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# CARBOMICS: The biological CARBon pump from OMICs to ecoSystem

Lionel Guidi

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**SORBONNE UNIVERSITÉ**  
**Habilitation à Diriger des Recherches**  
**Faculté Terre, Environnement, Biodiversité – UFR 918**

Présenté par

**Lionel Guidi**

Chargé de Recherche au CNRS

Laboratoire d'Océanographie de Villefranche sur Mer (LOV – UMR 7093)

Titre du Mémoire

**CARBOMICS:**  
**The biological CARBOn pump from OMICs to ecoSystem**

Composition du Jury :

Pr. Stéphane Blain (Président)  
Pr. Ardian Burd (Rapporteur)  
Dr. Catherine Jeandel (Rapporteuse)  
Dr. Laurent Memery (Rapporteur)  
Dr. Eric Rottinger (Membre)

Date de Soutenance

11 Décembre 2018

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## I. CURRICULUM VITAE

**Guidi, Lionel** (DOB, 22/06/1981, French):

Laboratoire d'océanographie de Villefranche sur Mer (LOV)

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BP 28 - 06230 Villefranche sur Mer - France

Researcher ID : B-3977-2012

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### CURRENT POSITIONS:

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2013-: CNRS (CR2) researcher at LOV, France

2011-: Affiliated researcher at the University of Hawaii at Manoa, HI, USA

### EDUCATION:

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2008: PhDs:

- Sorbonne University UPMC, CNRS (LOV, Villefranche sur Mer, France)

- Texas A&M University (Department of oceanography, College station, Texas, USA)

PhD supervisors: Pr. Gabriel Gorsky, Pr. George A. Jackson

2004: Master, Sorbonne University UPMC, France

*Specialization:* Marine ecosystem modeling, and data analyses

### PREVIOUS POSITIONS:

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2011-2013: Post-doctoral researcher, CNRS, LOV, France, (in Pr. G. Gorsky's Lab)

2008-2011: CMORE postdoctoral researcher, UH, HI, USA (in Pr. D. Karl's Lab)

*Invited visiting researcher:*

August 2010: COAS, OSU, OR, USA (in Pr. R. Letelier's Lab)

February 2010: WHOI, MA, USA (in Pr. S. Doney's Lab)

November 2009: Scripps, CA, USA (in Pr. D. Stramski's Lab)

### INSTITUTIONAL RESPONSIBILITIES:

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2016-: Team leader substitute (Team PEPS, LOV ~30 members)

2014-: Elected researcher at the "Conseil de Laboratoire" of LOV, France.

2014-: Elected at the city council of Sospel (Alpes Maritimes), France

2005-2007: Elected student at the committee of evaluation of the LOV, France.

### COMMISSIONS OF TRUST:

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2017-: Member of the "Collège de Direction Scientifique" of EMBRC-France

2016-: TARA Oceans coordinator

2014-: Member of the scientific committee of MOOSE, France

*Editorial Board member:* PeerJ

*Reviewer for funding agencies:* National Science Foundation (Biological Oceanography, Marine Chemistry), National Oceanic and Atmospheric Administration (Global Carbon Cycle), Natural Sciences and Engineering Research Council of Canada (NSERC), Natural Environment Research Council of the UK (NERC), Centre National de la Recherche Scientifique INSU-LEFE (France)

*Reviewer for journals:* Nature, Nature Geoscience, Proceedings of the National Academy of Sciences, Scientific Reports, Limnology and Oceanography, Limnology and Oceanography Methods, Deep-Sea Research part I and II, Aquatic Microbial Ecology, Marine Biology, Ecological Modelling, Biogeosciences, Global Change Biology, Journal of Marine Systems, Geophysical Research Letters, Progress in Oceanography, Journal of Geophysical Research-Ocean, PlosOne,

*PhDs Committee member:* 2016 - Nolwenn Lemaitre (PhDs advisors: Prof. Frank Dehairs & Dr. Géraldine Sarthou)

## FELLOWSHIPS, AWARDS, AND GRANTS

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### Fellowships

2008-2011: Gordon and Betty Moore postdoctoral fellowship, David Karl's Lab, HI, USA  
 2004-2008: French PhD Fellowship - University Pierre et Marie Curie

