Plankton food-webs: to what extent can they be simplified?

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ABSTRACT

Plankton is a hugely diverse community including both unicellular and multicellular organisms, whose individual dimensions span over seven orders of magnitude. Plankton is a fundamental part of biogeochemical cycles and food-webs in aquatic systems. While knowledge has progressively accumulated at the level of single species and single trophic processes, the overwhelming biological diversity of plankton interactions is insufficiently known and a coherent and unifying trophic framework is virtually lacking. We performed an extensive review of the plankton literature to provide a compilation of data suitable for implementing food-web models including plankton trophic processes at high taxonomic resolution. We identified the components of the plankton community at the Long Term Ecological Research Station MareChiara in the Gulf of Naples. These components represented the sixty-three nodes of a plankton food-web. To each node we attributed biomass and vital rates, *i.e.* production, consumption, assimilation rates and ratio between autotrophy and heterotrophy in mixotrophic protists. Biomasses and rates values were defined for two opposite system's conditions; relatively eutrophic and oligotrophic states. We finally identified 817 possible trophic links within the web and provided each of them with a relative weight, in order to define a diet-matrix, valid for both trophic states, which included all consumers, from nanoflagellates to carnivorous plankton. Vital rates for plankton resulted, as expected, very wide; this strongly contrasts with the narrow ranges considered in plankton system models implemented so far. Moreover, the amount and variety of trophic links highlighted by our review is largely excluded by state-of-the-art biogeochemical and food-web models for aquatic systems. Plankton models could potentially benefit from the integration of the trophic diversity outlined in this paper: first, by using more realistic rates; second, by better defining trophic roles of consumers in the planktonic web. We suggest that most trophic habits present in planktonic organisms must be contemplated in new generation plankton models.

Key words: Food-webs; grazing; plankton vital rates.

INTRODUCTION

Plankton is a morphologically, genetically and trophically diverse ensemble of both unicellular and multicellular organisms, whose individual dimensions span over seven orders of magnitude (Boyce *et al.*, 2015). Their phylogenetic differences are larger than those of terrestrial organisms covering the same size range. The only reason why they are grouped together is that they live suspended in the water, without relying on any substrate which is not produced by them. Nevertheless, plankton is a fundamental player in the biogeochemical cycles in aquatic systems and constitutes the essential source of carbon ultimately feeding the larger metazoans living in the ocean (Behrenfeld and Boss, 2014).

The general perception is that plankton is undergoing important modifications in the oceans due to global change (Chen *et al.*, 2012; Chust *et al.*, 2014). Yet, those modifications are often elusive, probably because the knowledge on the cascading processes which regulate the plankton food-web is still scarce. Indeed, while a deeper and deeper knowledge is accumulating at the level of single species and single trophic processes, the overwhelm-

ing biological diversity of plankton interactions is insufficiently known and only rarely, and partially, integrated within a coherent and unifying trophic framework (Boit *et al.*, 2012). Yet, advisable studies on plankton communities should move towards holistic/system ecological approaches considering several, if not all, components of the food-webs and possibly highlighting the emergent properties which hint at the regulating mechanisms of a complex system as plankton. For emergent properties we refer to those relying on interactions among system's components that are not predictable by analysing the response of individual components in isolation. These properties revealed to be crucial in regulating pelagic communities at the level of macroscopic organisms via mechanisms driven by food-web organization (Link *et al.*, 2015).

Food-web models should be seen at as networks including functional nodes (FNs), which, in turn, must be connected by trophic links. They should be based on a minimum number of nodes, thus impeding gross aggregations among taxa (Abarca-Arenas and Ulanowicz, 2002). For each node, a somewhat precise biomass value and vital rates, such as production, consumption and as-

simulation rates must be set. Moreover, network models should be developed starting from diet-matrices linking consumers and producers. The careful definition of nodes, their characteristics and 'roles' in the frame of a food-web must rely on trustable taxonomic data, such as those collected in long-term studies (Ribera d'Alcalà *et al.*, 2004). On the other hand, food-web models need a thorough biological accuracy and their parameterisations are largely time-consuming, which is one of the reasons why they are so scanty. All the above requirements are usually not matched in models dealing with plankton: in these models, the web of trophic links, especially for what concerns unicellulars, is usually grossly parameterised and the modelled feeding processes focus on simple trophic steps including mainly metazoan herbivory (Flynn *et al.*, 2013; Mitra *et al.*, 2014). As a consequence, while a vast, though fragmentary and often redundant, literature for trophic rates of planktonic organisms has been accumulated in the past decades, works on detailed plankton food-webs are still lacking.

In this paper we provide a careful compilation of data suitable to build food-web models including plankton, with a major emphasis on coastal ecosystems. Although this paper does not present model approaches, the compilation provided herein can be useful to develop models of plankton focused on trophic interactions, such as model recently described by D'Alelio *et al.* (2016). Our selection aims at describing putative processes in a coastal marine system. To this end, we identified the main components of the plankton community at the Long Term Ecological Research Station MareChiara in the Gulf of Naples (LTER-MC). These components represented the functional nodes (FNs) of a virtual food-web and, for each of these, we derived biomass and attributed vital rates, reviewing a vast literature on plankton organisms, which is reported in the reference section. We finally selected trophic links in the web on the base of literature review. We remark the fact that our parameterization might not be applied to off-shore and deep-sea systems, although our study may provide general conceptual criteria also useful to developing of modelling studies. A further limit of our work is that we were not able to include macrozooplankton, which were not routinely sampled at LTER-MC, in our conceptual framework.

The overall scope of this exercise is to provide a set of values and illustrate a procedure that may be used as a reference for other modelling studies. Furthermore, we compare and discuss the extensive suite of rates with the more compact parameterizations used in biogeochemical and fisheries models. The compilation presented herein is focused on summer, which is a crucial period for ecological processes of particular interest for coastal management, such as the development of harmful algal blooms and the recruitment of small pelagic fish.

METHODS

Study area and context

The plankton food-web described herein is localized in the Gulf of Naples (GoN), a Mediterranean coastal embayment open to the Tyrrhenian Sea. Data of plankton species and groups and their biomasses were derived from the Long Term Ecological Research MareChiara (LTER-MC, depth=75 m), at which sampling is routinely carried out since 1984 (Ribera d'Alcalà *et al.*, 2004). The present study refers to the plankton community occurring at the above-mentioned site and described by a previous papers by our group (D'Alelio *et al.*, 2015, 2016). The sampling was focused on unicellular plankton and mesozooplankton and it did not allow to effectively collect all juvenile stages of mesozooplankton - *i.e.*, among copepods, copepodites and not nauplii were routinely harvested by the 200 μm-size mesh used (Ribera d'Alcalà *et al.*, 2004). At the LTER-MC site, relatively eutrophic and oligotrophic states (herein Green and Blue) alternated during most of the Mediterranean summers (mid-June - late August, years 2002-2009) as an effect of the alternation between relatively coastal and offshore water displacement towards the monitoring station (D'Alelio *et al.*, 2015) (Fig. 1).
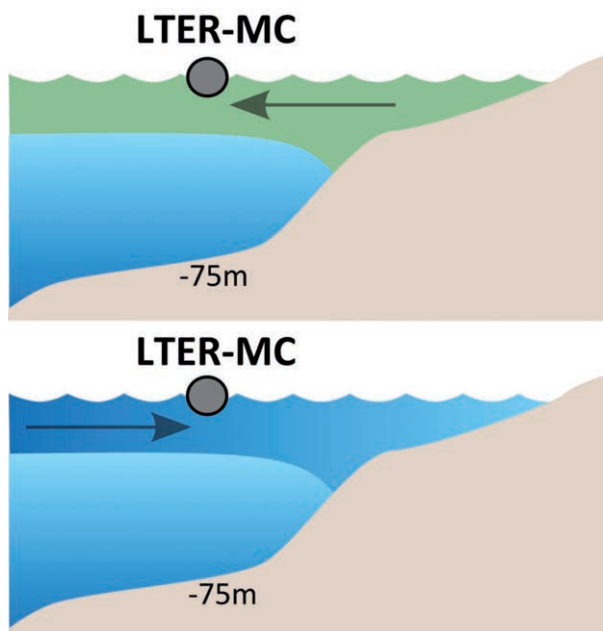
Fig. 1. The Green-Blue swing. The figure represents the intermittent horizontal displacement of surface waters (0-5 m) in the Gulf of Naples during summer, according to D'Alelio *et al.* (2015). The uppermost and lowermost panels indicate the arrival to LTER-MC station of waters from coastal or offshore areas, respectively. The Green water is richer in phytoplankton biomass than the Blue water.

The conceptual food-web herein presented is assumed to occupy the first 60-meter of the water column, despite the slightly deeper bottom at the LTER-MC. Two reasons justified this choice: i) mesozooplankton at LTER-MC was sampled by means of vertical nets covering the water-layer spanning 0-55 m in depth (Ribera d'Alcalà *et al.*, 2004); ii) we assumed that most trophic processes in the plankton occurred in the first 60 m of the water column, due to low-light conditions and sediment re-suspension below that depth. Since the water column was divided by two main layers by a steep density-gradient in the coastal planktonic system that we studied in the GoN during summer (Ribera d'Alcalà *et al.*, 2004), unicellular organisms in our case-study were divided between surface and subsurface communities (from 0 to -5 m and from -5 to -60 m, respectively). Yet, mesozooplankton and the protist *Mesodinium rubrum* (syn. *Myrionecta rubra*) were not separated between layers: in fact, these organisms are reported to perform large-scale diel vertical migrations across the pycnocline (Crawford, 1989; Stich and Lampert, 1981).

Construction of the conceptual plankton food-web

The biomasses for the nodes of the web were taken from D'Alelio *et al.* (2016), a former study in which the same food-web presented herein was investigated. They consist of average values (years 2002-2009, as in D'Alelio *et al.*, 2015) for a two-layer water column at LTER-MC over a two-months summer period (July-August). Our analysis (in the present paper and in the parallel one, D'Alelio *et al.*, 2016) tries to depict the typical pattern in carbon transfers within the analyzed food-web. Thus, we considered interannual variability as a second order term. In these works we used the POC available data (average values for summer of years 2007-2009) as a closure term, despite their reduced coverage (3 over 7 years). Each living FN is represented herein by a set of vital rates including a production rate (for all living organisms) and consumption and assimilation rates (for organisms featuring a heterotrophic metabolism). Vital rates are largely variable for any species, since they depend upon a wide spectrum of variables. For this reason, we provide a range of variability comprised between minimum and maximum values. Specific ranges are indicated for each of the two states of our case-study (*i.e.*, Green and Blue).

Biomass data for web-nodes were not used to reproduce biomass fluxes across the web, since the latter option can be only pursued by means of appropriate calculations, such as those provided by a mass-balanced model approach that is out of the scope of the present work and has been the main goal of D'Alelio *et al.* (2016). Yet, individual biomass data were used to modulate size-dependent rates to ranges pertaining the organisms present in our study system; the total biomass of unicellular organisms was used to set consumption rates in consumers in case these were reported in the literature as dependent from food concentrations.

Primary production rates were used to corroborate production rates of primary producers. All the above-mentioned rates are expressed per unit of biomass (*i.e.*, in d⁻¹ units). As a general rule for microbes in the surface layer, the maximum values of production rate were taken from the literature, while the minimum values were derived by multiplying the maximum value of the range by the ratio between the minimum and maximum primary production rates detected in the surface layer (T ~25°C) and at the specific system's state (see next Methods section). Concerning the deeper water-layer in our study system (5-60 m in depth, T ~15°C), the range of values of production rate for each unicellular FN (including auto-, mixo- and heterotrophic organisms) were derived analytically, *i.e.* by multiplying the minimum or maximum production rate of each FN at surface as derived from the literature by the ratio between the median primary production in the deeper layer and the median primary production in the surface layer. The latter choice stemmed from the assumption that production rates were correlated with the primary production of all phytoplankton in the deeper water-layer. Since diatoms in the deeper layer were represented by one and a single node (FN 30), the median values of minimum and maximum production rates of diatoms at surface (FN 4-10) were considered instead of the single value. Although laborious and indirect, the estimations derived from conceptual steps illustrated above provided production rates for unicellulars in the sub-surface water layer, which appeared more realistic than those merely taken with no modifications from the literature. Concerning metazoans, specific criteria have been applied depending on the life-cycle organization of each category of organism present in our case-study and also taking into account the time-scale which our case-study referred to.

As a general approach, consumption rates were derived from mass-specific ingestion rates (or daily carbon ration) recalculated from the literature. Consumption alone is not enough to characterize the trophic performances of heterotrophic organisms. In fact, a portion of the consumed biomass is not directed towards respiration and production and, being not assimilated by the animal, is eliminated. In this context, the assimilation efficiency, a variable usually estimated in feeding studies on planktonic animals, can be a good proxy for the non-assimilated fraction of consumed biomass, which is the fraction of undigested food emitted, *e.g.*, as faeces and, eventually, consumed by other organisms.

Derivation of primary production

The production rate of the phytoplankton community as a whole was estimated in order to evaluate the differences in growth of photoautotrophic organisms living in the two different layers of the water column considered

in our case-study. We analysed to this scope the only available data in our system, which were collected at LTER-MC on 1984. Thus, these data were only partially comparable to those used for defining the system's Carbon budget, which were collected during years 2000s.

