R8)	pht-PRO/(pht-PRO + pht-MET)	Consumption rate of total phytoplankton by PRO divided by consumption rate of total phytoplankton by PRO and MET	Importance of PRO in the consumption of total phytoplankton

*Pnet = Net production, pht = Total phytoplankton
**D2= Pnetpht + PnetBAC + PnetDET + PnetDOC

2.6. Ecological network analysis (ENA)

An ecological network analysis (ENA) was applied to describe the functioning of the ecosystem from the flux values obtained by the LIM-MCMC approach. ENA examines the food web structure within the ecosystem and its emerging properties (Ulanowicz, 1986; Fath and Patten, 1999; Tecchio et al., 2015; Meddeb et al., 2019). A number of calculated indices were considered to compare and characterize the stations:

- ***Total system throughput (TST):*** The total system throughput is the sum of all fluxes through all compartments (Kay et al., 1989). The TST is interpreted as an indicator of the system activity (Rutledge et al., 1976; Latham, 2006) and is calculated as:

$$TST = \sum_{i=1,j=1}^{n} T_{ij}$$

Where Tij is the flux from compartment i to compartment j. The size of the system is associated with its level of activity, which is determined by the number of compartments and the magnitude of the fluxes (Bodini et al., 2012; Ulanowicz, 1986).

Link: https://www.sciencedirect.com/science/article/abs/pii/S0924796323000921

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- ***Average mutual information (AMI):*** This index measures the efficiency with which materials are transported through the network. It describes the organization of exchanges between compartments (Latham and Scully, 2002; Ulanowicz, 2004) and is expressed as follows:

$$AMI = \sum_{i=1,j=1}^{n} T_{ij} Q_i \log\left(\frac{T_{ij}}{\sum_{k=1} T_{kj} Q_k}\right)$$

with T_{ij} is the flux from compartment i to compartment j; Q_i is the probability of a unit of energy passing through i; and T_{kj} and Q_k represent the total flux of j and the probability of a unit of energy passing through other compartments. Low values of AMI indicate that the system is evolving towards a web-like food web, while high values show an increase in specialization/constraints (Ulanowicz, 1997, 2004).

- **Ascendency/Development Capacity (*A/C) ratio:*** The A/C ratio shows the degree of organization of the food web (Ulanowicz et al., 2009). Ascendency (A) represents the organized part of the ecosystem and is more informative when expressed in relation to the development capacity (relative Ascendency, A/C). The development capacity (C) represents the maximum possible value of Ascendency that an ecosystem can reach.

It is calculated as follows:

$$A/C = \frac{AMI * T..}{-\sum_{ij} t_{ij} \log\left(\frac{t_{ij}}{T}\right)}$$

- ***Finn cycling index (FCI):*** The FCI (Finn, 1976) represents the fraction of the total flux through the system that is cyclic, i.e., the proportion of the flux that revisits the same node several times before exiting the system. The recycled flux from node i (TSTci) can be calculated from the following equation:

$$TST_{ci} = \left({}^{(n_i i - 1)}/_{n_i i}\right) T_i$$

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Thus, the FCI can be calculated by dividing the total cycling flux (TST_{ci}) by the total system throughput (TST):

$$FCI = \sum {TST_{ci}}/{TST_{flux}}$$

- ***Average path length (APL):*** The APL is the mean number of compartments crossed by a carbon unit from its entry to its exit from the system. It is an indicator of the amount of system activity (TSTflow) generated by each unit input into the system (Finn, 1976). It is calculated as follows:

$$APL = \frac{TST_{flux}}{\sum_{i=1}^{n} z_i}$$

APL is an indicator of the amount of system activity (TST_{flux}) generated by each unit of input to the system. Thus, Jørgensen et al. (2000) interpreted this index as an indicator of the growth and development of the system, which they renamed network aggradation since it forms an indicator of the organization of the system and its capacity to do more work with given resources (the input limit).

- ***Detritivory/herbivory (D/H) ratio:*** The D/H ratio measures the importance of grazing of phytoplankton relative to detrital carbon consumption. It is a simple ratio where detritivory represents the DET-MET and DOC-BAC fluxes and herbivory represents phytoplankton consumption fluxes by PRO and MET (Kay et al., 1989; Ulanowicz, 1992; Baird et al., 2009).

2.7. Statistical analyses

2.7.1. Multiple factor analysis (MFA)

A multiple factor analysis (MFA) was performed to identify the interrelationships between different ecological indicators (food web typology ratios and ENA indices) as well as environmental variables (inorganic and organic nutrients) and some of the calculated fluxes (GPP of PIC, NAN and MIC, bacterial production and sinking of NAN, MIC and MET). Each station was considered as a group, which by definition included variables measured at the same

date. The objective was to find a common or representative structure for all groups. Unlike individual principal component analysis, MFA can integrate groups of variables (at different sampling dates) in a single analysis, and analyzes the relationship within each group and over time (Escofier and Pagès, 1990).

The calculated indices as well as the environmental and biological data determined in the water column were organized in a matrix where the rows (individuals) represented the 50 randomly chosen values of LIM solutions and the columns (identified variables) were the parameters determined in each station. There were 200 individuals (or rows) in total, and 21 variables were used for each sample. The analysis consisted of a principal component analysis for each table, weighted by dividing each variable by its PCA eigenvalue for the final analysis. Four tables were considered: ENA indices, typology ratios, primary and bacterial production, and export.

All modeling and statistical analyses were performed in R software with LIM libraries for linear inverse modeling, NetIndices for ENA calculation as well as FactomineR, Ade4 and vegan for digital analyses of the results.

2.7.2. Cliff's δ test for comparing network indices between stations

The Cliff's δ test was used to statistically test ENA index differences between models (Tecchio et al., 2016). This method is necessary for large sample sizes (in our case 300,000 values for each stream). Four pairwise comparisons were performed for each ENA index. Then, the following values were used to define small, medium, and large effects (small, $|\delta| >= 0.11$; medium, $|\delta| >= 0.28$; large, $|\delta| >= 0.43$; Vargha and Delaney, 2000; Romano et al., 2006).

3. Results

3.1. Input, output and throughput flows

We calculated 34 carbon flows in each station using LIM-MCMC analysis (Table 2). Phytoplankton gross primary production (GPP) was the only carbon input in the food web.

453 Total GPP followed an ascending gradient from S1 (1,838.5 mg C m^{-2} d^{-1}), then S2, S3 (2,240.2
454 - 2,954 mg C m^{-2} d^{-1}) up to S4 (4,110.1 mg C m^{-2} d^{-1}) (Fig. 3 A). The contribution of each
455 phytoplankton size fraction to total GPP varied among stations (Fig. 3 B). PIC was the main
456 producer in S1 (76%), *versus* MIC in the other stations (56-80%). The contribution of NAN
457 was low (7-21%), but reached 33% in S4.

458 **Table 2.** Mean values of the fluxes estimated by the Monte Carlo Markov chain inverse linear
459 modeling (LIM-MCMC) approach for each station in the Gulf of Gabès.