### Travel Awards

2016: OCB, New Orleans, Louisiana, USA  
 2015: SOLAS, Santos, Brazil  
 2015: ASLO, Granada, Spain  
 2013: ASLO, New Orleans, Louisiana, USA  
 2010: GEOTRACES Data-Model synergy workshop, Barcelona, Spain  
 2009: AGU Chapman conference, Brockenhurst, Hampshire, England

### Grants

2017-2019: Optically Resolving Size and Composition Distributions of Particles in the Dissolved-Particulate Continuum from 20 nm to 20 mm to Improve the Estimate of Carbon Flux – NASA (Co-PI)  
 2017-2019: First Step - Linking Remotely-Detectable Optical Signals, Photic Layer Plankton Properties, and Export Flux - NASA (Collaborator)  
 2017-2018: MEGALODOM – CHRS – MI (Principal Investigator)  
 2017-2018: JIGA-TL: INSU - EC2CO (Collaborator)  
 2017-2018: DL-PIC: INSU - LEFE (MANU) (Collaborator)  
 2017-2019: ModelOmics: INSU - LEFE/EC2CO (Collaborator)  
 2016-2017: FunOmics: INSU - LEFE/EC2CO (Collaborator)  
 2012-2016: DEWEX: ANR Défi 1 (Collaborator)  
 2012-2016: PEACETIME: INSU – MISTRAL (Collaborator)  
 2014-2018: OUTPACE: INSU - MISTRAL (Collaborator)  
 2014-2017: SOCLIM: BNP FONDATION (Collaborator)  
 2104-2017: Can an Archipelago Fertilize the Ocean? Brazilian funding (Collaborator)

## Co-SUPERVISION OF GRADUATE STUDENTS:

---

PhDs: 2016-2019: Anne-Sophie Benoiston, (Université Pierre et Marie Curie, IBPS, France)  
 2015-2017: Simon Ramondenc, (Université Pierre et Marie Curie, LOV, France)  
 2011-2013: François Roullier, (Université Pierre et Marie Curie, LOV, France)

Masters: 2018 – Ophélie Da Silva (Université Paris Sud, Bioinformatic Master, France)  
 2017 - Marin Cornec (Université Pierre et Marie Curie, LOV, France)  
 2014 - Simon Ramondenc, (Université de Nice Sophia Antipolis, France)  
 2012 - Nicolas Mayot, 2012, M.S (Université Pierre et Marie Curie, LOV, France).

**TEACHING:**

2016: Lecturer at the [Ramon Margalef Summer Colloquia](#), “Microbes in a changing world: diversity and biogeochemistry” (~50 students).

**CONTRIBUTIONS TO AND/OR ORGANIZATION OF SCIENTIFIC WORKSHOP/SYMPOSIA:**

- 2017 : Biological Carbon Pump programmes, Institut Universitaire Européen de la Mer, Plouzané, France  
 2017 : The Tara Ocean Program: Structuring International Scientific Cooperation with South America, Conception, Chile  
 2017 : Global Challenges for Ocean Sciences and International Policies Today. Santiago, Chile ([Web](#))  
 2017: **Co-chair** of the workshop MEGALODOM: MarinE bioGeochemistry: Advancing the Link between Observations, Data, and Models, Villefranche sur Mer, France ([Web](#)) ~ 40 attendees  
 2017: Augmented observatories workshop. In the framework of the G7 working group “Promote increased G7 political action by identifying additional action needed to enhance the future routine ocean observation” as part of the Action “The future of Seas and Oceans”. Naples, Italy ([Web](#))  
 2017: Cycles biogéochimiques et diversité du vivant dans l’océan. Workshop LEFE-CYBER, Banuyls, France ([Web](#))  
 2017: Journée de restitution finale Enviromics. Mission pour l’Interdisciplinarité, Paris, France ([Web](#))  
 2016: **Co-Chair** of the Atelier RESOMAR – MOSSE: Observation du Zooplancton, Villefranche sur mer, France  
 2016: NSF Biology of the Biological Pump Workshop, New-Orleans, USA, ~40 attendees  
 2015: Effects of climate change on the biologically-driven ocean carbon pumps, Santos, Brazil, ([Web](#)) ~ 50 attendees  
 2014: **Co-chair** of the workshop: “Perspectives on particle flux from observations, measurements, and models at the Ocean Sciences Meeting, Honolulu, Hawaii, USA, ([Web](#)) ~ 90 attendees  
 2011: **Co-chair** of TARA oceans symposium in Honolulu Hawaii, USA, ([Flyer](#)) ~ 50 attendees.