Primary production data have been collected at the LTER-MC almost weekly during summer months of 1984-1988. The sampling was carried out , at 0.5, 2, 5, 10, 20, 30, 40, 50, 60 m of depth, as illustrated in Ribera d'Alcalà *et al.* (2004). The particulate primary production (PP) was estimated using a standard ^{14}C method. The integrated particulate primary production (PP) for the two layers (0-5 and 5-60 m in depth) considered in the present study was obtained by computing discrete values. Since the ^{14}C method estimated only PP, we inferred also the amount of exudates release (ER) to get the total primary production (TP), *i.e.* the sum of PP and ER. The latter quantity was derived using regressions pertaining all aquatic systems (Baines and Pace, 1991). Eventually, the production rate per unit of biomass was obtained by dividing TP by the total phytoplankton biomass (TB) estimated in D'Alelio *et al.* (2016). Production rates were estimated for each of the Green and Blue states. Production rates of phytoplankton FNs was set using as reference values both data collected as above and those obtained from the literature.

Review of literature data

Data collected from the literature and pertaining physiological and trophic properties of living nodes of the food-web were analysed statistically. The correlation between body-size and each vital rate (*i.e.* production, consumption and assimilation rates) was investigated considering all living nodes, in order to identify size-related trends. Separate correlations were carried out for the distinct trophic conditions investigated (*i.e.*, Green and Blue states). The large multivariate dataset including the ranges of all vital rates (production, consumption and assimilation rates and autotrophy/heterotrophy ratio) for all the studied conditions (*i.e.*, Green and Blue states) was reduced and interpreted by means of Principal Component Analysis, with the aim of identifying possible groupings of living nodes based on trophic characteristics. Statistical analyses were carried out with the open-source software PAST (http://palaeo-electronica.org/2001_1/past/issue1_01.htm). All trophic links detected by our compilation of data from the literature were organized within a single dataset represented by a predator/prey matrix. This matrix was visualized using a network approach. A single food-web was displayed, which was representative of both Green and Blue states of the system. Indeed, the food-web was un-weighted (*i.e.*, all links were quantitatively equivalent) and did not represent biomass fluxes, the latter option being out of the scope of the present work. This web aimed at aggregating links based on their directionality and displaying nodes hierarchically, based on

their topological/trophic position. The network representing the coastal plankton food-web in the Gulf of Naples was built and analysed with the open-source software yEd 3.11.1 (yWorks GmbH, http://www.yworks. com). Network connectance analyses were carried out according to Beckerman *et al.* (2006).

RESULTS AND DISCUSSION

Carbon budget of plankton in the Gulf of Naples during summer

The gross repartitions of the overall amount of carbon (*i.e.*, the sum of biomasses pertaining all nodes) in our system at Green and Blue states are presented in Fig. 2. Between the two trophic states, phytoplankton biomass underwent the largest variation in the surface water-layer (between 0 and 5 m in depth). Smaller changes were recorded in protozooplankton and heterotrophic bacteria pools at surface. Conversely, both mesozooplankton biomass and the whole particulate carbon pool in the deeper water-layer (5-60 m in depth) were almost unchanged at transitions between states. Overall, the mesozooplankton pool was lower than particulate carbon biomass. Mesozooplankton biomass was comparable to the collective unicellular biomass over the whole water column only during the Blue system state.

The plankton players in the studied food-web are represented by 63 FNs, including 17 for phytoplankton, 10 for mixotrophic-protozooplankton, 12 for heterotrophic-protozooplankton, 2 for heterotrophic bacteria, 5 for particulate detritus, 15 for mesozooplankton and 2 for dissolved organic carbon (DOM) (see nodes' list and description in Tab. 1). A wide spectrum of individual sizes characterized the plankton community (Fig. 3 A,D,G). Increasing of cell size was followed by a fairly regular increasing of the individual cell carbon, especially in unicellular organisms (compare Fig. 3A and B). Concerning metazoa, the picture was less regular, with *e.g.*, calanoid copepod species featuring comparable sizes (*i.e.*, prosomal length) but showing distinct individual biomasses (compare Fig. 3D and E).

Scaling-up to populations' biomasses, we estimated the differences for each FNs between the Green and Blue states (Fig. 3 C,F,H). Diatoms showed biomass changes of 2-3 orders of magnitude between the two states. Within the detritus pool, an increase of DOM was recorded at both surface and deeper layers at the Green state, as an effect of a larger amount of phytoplankton biomass, comparing to the Blue state. Moreover, the estimated salp faecal pellets also increased (of 1 order of magnitude) during the Green state. This fact stems from decreased assimilation efficiency for these animals into an environment with more abundant food particles.

Autotrophic unicellular organisms

In this section, we present the ratio behind the derivation of ranges of production rates for autotrophic organisms (Tab. 2, Fig. 4). In compiling production rates for unicellular organisms, we assumed that they were equivalent to individual growth rates, *i.e.*, cell doubling by mitotic division. However, while maximum production rates were considered equivalent to maximum growth rates found in the literature, the minimum production rates were derived as described in the Methods section and based on primary production data shown in the following subsection.

Primary production

In the Green state, minimum, maximum and median primary production rates accounted for 0.39, 0.99, 0.63 and 0.14, 0.96, 0.29 d^{-1} in the surface and deeper layers, respectively. In the Blue state, minimum, maximum and median primary production rates accounted for 0.22, 0.85, 0.52 and 0.17, 0.87, 0.48 d^{-1} in the surface and deeper layers, respectively. Thus, in the deeper layer, the median value for primary production in the Blue state was about double than the corresponding value at the Green state (*i.e.*, 0.48 *vs* 0.29 d^{-1}). This fact is highly plausible, due to a higher light penetration towards deeper waters during the Blue state in absence of high phytoplankton biomass at the surface.

Production rates

Data in the literature, including both *in situ* and *in vitro* observations at conditions similar to those in the present case-study, were almost comparable with our direct ob-
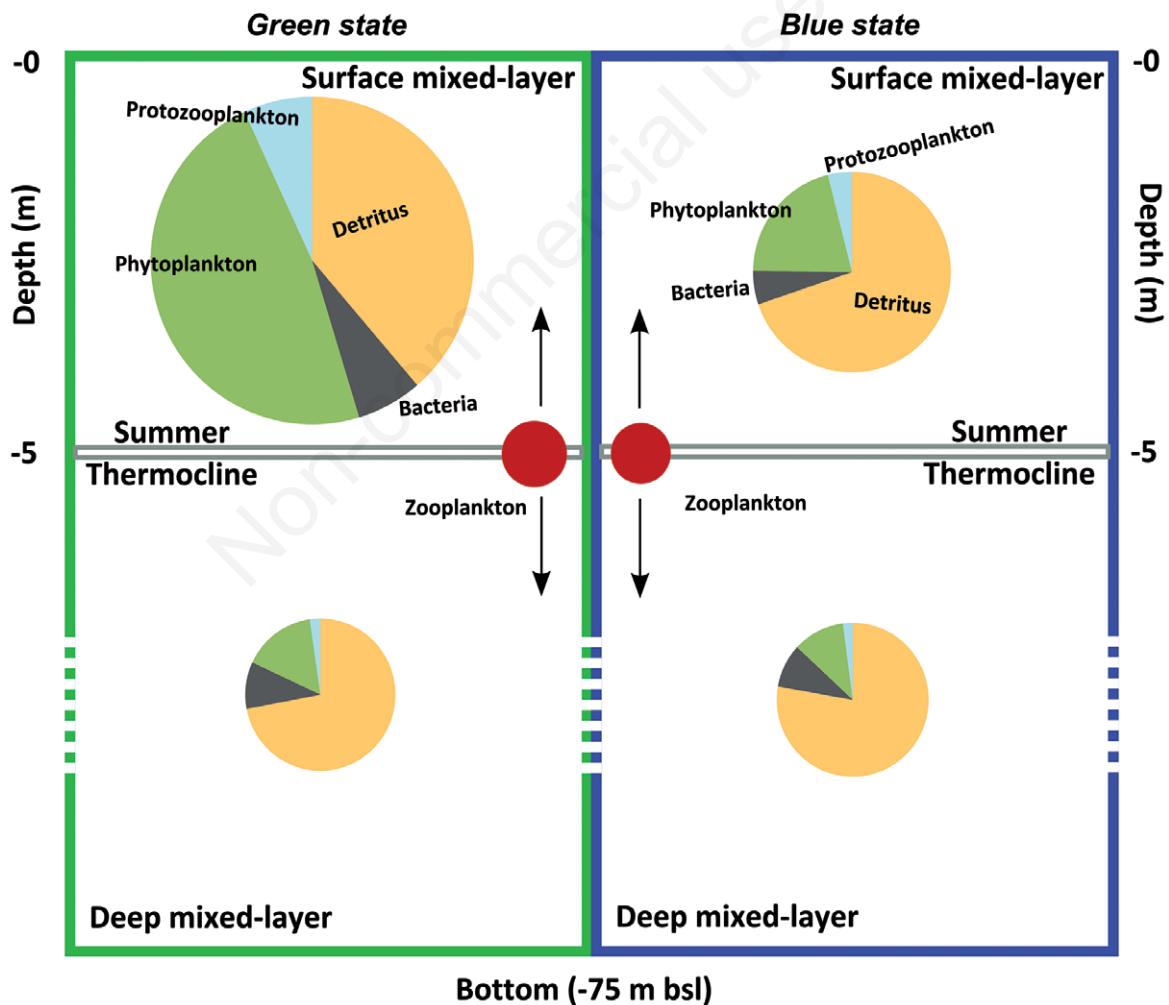
Fig. 2. Gross carbon-biomass budget during the Green-Blue swing. Panels represent the repartition of the total time-averaged (two months) amount of carbon among the main biomass compartments at LTER-MC, at the Green and Blue states of the system, respectively. Each panel is divided between surface and deeper water layers.
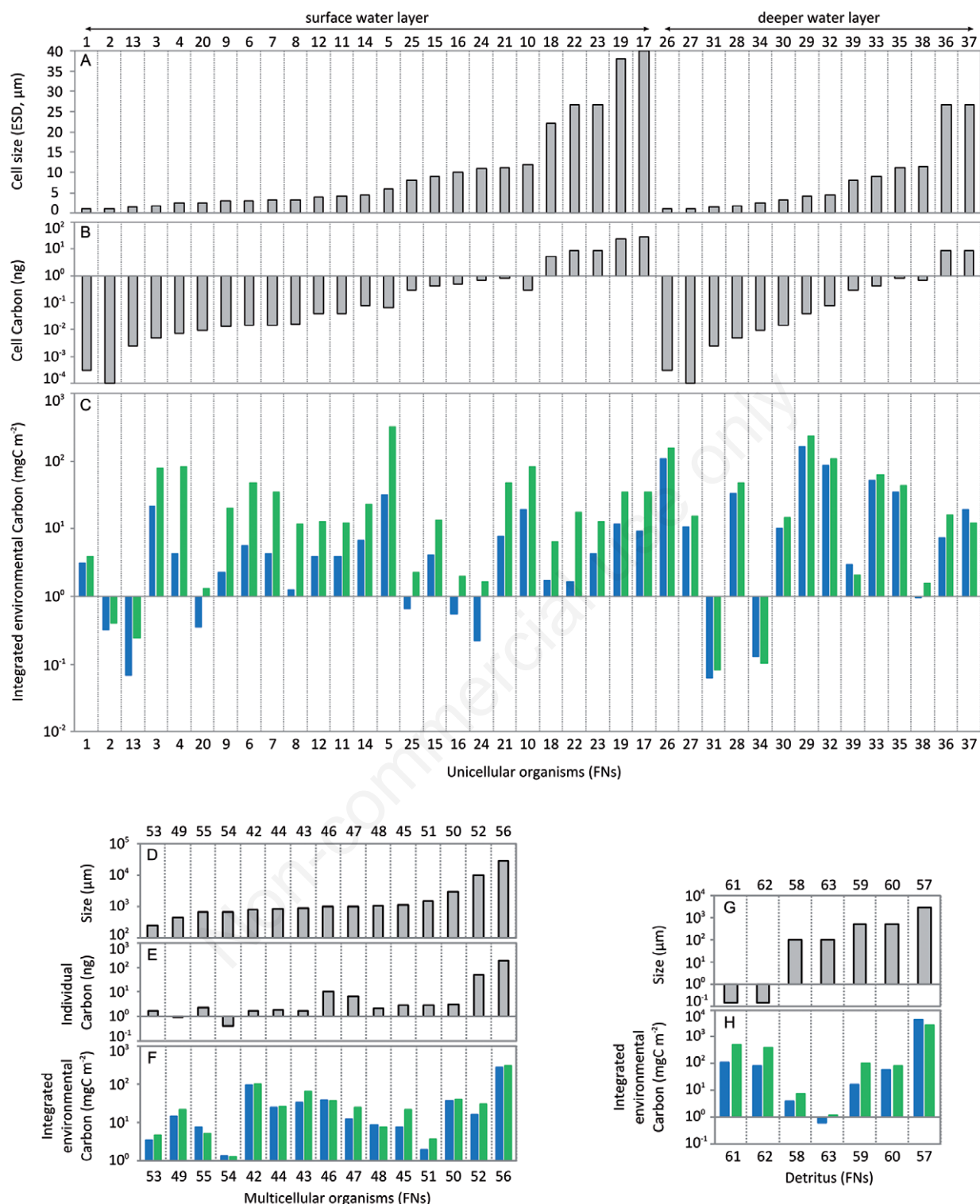
Fig. 3. Fine-scale carbon-biomass budget during the Green-Blue swing. In panels A-C, from top to bottom: cell-size (A) and individual cell-carbon (B) referring to unicellular functional nodes (FNs) of the food-web despite the specific trophic state; comparison of depth integrated environmental carbon-biomass (C) of unicellular FNs at the Green and Blue states (green and blue bars, respectively). In panels D-F: the individual size (D) and individual carbon (E) referring to metazoan FNs of the food-web despite the specific trophic state; comparison of depth integrated environmental carbon-biomass (F) of metazoan FNs at the Green and Blue states (green and blue bars, respectively). In panels G and H: size of detritus nodes (G) and the depth integrated environmental carbon-biomass (H) of detritus FNs at the Green and Blue states (green and blue bars, respectively). Functional nodes are listed in Tab. 1.

