

Article

Structure and Functionality of the Mesozooplankton Community in a Coastal Marine Environment: Portofino Marine Protected Area (Liguria)

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Abstract: This research is part of the LTER (Long-Term Ecological Research) project, a network of terrestrial, freshwater, transitional water and marine sites, on which ecological research is conducted on a multi-decade scale. LTER studies ecosystems, their dynamics and evolution, the relationships between biodiversity and ecological functionality, water quality, productivity, the role of resource availability, the effects of pollution and climate change. The research focuses on the study of the variability of zooplankton groups in the Portofino marine protected area, in Punta Faro. The samplings were carried out in the years 2018–2019, and the results were compared with the values of the years 2003–2005, interesting from a meteorological climatic and biological point of view. The plankton community of the Punta Faro system was analyzed by means of a modeling approach to obtain information on the functionality and health status of the system and to verify whether this has undergone any alterations in the last decade. The analyses carried out show a clear difference between the three-year period 2003–2005 and the two-year period 2018–2019, highlighting how environmental changes, such as the increase in temperature, have led to higher costs of system functioning in the last two years. The mesozooplankton community has changed both in terms of abundance of organisms and in terms of organization and functionality.

Keywords: ecological network analysis; emergy analysis; ascendancy; Ligurian Sea; Mediterranean Sea



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1. Introduction

The LTER-Italy Network is based on the general principles of the International LTER network and has the primary objective of promoting and supporting the acquisition of data and information relating to the basic variability and evolutionary trends of ecological processes and to support the development of sustainable management strategies of ecosystems, which can favor the integration of terrestrial and aquatic ecological research. The Protected Marine Area of Portofino has been part of the LTER network (site IT15 Ligurian Sea) since 2007 with two coastal stations, one in front of Punta Faro (zone B) and one in correspondence with Cala dell'Oro (zone A). The research is aimed at continuing the study of the structure and dynamics of zooplankton groups in the Portofino MPA, in Punta Faro.

Zooplankton plays a vital role in marine ecosystems. In particular, the organisms that make up mesozooplankton feed directly on phytoplankton, microzooplankton, other mesozooplankton and detritus and they are among the largest organisms that still have a significant feedback interaction with primary production [1].

Globally they are one of the main players in the flow of vertical particles in the oceans, so they are important both in the pelagic food web and in export processes, influencing the biogeochemical cycle of carbon and other nutrients in marine environment. Therefore,

understanding the structure and functioning of the planktonic community is crucial for tracking biogeochemical cycles and predicting the future responses of aquatic ecosystems to environmental changes [2,3].

Several studies have investigated whether these organisms could be used in the assessment of environmental quality status [4,5] and therefore be considered as indicators of ecosystem changes [6–8], organisms or group of organisms (populations, communities) which through a biochemical, physiological or ecological response allow to evaluate an alteration in the quality of the environment [9].

The zooplankton composition and abundance are influenced by various chemical, physical and biological variables, among these it is known how the zooplankton density is influenced by the properties of the water masses in which they live [10].

Several studies on zooplankton organisms as biological indicators focus on two main aspects: on the one hand, the analysis of the medium and long-term variations of the community in relation to the alterations induced by hydro-climatic variables on a local scale [11], regional [12] and global [13]; on the other hand, zooplankton changes due to the heavy anthropic impact on the coastal marine system [14].

Climate change is one of the aspects that have received the most attention in recent years; in fact, there are many studies that focus on how the increase in temperature can affect the marine ecosystem [15]. In several works, it is evident how these changes are reflected above all at the base of the trophic network (planktonic communities) which undergoes both quantitative and qualitative changes, such as the alteration of seasonal cycles, vertical migrations, and algal blooms.

All of this leads to important consequences at the ecosystem level, both from a socio-economic point of view, by decreasing the availability of fish resources [13,16], and from an ecological point of view, as variations of zooplankton communities affect the regeneration of nutrients [17] and the transport of organic matter.

In the works of Ribera d'Alcalà et al. [18] and Molinero et al. [19], it is highlighted that in different areas of the Mediterranean Sea, since the second half of the Eighties, the increase in temperatures influenced the zooplankton component, causing an increase in the population of gelatinous organisms and the consequent decline in copepod abundance.

A first attempt to analyze the changes in the planktonic community in LTER Italia sites was made by Morabito et al. [20]. In the Portofino site in the Ligurian Sea, an increase in the total abundance of mesozooplankton is evident, characterized by a reduction in the percentage contribution of copepods and an increase in Cladocera. Key species such as *Centropages typicus* decreased while small copepods (0.5–1 mm) increased, along with Appendicularia.

While the identification of changes in the community composition is important to detecting variations in the species composition and abundance, it gives poor information on the functioning of the system and on the adaptation strategies that complex natural systems may put in place to cope with changes in the surrounding environment. In this context, a series of whole system analyses based on the assessment and the investigation of the system functioning are here proposed. With the aim to cover different aspects of the complex functioning of the plankton community Energy Systems Theory and Emergy Analysis (Emergy is defined as the sum of the available energy of one kind, e.g., solar joules, which is used-up, directly and indirectly, within an ecosystem for the production of goods and services) were applied to quantify the health of these benthic ecosystems and evaluate differences in their structure, organization and functional capacities.

The application of a whole system perspective for the evaluation of the structure and functionality of the zooplankton community is not widely reported in the scientific literature. The role of these indices allows a more in-depth study of the observed system and thanks to these it has been possible to search for signals that can highlight changes at the environmental level. This study compared two periods 13 years apart (2003–2005; 2018–2019), highlighting an ongoing climate change which is leading to functional changes in the system.

2. Materials and Methods

2.1. Study Site

The Portofino Promontory (Figure 1) has a very complex circulation because it is linked both to the meteo-climatic (wind direction and intensity) and hydrodynamic (dominant circulation) forcing, and to the interference of the promontory itself together with the narrow continental shelf [21–24]. Current historical series show that the current off Sestri Levante in winter has a North-West direction (Ligurian Provençal current), consistent at all depths, while on the other side of the promontory it has the opposite direction (South-East) with some variation in the vertical component and, finally, off the coast of Bogliasco or 15 km downstream of the promontory it again has a north-west direction and consistency at all depths, also confirmed by numerical models [22].

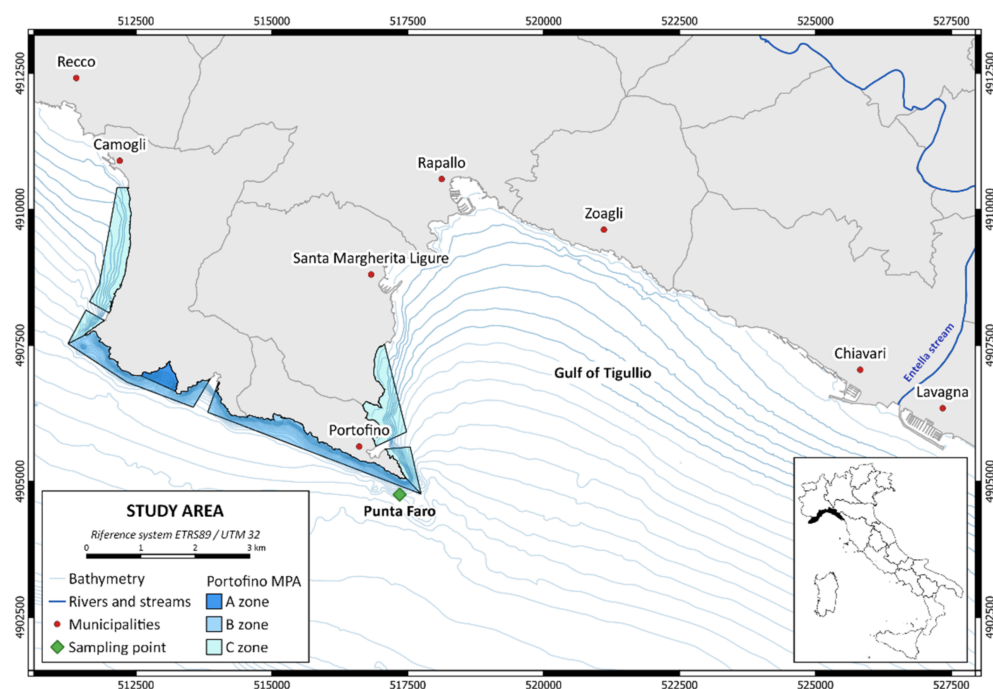


Figure 1. Study area.

The predominance of the current towards the Southeast during the surveys near Camogli suggests the existence of a recirculation or anticyclonic vortex with an intensity of the order of 10% of the inlet current and with an extension of less than 15 km. This vortex was highlighted in the spring by a superficial drifter, caught by the coastal current [23], but the presence of a fish trap, “tonnarella”, in the area overlooking Camogli since 1600, testifies how the vortex is a regularly occurring structure in the area. Occasional current reversals off Camogli can be induced by local winds. Facing the western cape of the Promontory (Punta del Faro), the main stream from east to west can intensify and be moved away from the promontory towards the open sea (in case of winds from NE and SE), while occasionally, in case of winds from SSW, the coastal circulation inside the Gulf of Tigullio intensifies, as a consequence of water accumulation along the coast, generating an upstream vortex and one against the coastal current from West to East [21].

Several torrential water courses flow into the Gulf of Tigullio, but generally do not lead to high inputs of fresh water. For this reason, the coastal waters around the Promontory maintain a marked oligotrophy [20], like the waters further offshore, which tends to be more pronounced in recent years than in the past [25]. The main supply of fresh water comes from the Entella stream that flows between Chiavari and Lavagna. The Entella stream, in fact, together with the other minor watercourses that flow into the Gulf of Tigullio, is important as it modifies the physical chemical and biological conditions of the

marine environment, both as an input of inorganic nutrients and as it favors stability of the water column, decreasing the salinity; this influences the dynamics of phytoplankton biomasses which are affected in a short time by the input of nutrients [26,27].

2.2. Field Activity

Both the zooplankton samplings and the seawater features were investigated as part of LTER program monitoring in Punta Faro station (Figure 1), around 80 m depth, every 15 days, according to the meteo-marine situation, on board the “M/B Veliger”, since 2000 for environmental features and since 2003 for zooplankton.

2.2.1. Environmental Features

Sea temperature and fluorescence were acquired by an Idronaut 301 (2003–2005) and 316 plus (2018–2019) probe equipped with a Turner Cyclops 7TM fluorometer along the entire water column. To calibrate the fluorometer, *in situ* seawater samples were collected and chlorophyll-a was determined in the laboratory [28]. CTD data were averaged for each meter and the monthly means were calculated in the 0–50 m layer.

2.2.2. Zooplankton Sampling and Laboratory Procedures

The collection of mesozooplankton was carried out using a WP2 type plankton net with 200 µm meshes, a mouth with a diameter of 57 cm for the years 2003–2005 and a General Oceanics net with a 200 µm mesh, a mouth with a diameter of 50 cm for the years 2018–2019. A vertical descent from –50 m depth to the surface was carried out. The collected samples were transferred into containers and suitably fixed for storage (final 4% formaldehyde solution) to perform taxonomic studies and to identify the feeding strategy. All samples were split with a Folsom plankton splitter into subsamples according to their abundance and were sorted into different taxa and identified under a stereomicroscope (Zeiss) to group level, while for copepods an aliquot of the whole samples was considered where at least 100 copepods could be identified [29] to species or genus level. A total of 100 samples were analyzed in this study (2003:24; 2004:20; 2005:19; 2018:18; 2019:19). In 2018–2019 two replicates were collected in order to determine also the total biomass (dry weight) filtering the samples through pre-weighted 200-µm nets. The zooplanktonic biomass was calculated by weighing the collected nets after drying overnight (60 °C).