**MEMBERSHIPS OF SCIENTIFIC SOCIETIES:**

- 2006-: Member of the Association for the Sciences of Limnology and Oceanography (ASLO)  
 2015-: Member of the American Geophysical Union (AGU)  
 2010-: Member of “[kahikai one ocean](#)” administrator board

**SYNERGISTIC ACTIVITIES AND OUTREACH:**

- 2017: Member of the NextGen Plankton 2.0 challenge asking students from SKEMA to invent an application which will show practical usage of “plankton” for general public or for industry.  
 2017: Mouans-Sartoux [Book festival](#): Conference on Plankton and presentation of “Étonnant vivant”  
 2016: [France-Inter](#): Chercheur d’avenir en compagnie d’Eric Karsenti et Sébastien Colin  
 2016: MEDITES- Séance Métier, Villefranche sur mer.  
 2016: Le Facebook des plactons, leur rôle clef sur le climat. Plan Climat Energie des Alpes maritimes. Conseil Départemental.  
 2016: La mission TARA et la découverte du Facebook du plancton. Journée de l’environnement, Mairie de Villefranche sur mer.  
 2015: TARA Oceans: 3 ans d’expédition pour mieux comprendre les écosystèmes marins et l’impact du changement climatique. Institut Français de Budapest.  
 2015: Road to COP21 - Paris Climat 2015 - [Ocean & Climate Science Meetings](#)  
 2015: “Quel est le lien entre les Océans et le Climat ?” for the “Lycée Saint Joseph” in Menton (~700 students)  
 2015: Contribution to the COP21 event [Ocean-Climax](#) organized by the Surfrider foundation: Participation to a round table with Hubert Reeves, Pascal Picq, and Odile Gauthier  
 2015-: Contribution to MEDITES- middle school initiation to oceanography (~100 students)

**SCIENTIFIC CRUISES:**

- 2013 (30 days): **Chief Scientist** of TARA Oceans Polar Circle expedition  
2008 (15 days): OPEREX: C-MORE cruise  
2006 (10 days): SCRIPPS cruise  
2005 (10 days): CIESM-SUB1 cruise  
2004 (30 days): BIOSOPE (Biogeochemistry and Optics South Pacific Experiment)