Tab. 1. Functional nodes of the web.

Functional nodes (FN)	Small description	Trophic status
1 Cyanobacteria (s)	Mainly *Synechococcus*	A
2 Prochlorophytes (s)	Mainly *Prochlorococcus*	A
3 Phyto-nanoflagellates (s)	Several genera and N.I.T.	A
4 *Chaetoceros* spp. (s)	Different species in this diatom genus	A
5 *Leptocylindrus* spp. (s)	Different species in this diatom genus	A
6 *Skeletonema* spp. (s)	Different species in this diatom genus	A
7 Small diatoms (s)	Several genera and N.I.T.	A
8 Pennate diatoms (s)	*Thalassionema* spp., N.I.T. (cell size >10 μm)	A
9 *Pseudo-nitzschia* spp. (s)	Different species in this diatom genus	A
10 Centric diatoms (s)	Several genera	A
11 Coccolithophores (s)	Mainly N.I.T. plus *Emiliania huxleyi* and several genera	A
12 Phyto-microflagellates (s)	Several genera and N.I.T.	A
13 Mixotrophic nanoflagellates (s)	Mainly *Ollicola vangorii*	M
14 Small dinoflagellates (s)	Several genera and N.I.T.	M
15 Medium dinoflagellates (s)	Several genera and N.I.T.	M
16 *Mesodinium rubrum* (a)	(Syn. *Myrionecta rubra*) ciliate	M
17 *Tontonia* spp. (s)	Oligotrichous ciliate genus	M
18 *Laboea* spp. (s)	Oligotrichous ciliate genus	M
19 *Strombidium* spp. (s)	Oligotrichous ciliate genus	M
20 HNF (s)	Heterotrophic nanoflagellates	H
21 Heterotrophic dinoflagellates (s)	Several genera	H
22 Prostomatids (s)	Ciliates	H
23 *Strobilidium* spp. (s)	Single ciliate genus	H
24 Tintinnids (s)	Several genera	H
25 Nanociliates (s)	Ciliates	H
26 Cyanobacteria (d)	Mainly *Synechococcus*	A
27 Prochlorophytes (d)	Mainly *Prochlorococcus*	A
28 Phyto-nanoflagellates (d)	Several genera and N.I.T.	A
29 Coccolithophorids (d)	Mainly *Emiliania huxleyi*	A
30 Diatoms (d)	Several genera	A
31 Mixotrophic nanoflagellates (d)	Mainly *Ollicola vangorii*	M
32 Small dinoflagellates (d)	Several genera and N.I.T.	M
33 Medium dinoflagellates (d)	Several genera and N.I.T.	M
34 HNF (d)	Heterotrophic nanoflagellates	H
35 Hetero- dinoflagellates (d)	Several genera	H
36 Prostomatids (d)	Ciliates	H
37 *Strobilidium* spp. (d)	Single ciliate genus	H
38 Tintinnids (d)	Several genera	H
39 Nanociliates (d)	Ciliates	H
40 Heterotrophic bacteria (s)	-	H
41 Heterotrophic bacteria (d)	-	H
42 *Penilia avirostris* (a)	Cladoceran	H
43 Cladocerans (a)	*Evadne* and *Pseudevadne* spp.	H
44 *Paracalanus parvus* (a)	Calanoid copepod (adults)	H
45 *Acartia clausii* (a)	Calanoid copepod (adults)	H
46 *Temora stylifera* (a)	Calanoid copepod (adults)	H
47 *Centropages typicus* (a)	Calanoid copepod (adults)	H
48 Other calanoids (a)	Genera (adults)	H
49 Juvenile calanoids (a)	Mainly juveniles stages of *Clausocalanus* spp., *Paracalanus parvus*	H
50 Appendicularia (a)	Different genera	H
51 Doliolids (a)	Mainly *Doliolum nationalis*	H
52 Salps (a)	Different genera	H
53 Meroplankton (a)	Larval stages of Anellida Polychaeta, Crustacea Maxillopoda, Echinodermata, Mollusca	H
54 *Oithona* spp. (a)	Different life stages of *O. atlantica*, *O. decipiens*, *O. longispin*a, *O. nana*, *O. setigera*, *O. similis*	H

Tab. 1. *Continued from previous page.*

Functional nodes (FN)	Small description	Trophic status
55 Detritivora (a)	*Corycaeus* spp., *Farranula rostrata* and Oncaeidae (Copepoda Cyclopoida) plus *Euterpina acutifrons* (Copepoda Harpacticoida)	H
56 Carnivora (a)	N.I.T. of Chaetognata, Mollusca Pteropoda, Cnidaria Siphonophora plus *Candacia* spp. and *Pleuromamma* spp. (Copepoda Calanoida)	H
57 Appendicularia houses (a)	-	D
58 Small faecal pellets (a)	Faecal pellets of small animals	D
59 Salp F.P. (a)	Faecal pellets of salps	D
60 Carnivora F.P. (a)	Faecal pellets of carnivores	D
61 DOC (s)	Dissolved organic carbon	D
62 DOC (d)	Dissolved organic carbon	D
63 Generic particulate detritus (a)	Amorphous particulate detritus	D

(s) In the surface water-layer; (d) in the deeper water-layer; (a) living all over the water column; A, autotrophic; H, heterotrophic; M, mixotrophic; D, detritus; N.I.T., non identified taxa.

servations based on C^{14} method. Moreover, the maximum values gained from primary production data were below the maximum values gained from growth rates retrieved from the literature. Relatively low values were recorded for prokaryotes - *i.e.*, 1.2 d^{-1} for *Synechococcus* (FN 1) during summer months (Sosik *et al.*, 2003), and 0.69-0.85 d^{-1} for prochlorophytes (FN 2) (Liu *et al.*, 1997); on the other hand, an exhaustive and recent review reported values up to 2.5 d^{-1} for unicellular planktonic photo-eukaryotes (Edwards *et al.*, 2012). After re-modulating growth rates based on primary production data shown in the previous paragraph, both maximum and minimum production rates of phototrophs (*e.g.*, coccolithophores and diatoms, FN 29-30) in the deeper water-layer where higher in the Blue than in the Green state. The analyses of primary production *in situ* informed us that the physiological state of phytoplankton species was comparable at Green and Blue states. Thus, in the surface and more productive water-layer, the same range of variability of production rates of phytoplankton species was assumed to occur in Green and Blue states.

Mixo- and heterotrophic unicellular organisms (protozooplankton)

In the following paragraphs, literature references and specific rationales for the calculation of production, consumption and assimilation rates of mixotrophic and heterotrophic unicellular organisms and presented in Tab. 3 and Fig. 4 are provided. Diet of unicellular consumers is discussed in the dedicated paragraph and presented in Fig. 5.

Production rates

Unlike phototrophic protists, the physiology of mixotrophic ciliates is largely unknown since these organisms are not easily cultivated in the laboratory or studied in the field. Mixotrophic ciliates in our system of study were mainly oligotrichous ciliates of the genera *Tontonia*, *Laboea* and *Strombidium* (FN 17-19). The maximum production rates indicated herein for these organisms (~1.5 d^{-1}) were obtained from multiple regression between growth, temperature and cell volume (Pérez *et al.*, 1997). We considered a temperature of 25°C (average value for the surface layer in the GoN during summer). The obtained values were in line with those reported in specific studies (*e.g.*, Schoener and McManus, 2012). A specific case was represented by *Mesodinium rubrum* (syn.

Tab. 2. Vital rates of phytoplankton.

FN	Blue state Production min-max d^{-1}		Green state Production min-max d^{-1}	
1	0.31	1.20	0.47	1.20
2	0.22	0.85	0.33	0.85
3	0.49	1.90	0.75	1.90
4	0.53	2.04	0.80	2.04
5	0.27	1.06	0.42	1.06
6	0.43	1.67	0.66	1.67
7	0.43	1.65	0.65	1.65
8	0.42	1.62	0.64	1.62
9	0.45	1.74	0.69	1.74
10	0.16	0.61	0.24	0.61
11	0.44	1.70	0.67	1.70
12	0.39	1.50	0.59	1.50
26	0.29	1.11	0.22	0.55
27	0.20	0.78	0.15	0.39
28	0.45	1.75	0.34	0.87
29	0.41	1.57	0.31	0.78
30	0.40	1.53	0.30	0.76

FN, functional node.

Living nodes (in order of increasing size)
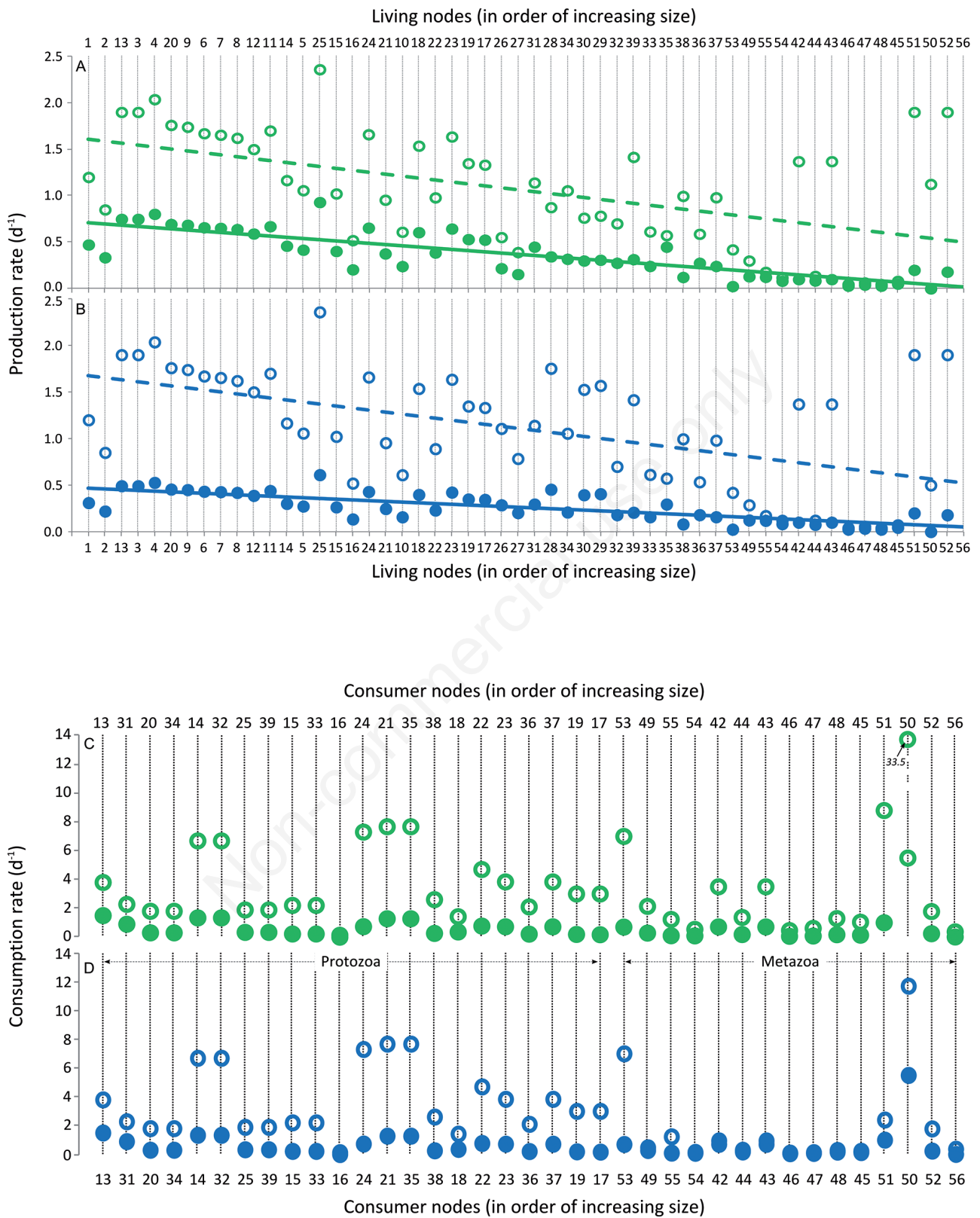
Fig. 4. Vital rates of FNs at Green and Blue states. In panels A and B, production rates for FNs during Green and Blue states, respectively. In panels C-D, consumption rates for FNs during Green and Blue states, respectively. Empty and full circles indicate maximum and minimum values, respectively. FNs are listed in Tab. 1.

Myrionecta rubra) (FN 16). This species blooms mainly at low salinity (about 10) in coastal transition systems (Johnson *et al.*, 2013). Although salinity in our system of study is usually higher (around 37), we considered a maximum production rate of 0.52 d^{-1} for *M. rubrum* based on estimation made in culture at 31 (Yih *et al.*, 2004), *i.e.*, the only data available. Finally, due to scanty background knowledge, we assigned to mixotrophic nanoflagellates (FN 13) the same value as for phyto-nanoflagellates (FN 3) (approaching 2 d^{-1}), which was derived from (Edwards *et al.*, 2012). Concerning mixotrophic dinoflagellates (FN 14-15), the maximum production rate (~1 d^{-1}) was obtained with the regression relating growth rate to metabolic state and cell size reported by (Jeong *et al.*, 2010).