2.3. Abundance to Biomass Conversion

The application of a mass balance trophic network model needs the estimation of biomass values for the functional groups in the system.

Chlorophyll-a concentrations were converted into carbon equivalents by applying the coefficient 40 µg C µg chl-a [30]. The abundance of zooplankton was converted into biomass through the application of conversion factors available in the literature (e.g., [31]). Whenever this conversion was not available, biomass was estimated by means of procedures based on the length/biomass ratio (e.g., [32]). This latter procedure was applied in this study to the pteropods. In particular, the length (L, mm) of the organisms was first converted to wet weight (WW, mg) and then transformed into DW using conversion factors available in the literature [32,33]. Finally, the biomass was transformed into carbon using a conversion factor of 0.25 [34]. Conversion factors applied in this study are reported in Appendix A (Table A1).

Aiming at a validation of the abundance of biomass conversion, the sum of all the estimated biomasses was compared to the total measured biomass values in each sample. Differences were always moderate and statistically not relevant (one-way ANOVA, $p > 0.1$)

2.4. Data Processing

Monthly standardized anomalies (zero mean and unit variance) were calculated for temperature (0–50 m average and 0–5 m average) and fluorescence (0–50 m average)

removing to each monthly mean the five years monthly mean and dividing for the five years standard deviation.

Differences in the anomalies and zooplankton biomass values were tested with ANOVA.

Moreover, the Redundancy Analysis multivariate technique (RDA) [35] was used to verify the influence of seawater temperature and fluorescence on the average annual zooplankton biomass of the functional groups. The response variables (zooplankton variables) were log-transformed prior to the analysis and then standardized to minimize the effects of outliers and extreme values, while standardized monthly anomalies of temperature in the 0–50 m layer (T_An), temperature in the 0–5 m layer (T5_An) and fluorescence in the 0–50 m layer (Chl_An) were used as explanatory variables.

To test the order of importance of the explanatory variables, an automated forward selection model was applied. First the “marginal effects”, namely the variance expressed by only one explanatory variable, were calculated; then the “conditional effects” that show the increase in total sum of eigenvalues after including a new variable during the forward selection. RDA analysis was performed using Brodgar 2.5.6 (2011, Highland Statistics Ltd., Newburgh, United Kingdom).

2.5. Modelling Approach

The plankton community has been analyzed through an ecosystem approach in terms of structure and functioning based on the quantification and characterization of flows acting within the system [36]. System flow analysis was performed through the development and calibration of simulations of the trophic web by means of Ecopath software. Ecopath uses a set of linear equations in order to balance the flows (in and out) of each element or functional group (species or groups of species) [37]. The simulation’s routine is based on a system of linear equations, which can be expressed for an arbitrary time period by:

$$B_i \times \left(\frac{P}{B}\right)_i \times EE_i = \sum_{j=1}^n \left[B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ij} \right] \quad (1)$$

Five parameters are needed for each group: biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B), ecotrophic efficiency (EE) and diet matrix (DC). If one of these parameters is not available, it could be calculated knowing 4 further parameters: unassimilated/consumption (Un/Q), net migration rate (E), biomass accumulation (BA), catch mortality (Y). Since ecotrophic efficiency was always lacking it has been estimated considering E, BA and Y null for each simulation. Employed data of P/B, Q/B and Un/Q are reported in Appendix A (Table A2) together with their reference sources. Whenever two or more species were characterized by the same parameters, they were collapsed into one single functional group in the simulations).

The software routine gives an error message if the simulation output is not realistic. If inconsistencies were detected (i.e., $EE > 1$) the diet matrix was slightly adjusted to get to a successful simulation [38]. Whenever the diet matrix was modified, the number (and obviously the position) of fluxes remained unchanged.

2.5.1. Model Outputs

Ecological indices were used to analyze the structure and functioning of the plankton community based on trophic flows analysis, thermodynamic concepts, information theory and trophodynamic indicators [38].

Mixed Trophic Impact

Direct and indirect trophic interactions among functional groups were analyzed by means of the Mixed Trophic Impact (MTI) approach [39,40].

Mixed trophic impact is able to account for the relative direct and indirect effects of any group within the mesozooplankton community on another group by applying hypothetical biomass changes.

MTI was calculated in accord with Ulanowicz and Puccia [40]:

$$[M] = ([I] - [Q])^{-1} - [I] \quad (2)$$

where M (MTI) is all the mixed trophic impacts that occur in the food web, Q is the net impact matrix involving all impacts, and I is the identity matrix. Each q_{ij} element of the Q matrix results from the differences between the positive effects d_{ji} (the fraction of the prey i in the diet of the predator j) and negative effects f_{ij} (the fraction of total consumption of i used by predator j) [40,41].

The MTI range from -1 to $+1$, and values close to these limits indicate strong effects. For the sake of clarity in this research only the five groups having the highest positive impacts and the highest negative impacts were taken into consideration.

Ecological Network Analysis

Functionality, efficiency, and ability to exploit, move and convey energy and matter are emergent properties of a complex living system. A whole system approach is necessary to identify, measure and combine the web of fluxes acting within the ecosystem. A set of metrics (here referred to as network analysis) based on a statistical approach to the study of ecosystem fluxes was proposed by Ulanowicz [42]. Network analysis is able to measure key signals of ecosystem functioning and to provide information regarding the ecosystem status. Total trophic flows within the community in terms of consumption, production, respiration, exports and imports and flow to detritus were quantified for the analyzed plankton community. The sum of all these flows represents the Total System Throughput (TST) that is here intended as the measure of the activity or size of the system functioning [43]. Complementary to the quantitative information provided by TST, the level of organization of the exchanges among components of the system can be assessed. Average mutual information (AMI) is based on the statistical evaluation of how much each flux acting in the considered web is forced to enter a specific compartment (j) when released by another one (i) [42,44] suggested the formulation for its calculation as:

$$AMI = \sum_{i=1}^n \sum_{j=1}^n \frac{T_{ij}}{T} \log \left(\frac{T_{ij} B^2}{B_i B_j T} \right) \quad (3)$$

where T_{ij} is the flux of biomass out of i-group and going in j-group, T is the sum of all the fluxes of biomass in the system and B_i and B_j are the biomasses of i-group a j-group, respectively. Ascendency (A) incorporates aspects of both a system's size (TST) and the degree of organization (AMI) with which the material is being processed [44]. Computation of Ascendency used the following equation:

$$A = TST * AMI = \sum_{i=1}^n \sum_{j=1}^n T_{ij} \log \left(\frac{T_{ij} B^2}{B_i B_j T} \right) \quad (4)$$

Emergy Analysis

Emergy accounting is an environmental accounting method proposed by [45] as a metric able to account for the differences in the energies flowing in a system that are not equivalent in terms of their ability to perform work. In this method, all inputs supporting a system are accounted for in terms of their solar energy, defined as the total amount of solar available energy (exergy) directly or indirectly required to make a given product or support a given flow, and measured as solar equivalent Joule (sej) [45]. An accounting method for the assessment of the emergy content of marine system has been recently proposed [46] (refer to this study for the methodology description) and applied to different systems from benthic [47,48] to oceans [49]. The emergy content of each element of the system is accounted for in function of different properties depending on the size of each element (i.e., biomass) and on the organization or complexity (i.e., rate of consumption and trophic level)

that are information retrieved by the modelling approach applied in this study. In this study, the accounting system for the emergy evaluation has been applied for the assessment of both the natural capital (i.e., the stock of biomass) and the functioning of the system (i.e., the resources exploited on a yearly basis).

In thermodynamic terms, the increase in size and complexity (and in turn in emergy) means that ecosystems gain order and move away from the state of thermodynamic equilibrium, and this thermodynamic property of natural systems can be used to assess the ecological condition (e.g., the health) of ecosystems [50].

3. Results

3.1. Environmental Features

Figure 2A shows the temperature trend along the water column in relation to the depth in the years 2003–2005.

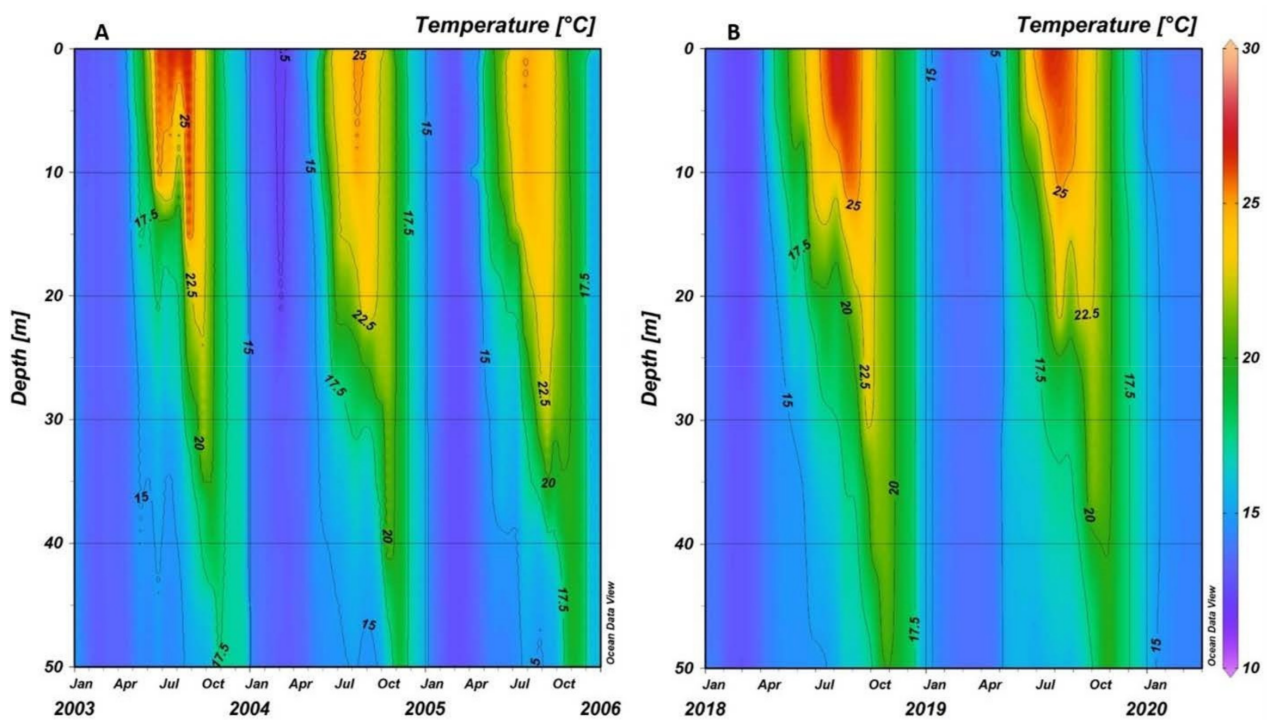


Figure 2. Temperature trend ($^{\circ}\text{C}$) in the water column during the three years (A) and the two years (B).

The graph shows a regular trend of this variable, with high summer-spring surface values (21.7 ± 3.4 $^{\circ}\text{C}$) and low autumn-winter surface values (16.6 ± 3.3 $^{\circ}\text{C}$), but high interannual variations are evident. The maximum temperatures were recorded on the surface in August 2003 (26.5 $^{\circ}\text{C}$); the minimums on the surface were recorded in March 2004 (12.5 $^{\circ}\text{C}$).