**PEER-REVIEWED PUBLICATIONS (\*WORKED BASED ON CO-SUPERVISION OF MASTERS/PHDs)**

- 1 Grébert, T. *et al.* (2018). Light color acclimation is a key process in the global ocean distribution of *Synechococcus cyanobacteria*. **Proceedings of the National Academy of Sciences**, doi:10.1073/pnas.1717069115.
- 2 Carradec, Q. *et al.* (2018). A global ocean atlas of eukaryotic genes. **Nat Commun** 9, 373, doi:10.1038/s41467-017-02342-1.
- 3 Tréguer, P. *et al.* (2017). Influence of diatom diversity on the ocean biological carbon pump. **Nat Geosci**, doi:10.1038/s41561-017-0028-x.  
*Press release:* [CNRS](#), [INSU](#)
- 4 Reygondeau, G. *et al.* (2017). Global biogeochemical provinces of the mesopelagic zone. **Journal of Biogeography**, n/a-n/a, doi:10.1111/jbi.13149.
- 5 \*Benoiston, A.-S. *et al.* (2017). The evolution of diatoms and their biogeochemical functions. **P. Roy. Soc. B-Biol Sci** 372, doi:10.1098/rstb.2016.0397.
- 6 Chust, G. *et al.* (2017). Mare incognitum: A glimpse into future plankton diversity and ecology research. **Frontiers in Marine Science** 4, doi:10.3389/fmars.2017.00068.
- 7 Durrieu de Madron, X. *et al.* (2017). Deep sediment resuspension and thick nepheloid layer generation by open-ocean convection. **Journal of Geophysical Research: Oceans**, doi:10.1002/2016JC012062.
- 8 \*Ramondenc, S. *et al.* (2016). An initial carbon export assessment in the Mediterranean Sea based on drifting sediment traps and the Underwater Vision Profiler data sets. **Deep-Sea Res. I.** 117, 107-119, doi:10.1016/j.dsr.2016.08.015.
- 9 Waite, A. M. *et al.* (2016). The Wine Glass Effect shapes particle export to the deep ocean in mesoscale eddies. **Geophys. Res. Lett.** 43, doi:10.1002/2015GL066463.
- 10 Chaffron, S., Guidi, L., Bittner, L. & Eveillard, D. (2016). Principles of Systems Biology, No. 5: From Molecular Oceanography to Ocean Systems Modeling. **Cell Systems** 2, 290, doi:10.1016/j.cels.2016.05.001.
- 11 Biard, T. *et al.* (2016). In situ imaging reveals the biomass of giant protists in the global ocean. **Nature** 532, doi:10.1038/nature17652.  
*Press release:* [CNRS](#), [INSU](#), [Nature](#), ...
- 12 Guidi, L. *et al.* (2016). Plankton networks driving carbon export in the oligotrophic ocean. **Nature** 532, 465-470, doi:10.1038/nature16942.  
*Press release:* [CNRS](#), [INSU](#), [Nature Review Microbiology](#), [Le Monde](#), ...
- 13 Waite, A. M. *et al.* (2016). Cross-shelf transport, oxygen depletion, and nitrate release within a forming mesoscale eddy in the eastern Indian Ocean. **Limnol. Oceanogr.** 61, 103-121, doi:10.1002/lno.10218.
- 14 Villar, E. *et al.* (2015). Environmental characteristics of Agulhas rings affect interocean plankton transport. **Science** 348, doi:10.1126/science.1261447.
- 15 Sunagawa, S. *et al.* (2015). Structure and function of the global ocean microbiome. **Science** 348, doi:10.1126/science.1261359.
- 16 \*Romagnan, J.-B. *et al.* (2015). Comprehensive Model of Annual Plankton Succession Based on the Whole-Plankton Time Series Approach. **PLoS ONE** 10, e0119219, doi:10.1371/journal.pone.0119219.
- 17 Lima-Mendez, G. *et al.* (2015). Determinants of community structure in the global plankton interactome. **Science** 348, doi:10.1126/science.1262073.
- 18 Legendre, L., Rivkin, R. B., Weinbauer, M., Guidi, L. & Uitz, J. (2015). The microbial carbon pump concept: potential biogeochemical significance in the globally changing ocean. **Prog. Oceanogr.** 134, 432-450, doi:10.1016/j.pcean.2015.01.008.