Flow description	**Symbol**	**estimated value (mg C m^{-2} d^{-1})**			
		S1	**S2**	**S3**	**S4**
Microphytoplankton gross primary production	GPP-MIC	206.40	1258.00	2359.00	2451.00
Nanophytoplankton gross primary production	GPP-NAN	228.10	481.00	195.70	1365.00
Picophytoplankton gross primary production	GPP-PIC	1404.00	501.20	339.30	294.10
Microphytoplankton respiration	MIC-RES	11.24	78.49	151.70	167.70
Microphytoplankton dissolved organic carbon exudation	MIC-DOC	20.35	144.77	333.20	268.00
Microphytoplankton net production	MIC-DET	0.91	175.88	1259.60	72.48
Microphytoplankton grazing by protozooplankton	MIC-PRO	64.78	441.70	310.90	994.00
Microphytoplankton grazing by metazooplankton	MIC-MET	58.07	281.80	209.80	650.50
Microphytoplankton sinking	MIC-LOS	51.03	135.00	93.60	298.50
Nanophytoplankton respiration	NAN-RES	19.67	39.65	21.41	131.43
Nanophytoplankton dissolved organic carbon exudation	NAN-DOC	29.01	69.71	30.58	182.43
Nanophytoplankton detritus production	NAN-DET	72.82	247.80	14.12	632.50
Nanophytoplankton grazing by protozooplankton	NAN-PRO	88.33	100.93	116.70	315.20
Nanophytoplankton grazing by metazooplankton	NAN-MET	16.40	22.54	12.72	102.71
Nanophytoplankton sinking	NAN-LOS	1.92	0.37	0.14	0.49
Picophytoplankton respiration	PIC-RES	298.23	76.28	96.51	81.57
Picophytoplankton dissolved organic carbon exudation	PIC-DOC	332.50	120.73	88.99	65.67
Picophytoplankton grazing by protozooplankton	PIC-PRO	773.10	304.10	213.80	146.90
Protozooplankton respiration	PRO-RES	464.70	374.10	352.60	547.60
Protozooplankton dissolved organic carbon excretion	PRO-DOC	146.80	248.00	248.60	277.90
Protozooplankton detritus production	PRO-DET	323.60	244.00	197.40	307.70
Protozooplankton consumption by MET	PRO-MET	317.30	484.70	406.90	684.70
Metazooplankton respiration	MET-RES	147.34	353.00	203.50	575.90
Metazooplankton dissolved organic carbon excretion	MET-DOC	63.31	234.50	125.25	270.20
Metazooplankton detritus production	MET-DET	93.79	228.80	105.15	324.00
Metazooplankton sinking	MET-LOS	125.20	313.90	201.90	541.70
Bacterial respiration	BAC-RES	219.30	308.50	338.00	302.70
Bacterial dissolved organic carbon production	BAC-DOC	112.94	250.65	263.24	100.02
Bacterial grazing by protozooplankton	BAC-PRO	326.10	504.00	564.00	361.90
Dissolved organic carbon uptake by bacteria	DOC-BAC	658.30	1063.20	1165.00	764.60
Dissolved organic carbon output	DOC-LOS	54.55	29.10	38.05	460.30
Detritus dissolution	DET-DOC	8.03	26.91	113.50	60.77
Detritus consumption by metazooplankton	DET-MET	37.88	338.10	6.35	273.90
Detritus sinking	DET-LOS	445.30	531.50	1456.00	1002.00

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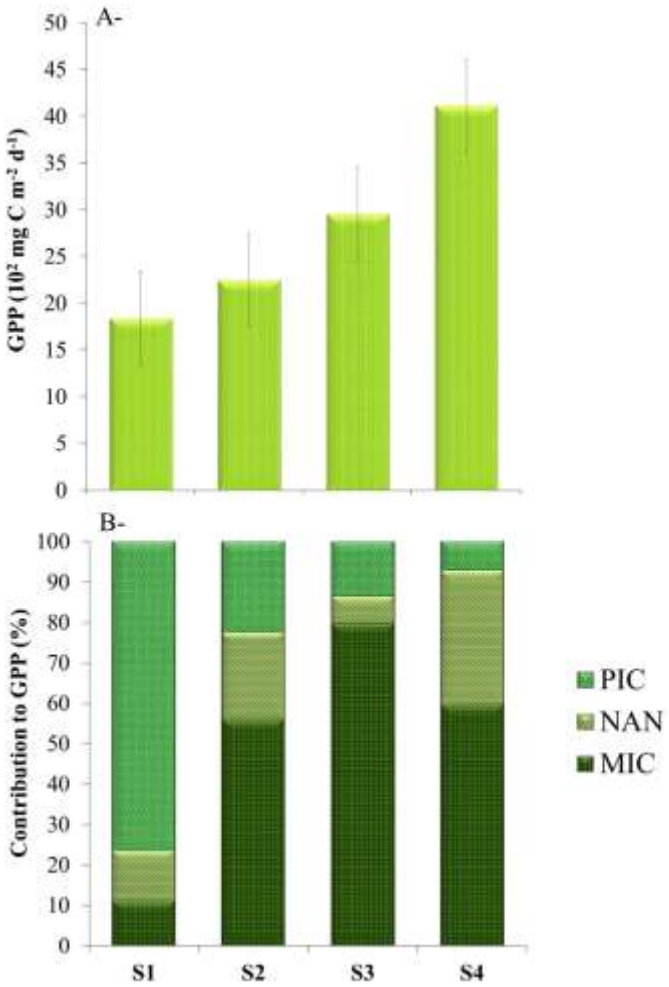

Fig. 3. Total gross primary production (GPP) (A), and contribution of each phytoplankton size fraction to GPP (B). PIC, picophytoplankton; NAN, nanophytoplankton; MIC, microphytoplankton.

The output flows were represented by respiration of all living organisms, DOC export, and particle vertical sinking of MIC, NAN, MET and DET. These outputs differed among stations (Table 2, Fig. 4 A). Respiration represented the main carbon output in S1 (63%) and S2 (55%) and to lesser extent in S3 and S4 (39-44%) (Fig. 4 A). Carbon loss through respiration was about 2-32% of GPP in S2, S3 and S4, and 1-40% in S1. PRO, MET and BAC altogether contributed 77-84% of respiration in S2, S3 and S4, while the total contribution of phytoplankton was ≤23%. In S1, the contribution of phytoplankton to this output increased (~30%) due to the enhancement of PIC respiration (Fig. 4 B). DOC export was low, except in S4 where it formed 11% of the carbon output. Particle sinking provided 34-45% of total carbon loss in S1, S2 and S4, and 59% in S3 (Fig. 4 A). Particle sinking formed the second main source

of carbon output (43-59%). MET and MIC represented most of the living sinking particles: they represented 12-32% and 5-16% of carbon loss, respectively (Fig. 4 C).

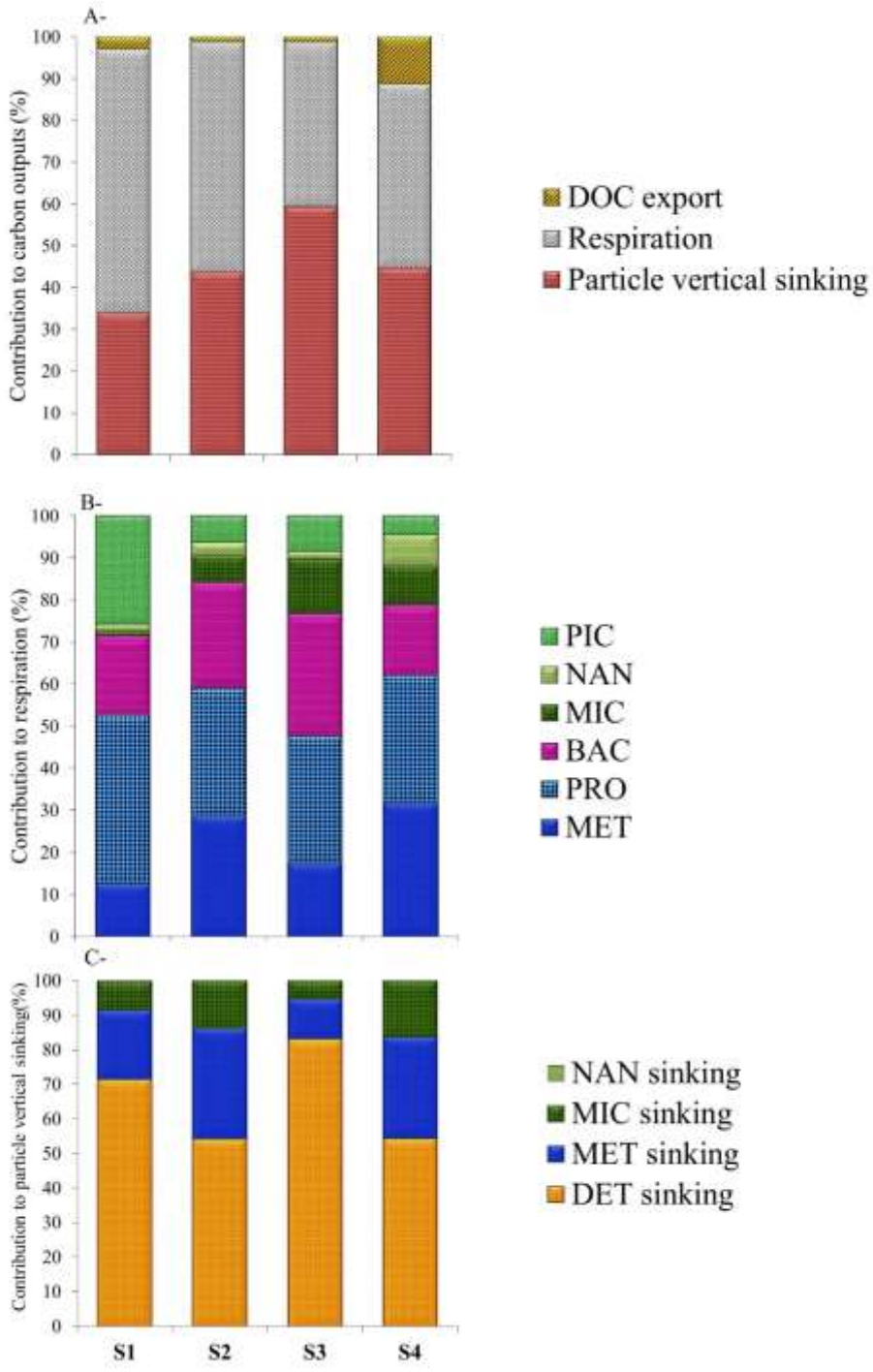

Fig. 4. Composition of total carbon outputs (A), contributions of living compartments to respiration (B) and contributions of living and non-living compartments to carbon sinking (C) in four stations in the Gulf of Gabès. PIC, picophytoplankton; NAN, nanophytoplankton; MIC, microphytoplankton; BAC, bacterioplankton; PRO, protozooplankton; MET, metazooplankton; DET, detritus; DOC, dissolved organic carbon.