Figure 2B shows the temperature trend along the water column in the years 2018–2019, a regular trend of the variable is observed, with high surface values in the warm seasons (23.3 ± 2.5 $^{\circ}\text{C}$) and low surface values in the winter autumn seasons (15.4 ± 2.5 $^{\circ}\text{C}$). The maximum temperatures were recorded on the surface in August 2018 (27.2 $^{\circ}\text{C}$); the surface minima were measured in March 2018 (12.6 $^{\circ}\text{C}$). Differences were analyzed using a one-way ANOVA followed by a Fischer post hoc test ($p < 0.01$)

In both graphs we can see the progressive establishment of the thermocline, which is evident in the months of July–August, with very warm surface waters and colder deep waters. In the following months, the surface heat is transferred to the deeper layers. Summer 2003 experienced a positive temperature anomaly, similar to those of summer 2018 and 2019.

Autotrophic biomass (Figure 3), expressed as chlorophyll-a ($\mu\text{g/L}$), in the 50 m-surface layer shows a clear seasonal cycle (one-way ANOVA, $p < 0.01$) with higher values in winter and decreasing trend up to summer, and an increase in autumn. The major interannual variation occurred in winter due to the high variability of the late winter/early spring blooms. The highest autotrophic biomass occurred in winter 2018 and in winters 2003 and 2004 the seasonal average values exceeded $0.50 \mu\text{g/L}$. Conversely, in autumn 2018 and 2004 the increase in concentration was almost missing, as the seasonal average values were very similar to the ones of the summer in those years ($<0.2 \mu\text{g/L}$). Analyzing the annual average values, the difference in the 2003–2005 period is low ($0.30 \pm 0.19 \mu\text{g/L}$ in 2003; $0.31 \pm 0.19 \mu\text{g/L}$ in 2004 and $0.29 \pm 0.08 \mu\text{g/L}$ in 2005), while 2018 shows the highest average and 2019 the lowest ($0.36 \pm 0.25 \mu\text{g/L}$ and $0.25 \pm 0.11 \mu\text{g/L}$, respectively).

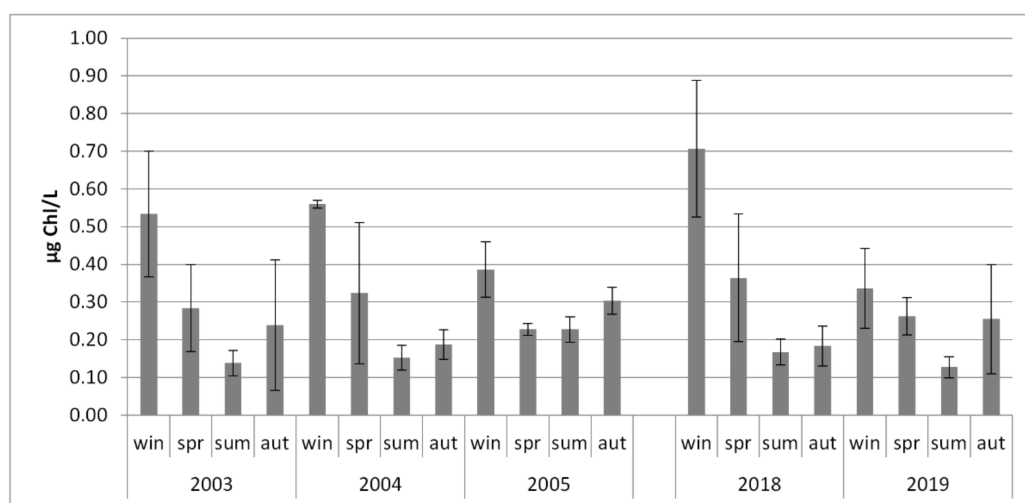


Figure 3. Seasonal autotrophic biomass as average chlorophyll-a ($\mu\text{g/L}$) in the 50 m-surface layer. Win: January–March; spr: April–June; sum: July–September; aut: October–December. Bars denote standard deviation.

3.2. Zooplankton Community

The complete list of the mesozooplankton species collected is reported in Appendix A (Tables A3–A7) together with abundances and sampling frequencies. Considering the annual mean abundance of the mesozooplankton organisms (both adults and juveniles) (Figure 4), it appears clear that copepods were the main abundant taxa in the five years, and the most abundant trophic group (ind/m^3) was represented by herbivorous copepods (HC). It accounted for more than 50% each year, with peaks of abundance in 2003, 2005 and 2019, close to $1000 \text{ ind}/\text{m}^3$ (46%), but only in 2005 they accounted for more than 60% of the total organisms. Among copepods, the least represented group were detritivorous copepods (DC), which accounted for less than 2% in the 2003–2005 period but increased their contribution in 2018 and 2019 (3.2 and 2.5%, respectively) with a percentage of about 3%. The omnivorous copepods (OC) contribution varied from 16.5 to 26.4% not showing differences between the periods. Carnivorous copepods (CC), as detritivorous, were less abundant in 2003–2005 period (1.2–2.2%) and increased in 2018–2019 reaching a percentage contribution like that of DC (3.3% and 2.6%, respectively, in 2018 and 2019).

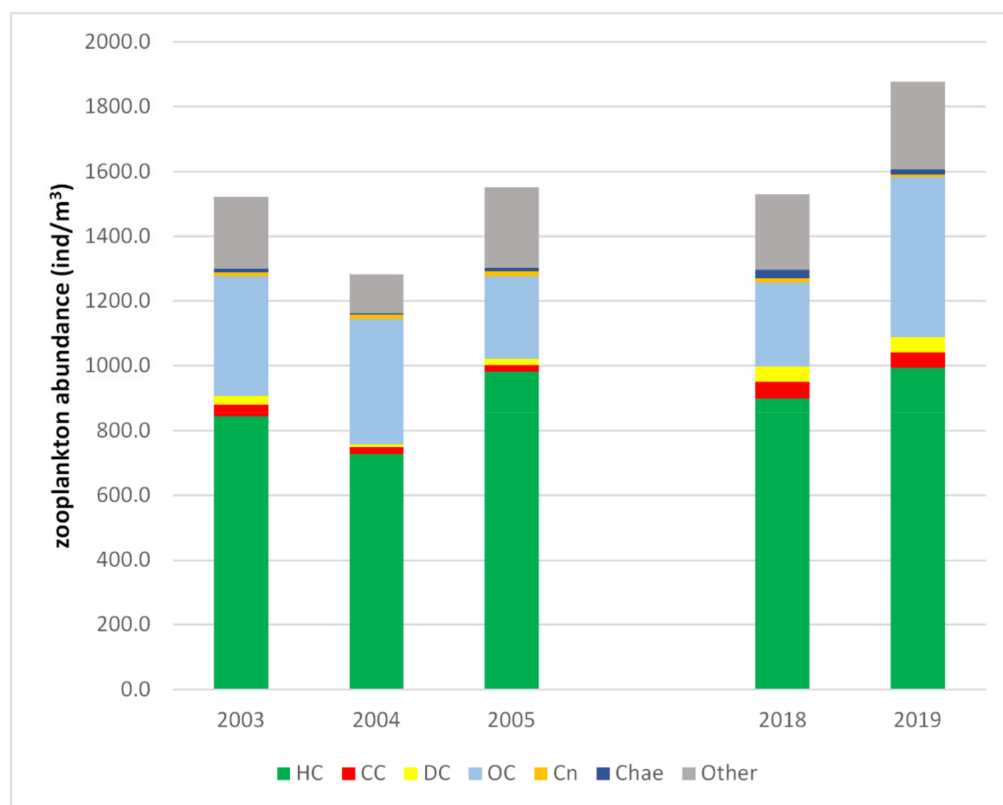


Figure 4. Zooplankton average abundance (ind/m³) in the five years according to main taxa (Copepods are divided by trophic strategy: HC-herbivorous copepods, CC-carnivorous copepods, DC-detritivorous copepods, OC omnivorous copepods; Cn-Cnidarians; Chae-Chaetognata; Other- other organisms mainly Cladocera, Appendicularia, Thaliacea and Thecosomata-Pteropoda).

Other carnivorous organisms, Cnidaria (Cn) and Chaetognata (Chae), showed low abundance: 22.30 ± 4.23 ind/m³ in 2003–2005 and a slightly higher 31.36 ± 12.81 ind/m³ in 2018–2019, while the contribution of other organisms (Other), mainly Cladocera, Appendicularia, Thaliacea and Pteropoda, varied from 7.9% to 16.1% according to the years.

Total abundance was higher in 2019 (>1800 ind/m³) and lower in 2004 (<1300 ind/m³).

The contribution of each taxa/trophic group in terms of biomass (mgC/m³) has been drawn up and Figure 5 shows the changes in the relationships between the years and between the trophic groups. Since most of the copepods have a small size, their overall contribution shifts below 50%. The HC are always the dominant group, but the percentage contribution of this trophic group is reduced to 43.5% in 2003–2005 period and to 39.7% in 2018–2019, with minimum percentages in 2018 (30.1%). The OC contributes for around 2% each period, while CC and DC contribute for even less, but their biomass is higher in 2018–2019 period (one-way ANOVA, $p < 0.05$ and $p < 0.001$, respectively, for CC and DC). Carnivorous larger organisms such as Cnidaria (Cn) and Chaetognata (Chae) acquire relevance every year: Cn contribution varies from 12.2% in 2019 to 31.9% in 2005 and Chae from 8.3% in 2004 to 41.2% in 2018, together accounting for nearly 50% of the total biomass. In particular, Chae have higher biomass in 2018–2019 period (one-way ANOVA, $p < 0.05$). The contribution of Other, conversely, decreases to less than 6%.

Total biomass was highest in 2018 (13.1 ± 9.2 mgC/m³) and lowest in 2004 (7.7 ± 3.0 mgC/m³) despite differences were not statistically relevant (one-way ANOVA, $p > 0.1$).

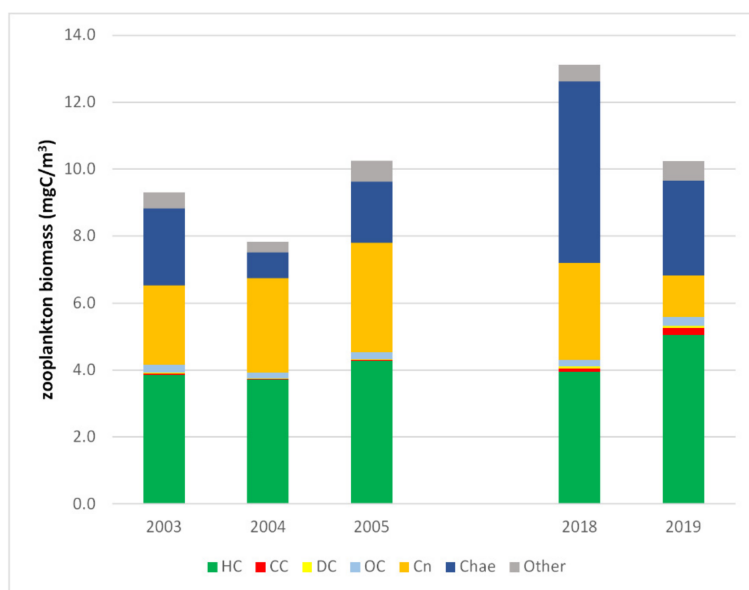


Figure 5. Zooplankton average biomass (mgC/m³) for five years according to main taxa (Copepods are divided by trophic strategy: HC-herbivorous copepods, CC-carnivorous copepods, DC-detritivorous copepods, OC omnivorous copepods; Cn-Cnidarians; Chae-Chaetognata; Other- other organisms mainly Cladocera, Appendicularia, Thaliacea and Thecosomata-Pteropoda).