- 19 Guidi, L. *et al.* (2015). A new look at ocean carbon remineralization for estimating deep-water sequestration. **Global. Biogeochem. Cy.** 29, 1044–1059, doi:10.1002/2014GB005063.  
Press release: [CNRS/INSU](#), [TARA](#), [Le Monde](#)
- 20 de Vargas, C. *et al.* (2015). Eukaryotic plankton diversity in the sunlit ocean. **Science** 348, doi:10.1126/science.1261605.
- 21 Brum, J. R. *et al.* (2015). Patterns and ecological drivers of ocean viral communities. **Science** 348, doi:10.1126/science.1261498.
- 22 Boss, E. *et al.* (2015). Optical techniques for remote and in-situ characterization of particles pertinent to GEOTRACES. **Prog. Oceanogr.**, 43-54, doi:10.1016/j.pocean.2014.09.007.
- 23 \*Roullier, F. *et al.* (2014). Particle size distribution and estimated carbon flux across the Arabian Sea oxygen minimum zone. **Biogeosciences** 11, 4541-4557, doi:10.5194/bg-11-4541-2014.
- 24 Robin, T., Guidi, L., Dufour, A. I. & Migon, C. (2013). Statistical distributions of trace metal concentrations in the northwestern Mediterranean atmospheric aerosol. **Environ. Monit. Assess.** 185, 9177–9189, doi:10.1007/s10661-013-3245-9.
- 25 Lombard, F., Guidi, L. & Kiørboe, T. (2013). Effect of Type and Concentration of Ballasting Particles on Sinking Rate of Marine Snow Produced by the Appendicularian *Oikopleura dioica*. **PLoS ONE** 8, e75676, doi:10.1371/journal.pone.0075676.
- 26 Smith, C. R. *et al.* (2012). A large population of king crabs in Palmer Deep on the west Antarctic peninsula shelf and potential invasive impacts. **P. Roy. Soc. B-Biol Sci.** 279, 1017-1026, doi:10.1098/rspb.2011.1496.  
Press release: [Nature](#), [Science NOW](#), [BBC](#), ...
- 27 Guidi, L. *et al.* (2012). Does eddy-eddy interaction control surface phytoplankton distribution and carbon export in the North Pacific Subtropical Gyre? **J. Geophys. Res.** 117, G02024, doi:10.1029/2012jg001984.
- 28 Ferraris, M. *et al.* (2012). Distribution of *Pelagia noctiluca* (Cnidaria, Scyphozoa) in the Ligurian Sea (NW Mediterranean Sea). **J. Plankton Res.** 34, 874-885, doi:10.1093/plankt/fbs049.
- 29 Calcagno, V. *et al.* (2012). Flows of Research Manuscripts Among Scientific Journals Reveal Hidden Submission Patterns. **Science** 338, 1065-1069, doi:10.1126/science.1227833.  
Press release: [Science Podcast](#), [Nature](#), [CNRS](#), ...
- 30 Jouandet, M.-P. *et al.* (2011). Optical imaging of mesopelagic particles indicates deep carbon flux beneath a natural iron-fertilized bloom in the Southern Ocean. **Limnol. Oceanogr.** 56, 1130-1140.
- 31 Picheral, M. *et al.* (2010). The Underwater Vision Profiler 5: An advanced instrument for high spatial resolution studies of particle size spectra and zooplankton. **Limnol. Oceanogr. Meth.** 8, 462–473, doi:10.4319/lom.2010.8.462.
- 32 Guidi, L., Calcagno, V., Ibanez, F. & Beaugrand, G. (2010). Reply to Comment on "A new procedure to optimize the selection of groups in a classification tree: Applications for ecological data". **Ecol. Model.** 221, 2739-2740, doi:10.1016/j.ecolmodel.2010.08.016.
- 33 Guidi, L. *et al.* (2009). Effects of phytoplankton community on production, size, and export of large aggregates: A world-ocean analysis. **Limnol. Oceanogr.** 54, 1951-1963.
- 34 Guidi, L., Ibanez, F., Calcagno, V. & Beaugrand, G. (2009). A new procedure to optimize the selection of groups in a classification tree: Applications for ecological data. **Ecol. Model.** 220, 451-461.
- 35 Stemmann, L. *et al.* (2008). Global zoogeography of fragile macrozooplankton in the upper 100-1000 m inferred from the underwater video profiler. **ICES J. Mar. Sci.** 65, 433-442, doi:10.1093/icesjms/fsn010.
- 36 Stemmann, L. *et al.* (2008). Effects of frontal processes on marine aggregate dynamics and fluxes: An interannual study in a permanent geostrophic front (NW Mediterranean). **J. Mar. Syst.** 70, 1-20.
- 37 Stemmann, L. *et al.* (2008). Volume distribution for particles between 3.5 to 2000  $\mu\text{m}$  in the upper 200 m region of the South Pacific Gyre. **Biogeosciences** 5, 299-310.
- 38 Guidi, L. *et al.* (2008). Relationship between particle size distribution and flux in the mesopelagic zone. **Deep-Sea Res. I.** 55, 1364-1374, doi:10.1016/j.dsr.2008.05.014.
- 39 Guidi, L. *et al.* (2008). Distribution and fluxes of aggregates  $>100 \mu\text{m}$  in the upper kilometer of the South-Eastern Pacific. **Biogeosciences** 5, 1361-1372.
- 40 Guidi, L. *et al.* (2007). Vertical distribution of aggregates ( $> 110 \mu\text{m}$ ) and mesoscale activity in the northeastern Atlantic: Effects on the deep vertical export of surface carbon. **Limnol. Oceanogr.** 52, 7-18.