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Throughput was defined as the sum of carbon flows coming into or leaving a compartment. The throughput of each compartment varied among stations (Fig. 5). In S1, PIC and PRO showed the highest value of carbon throughput (1,401 and 1,256 mg C m^{-2} d^{-1}, respectively), while both living compartments (MIC, BAC, PRO and MET) and non-living compartments (DET and DOC) showed similar carbon throughputs in S2 (896-1,258 mg C m^{-2} d^{-1}). However, MIC had the highest throughput (2,451 mg C m^{-2} d^{-1}) in S3 and S4, largely above its throughputs in S1 and S2. BAC, PRO, DET and DOC had relatively high throughputs in S3 (1,165-1,576 mg C m^{-2} d^{-1}), while MET and PRO had higher values (1,712-1,818 mg C m^{-2} d^{-1}) than DET and DOC (1,337-1,225 mg C m^{-2} d^{-1}) in S4.

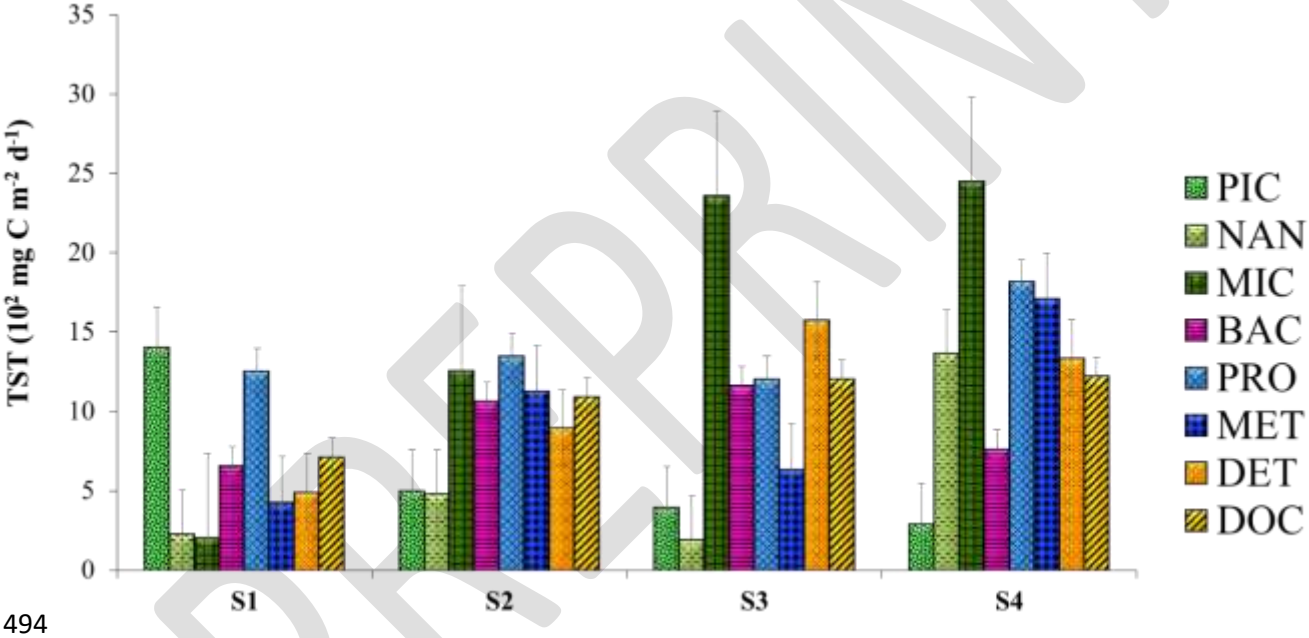


Fig. 5. Throughput of each compartment for the four models of four stations in the Gulf of Gabès. TST, total system throughput; PIC, picophytoplankton; NAN, nanophytoplankton; MIC, microphytoplankton; BAC, bacteria; PRO, protozooplankton; MET, metazooplankton; DET, detritus; DOC, dissolved organic carbon.

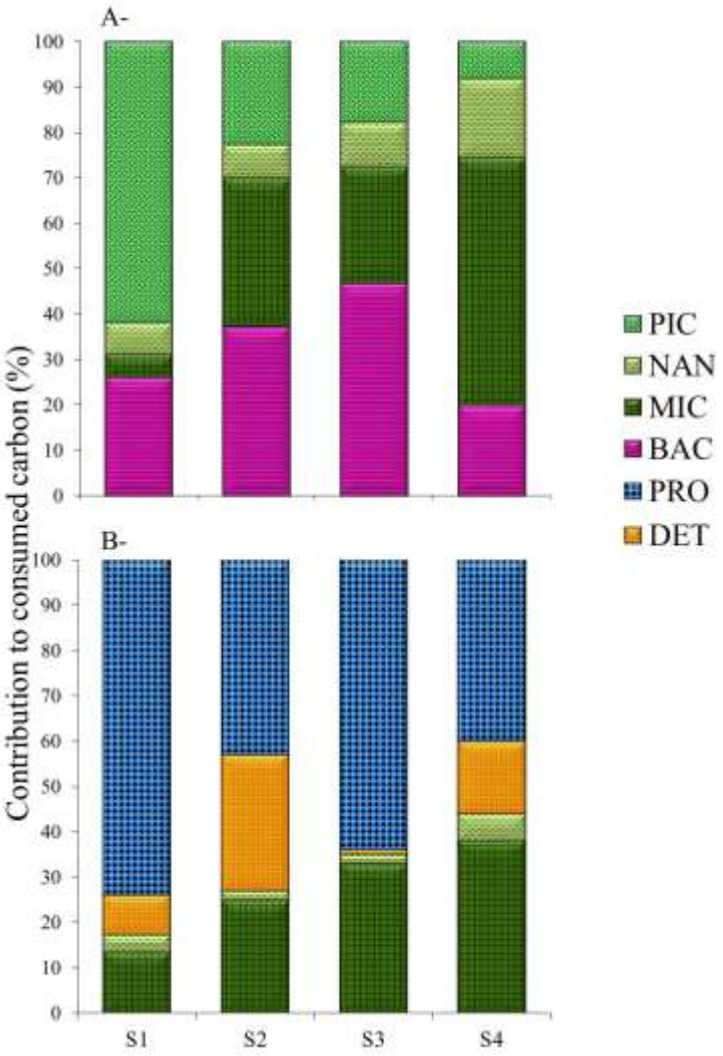
Error bars, 95% confidence intervals calculated from the probability of distribution of each flow and for 300,000 solutions *per* flow.

3.2. Protozooplankton and metazooplankton diets

The diets of PRO and MET were expressed as the contribution of each food source to the carbon consumed by grazers. The diets of both zooplankton compartments varied among stations (Fig. 6). PRO mainly fed on PIC (62%) followed by BAC (26%) in S1. In S2 and S3,

506 the diet of PRO was roughly divided between BAC (37-47%) and phytoplankton (mainly MIC:
507 33-26% and PIC: 23-18%). Conversely, phytoplankton were the main food source of PRO in
508 S4; MIC alone formed 54% of its diet (Fig. 6 A).

509 In S1, MET was mainly carnivorous, since PRO formed 74% of its diet, while
510 phytoplankton only provided 17%. In S2, PRO and DET were the main food source of MET,
511 forming 43% and 30% of its consumed carbon, respectively. In S3, the diet of MET mainly
512 relied on PRO (64%), and MIC contributed 33%. In S4, the contribution of phytoplankton
513 (mainly MIC) to MET diet increased to 44%. PRO formed 40% of MET diet, while DET only
514 represented 16% in this station (Fig. 6 B).