3.3. Influence of Environmental Features on Zooplankton

Redundancy analysis developed considering the three explanatory variables (T_An, Chl_An and T5_An) explains 84% of the variation in the annual zooplankton biomass data. The two-dimensional approximation in Figure 6 explains 80.0% of this (59.5% on axis 1 and 20.5% on axis 2). Therefore, the first two axes explain 67.2% of the total variation in the annual zooplankton biomass data.

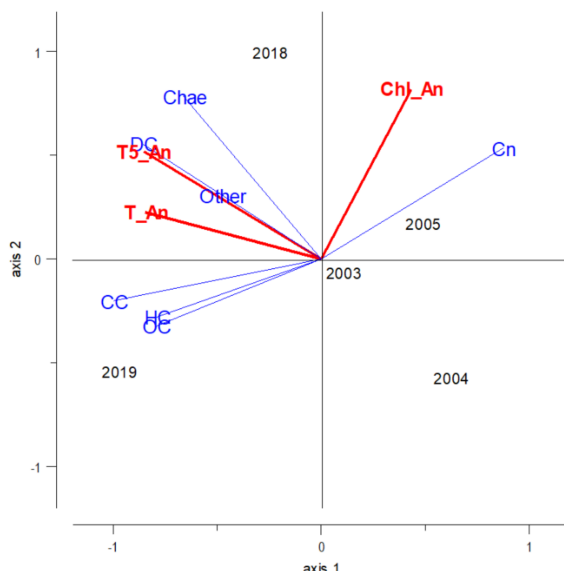


Figure 6. RDA correlation triplot for annual average zooplankton biomass and environmental variables anomalies. In blue: the response variables (zooplankton biomass functional groups); in red: the explanatory variables (monthly anomalies of temperature in the 0–50 m layer T_An, temperature in the 0–5 m layer T5_An, and fluorescence in the 0–50 m layer Chl_An); in black: the five years. (Copepods are divided by trophic strategy: HC-herbivorous copepods, CC-carnivorous copepods, DC-detritivorous copepods, OC omnivorous copepods; Cn-Cnidarians; Chae-Chaetognata; Other-other organisms mainly Cladocera, Appendicularia, Thaliacea and Thecosomata-Pteropoda).

The results of the forward selection and the permutation tests continue to explain a high percentage of variance (84.5%) and indicate that temperature anomalies have the main “marginal” effect (58.03% and 52.97%, respectively, T5_An and T_An, while Chl_An alone only explains 30.39%) and considering the “conditional effects” T5_An has the highest explained variation (0.49). The increase in explained variation due to adding an extra explanatory variable show Chl_An followed by T_An (0.27 and 0.08, respectively). The triplot in Figure 6 indicates that T5_An and T_An were positively related and T5_An was highly positively related to DC, Other and chaetognats, while T_An was partially positively correlated to CC, HC and OC. Chl_An instead was positively related to cnidarians. The five years grouped in different ways: the years of the period 2003–2005 grouped closer in the first and second quadrant while 2018 and 2019 were more apart in the third and fourth.

3.4. Modelling Approach

The main statistics describing the output of the ecological models estimated in each simulation together with the network flows and information indices were reported in Table 1.

Table 1. Output parameters from the Punta Faro mesozooplankton community model (TL: trophic level, TST: total system throughput).

	Groups Number	TL Mean	TL Max	Production (Sum)	Respiration (Tot)	Flows to Detritus	TST
mgC/m ³ /year							
2003							
Minimum	16.00	1.26	1.61	7.40	2.00	5.23	12.91
Maximum	22.00	1.98	2.41	31.06	8.44	29.15	45.12
Mean	19.83	1.67	2.10	17.57	4.50	12.76	28.90
St.dev.	1.59	0.26	0.22	9.94	2.24	8.46	12.43
2004							
Minimum	13.00	1.31	1.49	7.61	1.86	4.94	12.17
Maximum	23.00	1.79	2.35	28.26	6.52	26.53	42.17
Mean	18.45	1.53	1.95	16.13	3.66	13.94	26.87
St.dev.	2.46	0.17	0.28	10.08	1.36	9.40	10.22
2005							
Minimum	15.00	1.23	1.41	12.71	1.42	6.83	20.22
Maximum	20.00	1.94	2.48	25.96	10.48	20.14	53.01
Mean	17.82	1.62	2.00	17.21	4.90	12.13	30.10
St.dev.	1.60	0.20	0.27	4.15	2.30	4.13	9.00
2018							
Minimum	16.00	1.31	1.77	8.13	2.59	4.17	15.44
Maximum	22.00	2.22	2.45	47.97	7.40	41.42	56.06
Mean	19.09	1.75	2.18	22.13	4.54	16.37	33.36
St.dev.	1.76	0.27	0.19	14.05	1.61	12.69	15.38
2019							
Minimum	17.00	1.38	2.00	8.01	1.31	4.33	11.23
Maximum	22.00	2.26	2.66	36.93	13.67	17.64	50.45
Mean	19.58	1.77	2.26	21.12	5.28	10.75	28.93
St.dev.	1.44	0.24	0.19	5.85	3.29	3.96	10.92

A number of functional groups showed low variability among simulations and ranged from a minimum of 13 groups to a maximum of 23. The sum of all production displayed higher values in 2018–2019 while respiration, flow to detritus and the sum of all the flows in the network (total system throughput) did not show clear differences among years.

Both the average and the maximum values of the trophic levels show consistent trends in the two considered periods with higher values in the period 2018–2019. The highest trophic levels corresponded to the presence of Cnidaria (average TL = 3.06) and Chaetognata (average TL = 2.72). Differences in the average trophic levels of the networks are also mirrored by variations in the organization of the food chain and in the groups targeted for consumption (Figure 7). Despite the consumption of autotrophs playing a major role in all the considered years, the average food chain organization in 2018–2019 has shifted towards higher consumption of detritus and heterotrophs reducing the share of autotrophs consumption.

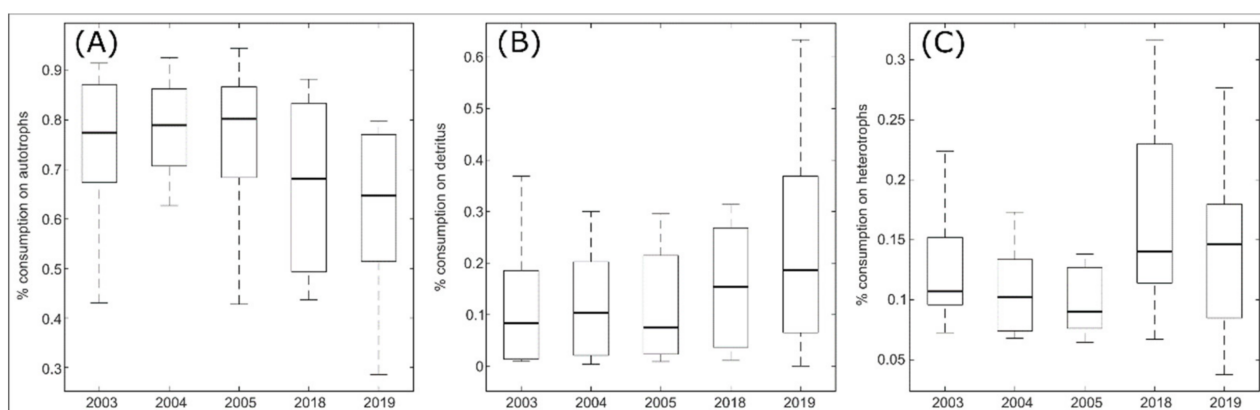


Figure 7. Percentage of total consumption on autotrophs (A), detritus (B) and heterotrophs (C).

3.4.1. Mixed Trophic Impact

The total MTI analysis was carried out for each simulation in order to identify the functional group with the highest influence on the biomass of the others in the analyzed trophic web. In all the simulated networks, primary producers played the top positive role in the system. For the sake of clarity, results are shown excluding the primary producers' role and taking into consideration the frequency each functional group was identified among ones having of the top five positive or negative effects (Figure 8). Juvenile copepods played a major positive role in the plankton community during the entire period, together with herbivorous copepods, despite these latter losing importance in recent years. During the 2003–2005 period Thecosomata often had a negative impact while *Oncaea* spp. as well as omnivorous cyclopoids (mainly *Oithona* spp.) played a major positive role only in the 2018–2019 samples. Regarding the negative overall effects, the highest impact on the web was always due to Appendicularia, Chaetognata, Cnidaria, Thecosomata and other omnivorous juveniles (as crustaceans' larvae).

3.4.2. Ecological Network Analysis

Average mutual information variations are very narrow ranging from 1.02 to 1.22 with an overall average value of 1.14 ± 0.05 (Figure 9). AMI values are consistent between the considered periods with the highest values during the warm season (spring and summer) and the lowest values in winter.

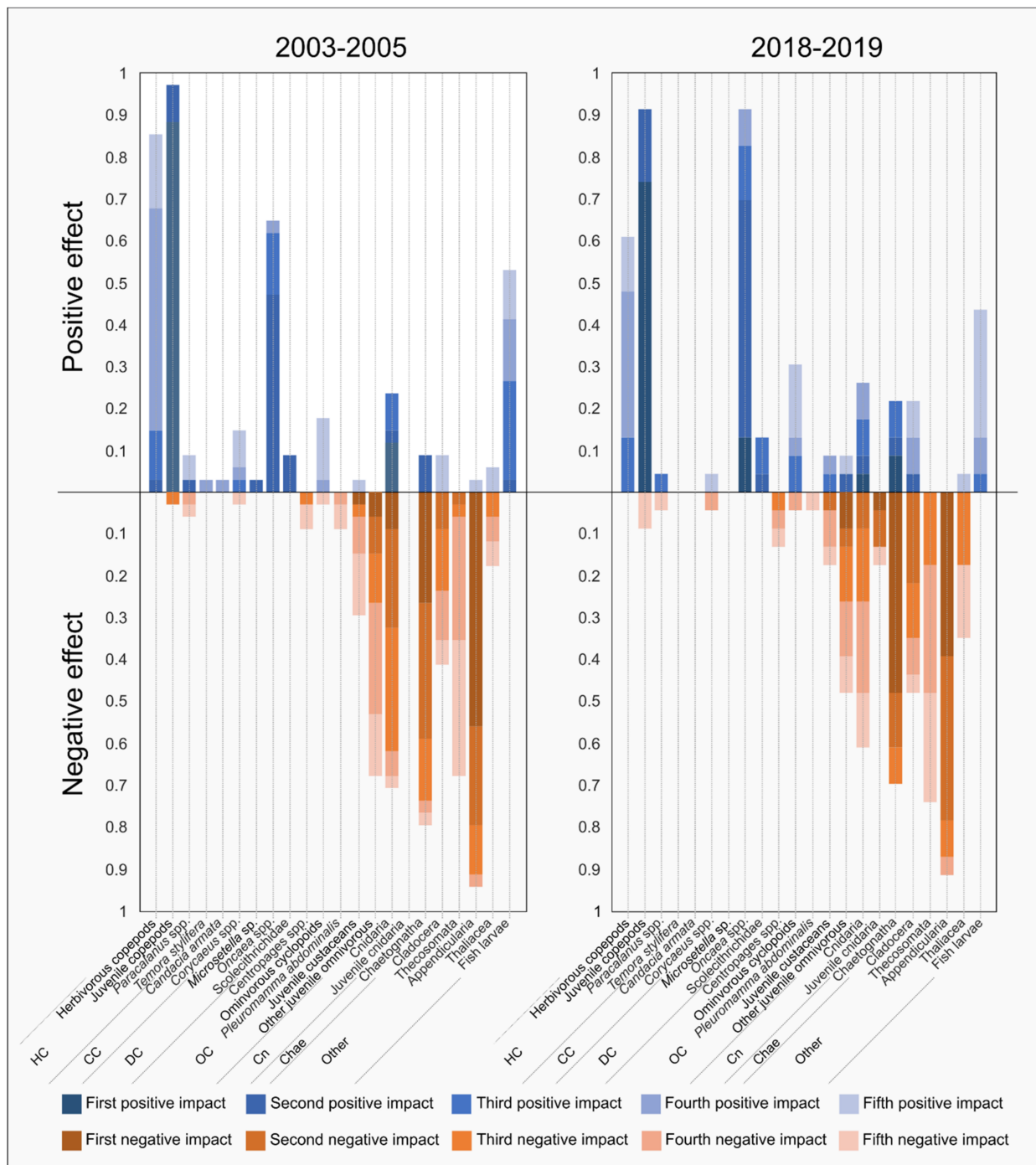


Figure 8. Positive and negative effects of considered functional group (values reported as frequency of appearance).