Scanty information was available also for obligate heterotrophic protists. The maximum production rate for Heterotrophic nanoflagellates (FN 20) (~1.5 d^{-1}) was based on Weisse (1997), *i.e.*, the only one study available. The maximum value for heterotrophic dinoflagellates was obtained with the same regression used for mixotrophic ones (Jeong *et al.*, 2010). Growth rate data for prostomatids (FN 22, cell size >20 μm) were also scarce in the literature. To the best of our knowledge, the physiological performance was studied only for the species *Tiarina fusus* and values of maximum production rate at 19°C were reported to range 0.1-0.47 d^{-1}, depending on the prey provided as food (Jeong *et al.*, 2002). By applying a Q_{10} of 2.8 - an average value for ciliates according to (Hansen and Bjørnsen, 1997) - the maximum production rate of prostomatids at 25°C resulted 0.98 d^{-1}. The maximum value for the heterotrophic oligotrichous ciliates of the genus *Strobilidium* spp. (FN 23) (~1.5 d^{-1}) was derived through the equation reported by Pérez *et al.* (1997), considering the specific biovolume and a temperature of 25°C. A wide literature was available for growth rates of tintinnids (FN 24) estimated from *in situ* observations carried out during summer (Verity, 1986). Finally, nanociliates in our case-study (FN 25, cell size <20 μm) included both prostomatids and other ciliates. Information about their growth performances were scarce and we

Tab. 3. Vital rates of protozooplankton.

FN	Blue state Production min-max d^{-1}		Green state Production min-max d^{-1}		Blue/Green states Consumption min-max d^{-1}		Assimilation efficiency -	Autotrophy *vs* Heterotrophy -
Mixotrophic protozooplankton								
13	0.49	1.90	0.75	1.90	1.50	3.80	0.90	0.50
14	0.30	1.17	0.46	1.17	1.34	6.69	0.90	0.59
15	0.26	1.02	0.40	1.02	0.22	2.20	0.90	0.59
16	0.13	0.52	0.20	0.52	0.00	0.13	0.90	0.90
17	0.34	1.33	0.52	1.33	0.17	3.00	0.90	0.83
18	0.40	1.54	0.61	1.54	0.36	1.42	0.90	0.64
19	0.35	1.35	0.53	1.35	0.19	3.00	0.90	0.81
31	0.30	1.14	0.45	1.14	0.90*	2.28*	0.90	0.50
32	0.18	0.70	0.28	0.70	1.34	6.69	0.90	0.59
33	0.16	0.61	0.24	0.61	0.22	2.20	0.90	0.59
Heterotrophic protozooplankton								
20	0.46	1.76	0.69	1.76	0.30	1.80	0.90	-
21	0.25	0.95	0.38	0.95	1.28	7.67	0.90	-
22	0.23	0.89	0.39	0.98	0.77	4.70	0.90	-
23	0.42	1.64	0.64	1.64	0.72	3.84	0.90	-
24	0.43	1.66	0.65	1.66	0.73	7.30	0.90	-
25	0.61	2.36	0.93	2.36	0.33	1.89	0.90	-
34	0.21	1.06	0.32	1.06	0.30	1.80	0.90	-
35	0.30	0.57	0.45	0.57	1.28	7.67	0.90	-
36	0.18	0.53	0.28	0.59	0.21	2.10	0.90	-
37	0.16	0.98	0.24	0.98	0.72	3.84	0.90	-
38	0.08	1.00	0.12	1.00	0.26	2.61	0.90	-
39	0.21	1.42	0.31	1.42	0.33	1.89	0.90	-

FN, functional node.

used data from Franzé and Modigh (2013), who reported max growth rates up to 2.36 d^{-1} for a nanociliate assemblage under laboratory conditions and relaxed intra-guild predation.

Consumption and assimilation rates

Autotrophy and heterotrophy alternate in the metabolism of mixotrophic organisms. A gross estimation of the extent of alternation between these life-strategies is given by the ratio of daily production associated to autotrophy, which is presented in Tab. 3. Scanty information was available about specific ingestion rates of mixotrophic flagellates, which were represented mainly by *Ollicola vangoorii* (FN 13 and FN 31, in surface and deeper layers, respectively). We assumed that consumption rates in these organisms were never lower than twice the production rates in the same organisms, a value largely enough to guarantee their metabolisms. Since no information was available in the literature regarding growth and metabolism in *Ollicola vangorii*, we assumed that 50% of the biomass production in this organism was carried out via photo-autotrophy.
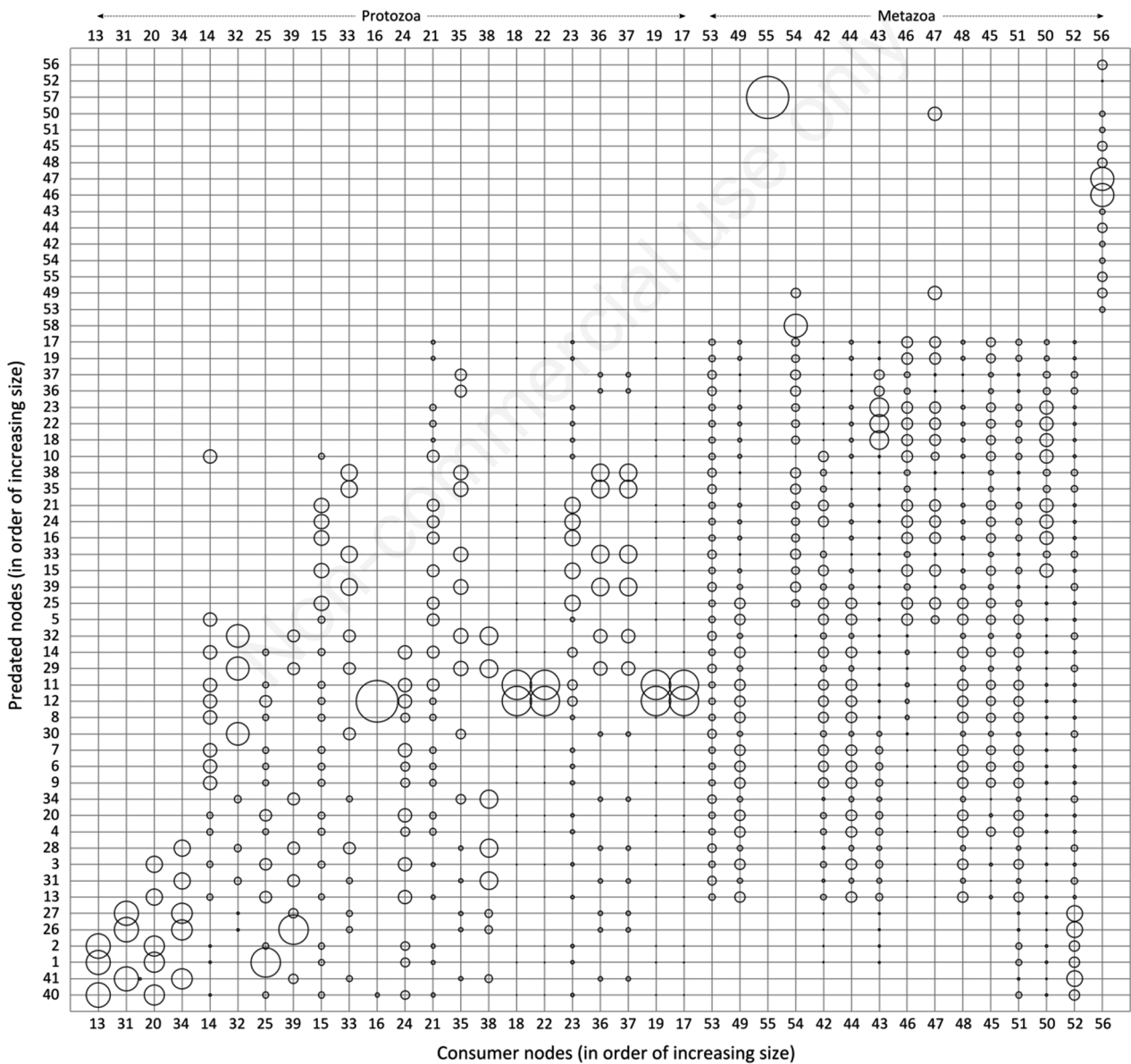
Fig. 5. Diet-matrix of FNs. Each data-point represents a trophic link; columns and rows represent consumers and preys, respectively. The dimension of a circle is proportional to the weight of the link in the diet of the consumer, which is represented by the spectrum of circles within the column. FNs are listed in Tab. 1.

The obligate mixotroph *M. rubrum* (syn. *M. rubra*) (FN 16) is reported to ingest a maximum amount of carbon corresponding to 13.1% of its body-mass, on a daily basis (recalculated data from Yih *et al.*, 2004). This value would be in line with the ratio of ingested versus autotrophically-produced carbon amounts (*i.e.*, 0.10 *vs* 0.90, respectively). Such a high value stems from the fact that the captured plastids can divide within this ciliate and can be transmitted throughout a clonal line, unlike for the other mixotrophic ciliates which need to acquire new plastids after some cellular divisions (Stoecker *et al.*, 2009 and references therein). The minimum consumption rate for *M. rubrum* was assumed close to zero, after considering the high photosynthetic performances of this species.

The oligotrichous ciliates *Laboea* spp., *Tontonia* spp. and *Strombidium* spp. (FN 17-19) engulf microalgae and retain their plastids but are not able to maintain plastidial-division (Stoecker *et al.*, 2009 and references therein). Aplastidic cells were rarely reported in these genera, which relied on photosynthesis to cover a large part of the respiration demand and showed growth limitation in absence of plastids; on average, the overall contribution of photosynthesis to production was around 55% (Stoecker *et al.*, 2009 and references therein). A meta-analysis based on published data (Dolan and Perez, 2000) estimated that, close to light-saturation (200 μE, *i.e.*, an amount of light comparable with that in the surface layer of the GoN during summer), the carbon-fixation rate in plastidic oligotrichous ciliates had an average value of 5 fg C per μm^{-3} of ciliate-biovolume per hour, and this rate was independent from the size of the ciliate. Based on these assessments, we calculated that the fraction of biomass obtained via photosynthesis at saturating light was 0.81, 0.64 and 0.83 in *Strombidium*, *Laboea* and *Tontonia* (FNs 17-19), respectively, considering a summer day-length of 14 h.

For what concerns the genus *Strombidium* spp. (FN 19), the ingestion rate of the species *S. rassoulzadeganii* was within 3 d^{-1} (*i.e.*, 300 % the body-mass) at concentrations of food comparable to those found in our system in the surface layer (<0.5 g C m^{-3}) (Schoener and McManus, 2012). Considering that a *Strombidium* cell should cover up to 81% of its metabolic needs via photosynthesis, the minimum consumption rate would account for about 0.19 d^{-1}. *Laboea strobila* (FN 18) can ingest up to 5.9% of its biomass per hour, giving a maximum consumption rate of 1.42 d^{-1} (Stoecker *et al.*, 2009), though assuming that ingestion rates were equivalent during day and night (but this is not always valid, see, *e.g.*, Jakobsen and Strom, 2004). Following the same rationale adopted for the other oligotrichous ciliates, minimum consumption rate for *L. strobila* should be about 0.36 d^{-1}. Since no information was found for the genus *Tontonia* (FN 17), we assumed that the consumption rate of this ciliate should be similar to that of *Strombidium*, based on similarities of cellular biomass and metabolism (*i.e.*, ratio between autotrophy and heterotrophy). The minimum consumption rate for this protist was assumed as ~0.17 d^{-1}, according with the criteria adopted for other mixotrophic oligotrich ciliates.

Tab. 4. Vital rates of mesozooplankton.

FN	Blue state Production min-max		Green state Production min-max		Blue state Consumption min-max		Green state Consumption min-max		Blue state Assimilation efficiency min-max		Green state Assimilation efficiency min-max	
	d^{-1}	d^{-1}	d^{-1}	d^{-1}	d^{-1}	d^{-1}	d^{-1}	d^{-1}				
42	0.10	1.37	0.10	1.37	0.65	0.95	0.71	3.50	0.50	0.68	0.45	0.70
43	0.10	1.37	0.10	1.37	0.65	0.95	0.71	3.50	0.50	0.68	0.45	0.70
44	0.08	0.12	0.08	0.13	0.15	0.30	0.18	1.37	0.40	0.68	0.40	0.68
45	0.05	0.07	0.05	0.08	0.11	0.23	0.14	1.04	0.40	0.68	0.40	0.68
46	0.03	0.04	0.03	0.05	0.05	0.10	0.06	0.46	0.40	0.68	0.40	0.68
47	0.04	0.06	0.04	0.06	0.07	0.13	0.08	0.61	0.40	0.68	0.40	0.68
48	0.03	0.04	0.03	0.05	0.14	0.28	0.17	1.29	0.40	0.68	0.40	0.68
49	0.12	0.29	0.13	0.30	0.23	0.47	0.28	2.14	0.73	0.73	0.73	0.73
50	0.00	0.50	0.00	1.13	5.50	11.70	5.50	33.50	0.40	0.91	0.06	0.91
51	0.20	1.90	0.20	1.90	0.90	2.40	1.00	8.80	0.42	0.72	0.32	0.72
52	0.18	1.90	0.18	1.90	0.24	1.78	0.24	1.78	0.75	0.87	0.75	0.87
53	0.03	0.42	0.03	0.42	0.06	7.00	0.06	7.00	0.80	0.80	0.80	0.80
54	0.08	0.12	0.08	0.12	0.07	0.15	0.09	0.54	0.65	0.76	0.65	0.76
55	0.12	0.17	0.12	0.18	0.10	1.23	0.10	1.23	0.65	0.76	0.65	0.76
56	0.05	0.19	0.05	0.19	0.01	0.37	0.01	0.37	0.80	0.82	0.80	0.82

FN, functional node.