515

516 **Fig. 6.** Diets of protozooplankton (A) and metazooplankton (B) in four stations in the Gulf of
517 Gabès. PIC, picophytoplankton; NAN, nanophytoplankton; MIC, microphytoplankton;
518 BAC, bacterioplankton; PRO, protozooplankton; DET, detritus.

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519

520 **3.3. Food web typology ratios**

521 The stations presented distinct carbon circulations through the food webs. The typology
522 ratios varied significantly among stations according to Cliff's δ test (Table 3, Fig. 7). Ratio R4
523 significantly differed among stations, with higher values in S4 (0.55) and S1 (0.48) than in S2
524 and S3 (0.43 and 0.42, respectively) (Fig. 7 A). R6 followed an opposite trend, with lower
525 values in S1 and S4 (0.39 and 0.38, respectively) than in S2 and S3 (0.41 and 0.44, respectively)
526 (Fig. 7 B). R7 and R8 were very high in S1 (0.73 and 0.92, respectively) and decreased in S2
527 (0.21 and 0.74) and S3 (0.11 and 0.74) to reach their lowest values in S4 (0.06 and 0.66) (Fig.
528 7 C, D).

529 **Table 3**. Results of Cliffs'δ test applied to ecological network indices and typology ratios
530 calculated for four stations of the Gulf of Gabès. The following values were used to define the
531 size of the effects: |δ| >= 0.43, large; ***, large.

	S1/S2	S1/S3	S1/S4	S2/S3	S2/S4	S3/S4
TST	-1 (***)	-1 (***)	-1 (***)	-1 (***)	-1 (***)	-1 (***)
A/C	1 (***)	-1 (***)	1 (***)	-1 (***)	1 (***)	1 (***)
AMI	1 (***)	-1 (***)	1 (***)	-1 (***)	1 (***)	1 (***)
APL	-0.93 (***)	0.93 (***)	1 (***)	1 (***)	1 (***)	1 (***)
FCI	-1 (***)	-1 (***)	0.73 (***)	0.99 (***)	1 (***)	1 (***)
D/H	-1 (***)	-1 (***)	1 (***)	-0.93 (***)	1 (***)	1 (***)
R4	1 (***)	1 (***)	-1 (***)	0.67 (***)	-1 (***)	-1 (***)
R6	-1 (***)	-1 (***)	0.66 (***)	-1 (***)	1 (***)	1 (***)
R7	1 (***)	1 (***)	1 (***)	1 (***)	1 (***)	1 (***)
R8	1 (***)	1 (***)	1 (***)	-0.89 (***)	1 (***)	1 (***)

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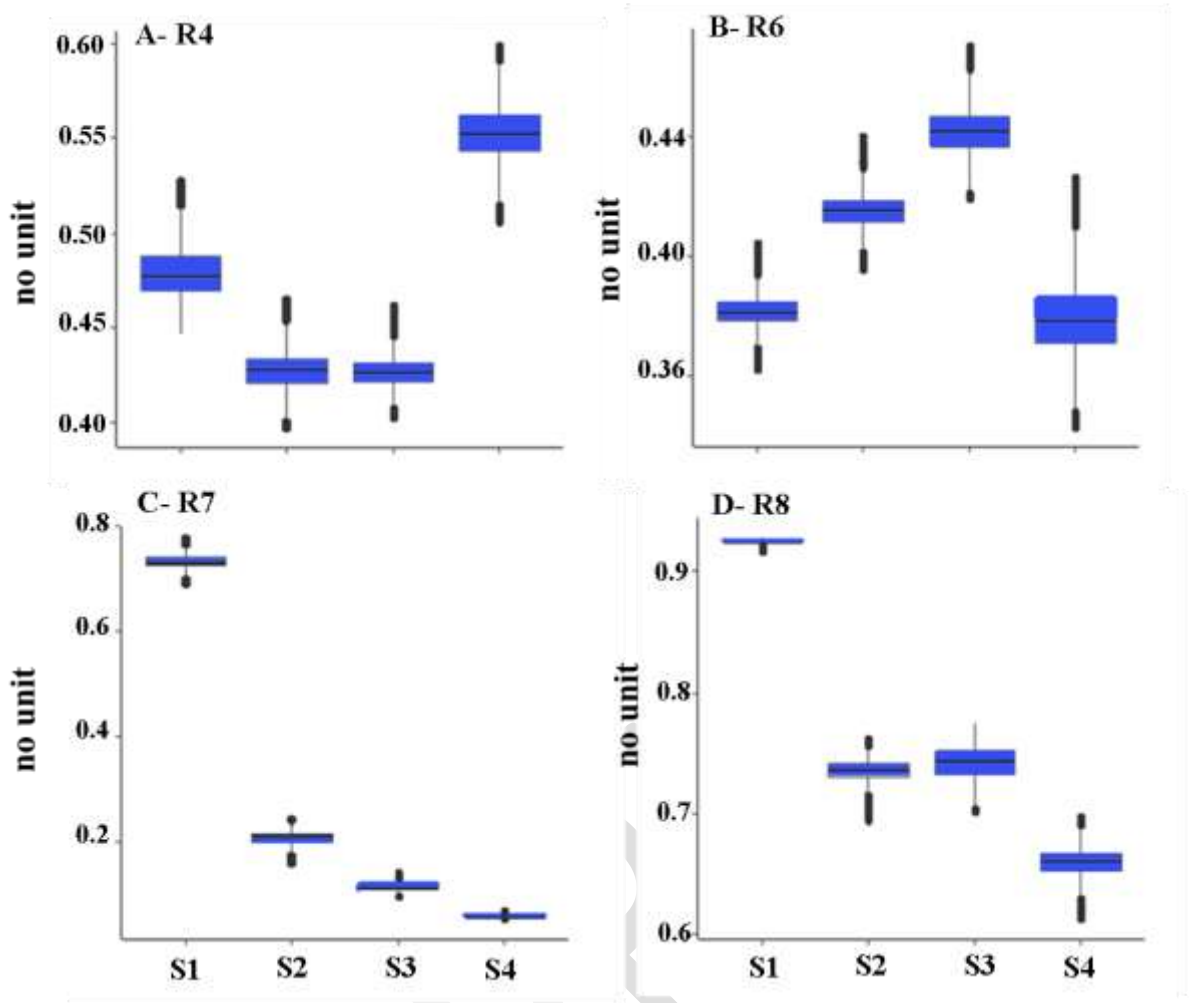
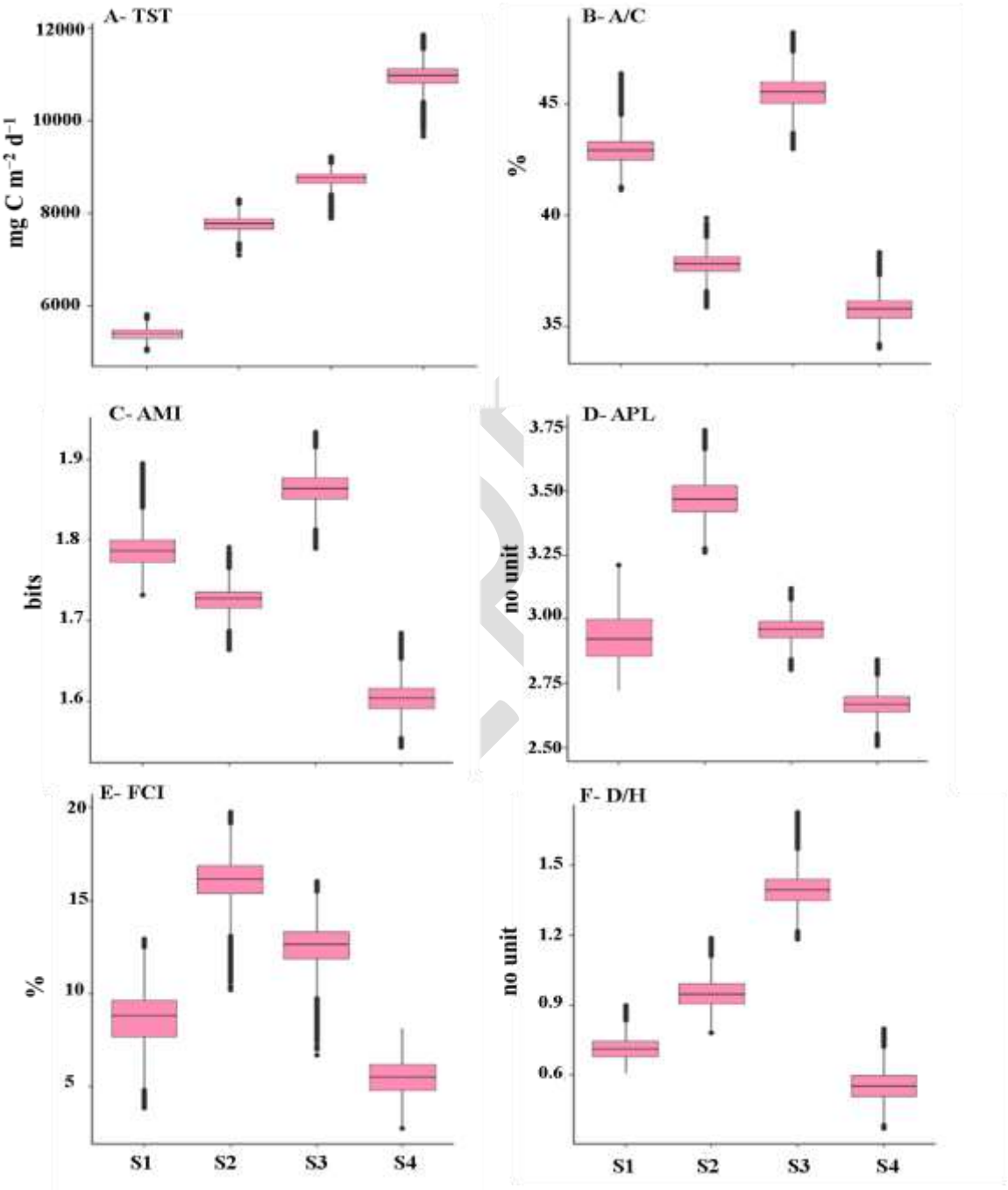