Ascendency ranges from 8.16 to 55.47 mgC/m³/year averaging 26.23 ± 10.81 mgC/m³/year. Maximum values and highest variability are displayed in spring (Figure 9). Ascendency in the two years period 2018–2019 always displayed larger maximum, minimum and average values than 2003–2005.

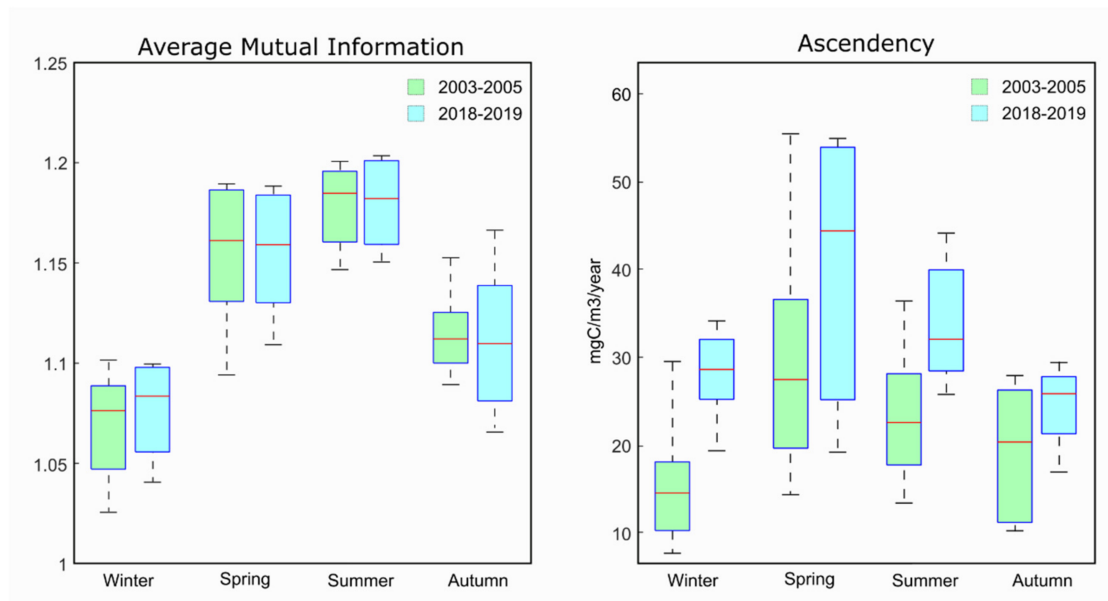


Figure 9. Seasonal Average Mutual Information and Ascendency ($\text{mgC}/\text{m}^3/\text{year}$) in the two periods (2003–2005 and 2018–2019).

3.4.3. Energy Analysis

Energy, intended here as a metric of the natural capital stored in the living biomass, ranged from 3.89×10^{10} sej to 4.46×10^{11} sej with an average value of $1.76 \times 10^{11} \pm 1.18 \times 10^{11}$ sej (Figure 10). Energy showed similar values in both the considered periods with minimum average values in summer and highest average values in spring. Energy exploited per unit of time (empower) ranged from 3.80×10^9 sej/year to 2.31×10^{10} sej/year averaging $1.19 \times 10^{10} \pm 8.55 \times 10^9$ sej/year (Figure 10). Despite natural capital stored did not differ in the considered periods, the functioning of the plankton community measured through the energy exploited to maintain the system (empower) always showed higher average values in 2018–2019. The two periods also showed different trends with maximum values in spring during 2003–2005 while empower kept growing until summer in 2018–2019.

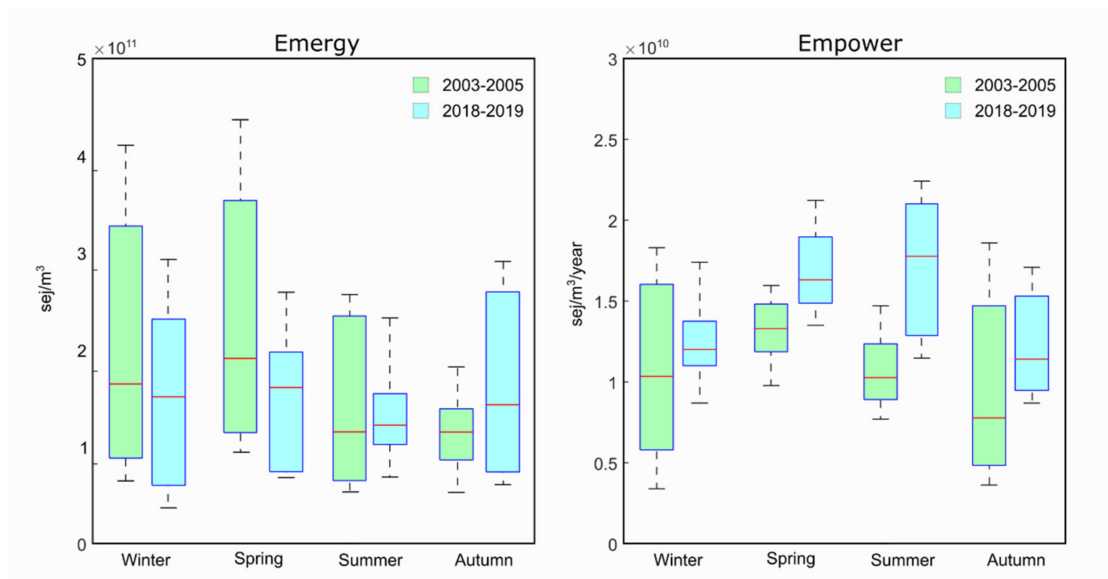


Figure 10. Seasonal average Energy (sej/m^3) and Empower ($\text{sej}/\text{m}^3/\text{year}$) in the two periods (2003–2005 and 2018–2019).

4. Discussion

Numerous long-term studies regarding the variations of plankton community due to climate and hydrological changing conditions are available mainly regarding the oceans [51–56]. Despite being recognized as an important hot spot of biodiversity, Mediterranean Sea is less studied and research regarding the plankton community is somewhat rare because of the lack of long-term datasets [52,57–62] although efforts have been made in recent years carrying on long-term programs (e.g., [63–67]). Even when the plankton community is investigated, the studies focused on the analysis of the variations in the composition of the community, comparing abundances of different species or assemblages of species. Very few studies are referred to the analysis of the plankton community functioning [68,69] while it is complementary information crucial for the interpretation of the ecosystem state, maturity and health status. Therefore, in this study, we analyzed the functioning of the plankton community sampled on a monthly base in front of the coast of Portofino (NW Mediterranean) comparing two periods 13 years apart (2003–2005 and 2018–2019). The functional analyses, based on whole system approaches such as network analysis and emergy analysis, allowed to analyze the functioning of the system in terms of its ability to store, move and exploit available energy. Both network and emergy analysis outputs have been considered as goal functions of the system since all the considered indicators are expected to increase when a system is free to develop and move towards a more mature and stable state [42,45].

The temperature of the water column showed that the environmental conditions have changed, leading to less diversified seasons with warmer seasons lasting longer and colder seasons showing higher temperature values all over the water column. This is expected to have relevant consequences in terms of system functionality and is in accord with a general increase in the surface temperatures of the Ligurian Sea but, in general, also of the Mediterranean Sea, although presenting interannual variations [23]. From the analyses carried out, in fact, it can be observed that 2005 is characterized by a low stratification, as the warm waters are not limited to the surface area but reach up to about 35–40 m deep, while 2003 shows a superficial thermal anomaly with very high temperature values compared to the average. In recent years, there has been a marked increase in temperatures which translates into a decidedly positive normalized anomaly for both 2018 and 2019, especially in late summer and autumn [70].

Autotrophic biomass in the two considered periods is generally low, reflecting the oligotrophy of the Ligurian Sea [71] and the characteristics of the Portofino Promontory marine area [20,72,73]. The seasonal cycle (principal blooms in late winter/early spring and an occasional secondary bloom in autumn) are typical of the Mediterranean Sea and at Punta Faro LTER site are also influenced by torrents discharge [27,74]. Since the 2000s a process of oligotrophication was highlighted in the area [25], and this process was also observed in other Italian LTER sites up to the middle 1990s/early 2000s, followed by a stabilization or a new increase, together with a reduction of the mean phytoplankton size [20].

Considering this scenario, possible structural (biomass composition) and functional differences of the system were investigated. For the zooplankton component, what is known for this study area is confirmed, namely that the zooplankton abundance is mainly dominated by copepods [62,73] which cover about 62% of the sampled community, among them the component mainly represented is that of herbivorous copepods. The main peak of abundance occurs in spring, after the late winter-early spring phytoplankton bloom. These five years are part of a context of increased abundance of zooplankton organisms, mainly due to the increase in small to medium-sized copepods (1 mm–0.5 mm) that were reported in other Tyrrhenian sites, although with interannual and decadal fluctuations [20,67]. Despite the increase in total mesozooplankton abundance in the 2000s compared to the past, specific organisms or groups showed different behaviors, such as the most abundant spring copepods *Centropages* spp. that is also decreasing because of an anticipation of the end of the season in relation to summer temperature anomalies in the Tyrrhenian Sea,

but other groups such as the Appendicularia and Chaetognata groups are increasing in abundance. Moreover, in Portofino LTER site an increase is reported in the abundance of small organisms, such as *Oithona* spp. and *Oncaea* spp. and the same process also occurs in the Northern Adriatic Sea [20]. This trend seems to be amplified in 2018–2019 biennium where average detritivores copepods contribution increased, together with CC and Chae contributions.

Looking at the biomass values, they are coherent with other findings in the oligotrophic Mediterranean Sea [75] ($<10 \text{ mgC/m}^3$). A high percentage contribution is due to herbivorous copepods (adults and juveniles) but also to Cnidaria and Chaetognata, which were particularly elevated in 2018 (41.2%), contributing to the highest value of mean annual biomass for that year. The year 2004, on the other hand, is the one with the lowest values in terms of biomass, as it was for the abundance values, but the difference in biomass is even more marked.

The web organization in the two considered periods showed an increase in the share of consumption directed towards detritus and heterotrophs coupled with a decrease in the share of primary producers' consumption. Primary producers in the water column and the primary productivity available for consumption do not display significant variations during the considered periods. We may hypothesize two different reasons for the decrease in the primary producers' consumption. In 2018, primary productivity and food availability were high due to the maximum values of primary producers biomass in the system (Figure 3) but this corresponds to the moment when the maximum values of non-herbivorous consumers biomass was detected (mainly Chaetognata and Cnidaria) (Figure 5) forcing the web organization to a functional change driven by the presence of a different set of organisms composing the zooplankton community rather than by a lack of resources availability (top-down effect). On the contrary, in 2019 the highest herbivorous biomass was sampled, and it was expected to address the consumption towards the autotrophs. This was not the case, due to a lack of primary productivity in the system which was not able to support the expected consumption that was diverted towards detritus exploitation (bottom-up effect). Primary productivity was in fact simulated to be completely consumed by autotrophs 5 out of 12 months in 2019.