Small and medium mixotrophic dinoflagellates (FN 14-15) bear proper plastids, which are transmitted to their progeny after cell-division. Autotrophy could account for 59% of their growth rate and, consequently, of their metabolism (recalculations from data in Fig. 4 and Tabs. 3 and 4 in Jeong *et al.*, 2010). The consumption rate for dinoflagellates in our study system was derived based on meta-analyses of published experimental data and relating regressions (Jeong *et al.*, 2010 and references therein). Smaller- and medium-sized mixotrophic dinoflagellates (in our study system, showing an ESD of 9 and 18 μm, respectively, and included in FN 14-15 for the surface and FN 32-33 for the deeper layer) showed a maximum consumption rate of 6.69 and 2.205 d^{-1}, respectively. Obligate heterotrophic dinoflagellates (in our study system, showing an ESD of about 22 μm and included in FN 21 and 35 for surface and deeper layer, respectively) showed a maximum consumption rate of 7.674 d^{-1}. For what concerns the minimum consumption rate of a dinoflagellate node, in absence of specific values in the literature, these were set as double the minimum production rate of the same node - *i.e.*, 1.338 and 0.22 d^{-1} for smaller and larger mixotrophic dinoflagellates and 1.279 d^{-1} for heterotrophic dinoflagellates. Since it was not possible to disentangle the effect of temperature on the ingestion rate from the information available in the literature, the consumption rates' ranges described above are considered as representing dinoflagellates present in both water layers considered in our study system.

The feeding performances of prostomatids (FN 22 and 36) have been poorly studied. The ingestion rates of *Tiarina fusus* at 17°C and at food concentrations comparable to those reached in the GoN during summer ranged 0.21-2.1 d^{-1} (Jeong *et al.*, 2002). The latter values were taken as the minimum-maximum consumption range for the deep prostomatids (FN 36) in our case study, living at T=15°C. Considering a Q_{10} of 2.8 specific for ciliates (Hansen and Bjørnsen, 1997), and references therein), the consumption rate for prostomatids in the surface layer (FN 22) should range 0.77-4.7 d^{-1}. Concerning *Strobilidium* (FN 23 and 37, in surface and deeper layers, respectively), weight-specific ingestion rates were in the range 0.03-0.16 h^{-1} in *Strobilidium* cf. *spiralis* (Verity, 1991), with the higher value gained at a saturating food concentration of 250 mg C m^{-3}, a value in the range of our system of study during summer. Since consumption rates of *Strobilidium* during the day and the night were comparable according to (Jakobsen and Strom, 2004), daily consumption rates for *Strobilidium* in our case-study (FN 23) should range 0.72-3.84 d^{-1}. This range referred to a single temperature (20°C, intermediate between our environmental extremes) but we assumed it as representative for both surface and deeper layers populations (FNs 23 and 37).

The consumption rates of tintinnids at 25°C ranged

0.73-7.3 d^{-1} (data for *Tintinnopsis acuminata*, recalculated from Verity (1985), assuming that ingestion rates during day and night were comparable). This range was herein considered for tintinnids in the surface layer (FN 24). When applying a Q_{10} of 2.8 (Hansen and Bjørnsen, 1997), the consumption rate for tintinnids in the deeper layer (FN 38) should range 0.26-2.61 d^{-1}. Nanociliates (FNs 25 and 39, in surface and deeper layers, respectively) included specimens with a cell-size <20 μm (average ESD=16 μm). A cell of the marine genus *Uronema* (ESD about 12 μm, comparable to those in our case-study) can ingest up to 31 *Synechococcus* cells hour^{-1} at light conditions (Christaki *et al.*, 1999). Considering that the ingestion rate of nanociliates is 120% higher in the dark (data for *Balanus comatum*, Jakobsen and Strom, 2004), the whole amount of cells ingested per day by one nanociliate should be 68.2, giving a specific rate of ingestion of 1.89 d^{-1}. Since the experimental data considered were gained at 20°C (intermediate between 15 and 25°C) (Christaki *et al.*, 1999), and since a Q_{10} specific for nanociliates was not available in the literature, maximum consumption rate for both the surface and deeper populations (FN 25 and 39) was considered as 1.89 d^{-1}. This value is relatively high, enabling these organisms to sustain their metabolism at the highest rate of production. Moreover, since the functional response (*i.e.*, the consumption rate in function of food concentration) for nanociliates was unknown, the minimum consumption rate at both surface and deeper layers was assumed to be proportional to the maximum consumption rate and the ratio between minimum and maximum consumption rates of other heterotrophic ciliates (*i.e.* prostomatids and *Strobilidium*), *i.e.*, 0.33 d^{-1}.

Finally, according with the literature, mixo- and heterotrophic unicellular organisms were assumed to be highly efficient in energetic terms and to have an assimilation efficiency ~1 (Stoecker *et al.*, 2009 and reference therein).

Diet

This paragraph describe in detail the derivation of values included in Fig 5. The trophic links presented herein are considered valid for both Green and Blue states.

Dinoflagellates, including both mixotrophic and heterotrophic taxa, were reported to eat a wide array of preys (Sailley and Buitenhuis, 2014). According to laboratory observations (Jeong *et al.*, 2010), mixotrophic and heterotrophic dinoflagellates were more actively feeding when predator:prey size ratios ranged 0.8-5.8 and 0.4-5.3, respectively; moreover, the higher ingestion rates were observed when predator to prey size ranged 0.8-1.4 and 0.9-2.6 for mixotrophic and heterotrophic dinoflagellates, respectively. According to size-selectivity, small mixotrophic dinoflagellates in our case-study (average equivalent sphere diameter, *i.e.*, ESD=4.5 μm, FN 14 and 32) would predate preferentially bacteria, prochlorophytes

(ESD <1 μm), other small-sized dinoflagellates (ESD within 10 μm; cannibalistic feeding) and diatoms. In turn, larger mixotrophic dinoflagellates (avg. ESD=9 μm, FN 15 and 33) would eat all other unicellular organisms, except for large ciliates (ESD >40 μm). Obligate heterotrophic dinoflagellates (avg. ESD 11.1 μm, FN 21 and 35) would eat over an even wider prey-range.

Heterotrophic nanoflagellates (HNF, FN 20 and 34) and nanociliates (FN 25 and 39) were among the smallest consumers in the studied food-web. Bacterivory was reported as the dominant feeding behaviour of HNF (Novarino *et al.*, 2002). HNF were reported to assume, at daily basis, from 12 to 60% of heterotrophic bacteria, from 0.6 to 19% of *Synechococcus* and from 0.02 to 21% of *Prochlorococcus* (Christaki *et al.*, 2001). Some species also graze pico-eukaryotes (<3 μm) (Christaki *et al.*, 2005). The latter were partially represented in our system of study within FNs 3 and 28. We included in HNF diet all the food-items listed above, giving much relative weight to trophic links involving prokaryotes. According with meta-analyses, nanociliates (FN 25) are reported to eat preferentially cell preys smaller than 9 μm ESD (Sailley and Buitenhuis, 2014). As an example, the prostomatid *Uronema* spp. (included in FN 25) eats preferentially more *Synechococcus* than *Prochlorococcus* and heterotrophic bacteria (Christaki *et al.*, 1999).

Larger ciliates, such as prostomatids and *Strobilidium* spp. (average ESD ~54 μm, FN 22, 36 and FN 23, 37, respectively), could ingest all unicellular plankters, from bacteria to ciliates (Sailley and Buitenhuis, 2014) but should prefer food items having an ESD > 12 μm (Jeong *et al.*, 2002). Diatoms appeared not to be selected by the above-mentioned organisms probably because these microalgae would provide low quality food to ciliates (Müller and Schlegel, 1999). Tintinnids ingest particles whose size is around 43% of the diameter of lorica at the oral opening (Heinbokel, 1978). The average diameter for tintinnids in the GoN (FN 24), weighted to each species' relative abundance, is about 20 μm and the probable maximum size of prey edible by tintinnids in our food-web should be 9 μm. In the laboratory, tintinnids consuming phytoflagellates (FN 12) grew at the same rates than those fed with diatoms lacking significant external processes (FN 7) (Verity and Villareal, 1986). Moderate growth was observed when tintinnids ate small dinoflagellates (FN 14) while extensive mortality was reported in tintinnids fed with *Synechococcus* (FN 1) (Verity and Villareal, 1986).

Heterotrophic metazoans

In the following paragraphs, literature references and specific rationales for the calculation of production, consumption, assimilation rates and the definition of diets of metazooplankton (Tab. 4, Figs. 4 and 5) are provided. Planktonic metazoans in our food-web include a large variety of groups and species with remarkably different life history traits and individual performances.

Production rates

Among marine cladocerans, *Penilia avirostris* (FN 42) which was extensively studied in the Mediterranean Sea and along Brazilian coasts, showed max growth rates higher than 1.0 day^{-1}, thus comparable to that of microbes (Atienza *et al.*, 2007, 2008; Egloff *et al.*, 1997). This species is characterized by intense population bursts pursued by fast parthenogenetic reproduction, especially during summer (Atienza *et al.*, 2007, 2008). In cladocerans, juveniles differ from adults only for their smaller size and occupy a niche comparable to the adult stage, which is reached very rapidly (<3 days) (Egloff *et al.*, 1997). In the studied food-web, the minimum-maximum values of production rates for *P. avirostris* were set assuming that population increasing dependended only on i) the animal birth rate, and ii) the hatching of parthenogenetic eggs', without considering somatic growth. Moreover, since the relation between population growth rates and food environment for cladocerans is still unknown, a single range of production rate, derived from the above-mentioned studies, was considered for both the Green and Blue states. Scanty information is available in the literature for the cladocerans *Evadne* spp. and *Pseudevadne tergestina* (FN 43) and we assumed that minimum-maximum production rates for these animals were the same of those set for *P. avirostris*, in both the Green and Blue states.

Unlike cladocerans, the copepod life-histories include several developmental stages. Both population and individual growth rates are good proxies of these animals' productivity (Frangoulis *et al.*, 2010). We used the weight-specific fecundity to define production rates for adults, assuming that adult-female production is completely realized by means of egg production (Hirst and Bunker, 2003) without any change in individual biomass at short-time scales. Conversely, the weight-specific (somatic) growth was used to define production rates in juvenile copepods, since they undergo changes in individual biomass at short time-scales (Hirst and Bunker, 2003). Production rates for both adult and juvenile copepods in our case-study were based on the extensive synopsis of growth rates of copepods published by Hirst and Bunker (2003), which linked growth rates to i) species body-mass, ii) temperature and iii) food concentration. Since copepods in our case-study were sampled in the upper 50 m layer of the water column, we set minimum-maximum values as the rates predicted for temperatures and food conditions present in the environment at the surface and at the bottom of the sampling layer in the Green and Blue states (T ranging 25-15°C and food ranging 203-21 and 37-17 mg C m^{-3} at Green and Blue states, respectively). Growth rates of copepods (FN 44-49) were

well below those reported for cladocerans (Fig. 4, Tab. 4).

Pelagic tunicates, represented by appendicularians, doliolids and salps in our case-study (FN 50-52), are semelparous organisms - *i.e.*, they reproduce only once in a lifetime and die after reproducing (Bone, 1998). Moreover, pelagic tunicates have no larval stage and newly born individuals are comparable to adults in terms of feeding performances, ecological role and, in some cases, body-size (Bone, 1998; Deibel and Lowen, 2012 and references therein). Adults undergo also an intense somatic growth, which must be considered when parameterizing the production rates of these animals. The growth rate of pelagic tunicates is represented by the so-called 'lifetime fitness', a parameter that in population ecology studies is a synonym of 'recruitment' (Deibel and Lowen, 2012). The lifetime fitness integrates both the timing of egg release and the somatic growth that precedes spawning and it expresses the maximum intrinsic rate of natural increase. Taking into account the short duration of life-cycle of pelagic tunicates and the time scale of our case-study, we considered the lifetime fitness as thoroughly suitable to represent production rates of pelagic tunicates in unit of biomass.

Oikopleura dioica was the main appendicularian species present in the GoN during summer and it is included herein within FN 50. A life-cycle-based model demonstrated that lifetime fitness of this species was strongly influenced by both temperature and food concentration (Lombard *et al.*, 2009b; Deibel and Lowen, 2012). Alike other pelagic tunicates, appendicularians are sensitive to high food concentrations: *i.e.*, they easily undergo super-saturation/engulfment, with negative effects on reproduction at food concentration >300 mg C m^{-3} (Lombard *et al.*, 2009b). However, in our system, food availability did not exceed 200 mg C m^{-3}. The range of production rate of appendicularians in our case-study was set based on the studies above (with maximum=1.13 d^{-1}).