Fig. 7. Spatial variation of the food web typology ratios.
R4 = Pnetpht/D2 (A), R6 = (PnetDET + PnetDOC)/D2 (B), R7 = PnetPIC/Pnetpht (C) and R8 = pht-PRO/(pht-PRO + pht-MET) (D)
Pnet, net production; pht, total phytoplankton; D2, Pnetpht + PnetBAC + PnetDET + PnetDOC; pht-PRO, consumption of pht by PRO; pht-MET, consumption of pht by MET.

3.4. Ecological network analysis (ENA) indices

Ecological network analysis (ENA) indices define emerging properties of the food web. They clearly distinguished the functioning of each station; all indices varied significantly and showed large differences among stations according to Cliff's δ test (Table 3, Fig. 8). The total system flux (TST) was higher in S4 (10,966 mg C m^{-2} d^{-1}) than in S2, S3 (7,770- 8,740 mg C m^{-2} d^{-1}) and S1 (5,386 mg C m^{-2} d^{-1}) (Fig. 8 A). Conversely, the lowest relative Ascendency (A/C) was found for the food webs of S4 (0.32 %) in comparison with the other stations (0.38-0.46 %) (Fig. 8 B). Average mutual information (AMI) followed a similar trend to that of A/C,

549 with higher values in S1, S2 and S3 (1.72-1.86 bits) than in S4 (1.60 bits) (Fig. 8 C). The
550 average path length (APL) and Finn cycling index (FCI) showed similar spatial variations, with
551 the highest values in S2 (3.46 and 0.16%, respectively) and the lowest ones in S4 (2.67 and
552 0.05%, respectively) (Fig. 8 D, E). Finally, the D/H ratios in S2 and S3 (1.22-1.36) significantly
553 exceeded those in S1 (0.70) and S4 (0.47) (Fig. 8 F).



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555 **Fig. 8.** Spatial variation of ENA indices calculated for the planktonic food webs in four stations
556 of the Gulf of Gabès. Total system throughput (TST; mg C m^{-2} d^{-1}) (A), relative
557 Ascendency (A/C; %) (B), average mutual information (AMI; bits) (C), average path
558 length (APL) (D), cycling index (FCI; %) (E), and detritivory to herbivory (D/H) (F).

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3.5. Relationships between ENA indices, typology ratios, input and output flows and environmental variables

Multiple factor analysis (MFA) was applied to the four stations on ENA indices, carbon flux ratios, inorganic and organic nutrients, size-fractioned GPP, bacterial production and particle sinking (Fig. 9). The first two axes of the MFA explained 47.84% and 35.98% of the total variance, respectively.

On the first axis of the MFA, the TST index (5%), GPP of NAN (6%) and MIC (6%), sinking of MIC (7%) and MET (7%) and nutrients (N_{inorg} 3%, P_{org} and P_{inorg} 3-4%, Si_{inorg} 4%) were projected onto its positive pole. Its negative pole was determined by the A/C index (2%), ratios R7 (6%) and R8 (8%), GPP of PIC (6%), sinking of NAN (6%) and N_{org} (4%) The positive pole of the second axis was related to several ENA indices (D/H 6%, FCI 4%, APL 2%, AMI 2%, and A/C 2%), R6 (10%) and bacterial production (23%), while its negative pole was related to R4 (7%) (Fig. 9 A).

Stations S1 and S4 were discriminated on the first axis. S1 projected on the negative pole of the axis was characterized by high values of PIC GPP and ratios R7 and R8, but hosted low concentrations of inorganic N, P and Si and low TST, indicating a poorly rich nutrient system dominated by small producers. S4 was at the opposite of S1. It was characterized by high values of GPP for MIC and NAN, inorganic nutrient concentrations, TST and sinking of MIC and MET. Stations S2 and S3 occupied the center of axis 1, indicating that the factors represented on axis 1 were not discriminating for these stations. However, S2 and S3 were projected on the positive pole of axis 2 and were characterized by high values of BAC production, D/H and FCI indices and R6, but a low R4 (Fig. 9 B).

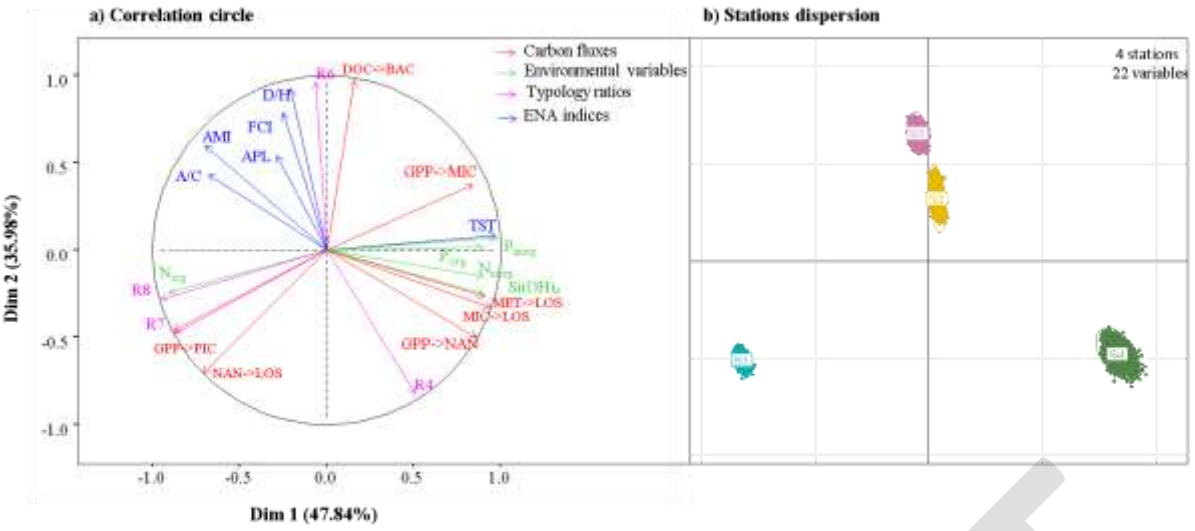

Fig. 9. Multiple factor analysis (MFA) ordination diagram showing the relationships between ecological indicators (food web typology ratios and ENA indices), environmental variables (inorganic and organic nutrients: N_{inorg}, P_{inorg}, Si_{inorg}, N_{org}, P_{org}) and carbon flows [GPP of PIC (GPP->PIC), NAN (GPP->NAN) and MIC (GPP->MIC), bacterial production (DOC->BAC) and sinking of NAN (NAN->LOS), MIC (MIC->LOS) and MET (MET->LOS)].

