## Plankton networks driving carbon export in the oligotrophic ocean

Lionel Guidi<sup>1,2\*</sup>, Samuel Chaffron<sup>3,4,5\*</sup>, Lucie Bittner<sup>6,7,8\*</sup>, Damien Eveillard<sup>9\*</sup>, Abdelhalim Larhlimi<sup>9</sup>, Simon Roux<sup>10</sup><sup>†</sup>, Youssef Darzi<sup>3,4</sup>, Stephane Audic<sup>8</sup>, Léo Berline<sup>1†</sup>, Jennifer R. Brum<sup>10</sup><sup>†</sup>, Luis Pedro Coelho<sup>11</sup>, Julio Cesar Ignacio Espinoza<sup>10</sup>, Shruti Malviya<sup>7</sup><sup>†</sup>, Shinichi Sunagawa<sup>11</sup>, Céline Dimier<sup>8</sup>, Stefanie Kandels-Lewis<sup>11,12</sup>, Marc Picheral<sup>1</sup>, Julie Poulain<sup>13</sup>, Sarah Searson<sup>1,2</sup>, *Tara* Oceans Consortium Coordinators<sup>‡</sup>, Lars Stemmann<sup>1</sup>, Fabrice Not<sup>8</sup>, Pascal Hingamp<sup>14</sup>, Sabrina Speich<sup>15</sup>, Mick Follows<sup>16</sup>, Lee Karp-Boss<sup>17</sup>, Emmanuel Boss<sup>17</sup>, Hiroyuki Ogata<sup>18</sup>, Stephane Pesant<sup>19,20</sup>, Jean Weissenbach<sup>13,21,22</sup>, Patrick Wincker<sup>13,21,22</sup>, Silvia G. Acinas<sup>23</sup>, Peer Bork<sup>11,24</sup>, Colomban de Vargas<sup>8</sup>, Daniele Iudicone<sup>25</sup>, Matthew B. Sullivan<sup>10</sup><sup>†</sup>, Jeroen Raes<sup>3,4,5</sup>, Eric Karsenti<sup>7,12</sup>, Chris Bowler<sup>7</sup> & Gabriel Gorsky<sup>1</sup>

The biological carbon pump is the process by which CO<sub>2</sub> is transformed to organic carbon via photosynthesis, exported through sinking particles, and finally sequestered in the deep ocean. While the intensity of the pump correlates with plankton community composition, the underlying ecosystem structure driving the process remains largely uncharacterized. Here we use environmental and metagenomic data gathered during the *Tara* Oceans expedition to improve our understanding of carbon export in the oligotrophic ocean. We show that specific plankton communities, from the surface and deep chlorophyll maximum, correlate with carbon export at 150 m and highlight unexpected taxa such as Radiolaria and alveolate parasites, as well as *Synechococcus* and their phages, as lineages most strongly associated with carbon export in the subtropical, nutrient–depleted, oligotrophic ocean. Additionally, we show that the relative abundance of a few bacterial and viral genes can predict a significant fraction of the variability in carbon export in these regions.

Marine planktonic photosynthetic organisms are responsible for approximately 50% of Earth's primary production and fuel the global ocean biological carbon pump<sup>1</sup>. The intensity of the pump is correlated with plankton community composition<sup>2,3</sup>, and controlled by the relative rates of primary production and carbon remineralization<sup>4</sup>. About 10% of this newly produced organic carbon in the surface ocean is exported through gravitational sinking of particles. Finally, after multiple transformations, a fraction of the exported material reaches the deep ocean where it is sequestered over thousand-year timescales<sup>5</sup>.

Like most biological systems, marine ecosystems in the sunlit upper layer of the ocean (denoted as the euphotic zone) are complex<sup>6,7</sup>, characterized by a wide range of biotic and abiotic interactions<sup>8–10</sup> and in constant balance between carbon production, transfer to higher trophic levels, remineralization, and export to the deep layers<sup>11</sup>. The marine ecosystem structure and its taxonomic and functional composition probably evolved to comply with this loss of energy by modifying organism turnover times and by the establishment of complex feedbacks between them<sup>6</sup> and the substrates they can exploit for metabolism<sup>12</sup>. Decades of ground-breaking research have focused on identifying independently the key players involved in the biological carbon pump. Among autotrophs, diatoms are commonly attributed to being important in carbon flux because of their large size and fast sinking rates<sup>13-15</sup>, while small autotrophic picoplankton may contribute directly through subduction of surface water<sup>16</sup> or indirectly by aggregating with larger settling particles or consumption by organisms at higher trophic levels<sup>17</sup>. Among heterotrophs, zooplankton such as crustaceans impact carbon flux via production of fast-sinking fecal pellets while migrating hundreds of meters in the water column<sup>18,19</sup>. These observations, focusing on just a few components of the marine ecosystem, highlight that carbon export results from multiple biotic interactions and that a better understanding of the mechanisms involved in its regulation requires an analysis of the entire planktonic ecosystem.