Despite different forcing factors, the changes in the food web organization might identify a shift of the plankton community from a grazing food web towards a detritus or microbial loop food web, typical of the tropical area [76], but already discussed for the Mediterranean Sea [19,68].

This is also supported by the analysis of the mixed trophic impact: the network functioning is characterized by the positive effect of herbivorous copepods and the negative overall effect due to Cnidaria, Chaetognata and other consumers. Still, in the 2018–2019 biennium the herbivorous copepods are less important being mainly compensated by the increased positive effect of *Oncaea* spp. and a few other minor changes (in example omnivorous copepods such as *Oithona* spp.) that may indicate an increased complexity in the web organization and a lower relevance of the first trophic levels in the web. Regarding the species with negative effects, changes are less evident highlighting that the community is changing mainly from the perspective of resource provisioning rather than from the resource exploitation one.

The modeling approach made it possible to investigate the functionality of the plankton community and its seasonal and interannual variations. The average mutual information here intended as a proxy of the organization and efficiency of the system displayed a decreasing seasonal trend with minimum values in autumn and consistent values throughout the years. Despite the species composition having changed, the system is able to maintain the flow organization, efficiently adapting to the changing conditions. On the contrary, ascendancy displayed consistently higher values in recent years, meaning that the overall level of activity of the system has increased and more energy is flowing in the system. Ecological network analysis theory states that this is expected to be correlated to an increase in maturity and complexity [42] but in this case this is not mirrored by a similar

trend of average mutual information indicating that the system is accelerating the rate of energy exchange without increasing its organization.

Ecological network analysis has been complemented by the analysis of the system complexity measured assessing the natural capital stored in the biomass (emergy) and the natural cost of maintaining the system complexity (empower). The comparison between the two analyzed periods displayed little variation in the system's capability to store natural capital in the plankton community that, despite being composed of a different set of organisms and being organized in a different way, kept the quantity of emergy stored in the living structures unchanged. On the contrary, the same complexity has been kept at a higher annual cost in recent years, pointing out that the plankton community has become less efficient at keeping the complexity level stable, having to spend more energy to maintain the natural capital.

As a matter of fact, the whole system analyses proposed here are able to analyze the system's functioning and complexity revealing that the plankton community has changed the species' composition, moving towards a more regeneration-dominated ecosystem [19] where small detritivorous copepods such as *Oncaea* spp. and omnivorous copepods such as *Oithona* spp., advantaged in an oligotrophic area [77], acquired importance. This is also mirrored by the different roles played by functional groups in the system with primary consumers (herbivores) that are losing relevance and an increasing importance of more complex species feeding on different resources and with higher trophic levels (increased contribution of detritivorous and carnivorous copepods, and carnivorous organisms). Considering the functional analyses, the system is able to organize the web of connections keeping the same level of exchange efficiency despite being characterized by an increase in the flow intensity and in the overall energy flowing in the system. This behavior was previously detected in benthic system under anthropic pressure [78,79] and was referred to as an increase effort put in place by the natural system to face or cope with the external disturbance. In this case, the plankton community affected by an increase in water temperature seems to react in the same way, accelerating processes without improving the general condition. This was also confirmed by the natural capital evaluation that showed the system was able to keep the stored capital at a constant level but at the cost of higher flows feeding the system. Again, the system is able to organize itself in a new, modified structure, probably adapted to the changed surrounding conditions but this is possible at the cost of higher energy flows and higher costs in terms of resources exploited by the system.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Individual Carbon weight for mesozooplankton species.

Functional Group	Species/Taxa	IC (mgC)
HC	<i>Acartia clausi</i>	0.0029
	<i>Acartia italica</i>	0.0029
	<i>Acartia margalefi</i>	0.0029
	<i>Acartia teclae</i>	0.0029
	<i>Calocalanus contractus</i>	0.0029
	<i>Calocalanus styliremis</i>	0.0029
	<i>Calocalanus tenuis</i>	0.0029
	<i>Clausocalanus arcuicornis</i>	0.0029
	<i>Clausocalanus furcatus</i>	0.0029
	<i>Clausocalanus lividus</i>	0.0029
	<i>Clausocalanus parapergens</i>	0.0029
	<i>Clausocalanus paululus</i>	0.0029
	<i>Clausocalanus pergens</i>	0.0029
	<i>Clausocalanus spp.</i>	0.0029
	<i>Ctenocalanus vanus</i>	0.0029
	<i>Euterpina acutifrons</i>	0.0029
	<i>Nannocalanus minor</i>	0.0049
	<i>Paracalanus denudatus</i>	0.0019
	<i>Paracalanus nanus</i>	0.0019
	<i>Paracalanus parvus</i>	0.0019
<i>Paracalanus spp.</i>	0.0019	
<i>Temora stylifera</i>	0.0102	
Juvenile copepods	0.0038	
CC	<i>Candacia armata</i>	0.0020
	<i>Corycaeus spp.</i>	0.0022
DC	<i>Microsetella sp.</i>	0.0012
	<i>Oncaea spp.</i>	0.0022
	<i>Scolecithricidae</i>	0.0063
OC	<i>Centropages kroyeri</i>	0.0065
	<i>Centropages typicus</i>	0.0065
	<i>Isias clavipes</i>	0.0068
	<i>Oithona nana</i>	0.0004
	<i>Oithona plumifera</i>	0.0004
	<i>Oithona similis</i>	0.0004
	<i>Pleuromamma abdominalis</i>	0.1000
<i>Pleuromamma gracilis</i>	0.0020	

Table A1. Cont.

Functional Group	Species/Taxa	IC (mgC)
Cn	Cnidaria	0.1885
	Juvenile Cnidarians	0.1885
Che	Chaetognatha	0.1885
	<i>Evadne spinifera</i>	0.0017
	<i>Evadne</i> spp.	0.0017
	<i>Penilia avirostris</i>	0.0017
Other	<i>Podon</i> spp.	0.0017
	Thecosomata	2.41×10^{-5}
	Appendicularia	0.0030
	Thaliacea	0.0028
	Fisch larvae	0.0016
	Malacostraca	0.0016
	Polychaeta	0.0016
	Bivalvia larvae	0.0016
	Bryozoa larvae	0.0016
	Echinodermata	0.0016
Other Juvenile	Cirripedia	0.0016
	Crustacea	0.0016

Table A2. List of model parameters.

Functional Group	Species	Model Parameters			References	
		P/B	Q/B	U/Q		
Chla		1.278				
	Herbivorous copepods	0.04	0.631	0.53		
HC	<i>Paracalanus</i> spp.	0.116	0.667	0.53		
	<i>Temora</i> spp.	<i>Temora stylifera</i>	0.04	0.223	0.53	
CC	<i>Candacia</i> spp.	<i>Candacia armata</i>	0.04	0.631	0.53	
	<i>Corycaeus</i> spp.		0.108	0.289	0.323	
	<i>Euchaeta</i> spp.		0.04	0.631	0.53	
DC	<i>Microsetella</i> sp.		0.04	0.631	0.53	
	<i>Oncaea</i> spp.		0.04	0.631	0.53	
	<i>Scolecithricella</i> spp.		0.04	0.631	0.53	
OC	<i>Centropages</i> spp.		0.108	0.289	0.323	[31,80,81]
	Omivores Cyclopoida		0.055	0.297	0.53	
	<i>Isias</i> spp.	<i>Isias clavipes</i>	0.04	0.631	0.53	
	<i>Pleuromamma</i> spp.	<i>Pleuromamma abdominalis</i>	0.04	0.631	0.53	
<i>Pleuromamma gracilis</i>		0.04	0.631	0.53		
Cn	Cnidaria	0.25	0.192	0.195		
Che	Chaetognata	0.25	0.192	0.195		
	Cladocera	0.793	1.452	0.496		
Other	Thecosomata	0.25	0.192	0.195		
	Appendicularia	0.494	14.012	0.604		
	Thaliacea	1.35	1.392	0.22		

Table A3. Abundance and frequency of species in 2003 samplings.

Functional Group	Trophic Refs.	Species/Taxa	2003							
			Winter		Spring		Summer		Autumn	
			Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)
HC	[82–86]	<i>Acartia clausi</i>	14.59	20	184.46	50	45.19	50	3.93	33
		<i>Acartia italica</i>	-	-	-	-	-	-	-	-
		<i>Acartia margalefi</i>	-	-	-	-	-	-	-	-
		<i>Acartia teclae</i>	-	-	-	-	-	-	-	-
		<i>Calocalanus contractus</i>	-	-	-	-	-	-	-	-
		<i>Calocalanus styliremis</i>	35.08	40	24.88	50	24.59	50	29.01	50
		<i>Calocalanus tenuis</i>	-	-	-	-	-	-	-	-
		<i>Clausocalanus arcuicornis</i>	19.94	20	3.13	33	7.36	33	6.17	33
		<i>Clausocalanus furcatus</i>	19.97	40	4.55	33	39.26	50	31.95	50
		<i>Clausocalanus lividus</i>	3.71	40	2.11	17	-	-	1.68	17
		<i>Clausocalanus parapergens</i>	-	-	-	-	-	-	-	-
		<i>Clausocalanus paululus</i>	56.35	60	7.91	33	145	50	20.90	50
		<i>Clausocalanus pergens</i>	38.40	40	41.22	50	5.67	50	15.96	50
		<i>Clausocalanus spp.</i>	47.97	20	12.22	33	28.54	26	19.94	50
		<i>Ctenocalanus vanus</i>	8.60	-	10.32	17	0.92	17	0.67	17
		<i>Euterpina acutifrons</i>	22.57	60	17.20	33	5.67	33	17.09	50
		<i>Nannocalanus minor</i>	-	-	-	-	-	-	2.18	17
		<i>Paracalanus denudatus</i>	2.32	40	22.05	33	-	-	-	-
		<i>Paracalanus nanus</i>	12.41	40	2.29	17	15.14	50	12.06	50
		<i>Paracalanus parvus</i>	54.57	40	128.65	50	23.46	50	43.87	50
<i>Paracalanus spp.</i>	7.80	20	11.95	50	3.40	17	2.09	33		
<i>Temora stylifera</i>	3.11	-	-	-	5.47	50	10.29	50		
Juvenile copepods	784.09	40	1251.86	50	414.17	50	643.67	50		
CC	[87–90]	<i>Candacia armata</i>	-	-	-	-	2.22	17	-	-
		<i>Corycaeus spp.</i>	15.15	40	9.95	50	24.17	50	46.03	50
DC	[87,91–93]	<i>Microsetella sp.</i>	-	-	-	-	1.65	17	-	-
		<i>Oncaea spp.</i>	11.71	20	11.95	50	3.93	33	7.34	50
		<i>Scolecithricidae</i>	-	-	-	-	2.45	17	1.09	17
OC	[82,83,94–96]	<i>Centropages kroyeri</i>	-	-	6.88	45	8.36	55	-	-
		<i>Centropages typicus</i>	13.61	20	27.69	54	5.39	10	4.89	09
		<i>Isias clavipes</i>	-	20	14.87	59	7.41	30	2.73	11
		<i>Oithona nana</i>	3.27	-	-	-	-	-	-	-
		<i>Oithona plumifera</i>	-	-	6.88	19	19.92	55	9.39	26
		<i>Oithona similis</i>	80.18	40	102.19	46	17.16	08	23.02	10
		<i>Pleuromamma abdominalis</i>	-	-	-	-	-	-	-	-
<i>Pleuromamma gracilis</i>	-	-	-	-	-	-	0.67	17		
Cn	[19,97,98]	Cnidaria	5.31	60	15.06	50	19.55	50	10.40	50
		Juvenile Cnidarians	-	-	-	-	-	-	-	-
Che	[99–102]	Chaetognatha	3.61	60	8.59	50	12.81	50	23.47	50

Table A3. Cont.