4. Discussion

4.1. Spatial change in planktonic food web characteristics

The complex hydrodynamic circulation in the Gulf of Gabès coupled with anthropogenic nutrient inputs created a north-south and coast-offshore ascending gradient of nutrients that induced a spatial change in the size community structure of phytoplankton (Chkili et al., 2023). As expected, the present study also showed a clear spatial variation of primary production, in quantity (Fig. 3 A) and composition (Fig. 3 B). Nutrients are always considered as the main factor controlling the size structure of primary producers, which in turn influence the food web organization (Legendre and Rassoulzadegan, 1995; Sakka Hlaili et al., 2008; Filiz et al., 2020; Hardikar et al., 2021). It is well admitted that identifying the dominant phytoplankton size fractions could play a crucial role in predicting food web types (Richardson and Jackson, 2007). For example, Bellinger et al. (2006) and Hardikar et al. (2021) highlighted that the size fraction of producers, i.e., small *versus* large phytoplankton, could be used as a robust indicator of the trophic level of the system and the carbon transfer pathway. In our study, nutrients appeared as significant environmental discriminant factors of the stations, in which small and large

phytoplankton played different roles in biogenic carbon production (MFA, Fig. 9). In addition, the increase in large phytoplankton relative to small cells can be an indicator of eutrophication (Bell and Elmetri, 1995; Garmendia et al., 2011; Machado et al., 2023). Nano and micro-phytoplankton were indeed dominant in S4 – the most nutrient-rich station –, which could confirm the eutrophication status of this station.

Phytoplankton size structure and production can change rapidly in response to environmental and anthropogenic disturbances such as vertical mixing patterns, light and temperature fluctuations, salinity or nutrient availability, together with industrial, urban and agricultural discharges. These changes are obviously followed by modifications in the composition and structure of zooplankton communities and their grazing activity (Legendre and Rassoulzadegan, 1995b; Kiørboe et al., 1996; Horňák et al., 2005; Bel Hassen et al., 2008; Drira et al., 2018), which could have significant effects on the structure of the marine food web (Froneman, 2004; Legendre and Rassoulzadegan, 1995; Vargas and González, 2004; Decembrini et al., 2009; Meddeb et al., 2019). The proto- and meta-zooplankton communities indeed varied from S1 to S4, and so did their microbivory and herbivory activities (Fig.6; Table 2).

Then, by looking at the size structure of phytoplankton, production, and the microbivory and herbivory of zooplankton, we can suggest that various food webs with different efficiencies in carbon export exist in the four stations. Going further with digital tools, we can identify the types of food web and characterize the emerging properties of each type.

4.2. Application of typology ratios and ENA indices to a description of the structure and function of planktonic trophic pathways

Typology ratios based on the size structure of the planktonic community as well as the interactions between the different compartments are useful to distinguish planktonic trophic pathway (PTP) types in marine systems (Sakka Hlaili et al., 2014).

In our study, all typology ratios showed significant spatial change (Table 3, Fig. 7), suggesting variation in the structure of PTP among stations. The spatial change in R7 (Fig. 7 C) evidenced a modification of the food web type among stations. In accordance with the range of R7 values given by Sakka Hlaili et al. (2014) and describing the importance of PIC in total carbon production, the microbial food web dominated in S1 (R7 = 0.7 > 0.6), while multivorous pathways prevailed in S2 and S3 (0.1 < R7 = 0.2-0.12< 0.6), but the food web in S4 acted as a herbivorous type (R7 = 0.06 < 0.1). This is in agreement with our observations of a high microbivory in S1, a shared role between microbivory and herbivory in carbon transfer in S2 and S3, and a strong herbivory in S4. In addition, PIC formed the most active compartment in S1, followed by PRO, while MIC was the most active compartment in the other stations, followed by PRO and MET (Fig. 5). This suggests an important role of these communities as producers (PIC and MIC) and grazers (PRO and MET). Furthermore, R8, which distinguished the main grazers in carbon channeling (i.e., PRO *versus* MET) corroborated R7. The high R8 in S1 (~1) indeed denoted that the main phytoplankton grazers in the microbial food web were PRO, while the lower values (0.66-0.74) found in the other stations (Fig. 7 D) indicated that PRO and MET altogether played an important role in carbon transfer when the dominant food web was herbivorous or multivorous. In addition, the relative importance of phytoplankton or non-living matter (DOC and DET) relatively to carbon production was specified by two other typology ratios – R4 and R6. Higher R4 than R6 values suggest that the system mainly relies on phytoplankton production, while the opposite means that non-living matter is important in circulating carbon production (Sakka Hlaili et al., 2014). These two ratios evolved differently among stations (Table 3, Fig. 7 A, B), showing that phytoplankton and/or non-living matter played different roles in carbon production across the three observed PTP. The higher R4 compared to R6 in S1 indicated that the microbial food web was more based on phytoplankton (mainly PIC) than on non-living matter. This coincides with a higher throughput of phytoplankton (1,838.5 mg C m^{-2} d^{-1}) than DOC and DET (1,204.05 mg C m^{-2} d^{-1}) in this station (Fig 5). In the herbivorous pathway of S4, phytoplankton (mainly MIC) also played a more

important role (R4>R6) and had a higher throughput (4,110.1 mg C m^{-2} d^{-1}) than non-living compartments did (2,561.7 mg C m^{-2} d^{-1}) (Figs. 4, 6 A, B). For the multivorous food web observed in S2 and S3, these same R4 and R6 values suggested that the systems were based on phytoplankton as well as on non-living matter. In both stations, non-living carbon throughputs (1,988.74-2,779.63 mg C m^{-2} d^{-1}) were close to phytoplankton throughputs (2,240.2-2,954 mg C m^{-2} d^{-1}) (Fig. 5). Unfortunately, despite the importance of these ratios, their application is rather limited in the literature. Therefore, it would be interesting to use these criteria more extensively by comparing them with those of other ecosystems. Using these criteria, researchers and managers can identify the dominant trophic pathway in a planktonic assemblage and determine the fate of the carbon that passes through it: they can identify the main trophic pathway (i.e. herbivorous, multivorous or microbial food webs) using ratio R7, identify the main consumers of total phytoplankton using ratio R8, and specify whether the system is rather based on non-living material or phytoplankton using ratios R4 and R6 (Sakka Hlaili et al., 2014).

ENA indices were also used to characterize PTPs, as they are powerful tools for understanding carbon circulation through the whole food web (Ulanowicz, 1986; Ulanowicz et al., 2009). In fact, both ecological indicators (typology ratios and ENA indices) could be discriminant in the description of the food web structure (Fig. 9). However, coupling ENA indices and typology ratios required selecting complementary indices.

ENA indices are potentially powerful tools when assessing ecosystem health (Niquil et al., 2014) and are sensitive to different impacts on marine ecosystems (Baird et al., 2009; Tecchio et al., 2016; Pezy et al., 2017). However, they can only partially capture the anthropogenic or natural stress levels of different types of food webs in aquatic ecosystems (Tecchio et al., 2016). Therefore, food web types can also be used as an indicator of the stress level in the ecosystem and its carbon transfer capacity (Legendre and Rassoulzadegan, 1995; Siokou-Frangou et al., 2010). For example, when a microbial food web exists, particularly in

682 oligotrophic environments, primary production is maintained through recycled nutrients and is
683 mostly lost through remineralization (Goldman et al., 1987; Legendre and Rassoulzadegan,
684 1995; Meddeb et al., 2018). This may demonstrate stress of the system, which has become
685 inefficient in carbon transfer (López-Abbate et al., 2019). In contrast, when herbivorous or
686 multivorous food webs dominate, primary production is based on nutrient inputs and
687 significantly transferred to large consumers or efficiently exported to deep waters (Michel et
688 al., 2002; Turner, 2002). Herbivorous food webs are known for their strong capacity to channel
689 carbon to higher pelagic and benthic consumers: low carbon is recycled (Legendre and
690 Rassoulzadegan, 1995; Meddeb et al., 2019), indicating a stable ecosystem (Meddeb et al.,
691 2019). Based on these statements, our study highlights the links between ecosystem typology
692 and properties derived from ENA indices that characterize the system's activity, stability,
693 maturity and organization.

694 The TST index is a measure of ecosystem activity and is considered as a basic index of
695 food web models used to discriminate food webs (Finn, 1976; Ulanowicz, 1986; Borrett and
696 Scharler, 2019). Several works have showed that high TST values correspond to productive
697 ecosystems, such as coastal areas influenced by nutrient-rich upwelling or riverine inputs and
698 productive continental shelves (Coll et al., 2007; Grami et al., 2008; Corrales et al., 2015;
699 Meddeb et al., 2018). TST varied significantly among the three PTPs found in our study
700 (Table 3, Fig. 8 A). This can obviously be linked to the variations in GPP and in the eutrophic
701 degree of the stations. Like GPP, TST followed an increasing gradient from the least nutrient-
702 rich station dominated by the microbial food web (S1) to the highly eutrophic station governed
703 by the herbivorous pathway (S4). Our results corroborate other studies showing that the
704 herbivorous food web is more active than the microbial and multivorous food webs (Meddeb
705 et al., 2019; Decembrini et al., 2021).