Growth rates of doliolids were studied less extensively than those of appendicularians. In our case-study, the genus *Doliolum* was the most represented doliolid in the GoN during summer (FN 51), mainly with the species *D. nationalis*. A lifetime fitness of 0.26 d^{-1} at 20°C was estimated for *D. gegenbauri* (Deibel and Lowen, 2012), featuring also a slight dependence from the food concentrations (Gibson and Paffenhöfer, 2000). Assuming a linear dependence between temperature and growth rates in the range of 15-25°C, this parameter would be 0.20-0.33 d^{-1} between 15 and 25°C (based on Q_{10} assumed for pelagic tunicates, according to Broms and Tiselius, 2003). We assumed the lowest number in the above-mentioned range as the minimum production rate for doliolids in our system. This rate would refer to the complete life-cycle of *D. gegenbauri* (encompassing up to six different life stages). Yet, *D. nationalis* is characterized by a bi-phasic life-cycle in which asexual production of new individuals can strongly shorten the generation time (Godeaux *et al.*, 1998). To the best of our knowledge, no estimation of growth rates for *D. nationalis* has been carried out so far. We thus assigned a maximum production rate of ~1.9 d^{-1} to doliolids, which is a value similar to that reported for salps (Madin and Deibel, 1998).

Salps have both sexual and asexual reproduction in their life cycle (Bone, 1998). Scanty information is available about growth rates of these animals (FN 52), due to the difficulty to breed them in laboratory at controlled conditions. *Thalia democratica* was the most represented species in the GoN during summer. The lifetime fitness of this species reported in the literature ranged 0.18-1.9 d^{-1}, within a temperature range of 14-22°C (Deibel and Lowen, 2012 and references therein). Interestingly, temperature does not seem to affect salp growth rate, based on the data available. Also, the lower rates were measured in the lab, while the highest ones were estimated from the field. While fast growth (up to 1.9 d^{-1}) could theoretically occur only in particular circumstances, such as the still poorly explained massive outbreaks occurring in nature (Deibel and Lowen, 2012 and references therein), slower growth was probably due to the confinement of large animals in a limited space in the laboratory. Based upon these considerations, we considered the whole range of variability of salps lifetime fitness.

In our case-study, we included also meroplankton (FN 53), which features planktonic larvae of benthic organisms. We used the rate of somatic growth of larvae as a proxy of production rate for meroplankton at the time scale of our case-study. Growth rates ranging 0.025-0.15 d^{-1} were reported for larvae of the polychaete *Polydora ciliata* at 16°C in the laboratory (Almeda *et al.*, 2009), with the highest rates attained at food saturation, *i.e.* about 1 mg C L^{-1}, a value about double the highest concentration of POC in our study system. After applying a Q_{10} of 2.8 (Hansen and Bjørnsen, 1997), the rates ranged 0.07-0.42 d^{-1}. Due to the scarce knowledge on the relation between growth, food and temperature in meroplankton, we assigned an identical minimum-maximum production range (0.025-0.42 d^{-1}, respectively) in both the Green and Blue states.

Finally, no information was gathered for the growth rates of chaetognaths, the most abundant carnivorous mesozooplankton group (FN 60) in our case study.

Consumption rates

Penilia avirostris (FN 42) from the Mediterranean Sea showed in the laboratory weight-specific ingestion rates ranging 0.26-1.57 d^{-1} in summer conditions (natural photoperiod and temperature 22-27°C) (Atienza *et al.*, 2006). However, a significantly wider range of 0-7 d^{-1} was re-

ported at about 22°C (Katechakis *et al.*, 2004), with minimum-maximum values corresponding to food concentrations of about 0 and >250 mg C m^{-3} (saturating condition). At food concentration of 203 mg C m^{-3}, *i.e.*, the maximum food concentration for a metazoan in our case study, the consumption rate should be 3.50 d^{-1} (recalculated data from Katechakis *et al.*, 2004). Since mesozooplankton in our case-study are likely able to cross the seasonal thermocline, the above mentioned range should be representative for the natural food range in our study system. Based on regression derived from the literature (Katechakis *et al.*, 2004), the minimum-maximum consumption rates should range 0.71-3.5 d^{-1} in the Green state (*i.e.*, with food concentrations ranging 21-203 mg C m^{-3}), and 0.65-0.95 d^{-1} in the Blue state (*i.e.*, with food concentrations ranging 17-37 mg C m^{-3}).

The literature available for the feeding performances of copepods features both *in situ* and laboratory studies. Various authors have conducted meta-analyses based on published data to search for global relations between feeding rates and i) food concentration, ii) body-mass, and iii) temperature, with the first variable being the main driver of feeding rates of copepods in nature as food concentration can explain 52% of the variance of ingestion rates (Saiz and Calbet, 2011, 2007). Herein, we derived the most probable values of consumption rates for the main calanoid copepods in our case-study by using multiple regression relations between ingestion rates and the main driving factors, as described in Saiz and Calbet (2011, 2007). Known variables in our calculations were i) FNs' body-mass and ii) the amount of carbon allocated into unicellular FN with ESD ≥3 μm - *i.e.*, the lowest size of food particles edible by copepods (Bartram, 1981) - in the Green and Blue states and in the surface and deeper layers (*i.e.*, 203-21 and 37-17 mg C m^{-3}, respectively). As shown in Fig. 4, these rates were always lower than 0.5 d^{-1}, thus significantly lower than those of most unicellular organisms. Differently from calanoid copepods, ingestion rates of the cyclopoid *Oithona* spp. (FN 54, including copepodites and adults of different species) were herein based on regression derived from data referring to *O. davisae* at different life stages (Almeda *et al.*, 2010; Saiz *et al.*, 2003). The minimum-maximum consumption rates for this animal were derived at the four key-concentrations considered also for other copepods; *Oithona*'s consumption rates were slightly higher than those for calanoid copepods, although they exceeded to some extent 0.5 d^{-1} only in the Green state.

The knowledge about trophodynamics of gelatinous filter-feeders presented some discrepancies: although consumption rates were well assessed in the laboratory for appendicularians, the same was not true for doliolids and salps. The ingestion rates of the appendicularian *O. dioica* was described in detail in laboratory conditions (T=15°C)

(Lombard *et al.*, 2009a, 2009b). Ingestion in these animals was directly related to temperature and inversely related to food concentration. Consumption rates for appendicularians (FN 50) were obtained from published regressions (Lombard *et al.*, 2009a, their Tab. 2), applied at the four key food-concentrations at the two system states (see above). The maximum consumption rate, corresponding to the surface layer, was increased according to a Q_{10} of 1.78 specific for grazing rates of *O. dioica* (Broms and Tiselius, 2003). According to our recalculations, a maximum consumption rate of more than 30 d^{-1} could be possible in appendicularians in the Green state. Though very high, such rate is not improbable, considering the low body-mass of these gelatinous filter feeders and the possibility to eliminate the food in excess by abandoning engulfed houses (Bone, 1998).

Concerning other gelatinous filter-feeders, the ingestion rate in relation with food concentrations was described in detail for *Doliolum denticulatum* from the North Western Mediterranean at laboratory conditions and using a natural microplankton community as food (Katechakis *et al.*, 2004). The animals used in the above-mentioned study had a size comparable to that of *D. nationalis*. The range of consumption rate of doliolids in our study case (FN 51, with maximum value up to 8 d^{-1} in the Green state, Fig. 4C,D) were based on regressions derived from the study above and applied at the four key food concentrations for metazoans in our study-case (see above). Ingestion rates of salps (FN 52) were scarcely investigated in comparison with other gelatinous filter feeders. Individuals of salps <10 mm in size (the individual size more frequently found in samples collected at station LTER-MC) showed weight-specific ingestion rates ranging 2-8.3% of the body carbon per hour, *i.e.*, ~ 0.24-1 d^{-1}, assuming that an individual feeds at least for 12 h a day (Madin and Deibel, 1998). This range is similar to the one observed in nature in the Southern Ocean at temperature <15°C, *i.e.*, 0.1-1 d^{-1} (von Harbou *et al.*, 2011). Assuming that a Q_{10} of 1.78 was applicable to salps as for appendicularians (Broms and Tiselius, 2003), the maximum consumption rate should be 1.78 d^{-1} for both the Green and Blue states in the GoN. Thus, salps' consumption rate would range 0.24-1.78 d^{-1}, likely enough to sustain the potentially high production rates of these organisms (Fig. 4). Moreover, since in our study system the concentration of food available to salps always exceeded 10 μg C L^{-1}, *i.e.*, the saturation limit of these animals (Andersen, 1985; Deibel, 1982), we believe that the same value of maximum consumption rate can be applicable to both the Green and Blue states.

Feeding rates of meroplanktonic larvae (FN 53) typically found during summer in the GoN, *i.e.*, polychaets, echinoderms, cirripedes, bivalves and gastropods, were measured over natural microplankton concentrations and

a specific ingestion rate of 2.5 d^{-1} was reported for each of these groups (Almeda *et al.*, 2011b). These rates referred to a natural phytoplankton bloom in the Vancouver bay during July with temperature ranging 13-17°C and at food concentration of 2-6 µg Chl *a* L^{-1}, thus comparable to the Green state in the GoN in surface waters. Assuming a Q$_{10}$ of 2.8 (Hansen and Bjørnsen, 1997), the maximum consumption rate during summer in the GoN accounted for 7 d^{-1}, which was a very high rate. However, meroplanktonic larvae have high energetic requirements to pursue an intense somatic growth and such high rates were not improbable. Being information on functional response of meroplankton scarce in the literature, the minimum rate can be only set herein as double the production rate.

Scantier information was available for the other animals in the food-web. Planktonic detritivores in our case-study (FN 55) included only cyclopoid and harpacticoid copepods whose feeding appendages are suited to scrap food particles from discharged appendicularian houses. *Oncaea mediterranea* was reported to eat up to 100% of its body-biomass at 20°C (Paffenhofer, 1993). According to the regression described by Saiz and Calbet (2007), the maximum potential consumption rate for these animals should be 1.23 d^{-1} in our case study and considering their body-size. The minimum consumption was assumed as ~0.1 d^{-1}, a value similar to the minimum ingestion rate of other copepods.

Finally, the ingestion rate of carnivores (FN 56) was assumed as driven mainly by that of chaetognaths. Different *Sagitta* species were studied at different maturity stages and across a coast-offshore trophic gradient in the Western Mediterranean during summer (Duró and Saiz, 2000): in that study, between 0.13 and 3.76 preys were ingested per chaetognath per day and no relation with food concentration was recorded. In our system, considering an average weight of 18.35 µg C per animal/prey for the FNs potentially eaten by chaetognaths, consumption rate of these predators should range 0.013-0.37 d^{-1}, both in the Green and Blue states.

Assimilation rates

In the literature, mesozooplankton were reported to have variable assimilation efficiency values, depending upon the actual food environment. Synthetic data are shown in Tab. 4. The assimilation efficiency of cladocerans (FN 42-43) was ranged 0.70-0.45 from lowest to highest food concentrations, respectively, within the range of variability of our study system (Katechakis and Stibor, 2004; Katechakis *et al.*, 2004). The assimilation efficiency of calanoid copepods (FN 44-48) was set based on the information available for *A. clausi,* which showed assimilation efficiency ranging 0.78-0.45, within a wide range of food concentrations from ~0 to over 800 µg C L^{-1} (Katechakis *et al.*, 2004). Yet, the relation between assimilation effi-

ciency and food concentration was not statistically significant (Katechakis *et al.*, 2004), since some values were comprised between 0.6 and 0.8 at super-saturating food concentrations. In the range of food variability of our study system, and considering a linear regression fitting data-points, assimilation efficiency would range ~0.68-0.40, for both the Green and Blue states. This range was considered valid for all calanoid copepods (FN 44-48) excepting juvenile stages (FN 49, including mainly copepodites). The assimilation efficiency for the latter was a fixed value of 0.73, assuming that it was equal to that of *O. davisae* juveniles at 20°C (Almeda *et al.*, 2011a). Higher assimilation in juveniles is likely due to the need to sustain a strong somatic growth, which is absent in adults. Concerning the cyclopoid copepod *Oithona* spp., assimilation efficiency ranged 0.65-0.76 in different life stages of *Oithona* (FN 54) (Almeda *et al.*, 2011a). Considering that *Oithona* spp. are ambush feeders, the saturation likely emerges at concentrations higher than those critical for suspension feeders, thus giving a relatively narrower assimilation efficiency range. Concerning detritivores, assimilation efficiency can be assumed equal to that of *Oithona*.

In comparison with copepods, the assimilation efficiency (and, in general, the feeding dynamics) of gelatinous mesozooplankton is more influenced by external conditions. Assimilation efficiency of appendicularians (FN 50) was strongly and inversely related to food concentration (Lombard *et al.*, 2009a, 2009b). A regression linking assimilation efficiency to food concentration was used to infer values relating to concentration and temperature extremes in our study-system (recalculated data from Lombard *et al.*, 2009a, 2009b), considering also a Q$_{10}$ of 1.78 as reported by Broms and Tiselius (2003). In our system, assimilation efficiency for appendicularians ranged 0.40-0.91 in the Blue state, and 0.06-0.91 in the Green state, with relatively higher values at lower food concentrations. Assimilation efficiency for doliolids (FN 51) ranged 0.32-0.72 in the range of food concentration of our study system (Katechakis *et al.*, 2004). Using the regression described by Katechakis *et al.* (2004), this parameter ranged 0.42-0.72 and 0.32-0.72 in the Blue and Green states, respectively. Assimilation efficiency of salps (FN 52) within 10 mm in length (like in our case-study) should be around 0.67 (Pakhomov, 2004), and this value was comparable to estimations made during an iron fertilization experiment, when assimilation efficiency ranged 0.75-0.87 at two fairly distant carbon concentrations (von Harbou, 2010). We can thus hypothesize that stable assimilation efficiency for salps, likely also at 'our' Green and Blues states, can stem from the regulation of feeding by eliminating water and food in excess by means of backwashing (Madin and Deibel, 1998).