Functional Group	Trophic Refs.	Species/Taxa	2003							
			Winter		Spring		Summer		Autumn	
			Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)
Other	[103–105]	<i>Evadne spinifera</i>	1.10	-	117.42	50	11.66	50	0.21	33
		<i>Evadne</i> spp.	0.21	-	3.35	50	7.79	50	-	-
		<i>Penilia avirostris</i>	-	-	2.82	50	73.14	50	0.26	33
		<i>Podon</i> spp.	11.66	40	11.03	50	2.88	50	-	-
		Thecosomata	14.90	60	75.60	50	19.08	50	21.64	50
		Appendicularia	69.22	60	156.26	50	184.08	50	61.64	50
		Thaliacea	0.94	40	24.78	50	2.40	50	4.08	33
		Fisch larvae	0.52	20	4.71	50	2.14	50	0.31	33
Other Juvenile		Malacostraca	20.86	40	8.42	50	6.85	50	9.51	50
		Polychaeta	5.96	40	0.68	50	1.15	50	5.76	50
		Bivalvia larvae	23.84	40	58.61	50	2.67	50	2.35	50
		Bryozoa larvae	5.44	40	11.66	50	-	-	0.26	33
		Echinodermata	6.12	40	27.86	50	1.15	50	1.52	50
		Cirripedia	0.05	-	0.05	17	0.05	17	-	-
		Crustacea	10.87	40	2.67	50	4.55	50	1.46	50

Table A4. Abundance and frequency of species in 2004 samplings.

Functional Group	Trophic Refs.	Species/Taxa	2004							
			Winter		Spring		Summer		Autumn	
			Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)
HC	[82–86]	<i>Acartia clausi</i>	3.35	25	55.99	50	8.36	50	18.90	33
		<i>Acartia italica</i>	-	-	-	-	-	-	-	-
		<i>Acartia margalefi</i>	-	-	-	-	-	-	-	-
		<i>Acartia teclae</i>	-	-	-	-	-	-	-	-
		<i>Calocalanus contractus</i>	-	-	-	-	-	-	-	-
		<i>Calocalanus styliremis</i>	60.48	50	9.95	50	24.96	50	8.53	67
		<i>Calocalanus tenuis</i>	-	-	-	-	-	-	-	-
		<i>Clausocalanus arcuicornis</i>	4.56	25	3.14	33	4.42	50	-	-
		<i>Clausocalanus furcatus</i>	4.87	50	-	-	2.03	33	12.43	33
		<i>Clausocalanus lividus</i>	7.59	50	1.33	17	-	-	-	-
		<i>Clausocalanus parapergens</i>	-	-	-	-	-	-	-	-
		<i>Clausocalanus paululus</i>	27.27	75	17.17	50	20.51	33	33.77	67
		<i>Clausocalanus pergens</i>	38.40	50	46.15	50	12.23	33	3.36	67
		<i>Clausocalanus</i> spp.	12.87	25	6.02	17	7.87	33	55.77	67
		<i>Ctenocalanus vanus</i>	-	-	-	-	-	-	-	-
		<i>Euterpina acutifrons</i>	18.46	75	5.86	33	2.73	33	1.00	33
<i>Nannocalanus minor</i>	-	-	0.51	17	-	-	-	-		

Table A4. Cont.

Functional Group	Trophic Refs.	Species/Taxa	2004							
			Winter		Spring		Summer		Autumn	
			Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)
HC	[82–86]	<i>Paracalanus denudatus</i>	8.68	50	-	-	-	-	-	-
		<i>Paracalanus nanus</i>	11.93	50	3.27	33	3.04	17	2.00	33
		<i>Paracalanus parvus</i>	56.13	50	40.74	50	60.45	50	17.79	67
		<i>Paracalanus</i> spp.	6.70	25	18.02	50	9.09	33	-	-
		<i>Temora stylifera</i>	-	-	-	-	2.74	33	2.09	33
		Juvenile copepods	1057.50	50	1211.49	50	413.90	50	555.83	1.00
CC	[87–90]	<i>Candacia armata</i>	-	-	0.51	17	1.12	17	-	-
		<i>Corycaeus</i> spp.	6.33	50	7.23	50	7.28	50	29.88	67
DC	[87,91–93]	<i>Microsetella</i> sp.	-	-	-	-	-	-	-	-
		<i>Oncaea</i> spp.	10.05	25	3.27	33	2.73	33	-	-
OC	[82,83,94–96]	<i>Scolecithricidae</i>	-	-	-	-	1.21	17	-	-
		<i>Centropages kroyeri</i>	-	-	-	-	1.36	17	-	-
		<i>Centropages typicus</i>	8.93	25	32.10	50	12.85	50	2.36	33
		<i>Isias clavipes</i>	1.77	25	1.59	17	11.91	33	2.36	33
		<i>Oithona nana</i>	-	-	52.13	50	4.80	33	4.17	33
		<i>Oithona plumifera</i>	-	-	-	-	5.00	50	7.72	67
		<i>Oithona similis</i>	80.89	50	73.20	50	12.06	50	8.53	67
		<i>Pleuromamma abdominalis</i>	-	-	-	-	-	-	-	-
Cn	[19,97,98]	Cnidaria	16.42	75	14.06	50	15.84	50	12.63	67
		Juvenile Cnidarians	-	-	-	-	-	-	-	-
Che	[99–102]	Chaetognatha	4.13	75	3.61	50	1.88	50	8.00	67
Other	[103–105]	<i>Evadne spinifera</i>	-	-	5.38	33	8.36	50	2.67	33
		<i>Evadne</i> spp.	-	-	0.21	17	3.55	50	0.47	33
		<i>Penilia avirostris</i>	-	-	0.31	17	35.97	50	1.57	67
		<i>Podon</i> spp.	19.81	50	12.49	50	3.82	50	1.49	67
		Thecosomata	12.97	75	35.71	50	9.67	50	8.16	67
		Appendicularia	27.76	75	86.94	50	136.82	50	86.42	67
		Thaliacea	2.25	50	9.31	33	0.73	50	3.29	67
		Fisch larvae	0.05	25	3.08	33	1.15	50	0.16	67
Other Juvenile		Malacostraca	18.14	50	11.61	50	5.23	50	2.12	1.00
		Polychaeta	3.14	50	1.46	50	1.88	50	1.57	1.00
		Bivalvia larvae	5.33	50	12.01	50	1.57	50	0.71	67
		Bryozoa larvae	4.65	50	1.93	50	0.05	33	-	-
		Echinodermata	5.86	50	1.93	50	0.94	33	0.78	1.00
		Cirripedia	-	-	-	-	0.10	17	-	-
		Crustacea	10.19	50	1.10	50	1.46	50	1.49	1.00

Table A5. Abundance and frequency of species in 2005 samplings.

Functional Group	Trophic Refs.	Species/Taxa	2005							
			Winter		Spring		Summer		Autumn	
			Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)
HC	[82–86]	<i>Acartia clausi</i>	131.20	75	183.61	50	42.75	40	4.30	25
		<i>Acartia italica</i>	-	-	-	-	3.27	20	-	-
		<i>Acartia margalefi</i>	-	-	-	-	-	-	-	-
		<i>Acartia teclae</i>	-	-	-	-	-	-	-	-
		<i>Calocalanus contractus</i>	-	-	-	-	-	-	-	-
		<i>Calocalanus styliremis</i>	46.90	75	24.54	50	8.48	40	12.33	25
		<i>Calocalanus tenuis</i>	-	-	-	-	-	-	-	-
		<i>Clausocalanus arcuicornis</i>	6.84	50	7.69	17	4.14	40	3.28	50
		<i>Clausocalanus furcatus</i>	11.35	50	-	-	1.42	20	33.23	50
		<i>Clausocalanus lividus</i>	10.40	50	4.06	33	3.63	20	8.61	25
		<i>Clausocalanus parapergens</i>	-	-	4.03	17	-	-	-	-
		<i>Clausocalanus paululus</i>	29.44	75	6.31	33	9.08	40	7.67	25
		<i>Clausocalanus pergens</i>	28.66	75	23.15	50	17.06	40	3.72	25
		<i>Clausocalanus spp.</i>	32.73	75	45.86	50	61.35	60	31.71	50
		<i>Ctenocalanus vanus</i>	3.75	25	-	-	3.27	20	-	-
		<i>Euterpina acutifrons</i>	14.59	50	2.40	33	-	-	7.03	50
		<i>Nannocalanus minor</i>	-	-	-	-	-	-	-	-
		<i>Paracalanus denudatus</i>	-	-	-	-	10.89	20	-	-
		<i>Paracalanus nanus</i>	4.54	25	15.38	17	1.42	20	6.33	23
		<i>Paracalanus parvus</i>	47.09	50	174.69	50	129.95	60	46.68	12
<i>Paracalanus spp.</i>	-	-	5.16	17	18.05	60	-	-		
<i>Temora stylifera</i>	-	-	0.87	17	1.42	20	1.24	35		
Juvenile copepods	906.54	75	1266.04	50	686.01	60	515.98	50		
CC	[87–90]	<i>Candacia armata</i>	13.56	27	7.75	16	10.56	21	17.68	36
		<i>Corycaeus spp.</i>	4.18	50	31.73	33	15.30	60	18.51	50
DC	[87,91–93]	<i>Microsetella sp.</i>	-	-	-	-	-	-	-	
		<i>Oncaea spp.</i>	22.31	75	16.30	33	1.36	20	1.24	25
		<i>Scolecithricidae</i>	-	-	-	-	-	-	-	-
OC	[82,83,94–96]	<i>Centropages kroyeri</i>	-	-	3.19	17	3.27	20	-	-
		<i>Centropages typicus</i>	5.56	25	43.32	50	18.83	60	1.13	25
		<i>Isias clavipes</i>	0.91	25	-	-	7.26	20	-	-
		<i>Oithona nana</i>	2.11	25	9.41	33	3.27	20	1.13	25
		<i>Oithona plumifera</i>	2.11	25	10.35	33	13.89	40	29.64	50
		<i>Oithona similis</i>	78.39	75	74.55	50	33.57	40	39.12	50
		<i>Pleuromamma abdominalis</i>	-	-	-	-	-	-	-	-
		<i>Pleuromamma gracilis</i>	-	-	-	-	-	-	4.96	25
Cn	[19,97,98]	Cnidaria	4.18	75	31.73	50	15.30	60	18.51	50
		Juvenile Cnidarians	-	-	-	-	-	-	-	-
Che	[99–102]	Chaetognatha	5.02	75	1.57	33	6.27	40	34.11	50

Table A5. Cont.