706 Relative Ascendency (A/C) is an indicator of the degree of ecosystem organization
707 (Ulanowicz, 1997; Patrício et al., 2004) that negatively correlates to the degree of maturity

(Christensen et al., 2005). The highest A/C value was recorded in S3 (Fig. 8 B), indicating that the multivorous pathway in this station was more organized than the food webs of the other stations. More particularly, A/C was lowest in contrast to TST in S4 and its herbivorous pathway, indicating a more active but less organized system. The AMI index is a measure of flow specializations within a system (Ulanowicz, 1986). It yields lower values at the early stages of ecosystem development (when the system is immature) and higher values under pristine conditions (least disturbed ecological functioning). In our study, AMI followed the same trend as A/C, i.e., highest in S3 and lowest in S4 (Fig. 8 C). This means that higher fluxes of BAC and DET, in parallel to MIC, may allow a greater fraction of the total system flux to pass through specialized pathways in the multivorous food web of S3. Other ENA indices that reflect stability, maturity and organization varied significantly according to the different PTPs (Table 3). The FCI index is an important indicator of changes in system functioning (Fath et al., 2019; Safi et al., 2019) and gives information about carbon cycling in the ecosystem (Finn, 1976; Saint-Béat et al., 2018). This index can indicate the degree of maturity, resilience and stability of the ecosystem (Vasconcellos et al., 1997; Duan et al., 2009; Niquil et al., 2012). Recycling can indeed reduce the impact of stress on the ecosystem by acting as a buffer. Therefore, increased recycling can give better resilience and stability to the system (Saint-Béat et al., 2015). In addition, the APL index – which measures the retention capacity of the system (Fath et al., 2019b; Kay et al., 1989) – is expected to be high in systems with high degrees of flow diversity and cycling (Christensen, 1995; Thomas and Christian, 2001). Both indexes showed similar spatial evolution, i.e., lower values in S4 than in the other stations (Fig. 8 D, E), indicating that the herbivorous food web observed in S4 was less stable than the multivorous and microbial pathways observed in the others stations. This is in agreement with Legendre and Rassoulzadegan (1995) and Meddeb et al. (2019), who reported lower stability of the herbivorous food web in comparison to the microbial and multivorous ones. The highest values of FCI and APL coincided with the multivorous food web in S2 – the station most exposed to the source of disturbance in the Gulf – TCG (Fig. 1). Thus, the increase in recycling and flow

diversity seemed to endow the system with a certain resistance to the strong disturbance that the PTP underwent in S2. According to the MFA results, the APL seemed to be less structuring in the system since its contribution was not significant on the first two axes. In this case, considering the first two axes of the MFA, FCI seemed to be more efficient in the stability analysis.

The detritivory/herbivory ratio (D/H), which was initially adapted from Odum (1969), was applied to show the importance of detritivory compared to herbivory. Several authors have used this index to provide information on carbon transfer to consumers *via* detritus and/or autotrophs (Kay et al., 1989; Ulanowicz, 1992; Chrystal and Scharler, 2014; Niquil et al., 2014; Fath et al., 2019; Safi et al., 2019). High D/H values reflect an ecosystem where detritus plays an important role in carbon recycling, while low D/H values indicate an ecosystem where primary producers play a vital role as food for the second level (Chrystal and Scharler, 2014; Luong et al., 2014). During our study, the ratio indeed showed significant spatial variation (Table 3, Fig. 8 F), indicating a shift from systems based on the primary production pathway in S1 and S4 (D/H: 0.7 and 0.5, respectively) to systems based on phytoplankton and the detrital energy pathway, which played an important role in S2 and S3 (D/H ~ 1). This is consistent with the fact that R6 and R4 were similar in S2 and S3 (Fig. 7A, B). Therefore, both phytoplankton and non-living carbon production played an important role for the multivorous food web observed in these stations. The lowest D/H value coincided with the herbivorous food web acting in the most eutrophic station S4. This is in agreement with the results of Luong et al. (2014), who reported that nutrient-rich environments favor herbivory over detritivory.

4.3. Importance of coupling ENA and typology ratios for ecosystem health monitoring and management perspectives

A representation of ecosystem dynamics based on the coupling of typology with ENA indicators may be considered as an effective tool for environmental managers. ENAs are sensitive tools for characterizing the ecosystem health status that have been repeatedly used to

assess the impact of natural and anthropogenic pressures on coastal marine ecosystems (Niquil et al., 2014; Pezy et al., 2017; Tecchio et al., 2016; de la Vega et al., 2018a, b; Safi et al., 2019; Fath et al., 2019). However, they can only partially capture the anthropogenic or natural stress levels of different types of food webs in aquatic ecosystems (Tecchio et al., 2016).

Thus, ecosystem models are increasingly used to advise water and marine policy makers in European Union countries (e.g. Heymans et al., 2020), but given the complexity of interactions within an ecosystem (Fath et al., 2007; Baird et al., 2009) and that model results represent projections of reality in a digital form, using and understanding these models is difficult for non-experts. Fath et al. (2019) recently reported that ENA indices are important, but currently difficult to understand for non-specialists and therefore difficult to use in communications. Typology ratios could be more practical for experts and non-experts alike. The advantage of these ratios is that if we consider some of them, we can directly access the specific fluxes without having to recur to modeling and calculate all the fluxes of the entire food web, as in the case of most ENA indices. For example, the identification of the dominant trophic pathway in a plankton assemblage could be based on these ratios, which can be calculated from flow values relatively easy to estimate in the field such as net picophytoplankton production divided by total phytoplankton production (R7), or the rate of consumption of total phytoplankton by protozooplankton divided by the rate of total consumption by proto- and metazooplankton (R8) (Fig. 10). Similarly, the material on which the system is based could be determined using criteria calculated from field-estimated fluxes, namely, total phytoplankton production divided by potential food production by protozooplankton (R4) or DOC and detritus production divided by potential food production by protozooplankton (R6) (Fig. 10) (Sakka Hlaili et al., 2014). This would facilitate decision-making about ecosystems. ENA results provide a better understanding of the functioning of the various structures of the planktonic food web under anthropogenic pressure, namely its activity (TST) and the importance of detritus in relation to phytoplankton production (D/H) in the system. Thus, from a planktonic perspective, these two indices often recommended by several

788 authors (Ulanowicz, 2004; Bodini et al., 2012; Fath et al., 2019; Safi et al., 2019) could also be
789 easily estimated from field data (Fig. 10). They could be coupled with trophic typology ratios
790 (R4, R6, R7 and R8) to better understand the functioning of different planktonic food web
791 structures under anthropogenic pressure. In fact, the MFA carried out in this study showed that
792 these ecological indicators (TST, D/H, R4, R6, R7 and R8) were the most structuring ones in
793 the studied systems. Thus, the coupling of different indices could be more descriptive of food
794 web functioning. For example, R4 and R6 indicate whether the system is based on non-living
795 matter (DET, DOC) (low R4 and high R6) or instead on phytoplankton (low R4 and high R6)
796 (Sakka Hlaili et al., 2014). The D/H index can be used in addition to these typology ratios to
797 determine which of these two sources dominates (Fath et al., 2019). According to the MFA
798 results (Fig. 9 A), the anti-correlation between D/H and R6 on the positive pole and R4 on the
799 negative pole of axis 2 indeed reflects different ecosystems (Fig. 9 B). The high D/H values can
800 be sustained by a higher R6 than R4, indicating that detritus play an important role in ecosystem
801 recycling, e.g., carbon recycling. Conversely, low D/H values can be maintained by a higher
802 R4 than R6, indicating an ecosystem where primary producers (phytoplankton and/or algae)
803 play a substantial role as feed for consumers (PRO and MET) (Luong et al., 2014). R7, R8 and
804 TST may be also complementary and interact in the description of the primary production of
805 the planktonic food web type and its fate (Fig. 9). R7 provides information on the relative
806 contribution of large and small phytoplankton to total primary production (Sakka Hlaili et al.,
807 2014). Thus, it provides indirect information on the amount of primary production in the
808 system, which may have an effect on the ecosystem activity measured by the TST (Finn, 1976;
809 Ulanowicz, 1986; Borrett and Scharler, 2019). Moreover, we can refer to R8 to identify the
810 main grazers of production. Grazers switch from MET (high R8) when herbivorous or
811 multivorous food webs are dominant to PRO (low R8) when microbial pathways prevail (Sakka
812 Hlaili et al., 2014).

