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Ecological-network models link diversity, structure and function in the plankton food-web

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A planktonic food-web model including sixty-three functional nodes (representing auto- mixo- and heterotrophs) was developed to integrate most trophic diversity present in the plankton. The model was implemented in two variants - which we named 'green' and 'blue' - characterized by opposite amounts of phytoplankton biomass and representing, respectively, bloom and non-bloom states of the system. Taxonomically disaggregated food-webs described herein allowed to shed light on how components of the plankton community changed their trophic behavior in the two different conditions, and modified the overall functioning of the plankton food web. The green and blue food-webs showed distinct organizations in terms of trophic roles of the nodes and carbon fluxes between them. Such re-organization stemmed from switches in selective grazing by both metazoan and protozoan consumers. Switches in food-web structure resulted in relatively small differences in the efficiency of material transfer towards higher trophic levels. For instance, from green to blue states, a seven-fold decrease in phytoplankton biomass translated into only a two-fold decrease in potential planktivorous fish biomass. By linking diversity, structure and function in the plankton food-web, we discuss the role of internal mechanisms, relying on species-specific functionalities, in driving the 'adaptive' responses of plankton communities to perturbations.

The evolutionary causes and ecological implications of plankton diversity have challenged ecologists ever since Hutchinson's classical paper¹. He wrote: "...how it is possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials?". Biological diversity and community organization are believed to have a central role in the functioning of ecosystems in general²⁻⁴. However, in most holistic approaches to aquatic systems, plankton diversity and food-web structure are rarely detailed^{5,6}. In contrast, detailed 'food-web' studies, i.e., those focusing on species-species interactions, trophic links and cascading effects, are considered as the most appropriate approaches to integrate biodiversity, structure, i.e. community organization, and function, i.e. energy and elemental fluxes^{7,8}.

Plankton is very diverse taxonomically, and encompasses extremely distant groups in evolutionary terms⁹. It includes unicellular and multicellular, autotrophic and heterotrophic organisms⁹, occurring in highly-timed populations' successions¹⁰⁻¹², organized in complex communities^{13,14} and deeply entangled in food-webs and biogeochemical cycles¹⁵⁻¹⁷. But little attention has been paid to the profusion of trophic processes among plankton organisms (i.e., the real plankton food-web)¹⁸, either by biogeochemical or fishery modelling, based on either the nutrient-phytoplankton-zooplankton scheme (NPZ¹⁹) or the slightly more detailed 'plankton functional type' (e.g., as in the BFM approach, <http://bfm-community.eu>) approaches. Both approaches aggregate plankton organisms into a few large groups ruled by two or a few trophic steps, and thus ignore a large number of species and trophic processes. On the other hand, the more recent and promising 'trait-based' approach, which considers morphological, functional and behavioral diversity in full, is still in its infancy²⁰.

The trophic diversity of plankton is huge. For instance, planktonic protists can eat other unicellular organisms^{21,22} and close the very first step of the pelagic food-chain within 'trophic loops'^{23,24}. Moreover, mesozooplankton (i.e. metazoans) include filter-feeding animals²⁵, suspension feeders capable of both prey-selectivity and omnivory^{26,27}, obligate and occasional predators (i.e., eat other metazoans)^{26,28}. All this diversity, in both

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