Functional Group	Trophic Refs.	Species/Taxa	2005							
			Winter		Spring		Summer		Autumn	
			Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)
Other	[103–105]	<i>Evadne spinifera</i>	-	-	26.82	33	16.68	34	5.80	12
		<i>Evadne</i> spp.	-	-	2.77	17	8.21	60	1.25	50
		<i>Penilia avirostris</i>	0.10	25	1.88	17	217.53	60	46.97	50
		<i>Podon</i> spp.	9.10	75	10.19	50	10.40	60	0.71	50
		Thecosomata	13.17	75	38.01	50	19.81	60	26.35	50
		Appendicularia	73.98	75	198.03	50	157.10	60	99.91	50
		Thaliacea	-	-	16.76	50	22.06	60	50.19	50
		Fisch larvae	0.21	25	2.67	50	0.31	40	0.24	50
Other Juvenile		Malacostraca	9.41	75	8.84	50	8.52	60	2.27	50
		Polychaeta	4.91	75	1.20	50	1.20	60	4.78	50
		Bivalvia larvae	9.41	75	9.51	50	3.29	60	3.92	50
		Bryozoa larvae	3.35	50	4.08	33	0.05	20	0.63	50
		Echinodermata	5.23	75	3.71	50	0.73	40	11.61	50
		Cirripedia	-	-	0.31	17	0.10	20	-	-
		Crustacea	26.56	75	0.84	50	0.63	40	1.88	50

Table A6. Abundance and frequency of species in 2018 samplings.

Functional Group	Trophic Refs.	Species/Taxa	2018							
			Winter		Spring		Summer		Autumn	
			Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)
HC	[82–86]	<i>Acartia clausi</i>	25.46	50	6.17	33	10.14	60	9.79	67
		<i>Acartia italica</i>	-	-	-	-	-	-	-	-
		<i>Acartia margalefi</i>	-	-	-	-	-	-	0.25	67
		<i>Acartia teclae</i>	5.66	25	-	-	1.77	20	-	-
		<i>Calocalanus contractus</i>	-	-	1.83	17	3.54	20	-	-
		<i>Calocalanus styliremis</i>	12.73	75	20.49	50	15.13	60	22.03	67
		<i>Calocalanus tenuis</i>	-	-	0.91	17	1.77	0.20	0.10	33
		<i>Clausocalanus arcuicornis</i>	21.29	75	9.97	33	5.29	40	4.43	33
		<i>Clausocalanus furcatus</i>	16.16	50	7.21	33	18.24	40	24.14	67
		<i>Clausocalanus lividus</i>	-	-	1.42	17	3.54	20	4.30	67
		<i>Clausocalanus parapergens</i>	-	-	-	-	-	-	-	-
		<i>Clausocalanus paululus</i>	70.14	75	20.38	50	12.38	20	8.03	33
		<i>Clausocalanus pergens</i>	36.82	50	11.53	33	9.26	60	7.24	67
		<i>Clausocalanus</i> spp.	14.01	50	18.00	33	39.53	60	7.24	67
		<i>Ctenocalanus vanus</i>	11.97	75	0.98	17	3.54	20	3.06	67
		<i>Euterpina acutifrons</i>	26.32	75	12.31	17	1.09	20	5.28	67
<i>Nannocalanus minor</i>	-	-	-	-	1.09	20	-	-		

Table A6. Cont.

Functional Group	Trophic Refs.	Species/Taxa	2018							
			Winter		Spring		Summer		Autumn	
			Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)
HC	[82–86]	<i>Paracalanus denudatus</i>	-	-	-	-	-	-	-	-
		<i>Paracalanus nanus</i>	11.08	50	-	-	1.09	20	0.85	33
		<i>Paracalanus parvus</i>	90.57	75	104.94	50	88.21	60	10.44	33
		<i>Paracalanus</i> spp.	-	-	2.93	17	2.65	20	-	-
		<i>Temora stylifera</i>	2.93	25	5.73	33	11.01	40	3.40	33
		Juvenile copepods	1332.10	75	947.31	50	633.76	60	366.42	67
CC	[87–90]	<i>Candacia armata</i>	-	-	-	-	-	-	-	-
		<i>Corycaeus</i> spp.	27.84	75	46.84	50	52.12	60	43.17	67
DC	[87,91–93]	<i>Microsetella</i> sp.	-	-	-	-	-	-	-	-
		<i>Oncaea</i> spp.	35.94	75	23.57	50	21.15	60	18.78	67
OC	[82,83,94–96]	<i>Scolecithricidae</i>	-	-	-	-	-	-	6.27	33
		<i>Centropages kroyeri</i>	-	-	-	-	-	-	-	-
		<i>Centropages typicus</i>	36.88	75	15.77	50	3.98	20	2.09	33
		<i>Isias clavipes</i>	10.15	25	-	-	1.39	20	-	-
		<i>Oithona nana</i>	38.50	50	5.62	17	-	-	-	-
		<i>Oithona plumifera</i>	8.06	50	11.52	50	10.23	40	19.44	67
		<i>Oithona similis</i>	23.32	50	52.28	50	5.72	40	15.32	67
		<i>Pleuromamma abdominalis</i>	-	-	-	-	-	-	-	-
Cn	[19,97,98]	<i>Pleuromamma gracilis</i>	-	-	-	-	-	-	0.85	33
		Cnidaria	6.79	75	35.97	50	9.51	60	6.32	67
Che	[99–102]	Juvenile Cnidarians	-	-	-	-	-	-	-	-
		Chaetognatha	26.73	75	54.15	50	8.70	60	23.44	67
Other	[103–105]	<i>Evadne spinifera</i>	-	-	79.76	33	34.90	60	11.72	33
		<i>Evadne</i> spp.	-	-	12.54	50	18.48	60	2.75	33
		<i>Penilia avirostris</i>	-	-	14.47	33	169.58	60	53.61	67
		<i>Podon</i> spp.	1.70	50	21.84	50	6.52	60	0.92	67
		Thecosomata	32.61	75	77.86	50	17.26	60	12.13	67
		Appendicularia	32.61	75	109.32	50	136.49	60	67.87	67
		Thaliacea	10.97	75	10.70	50	9.92	60	46.68	67
		Fisch larvae	0.20	25	1.90	50	2.85	40	0.31	67
Other Juvenile		Malacostraca	9.24	75	8.90	50	5.77	60	1.83	67
		Polychaeta	5.37	75	1.83	50	0.41	40	2.96	67
		Bivalvia larvae	11.62	75	9.61	50	1.36	40	1.12	33
		Bryozoa larvae	10.87	75	24.63	50	-	-	-	-
		Echinodermata	9.99	75	14.85	50	3.94	60	11.21	67
		Cirripedia	-	-	-	-	0.14	20	-	-
		Crustacea	14.88	75	2.65	50	1.49	60	0.51	67

Table A7. Abundance and frequency of species in 2019 samplings.

Functional Group	Trophic Refs.	Species/Taxa	2019							
			Winter		Spring		Summer		Autumn	
			Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)
HC	[82–86]	<i>Acartia clausi</i>	8.52	33	40.54	75	13.48	75	0.64	20
		<i>Acartia italica</i>	-	-	-	-	-	-	-	-
		<i>Acartia margalefi</i>	-	-	-	-	2.18	25	1.22	20
		<i>Acartia teclae</i>	-	-	-	-	-	-	-	-
		<i>Calocalanus contractus</i>	3.41	17	-	-	-	-	-	-
		<i>Calocalanus styliremis</i>	31.31	50	7.83	50	16.14	75	39.04	60
		<i>Calocalanus tenuis</i>	1.42	17	-	-	-	-	1.29	20
		<i>Clausocalanus arcuicornis</i>	1.21	17	19.07	50	14.48	50	-	-
		<i>Clausocalanus furcatus</i>	9.32	50	9.64	50	36.69	50	55.71	60
		<i>Clausocalanus lividus</i>	2.57	17	5.23	25	-	-	-	-
		<i>Clausocalanus parapergens</i>	-	-	-	-	-	-	-	-
		<i>Clausocalanus paululus</i>	47.13	50	42.03	75	10.29	50	17.21	20
		<i>Clausocalanus pergens</i>	49.41	50	131.02	75	3.25	50	-	-
		<i>Clausocalanus spp.</i>	8.29	17	38.15	75	43.20	75	27.32	60
		<i>Ctenocalanus vanus</i>	3.71	33	9.44	25	4.30	50	2.43	20
		<i>Euterpina acutifrons</i>	60.11	50	1.81	25	1.62	25	5.67	40
		<i>Nannocalanus minor</i>	2.92	33	-	-	-	-	3.69	20
		<i>Paracalanus denudatus</i>	1.25	17	-	-	-	-	-	-
		<i>Paracalanus nanus</i>	1.42	17	-	-	3.76	50	1.21	20
		<i>Paracalanus parvus</i>	50.41	50	26.61	50	80.71	75	42.24	60
<i>Paracalanus spp.</i>	2.63	17	9.44	25	-	-	-	-		
<i>Temora stylifera</i>	4.28	17	-	-	17.24	75	18.61	40		
Juvenile copepods	1170.71	50	2064.95	75	534.42	75	614.77	60		
CC	[87–90]	<i>Candacia armata</i>	-	-	-	-	-	-	1.85	20
		<i>Corycaeus spp.</i>	14.62	33	5.73	25	64.11	75	65.79	60
DC	[87,91–93]	<i>Microsetella sp.</i>	-	-	-	-	-	-	-	
		<i>Oncaea spp.</i>	13.06	50	8.33	50	35.70	75	21.07	60
OC	[82,83,94–96]	<i>Scolecithricidae</i>	-	-	6.79	25	-	-	0.64	20
		<i>Centropages kroyeri</i>	-	-	-	-	-	-	-	
		<i>Centropages typicus</i>	8.09	33	58.89	75	37.28	75	1.33	20
		<i>Isias clavipes</i>	2.50	33	4.92	25	-	-	-	
		<i>Oithona nana</i>	8.00	50	20.68	50	5.86	50	9.45	60
		<i>Oithona plumifera</i>	1.70	17	-	-	3.74	50	46.67	60
		<i>Oithona similis</i>	27.46	50	83.79	50	15.54	75	55.76	60
		<i>Pleuromamma abdominalis</i>	-	-	-	-	-	-	1.21	20
<i>Pleuromamma gracilis</i>	-	-	1.31	25	-	-	1.33	20		
Cn	[19,97,98]	Cnidaria	5.16	50	5.98	75	13.79	75	4.42	60
		Juvenile Cnidarians	-	-	2.65	50	0.14	25	0.14	20
Che	[99–102]	Chaetognatha	10.94	50	7.34	75	11.96	75	29.62	60

Table A7. Cont.

Functional Group	Trophic Refs.	Species/Taxa	2019							
			Winter		Spring		Summer		Autumn	
			Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)	Ab.	Freq. (%)
Other	[103–105]	<i>Evadne spinifera</i>	1.29	33	10.60	50	14.62	75	0.34	20
		<i>Evadne</i> spp.	-	-	2.17	50	18.28	75	0.61	20
		<i>Penilia avirostris</i>	-	-	8.42	50	425.24	75	52.38	60
		<i>Podon</i> spp.	6.59	50	4.01	75	8.97	75	0.20	20
		Thecosomata	12.30	50	9.72	75	25.27	75	19.57	60
		Appendicularia	62.64	50	119.44	75	172.37	75	53.13	60
		Thaliacea	4.62	50	6.45	75	31.12	75	10.87	60
		Fisch larvae	0.204	33	2.310	50	1.223	50	0.272	40
Other Juvenile		Malacostraca	5.16	50	12.70	75	5.16	75	14.61	60
		Polychaeta	4.01	50	0.48	50	0.82	75	12.03	60
		Bivalvia larvae	4.21	50	4.01	75	1.97	75	1.56	60
		Bryozoa larvae	0.54	50	4.14	75	0.14	25	1.29	20
		Echinodermata	11.28	50	2.38	75	1.49	75	7.95	60
		Cirripedia	0.14	17	-	-	0.20	50	-	-
		Crustacea	15.35	50	4.01	50	0.54	50	3.87	40

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