OCEAN PLANKTON

Determinants of community structure in the global plankton interactome

Gipsi Lima-Mendez,[1,2,3]* Karoline Faust,[1,2,3]* Nicolas Henry,[4,5]* Johan Decelle,[4,5]
Sébastien Colin,[4,5,6] Fabrizio Carcillo,[1,2,3,7] Samuel Chaffron,[1,2,3]
J. Cesar Ignacio-Espinosa,[8]† Simon Roux,[8]† Flora Vincent,[2,6] Lucie Bittner,[4,5,6,9]
Youssef Darzi,[2,3] Jun Wang,[1,2] Stéphane Audic,[4,5] Léo Berline,[10,11] Gianluca Bontempi,[7]
Ana M. Cabello,[12] Laurent Coppola,[10,11] Francisco M. Cornejo-Castillo,[12]
Francesco d'Ovidio,[13] Luc De Meester,[14] Isabel Ferrera,[12] Marie-José Garet-Delmas,[4,5]
Lionel Guidi,[10,11] Elena Lara,[12] Stéphane Pesant,[15,16] Marta Royo-Llonch,[12]
Guillem Salazar,[12] Pablo Sánchez,[12] Marta Sebastian,[12] Caroline Souffreau,[14] Céline Dimier,[4,5,6]
Marc Picheral,[10,11] Sarah Searson,[10,11] Stefanie Kandels-Lewis,[17,18] Tara Oceans coordinators‡
Gabriel Gorsky,[10,11] Fabrice Not,[4,5] Hiroyuki Ogata,[19] Sabrina Speich,[20,21] Lars Stemmann,[10,11]
Jean Weissenbach,[22,23,24] Patrick Wincker,[22,23,24] Silvia G. Acinas,[12] Shinichi Sunagawa,[17]
Peer Bork,[17,25] Matthew B. Sullivan,[8]† Eric Karsenti,[6,18]§ Chris Bowler,[6]§
Colomban de Vargas,[4,5]§ Jeroen Raes[1,2,3]§

Species interaction networks are shaped by abiotic and biotic factors. Here, as part of the *Tara* Oceans project, we studied the photic zone interactome using environmental factors and organismal abundance profiles and found that environmental factors are incomplete predictors of community structure. We found associations across plankton functional types and phylogenetic groups to be nonrandomly distributed on the network and driven by both local and global patterns. We identified interactions among grazers, primary producers, viruses, and (mainly parasitic) symbionts and validated network-generated hypotheses using microscopy to confirm symbiotic relationships. We have thus provided a resource to support further research on ocean food webs and integrating biological components into ocean models.

The structure of oceanic ecosystems results from the complex interplay between resident organisms and their environment. In the world's largest ecosystem, oceanic plankton (composed of viruses, prokaryotes, microbial eukaryotes, phytoplankton, and zooplankton) form trophic and symbiotic interaction networks (1–4) that are influenced by environmental conditions. Ecosystem structure and composition are governed by abiotic as well as biotic factors. The former include environmental conditions and nutrient availability (5), whereas the latter include grazing, pathogenicity, and parasitism (6, 7). Historically, abiotic factors have been considered to have a stronger effect, but recently, appreciation for biotic factors is growing (8, 9). We sought to develop a quantitative understanding of biotic and abiotic interactions in natural systems in which the organisms are taxonomically and trophically diverse (10). We used sequencing technologies to profile communities across trophic levels, organismal sizes, and geographic ranges and to predict organismal interactions across biomes based on co-occurrence patterns (11). Previous efforts addressing these issues have provided insights on the structure (12, 13) and dynamics of microbial communities (14–16).

We analyzed data from 313 plankton samples the *Tara* Oceans expedition (17) derived from seven size-fractions covering collectively 68 stations at two depths across eight oceanic provinces (table S1). The plankton samples spanned sizes that include organisms from viruses to small metazoans. We derived viral, prokaryotic, and eukaryotic abundance profiles from clusters of metagenomic contigs, Illumina-sequenced metagenomes ($_{mi}$tags), and 18S ribosomal DNA (rDNA) V9 sequences, respectively (table S1) (10, 18, 19) and collected environmental data from on-site and satellite measurements (17, 20, 21). We used network inference methods and machine-learning techniques so as to disentangle biotic and abiotic signals shaping ocean plankton communities and to construct an interactome that described the network of interactions among photic zone plankton groups. We used the interactome to focus on specific relationships, which we validated through microscopic analysis of symbiont pairs and in silico analysis of phage-host pairings.

Evaluating the effect of abiotic and biotic factors on community structure

We first reassessed the effects of environment and geography on community structure. Using variation partitioning (22), we found that on average, the percentage of variation in community composition explained by environment alone was 18%, by environment combined with geography 13%, and by geography alone only 3% (23, 24). In addition, we built random forest-based models (25) in order to predict abundance profiles of the Operational Taxonomic Units (OTU) using (i) OTUs alone, (ii) environmental variables alone, and (iii) OTUs and environmental variables combined and tested for each OTU whether one of the three approaches outcompeted the other. These analyses revealed that 95% of the OTU-only models are more accurate in predicting OTU abundances than environmental variable models, and that combined models were no better than the OTU-only models (26, 27). This suggests that abiotic factors have a more limited effect on community structure than previously assumed (8).

To study the role of biotic interactions, we developed a method with which to identify robust species associations in the context of environmental conditions. Twenty-three taxon-taxon and taxon-environment co-occurrence networks were constructed based on 9292 taxa, representing the combinations of two depths, seven organismal