Carnivorous mesozooplankton (FN 56), mainly chaetognats in our case-study, were reported to have as-

similation efficiency ranging 0.80-0.82 (Cosper and Reeve, 1975; Giesecke *et al.*, 2010). These rates were similar to those reported for siphonophores (Purcell and Kremer, 1983), other strictly carnivorous zooplankters occurring sporadically in our system, and we considered them valid in both the Green and Blue states. No information was available for meroplankton and detritivores (FN 53 and 55, respectively). About the former animals, we can assume a fixed assimilation efficiency of 0.8 in both the Green and Blue states, since larvae should convert in somatic growth a large part of the ingested food.

Diet

This paragraph describe in detail the derivation of values included in Fig. 5. The trophic links presented herein are considered valid for both Green and Blue states.

Unlike protistan grazers, mesozooplankton in our case-study were supposed to be eating in both surface and deeper water- layers. Cladocerans (FN 42-43) are suspension feeders: *i.e.*, their food particles are conveyed to oral apparatus by feeding currents produced by their appendages. Among cladocerans, *P. avirostris* (FN 42) was reported to eat plankton particles of size ≥1 µm, *i.e.*, the size of cyanobacteria and prochlorophytes, although flagellates, diatoms and dinoflagellates appeared to be the preferred preys (Atienza *et al.*, 2006). Yet, ciliates tended to be excluded due to their motility and larger size (Atienza *et al.*, 2006). When considering the size-spectra, the highest selectivity was detected for food particles between 15 and 70 µm in size, corresponding to 6-28 µm ESD, and decreased for values outside this size range (Katechakis *et al.*, 2004). *Evadne*, another cladoceran genus present in the GoN (FN 43), seemed to prefer food particles with an ESD between 40 and 60 µm, different from those selected by *Penilia* (Katechakis and Stibor, 2004).

The majority of calanoid copepods present in the GoN during the time period object of this study were suspension feeders reported to eat mainly unicellular organisms, with the exception of prokaryotes. *Paracalanus* spp. (FN 44) was reported to collect relatively small particles (<5 µm, ESD 2 µm) only passively (Price *et al.*, 1983) and animals under laboratory conditions appeared to select for medium-sized diatoms (<30 µm in length) when exposed to a mixed-diatoms diet (Mahadik, 2014). *Acartia clausi* (FN 45) was reported to eat particles between 7.5 and 210 µm in size, to select cells ranging 70-100 µm, and to neglect particles <7.5 µm (Katechakis *et al.*, 2004). Within the size-limits of ingestion, the selectivity observed in *A. clausi* matched always the peak of available food particles (Katechakis *et al.*, 2004). This species feeds also on protozooplankton (Fileman *et al.*, 2010), being able to switch from a suspension to an ambush feeding (Saiz and Kiørboe, 1995) as its congeneric species *A. tonsa* (Kiørboe *et al.*, 1997).

The lower size of plankton particles eaten by the cruiser/suspension-feeder *Temora stylifera* (FN 46) seemed larger than that for *A. clausi* (Dam, 1986). Individuals of *T. stylifera* from the GoN selected mainly cells and colonies ranging 30-200 µm when offered diatoms (Mahadik, 2014). *Centropages typicus* (FN 47) was reported to eat a wide array of organisms: small algae (Tomasini and Mazza, 1979), large ciliates or dinoflagellates (Calbet *et al.*, 2007), appendicularian juveniles and eggs (López-Urrutia *et al.*, 2004) and juvenile copepods (Titelman, 2001). The lower size-limit of food-items for this species was 10 µm; yet, the upper size-limit appeared less precise, since *C. typicus* could ingest prey larger than its own size (*e.g.*, yolk-sac fish larvae, Calbet *et al.*, 2007 and references therein). Indeed, *C. typicus* was reported to behave both as a cruiser (and suspension feeder) and as an ambush predator, thus selecting for large motile preys. Stable Isotope Analyses showed recently that *Acartia*, *Centropages, Paracalanus* and *Temora* in the Tyrrhenian Sea had behaved as herbivorous or omnivorous according to different areas (Rumolo *et al.* 2016). Different species of calanoid copepods of the genera *Clausocalanus* and *Paracalanus* were aggregated in the present study (FN 48). These genera being morphologically and dimensionally similar, we roughly assumed that their diets overlapped that of *P. parvus* (FN 44), though their different swimming behaviours indicate differences in particle capture (Mazzocchi and Paffenhöfer, 1999; Paffenhöfer, 1998). The trophic behavior of juveniles of calanoid copepods (FN 49, including mainly *Paracalanus* and *Clausocalanus* in our study system) was considered similar to that of adults of *P. parvus*.

Species of the genus *Oithona* were the most numerous cyclopoid copepods in our system and period of study. It was estimated that the daily ration of these animals came for the 20-30% from faecal pellets (Gonzalez and Smetacek, 1994) and for at least 25% from copepod juveniles (Lampitt, 1978). Moreover, ciliates represented preferred preys among microplankton and accounted for at least the 25% of the daily ration (Castellani *et al.*, 2005). In some cases, ciliates and dinoflagellates represented up to 80% of *Oithona* diet (Castellani *et al.*, 2008). Considering the percentages above, ciliates and dinoflagellates should not contribute less than 40% of the daily ration of *Oithona* spp. Concerning phytoplankton, only particles larger than 10 µm were reported to be eaten by *Oithona* spp. (Drits and Semenova, 1984), and these food particles should not contribute more than 10% of the daily ration of this copepod genus.

Three categories of non-selective filter-feeding animals were considered in our case-study: appendicularians, doliolids and salps (Bone, 1998). Appendicularians ingest a wide spectrum of particulate material, including bacteria and microzooplankton. Although these animals would not select for food particles, specimens belonging to the genus

Oikopleura showed the highest uptake for particles with ESD ranging 20-60 μm (Vargas and González, 2004). Moreover, ingestion of eukaryotes with ESD <13 μm was reported as almost three times higher than that of smaller prokaryotes (Scheinberg *et al.*, 2005). Deibel (1985) and Madin and Deibel (1998) reported doliolids feeding preferentially on particles <50 μm ESD. Salps are also non-selective feeders eating particles of size larger than doliolids (Madin & Deibel 1998). Doliolids ingest food-particle with a size range similar to that of particles eaten by appendicularians. Though, higher selectivity was reported for particles between 2.5-7.5 μm in size, while particles larger than 100 μm were not grazed (Katechakis *et al.*, 2004). Selectivity indexes for picoplankton (including bacteria) and for microplankton between 15 and 100 μm were half the maximum (Katechakis *et al.*, 2004). However, they have been recently reported to have high affinity for particles with size <3 μm, *i.e.*, bacteria, virus and colloids, which could be an important source of food at low microplankton concentration (Sutherland *et al.*, 2010). Indeed, in the course of a feeding experiment in which animals were fed with microspheres, about 60 % of particles found in the gut were within 1 μm in size at concentrations in the order of 10^3 cell mL^{-1}, thus comparable to those found in our system at any state and depth of the water column (Sutherland *et al.*, 2010). Though flagellates and small diatoms (>1 μm) might represent a larger carbon-pool in nature due to their abundance, prokaryotes and smaller particles (0.1-1 μm) are easier to be digested than larger microbes since they show a relatively high surface area to volume ratio.

Meroplankton were reported to eat different kinds of particles, *e.g.*, nanoflagellates (both auto- and heterotrophic), diatoms, dinoflagellates (of different sizes) and ciliates (Almeda *et al.*, 2011b). Finally, in our case-study, we assimilated the diet of carnivores (FN 56) to that of chaetognaths. Copepods were the most abundant prey among those identified in the gut of these animals, while cladocerans were ten times less abundant (Duró and Saiz, 2000). Among copepods, larger animals (*i.e.*, *C. typicus*, *T. stylifera*, *Candacia* spp., *Pleuromamma* spp.) were more oftencaptured than smaller ones (*Paracalanus* spp., *Acartia* spp., *Clausocalanus* spp.). Other crustaceans and chaetognats were also present in the diet, but at lower abundance.

Synthetic characterization of the Green and Blue plankton food-web

The production rates of organisms in our model system are collectively presented in Fig. 4. Both minimum and maximum values of production rates are included, in order to provide evidence about the variability of these rates. Despite overlapping ranges of production rates pertaining to distant species (in terms of both dimension and evolutionary history), a decreasing trend of maximum values of production rate with increasing size, which is not unexpected for plankton (Kiørboe and Hirst, 2014) was detected (Fig. 4 A,B). Yet, minimum values appeared less affected by individual size, especially at the Blue state (Fig. 4 A,B). The highest correlation was found for the Green dataset, with a statistically significant inverse correlation between production rates and size (r=-0.7; P<0.001).

The minimum and maximum values of consumption rates for protozooplankton and metazoan grazers are presented in Fig. 4C,D. The only variations between minimum and maximum values between Green and Blue states were recorded for metazoans. The resolution gained in studies regarding feeding performances of protozooplankton was not high enough to define distinct ranges between Green and Blue conditions. No particular trend of consumption rates per unit of biomass vs. individual size was apparent in the plankton community that we studied (Fig. 4C,D).

All trophic combinations within a hypothetical plankton food-web derived for our case-study are presented in Fig. 5. In this figure we provide a tentative diet-matrix that includes also selective preferences among the food-items pertaining each consumer. This 'semi-quantitative' elaboration was obtained from a thorough revision of the literature (see previous sections). However, a degree of uncertainty never less than 5% should be considered as affecting the relative weight of trophic links. In the present form, a single elaboration of food-web was provided, which is representative of both Green and Blue states. Indeed, the production of distinct food-webs for each state was not possible without using network approaches weighting trophic fluxes based on the biomass present at each node. This issue has been discussed in the modelling exercise carried out in D'Alelio *et al.* (2016). In the present work, we only extrapolated the trophic diversity present into a coastal plankton food-web, based on the organisms that were detected at LTER-MC.

A wide array of trophic connections involved both unicellular and multicellular organisms, and cases of specialized feeding were rare, although present in both groups of organisms. For instance, *M. rubrum* appeared to feed mainly small cryptophytes (size <10 μm, grouped in FN 12) (Crawford, 1989; Gustafson *et al.*, 2000; Johnson and Stoecker, 2005; Johnson *et al.*, 2013; Stoecker *et al.*, 2009). According to predator-prey size ratios, mixotrophic ciliates (ESD 30-40 μm) could eat from bacteria to the largest ciliates (Sailley and Buitenhuis, 2014). Nonetheless, the fact that this species keeps functional ingested plastids should drift predation mainly towards autotrophic taxa, such as prasinophytes, cryptophytes, haptophytes and chlorophytes (Stoecker *et al.*, 2009 and references therein). Another example of specialized trophic connection is that of cyclopoid and harpacticoid copepods (within FN 55) that are mainly

reported as scrapers of Appendicularia houses (Paffenhofer, 1993).

A Principal Component Analysis, carried out using all data in Tabs. 2 to 4, showed that most variance in the vital rates was generated by the maximum values of consumption rates, in the Green more than in the Blue state. Primary producers constituted the only homogeneous group in the PCA output, while metazoan filter feeders were the most heterogeneous group (Fig. 6A). In a second analysis, we excluded primary producers (the most homogeneous group), filter feeders (the most heterogeneous group) and bacteria, while we included only protozooplankton and metazoans. The first two PCA components explained 89 and 6% of the variance, respectively (Fig. 6B). The first component was affected mainly by maximum consumption rates, the second by maximum production rates. In plot in Fig. 6, nodes having similar biological characteristics (*i.e.*, *a priori* defined trophic guilds, such as suspension feeders, mixotrophic protozooplankton, heterotrophic protozooplankton) were represented with the same colour and included in the same polygon. As shown in Fig. 6, each polygon included a heterogeneous group of data-point in terms of their position in the two-dimensional space. Some

omnivorous mesozooplankton (mainly copepods, FN 44-49 and 54) formed a somewhat defined cluster but other mesozooplankton organisms, such as cladocerans, were instead closer to protistan consumers. A wide overlapping was recorded between mixo- and heterotrophic protists from the deeper layer. Finally, a strong expansion in terms of ranges of consumption rates affected each *a-prori* defined guild. In synthesis, the PCA suggested the existence of planktonic 'meta-guilds' including distantly related organisms, such as protozooplankton and metazoans, and supported the view that trophic guilds should not be defined *a-priori* in a plankton community.