Advanced sequencing technologies offer the opportunity to simultaneously survey whole planktonic communities and associated

<sup>1</sup>Sorbonne Universités, UPMC Université Paris 06, CNRS, Laboratoire d'oceanographie de Villefranche (LOV), Observatoire Océanologique, 06230 Villefranche-sur-Mer, France. <sup>2</sup>Department of Oceanography, University of Hawaii, Honolulu, Hawaii 96822, USA. <sup>3</sup>Department of Microbiology and Immunology, Rega Institute, KU Leuven, Herestraat 49, 3000 Leuven, Belgium. <sup>4</sup>Center for the Biology of Disease, VIB, Herestraat 49, 3000 Leuven, Belgium. <sup>5</sup>Department of Applied Biological Sciences, Vrije Universiteit Brussel, Pleinlaan 2, 1050 Brussels, Belgium. <sup>6</sup>Sorbonne Universités, UPMC Univ Paris 06, CNRS, Institut de Biologie Paris-Seine (IBPS), Evolution Paris Seine, F-75005, Paris, France. 7 Ecole Normale Supérieure, PSL Research University, Institut de Biologie de l'Ecole Normale Supérieure (IBENS), CNRS UMR 8197, INSERM U1024, 46 rue d'Ulm, F-75005 Paris, France. 8 Sorbonne Universités, UPMC Université Paris 06, CNRS, Laboratoire Adaptation et Diversité en Milieu Marin, Station Biologique de Roscoff, 29680 Roscoff, France. <sup>9</sup>LINA UMR 6241, Université de Nantes, EMN, CNRS, 44322 Nantes, France. <sup>10</sup>Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA. <sup>11</sup>Structural and Computational Biology, European Molecular Biology Laboratory, Meyerhofstr. 1, 69117 Heidelberg, Germany. <sup>12</sup>Directors' Research European Molecular Biology Laboratory Meyerhofstr. 1, 69117 Heidelberg, Germany. <sup>13</sup>CEA - Institut de Génomique, GENOSCOPE, 2 rue Gaston Crémieux, 91057 Evry, France. <sup>14</sup>Aix Marseille Université, CNRS, IGS, UMR 7256, 13288 Marseille, France. <sup>15</sup>Department of Geosciences, Laboratoire de Météorologie Dynamique (LMD), Ecole Normale Supérieure, 24 rue Lhomond, 75231 Paris CEDEX 05, France. <sup>16</sup>Dept of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139, USA. <sup>17</sup>School of Marine Sciences, University of Maine, Orono, Maine 04469, USA. <sup>18</sup>Institute for Chemical Research, Kyoto University, Gokasho, Uji, Kyoto, 611-0011, Japan. <sup>19</sup>PANGAEA, Data Publisher for Earth and Environmental Science, University of Bremen, 28359 Bremen, Germany.<sup>20</sup>MARUM, Center for Marine Environmental Sciences, University of Bremen, 28359 Bremen, Germany.<sup>21</sup>CNRS, UMR 8030, CP 5706 Evry, France. <sup>22</sup>Université d'Evry, UMR 8030, CP 5706 Evry, France. <sup>23</sup>Department of Marine Biology and Oceanography, Institute of Marine Sciences (ICM)-CSIC, Pg. Marítim de la Barceloneta 37-49, Barcelona E0800, Spain. 24 Max-Delbrück-Centre for Molecular Medicine, 13092 Berlin, Germany. 25 Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Naples, Italy. †Present addresses: Department of Microbiology, The Ohio State University, Columbus, Ohio 43210, USA (S.R., J.R.B.); Department of Microbiology, and Department of Civil, Environmental and Geodetic Engineering, The Ohio Sate University, Colombus, Ohio 43210, USA (M.B.S.); Aix Marseille Université, CNRS/INSU, Université de Toulon, IRD, Mediterranean Institute of Oceanography (MIO) UM 110, 13288, Marseille, France (L.B.); Biological Oceanography Division, CSIR-National Institute of Oceanography, Dona Paula, Goa 403 004, India (S.M.). \*These authors contributed equally to this work.

‡A list of authors and affiliations appears at the end of the paper.