

Tara Oceans studies plankton at PLANETARY SCALE

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The ocean is the largest ecosystem on Earth, and yet we know very little about it. This is particularly true for the plankton that inhabit the ocean. Although these organisms are at least as important for the Earth system as the rainforests and form the base of marine food webs, most plankton are invisible to the naked eye and thus are largely uncharacterized. To study this invisible world, the multinational *Tara Oceans* consortium, with use of the 110-foot research schooner *Tara*, sampled microscopic plankton at 210 sites and depths up to 2000 m in all the major oceanic regions during expeditions from 2009 through 2013 (1).

Success depended on collaboration between scientists and the *Tara* Expeditions logistics team. The journey involved not only science but also outreach and education as well as negotiation through the shoals of legal and political regulations, funding uncertainties, threats from pirates, and unpredictable weather (2). At various times, journalists, artists, and teachers were also on board. Visitors included Ban Ki-moon (Secretary-General of the United Nations) and numerous youngsters, including schoolchildren from the favelas in Rio de Janeiro.

Sampling, usually 60 hours per site, followed standardized protocols (3) to capture the morphological and genetic diversity of the entire plankton community from viruses to small zooplankton, covering a size range from 0.02 μm to a few millimeters, in context with physical and chemical information. Besides the sampling, a lab on board contained a range of online instruments and microscopes to monitor the content of the samples as they were being collected. The main focus was on the organism-rich sunlit upper layer of the ocean (down to 200 m), but the twilight zone below was also sampled. Guided by satellite and in situ data, scientists sampled features such as mesoscale eddies, upwellings, acidic waters, and anaerobic zones, frequently in the open ocean. In addition to being used for genomics and oceanography, many samples were collected for other analyses, such as high-throughput microscopy imaging and flow cytometry. The samples and data collected on board were archived in a highly structured

way to enable extensive data processing and integration on land (4). The five Research Articles in this issue of *Science* describe the samples, data, and analysis from *Tara Oceans* (based on a data freeze from 579 samples at 75 stations as of November 2013).

De Vargas *et al.* used ribosomal RNA gene sequences to profile eukaryotic diversity in the photic zone. This taxonomic census shows that most biodiversity belongs to poorly known lineages of uncultured heterotrophic single-celled protists. Sunagawa *et al.* used metagenomics to study viruses, prokaryotes, and picoeukaryotes. They established a catalog with >40 million genes and identified temperature as the driver of photic microbial community composition. Brum *et al.*, by sequencing and electron microscopy, found that viruses are diverse on a regional basis but less so on a global basis. The viral communities are passively transported by oceanic currents and structured by local environments. Lima-Mendez *et al.* modeled interactions between viruses, prokaryotes, and eukaryotes. Regional and global parameters refine resulting networks. Villar *et al.* studied the dispersal of plankton as oceanic currents swirl around the southern tip of Africa, where the Agulhas rings are generated. Vertical mixing in the rings drives nitrogen cycling and selects for specific organisms.

Tara Oceans combined ecology, systems biology, and oceanography to study plankton in their environmental context. The project has generated resources such as an ocean microbial reference gene catalog; a census of plankton diversity covering viruses, prokaryotes, and eukaryotes; and methodologies to explore interactions between them and their integration with environmental conditions. Although many more such analyses will follow, life in the ocean is already a little less murky than it was before.

REFERENCES

1. E. Karsenti *et al.*, *PLoS Biol.* **9**, e1001177 (2011).
2. E. Karsenti, *Mol. Syst. Biol.* **11**, 811 (2015).
3. S. Pesant *et al.*, *BioRxiv*, <http://biorxiv.org/content/early/2015/05/08/019117> (2015).
4. S. Sunagawa *et al.*, *Mol. Syst. Biol.* **11**, 809 (2015).

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Research schooner *Tara* supported a multinational, multidisciplinary team in sampling plankton ecosystems around the world.

Eukaryotic plankton diversity in the sunlit ocean

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Marine plankton support global biological and geochemical processes. Surveys of their biodiversity have hitherto been geographically restricted and have not accounted for the full range of plankton size. We assessed eukaryotic diversity from 334 size-fractionated photic-zone plankton communities collected across tropical and temperate oceans during the circumglobal *Tara Oceans* expedition. We analyzed 18S ribosomal DNA sequences across the intermediate plankton-size spectrum from the smallest unicellular eukaryotes (protists, >0.8 micrometers) to small animals of a few millimeters. Eukaryotic ribosomal diversity saturated at ~150,000 operational taxonomic units, about one-third of which could not be assigned to known eukaryotic groups. Diversity emerged at all taxonomic levels, both within the groups comprising the ~11,200 cataloged morphospecies of eukaryotic plankton and among twice as many other deep-branching lineages of unappreciated importance in plankton ecology studies. Most eukaryotic plankton biodiversity belonged to heterotrophic protistan groups, particularly those known to be parasites or symbiotic hosts.