The virtual plankton food-web presented herein includes a total of 817 links distributed among the 63 FNs organized hierarchically from primary producers to carnivorous mesozooplankton (Fig. 7). This network includes links valid for both Green and Blue states, since it was not possible to produce distinct food-webs for either states with the approach used in the present paper. However, the analyses carried out by D'Alelio *et al.* (2016), which used weighted-network models, suggested that the 95% of the link present in the present work could be present at both Green and Blue states, despite the fairly distant
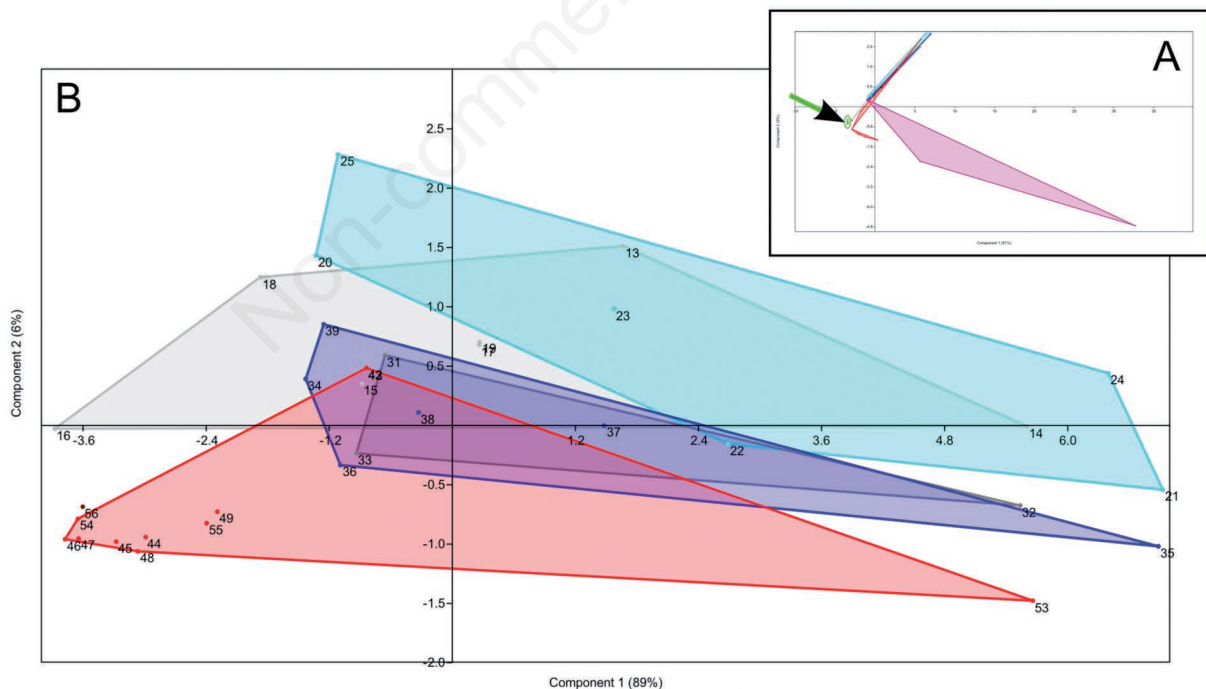
Fig. 6. PCA analysis based on plankton vital rates. The analysis was based on data presented in Tabs. 2 to 4. A PCA including all nodes and related vital rates is shown in panel A. Therein, the arrow indicates the cluster including primary producers, while the pink polygon connects filter-feeding metazoans. In panel B, a higher-resolution PCA, excluding primary producers and filter-feeders, is presented. The red polygon connects suspension feeding metazoans (cladocerans and copepods). The bright and dark gray polygons connect mixotrophic protists in either the surface or deeper layers, respectively. The bright and dark blue polygons connect heterotrophic protists in either the surface or deeper layers, respectively. Numbers indicate functional nodes (see Tab. 1).

conditions of overall biomass at the primary producers' level. The main picture shown in Fig. 7 translates into a connectance of 0.21, which is lower than that reported in a previous network study on the same GoN's plankton community (D'Alelio *et al.*, 2015), in which a connectance of ~ 0.30 was derived from time-trends of abundances of most nodes considered in the present paper. Links in trophic (this paper), association (D'Alelio *et al.*, 2015) and biomass-flow (D'Alelio *et al.* 2016) networks showed a power-law distribution across links, *sensu* Bascompte and Stouffer (2009), with few nodes (mainly protozooplankton and mesozooplankton filter-feeders) much more connected than others. This observation calls for further studies to clarify the dynamics of aggregation of plankton community as driven by the organization of the network of trophic links.

Plankton trophic links within biogeochemical and fishery models

The integrative analysis presented in this paper enabled us to i) gain a synthetic view of our system in terms of trophic processes, and ii) compare the overwhelming

trophic diversity existing within plankton with the conceptual setting adopted in the most used modelling approaches to aquatic systems. In our opinion, plankton models could potentially benefit from the integration of the trophic diversity shown in the present paper: first, by using more realistic rates, not in absolute terms, but relative to differences existing among consumers; second, by better defining trophic roles of consumers in the planktonic web. Indeed, organisms switch among different prey items or, more in general, among resources. This makes the food-web 'plastic'. Such plasticity can affect system functioning: *e.g.,* the modulation of trophic interactions drives the 'adaptive' transition among fairly different trophic regimes (D'Alelio *et al.*, 2016). Dissecting food-webs' plasticity is thus a crucial challenge of plankton ecology.

Many ecological models focusing on aquatic systems include trophic links among plankton organisms. For instance, a biogeochemical-flux model focusing on a Mediterraneann site (Auger *et al.*, 2011) included three categories of zooplankton and a diet matrix including three consumers (nano-, micro- and mesozooplankton) and seven preys (bacteria, three phytoplankton categories, nano- and micro-zooplankton and particulate organic mat-
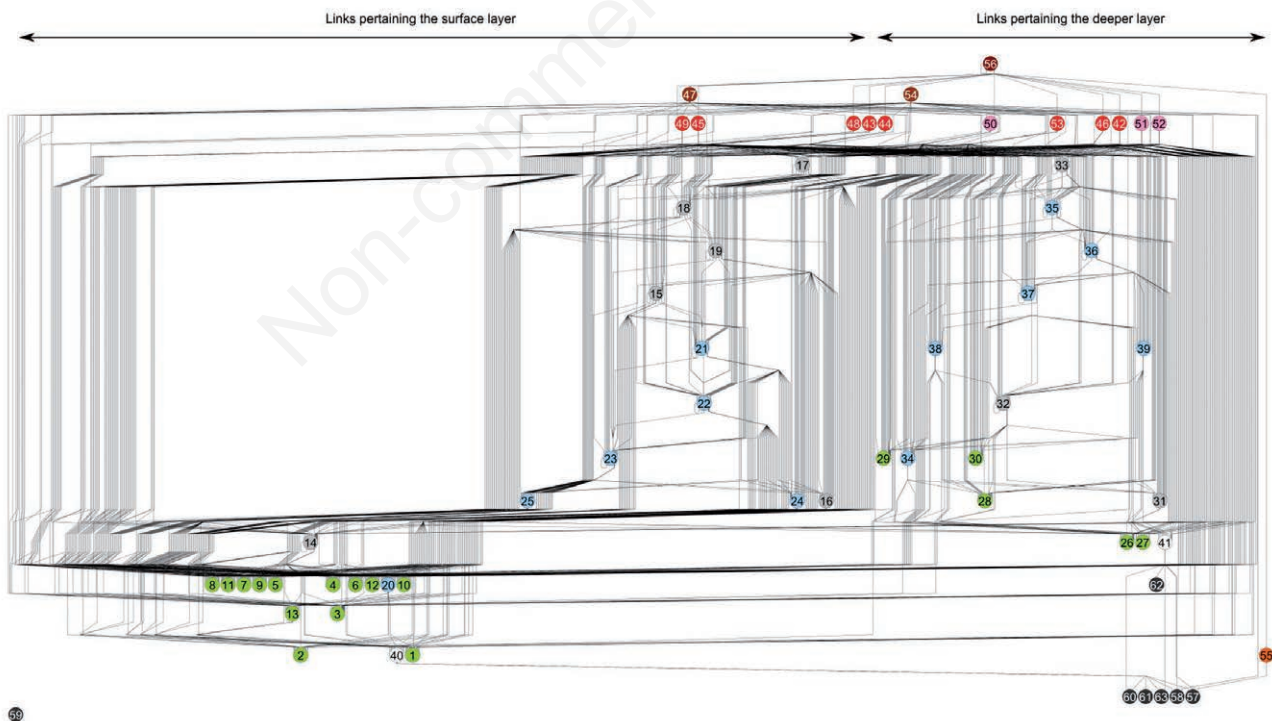
Fig. 7. Virtual plankton food-web. The network was built using links represented in Fig. 5. Red nodes are suspension feeding metazoans. Pink nodes are filter-feeding metazoans. Gray and blue nodes are protist with mixotrophic and heterotrophic metabolism, respectively. Green nodes are primary producers. White and black nodes are bacteria and detritus, respectively. Number at each node refers to FN code (Tab. 1). The network was built using an algorithm that displayed the nodes hierarchically, from the bottom to the top, based on the density of links. Relatively more and less linked nodes set at the bottom and at the top of the web, respectively.

ter, see Tab. A6 in Auger *et al.*, 2011). Being aware of the fact that the above-mentioned paper was focused on the large-scale dynamics of biogeochemical processes more than on the actual plankton food-web, we try to make some comparisons. The diet-matrix presented by Auger *et al.* (2011) showed a connectance of 0.24, but it is scarcely comparable with that reported herein (Figs. 5 and 7). For instance, mesozooplankton, was enabled to eat only phyto- and nano-/microzooplankton, thus excluding the possibility of 'cannibalistic' (intra-guild) predation, which is however a determinant characteristic of the system (*e.g., C. typicus* feeding on copepods' juveniles, and the strict carnivory of chaetognaths). A further and more important issue concerns the maximum grazing rates per unit of biomass (as d^{-1}) assumed in the model by Auger *et al.* (2011): the magnitude of the rate for micro-zooplankton was ~10% less of that for nanozooplankton (*i.e.*, 3.63 *vs* 3.89 d^{-1}), while mesozooplankton rate (0.43 d^{-1}) was 88% lower than that of microzooplankton. In light of the data compiled in the present paper (see Tabs. 3 an 4), the assumption made by Auger *et al.* (2011) might lead to significant errors in the estimate of grazing impact. First, some important (in terms of biomass) metazoans, such as Appendicularia, can consume up to four-fold more food than protists, proportionally to the specific body-biomass; second, within protists, also due to mixotrophy, there can be a 98% variability in the maximum consumption rate, thus exceeding the variability considered in the paper cited above between meso- and microzooplankton. In our opinion, biogeochemical-flux modellers should consider the option of including detailed feeding processes at the level of zooplankton, as already suggested by other authors (Flynn *et al.*, 2013; Mitra *et al.*, 2014).

An approach with a more detailed food-web representation comes from Allometric Trophic Network models (ATN), recently applied to the plankton community from Lake Constance (Boit *et al.*, 2012). That model included 24 nodes and 107 links (connectance 0.19) and reproduced with a significant accuracy the observed seasonal dynamics of plankton groups. In ATN models, trophic interactions are parameterised by allometric scaling rules, *i.e.*, based on individual size. However, a limit of this approach is that vital rates are represented by fixed values - namely, larger sizes correspond to lower metabolic rates - despite the large variability of vital rates present in the plankton system. ATN are thus applicable as interpolators of biomass fluxes for those closed systems - such as lakes - in which the mass-balanced budget (*e.g.*, in terms of carbon) can be well assessed and rates can be corrected to realistic values. See, as an example, corrections operated to allometrically-predicted rates for phytoplankton, heterotrophic bacteria and filamentous blue and green algae in Tab. 1 in Boit *et al.* (2012). In fact, as shown in the present paper (Fig. 4), while plankton production rates are in some way

inversely correlated to individual size, the same is not true for consumption rates. Moreover, ATN lack, at the present stage, the inclusion of mixotrophic organisms.

Ecological-network models similar to ATN can be also produced for systems in which the mass-balance is unknown. In fact, the latter can be tested *in-silico* in the frame of modelling approaches focusing on resource-based growth and losses due to consumption and metabolic costs. These models are developed in the frame of the 'Ecopath' approach (http://www.ecopath.org/, (Christensen and Walters, 2004)), which is often used to derive biomass fluxes in commercially exploited food-webs (Coll *et al.*, 2008). These are purely trophodynamic models based on trophic links and biomass fluxes among nodes. In Ecopath models, vital rates of each node are derived (also iteratively, via Markov Chain Monte Carlo methods) from the respective ranges in a way that the final matrices guarantee the overall biomass balance of the system, based on the initial distribution of biomass among nodes. Moreover, the Ecopath software enables the definition of autotrophy/heterotrophy ratio in consumer nodes and, in the variant Ecosim of the same package, it permits to run time-simulation of the mass-balanced web. Ecopath models are currently used to model marine food-webs (Libralato *et al.*, 2010) but rarely they included more than three plankton groups. Yet, high resolution Ecopath models for plankton are doable and very informative on the bioenergetics of plankton community (D'Alelio *et al.* 2016).

CONCLUSIONS

We performed an extensive review of the plankton literature to provide a compilation of data suitable for implementing food-web models including plankton trophic processes at high taxonomic resolution. Our analysis highlights that the ranges of trophic rates in planktonic organisms are very wide. As a consequence, there should be a wide range of possible rearrangements of fluxes and community structure after a change in external forcing. This implies that a drastic aggregation of taxa will never allow to predict the role of biological diversity on ecosystem functioning.

The compilation of data in the present case-study is particularly useful if applied to ecological network models like those developed into Ecopath approaches (D'Alelio *et al.* 2016). Being aware that the ranges reported also show that values may change from place to place or from trophic state to trophic state, our compilation is more a proof-of-concept of a procedure than a cookbook for model parameterization. However our tables can be used as a reference for future studies, especially if focused on coastal areas and on the summer season, a period crucial for ecological processes like development of harmful

algal blooms nearby large coastal towns and recruitment of small pelagic fish eating on plankton and exploited in coastal fisheries.

In conclusion, our reasoned synthesis supports the view that biological complexity and diversity cannot be simplified beyond certain limit, without losing any possibility of understanding of how planktonic systems really work. Our study shows that expanding the biological resolution within biogeochemical models could be feasible, having the proper data inputs. It also calls for further efforts to include into the food-web framework presented herein also larger organisms, like macrozooplankton, which play an important role in transferring energy from the mesozooplankton to high-trophic level consumers.

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