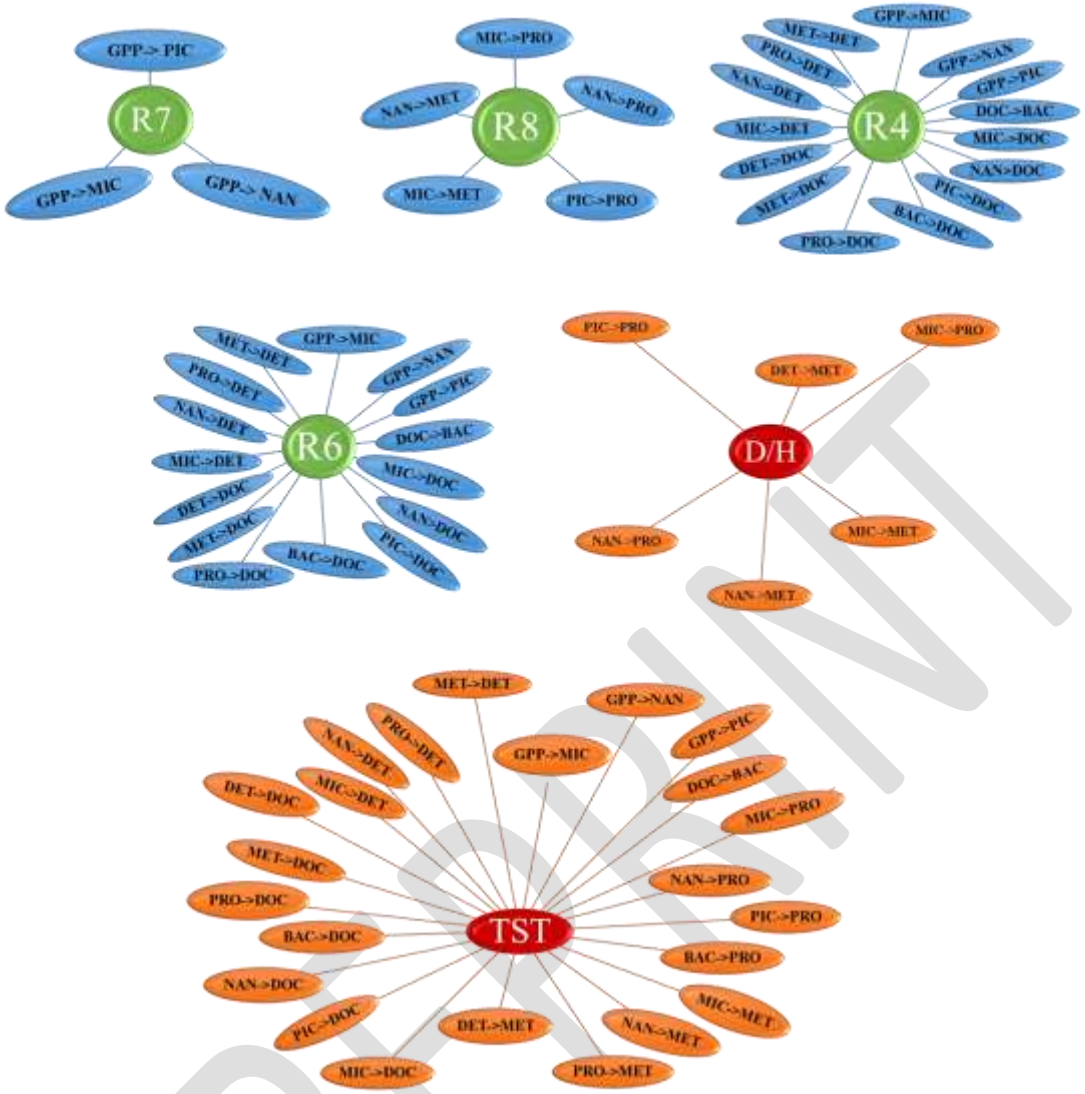

Fig.10. Diagram illustrating the different flows involved in estimating the typology ratios (R4, R6, R7 and R8) and ENA indices (D/H, TST). The description of each flow is detailed in Table 2.

In general, although ENA indices faithfully characterize carbon circulation within planktonic food webs, they could be complemented with typological indices to make their interpretation easier and describe the main trophic pathways.

Despite efforts in the management of marine ecosystems, there are still gaps in the relationships between planktonic food web levels and benthic/pelagic organisms. The planktonic food web typology approach has only been partially addressed by managers. This is the first time that a local approach to a eutrophication gradient has been based on differences in PTP typology. The same approach is currently used by OSPAR to define MSFD D4

indicators, as stated in Schückel et al. (2022) (OSPAR quality report status validated for publication in September 2023). However, OSPAR uses complete models, where plankton is often represented in a rather incomplete way (for example, protozooplankton is not considered).

At the base of the pelagic food web, plankton and the existing fluxes of matter among planktonic compartments largely condition the functioning of the ecosystem because they are a source of primary production, are exported to the benthos or related ecosystems, and condition trophic efficiency towards the upper links (Legendre and Rassoulzadegan, 1995; Dupuy et al., 1999; Sintes et al., 2004; Leguerrier, 2005; Marquis et al., 2007). As a result, indices of the typology and functioning of the planktonic food web can be linked to the benthos and the higher trophic links from the export estimate. In addition, they can also give an idea of the emerging properties of the whole ecosystem (activity, export, recycling...).

The present study is based on a correlative approach, using MFA that links three levels: i) the nutrient gradient, ii) the type of RTP, and iii) the indicators that seemed best able to distinguish the four stations and their ecological functioning. On the basis of our conclusions, we can propose a new, original monitoring protocol that links typology ratios and ENA. Like ENA, ratios are based on food web flows, but they involve fewer flows, so that they can be estimated without necessarily quantifying the entire system. This approach differentiates ratios locally. Therefore, typology ratios appear as the best candidates for more operational development in the future.

Issues still remain to be solved. The first issue is that our study is local, so that our conclusions are not generic – further studies are needed for that –, but we do propose a protocol that can be applied to other sites to generalize our conclusions. This protocol should be tested in other cases of pollution (other than eutrophication) to determine the extent to which it is applicable and can be taken into account by managers. Another issue is that ecosystem management is in its formulation clearly intended to represent a complete food web (and therefore a complete ecosystem). Since typology ratios can be used to analyze planktonic food

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webs (Sakka Hlaili et al., 2014), we now need to test them with ENAs in complete food webs, i.e. taking pelagic and benthic webs into account in the analyses.

5. Conclusion

The present study provides an analysis of the food web structure in the permanently disturbed Gulf of Gabès. An approach combining ecological network analysis (ENA) selected on the basis of previous literature and typology reports was tested. The study site was characterized by nutrient inputs (mainly from TCG), whose association with hydrodynamics has created a gradient of nutrient richness. The size structure of primary production, trophic interactions, the food web structure and function differed among the stations. The main results showed that:

- The microbial food web dominated in the least nutrient-rich system S1. It was identified by the highest value of R7 and formed a phytoplankton-based food web (R4>R6) primarily assigned to PRO (higher R8). PRO was inefficient in channeling biogenic carbon. This food web showed the lowest total system throughput (TST), and a low detritivory to herbivory (D/H) ratio, indicating a less active system relying on primary production (phytoplankton).
- In contrast, the herbivorous food web indicated by the lowest value of R7 was identified in the most eutrophic system S4, where large phytoplankton dominated primary production (R4>R6) and were assigned to PRO and MET (lowest R8). These were efficiently exported to higher consumers. Thus, all ecological indicators were lowest in this food web, except TST that was highest. This indicates that the herbivorous food web of the system was more active based on primary production (low D/H) but less organized (low A/C) and less stable (low FCI).
- The multivorous food web, as indicated by R7, dominated in the moderately nutrient-rich systems S2 and S3, and carbon production was based on both phytoplankton and non-living carbon (R4~R6) assigned to PRO and MET (low R8). These can be

efficient in carbon transfer. This food web was characterized by the highest relative ascendency and cycling values (A/C and FCI), and was more organized, specialized and stable. It also showed a higher total system throughput and the highest D/H, reflecting a more active system where detritus play an important role in carbon recycling.

From an ecosystem management perspective, we propose a comprehensive assessment of ecosystem health based on appropriate indicators of food web typology and ENA indices, to be used by managers to assess the structure, functioning, and emerging properties of ecosystems under anthropogenic pressure. We suggest combining typology ratios to identify food web types with ENA indices to distinguish different food web functions across nutrient gradients. This combination can provide an effective tool for managing and assessing ecosystem health, and for investigating the occurrence of anthropogenic pressures.

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