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Read the full article at <http://dx.doi.org/10.1126/science.1261605>

Structure and function of the global ocean microbiome

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Microbes are dominant drivers of biogeochemical processes, yet drawing a global picture of functional diversity, microbial community structure, and their ecological determinants remains a grand challenge. We analyzed 7.2 terabases of metagenomic data from 243 *Tara Oceans* samples from 68 locations in epipelagic and mesopelagic waters across the globe to

generate an ocean microbial reference gene catalog with >40 million nonredundant, mostly novel sequences from viruses, prokaryotes, and picoeukaryotes. Using 139 prokaryote-enriched samples, containing >35,000 species, we show vertical stratification with epipelagic community composition mostly driven by temperature rather than other environmental factors or geography. We identify ocean microbial core functionality and reveal that >73% of its abundance is shared with the human gut microbiome despite the physicochemical differences between these two ecosystems.

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Read the full article at <http://dx.doi.org/10.1126/science.1261359>

Patterns and ecological drivers of ocean viral communities

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Viruses influence ecosystems by modulating microbial population size, diversity, metabolic outputs, and gene flow. Here, we use quantitative double-stranded DNA (dsDNA) viral-fraction metagenomes (viromes) and whole viral community morphological data sets from 43 *Tara Oceans* expedition samples to assess viral community patterns and structure in the upper ocean. Protein cluster cataloging defined pelagic upper-ocean viral community pan and core gene sets and suggested that this sequence space is well-sampled. Analyses of viral protein clusters, populations, and morphology revealed biogeographic patterns whereby viral communities were passively transported on oceanic currents and locally structured by environmental conditions that affect host community structure. Together, these investigations establish a global ocean dsDNA viromic data set with analyses supporting the seed-bank hypothesis to explain how oceanic viral communities maintain high local diversity.

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Determinants of community structure in the global plankton interactome

G. Lima-Mendez, K. Faust, N. Henry, J. Decelle, S. Colin, F. Carcillo, S. Chaffron, J. C. Ignacio-Espinoza, S. Roux, F. Vincent, L. Bittner, Y. Darzi, J. Wang, S. Audic, L. Berline, G. Bontempi, A. M. Cabello, L. Coppola, F. M. Cornejo-Castillo, F. d'Ovidio, L. De Meester, I. Ferrera, M.-J. Garet-Delmas, L. Guidi, E. Lara, S. Pesant, M. Royo-Llonch, G. Salazar, P. Sánchez, M. Sebastian, C. Souffreau, C. Dimier, M. Picheral, S. Searson, S. Kandels-Lewis,

Plankton diversity

Tara Oceans sampled the smallest in the planktonic world, including viruses, bacteria, protists, and zooplankton. These spectacular and plentiful organisms form the microscopic basis of marine food webs. Analysis of their genes and genomes provides the basis for research insights into identities and interactions.

Podovirus



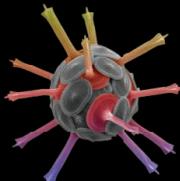
50 nm

Siphovirus



100 nm

Coccolithophore,
Rhabdosphaera sp.



5 μm

Eubacteria,
Bacteroidetes sp.



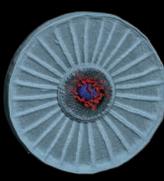
10 μm

Dinoflagellate,
Ceratium sp.



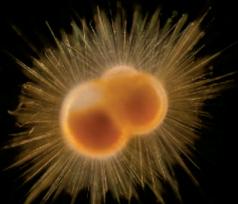
20 μm

Diatom,
Planktoniella sp.



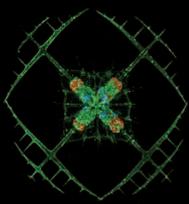
20 μm

Foraminiferan,
Globigerinoides sp.



50 μm

Acantharian,
Lithoptera sp.



60 μm

Copepod,
Centropages sp.



500 μm

Polychaete annelid,
Myrianida sp.



500 μm

Colonial radiolarian,
Sphaerozoum sp.



1000 μm

Siphonophore,
Lesia sp.



2000 μm

Tara Oceans Coordinators, G. Gorsky, F. Not, H. Ogata, S. Speich, L. Stemmann, J. Weissenbach, P. Wincker, S. G. Acinas, S. Sunagawa, P. Bork, M. B. Sullivan, E. Karsenti,* C. Bowler,* C. de Vargas,* J. Raes*

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.

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Environmental characteristics of Agulhas rings affect interocean plankton transport

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Agulhas rings provide the principal route for ocean waters to circulate from the Indo-Pacific to the Atlantic basin. Their influence on global ocean circulation is well known, but their role in plankton transport is largely unexplored. We show that, although the coarse taxonomic structure of plankton communities is continuous across the Agulhas choke point, South Atlantic plankton diversity is altered compared with Indian Ocean source populations. Modeling and in situ sampling of a young Agulhas ring indicate that strong vertical mixing drives complex nitrogen cycling, shaping community metabolism and biogeochemical signatures as the ring and associated plankton transit westward. The peculiar local environment inside Agulhas rings may provide a selective mechanism contributing to the limited dispersal of Indian Ocean plankton populations into the Atlantic.

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