### BOOKS & BOOK CHAPTERS & CONFERENCE PAPERS

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- 1 Jessup C. (2017). Étonnant vivant, Découvertes et promesses du XXI<sup>e</sup> siècle. Eds., CNRS, Institut des sciences biologique, France, p. 328.
- 2 Bopp L., C. Bowler, L. Guidi, E. Karsenti, C. de Vargas. (2015). L'Océan pompe à carbone. In Fiche Scientifiques from the Ocean & Climate Platform, Label COP21. [English version](#) / [French version](#)
- 3 Stemmann, L., M. Picheral, L., Guidi, L., Lombard, F., Prejer, F., Claustre, H. & Gorsky, G. (2012). Assessing the spatial and temporal distributions of zooplankton and marine particles using the Underwater Vision Profiler, In *Sensors for ecology: Towards integrated knowledge of ecosystems*. Le Galliard, J.-F., Guarini, J.-M. & Gaill, F., Eds., CNRS, Institut Ecologie et Environnement, France, pp. 119-137.
- 4 Picheral, M., L. Stemmann, L. Guidi, D. Karl, A. Waite, L. Legendre, L., & Gorsky, G. (2009). Underwater vision profiler-a sensor for detailed assessment of particles (> 100 µm) and large plankton distribution. In *OceanObs'09 Conference* (pp. 21-25).

### INTERNATIONAL COMMUNICATIONS (\*INVITED SPEAKER)

---

- 1 \*Guidi, L. 2017. The Biological Carbon Pump seen through High Throughput Imaging and “Omics”. Seminars, Alfred Wegener Institute. Bremerhaven, Germany, 20<sup>th</sup> November.
- 2 \*Guidi, L. 2017. The Biological Carbon Pump seen through High Throughput Imaging and “Omics”. Friday Seminars, National Oceanography Center. Southampton, UK, 3<sup>rd</sup> November.
- 3 \*Guidi, L. 2017. Ship Opportunity: From Tara Oceans to Monaco Explorations. Scripps. San-Diego, California, USA, 22<sup>nd</sup> September.
- 4 \*Guidi, L. 2017. The planktonic social network of the biological carbon pump. ICES. Annual Science Conference. Florida, 18th-21th September (**plenary**)
- 5 \*Guidi, L. 2017. Issues on modeling linked to climate change impacts on ocean biodiversity. Global Challenges for Ocean Sciences and International Policies Today. Santiago, Chile, 7<sup>th</sup> September
- 6 \*Guidi, L. 2017. Genocyanography. The Tara Ocean Program: Structuring International Scientific Cooperation with South America, Conception, Chile, 4<sup>th</sup> – 6<sup>th</sup> September
- 7 \*Guidi, L. 2017. Tara Oceans: Results of 3 years around the world to study plankton. Universidad de Buenos Aires, Buenos Aires, Argentina, 1<sup>st</sup> to 3<sup>rd</sup> September.
- 8 \*Guidi, L. 2017. Plankton networks driving carbon export in the oligotrophic ocean. 2017. Journée de restitution finale du défi ENVIROMICS, Paris, 25<sup>th</sup>-26<sup>th</sup> April.
- 9 \*Guidi, L. 2017. Tara Oceans: The Biological Carbon Pump from Genes to Ecosystems. ASLO. Hawaii, 26<sup>th</sup> February- 3<sup>rd</sup> March (**plenary**).
- 10 \*Guidi, L. 2016. From satellite to genes: A new view of the biological carbon pump. Laboratoire Leprince-Ringuet. Paris, France. 23<sup>rd</sup> May.
- 11 \*Guidi, L. 2016. The biological carbon pump from satellite to genes. Laboratoire de Biologie du développement. Villefranche sur mer, France. 2<sup>nd</sup> May.
- 12 \*Guidi, L. 2016. The biological carbon pump: How to move beyond JGOFS? Silica Day 1. Laboratoire de Sciences de l'environnement marin. Brest, France. 18<sup>th</sup> March.
- 13 Guidi, L., S. Chaffron, L. Bittner, D. Eveillard, E. Karsenti, C. Bowler, M. Gehlen. 2016. Integrating plankton networks in oceans biogeochemical modelling. Networks for plankton systems, Ecology & Evolution. Paris, France. 9-10 March.
- 14 \*Guidi, L., S. Chaffron, L. Bittner, D. Eveillard, J. Raes, E. Karsenti, C. Bowler, G. Gorsky. 2016. Combining Bioinformatics and oceanography to understand biological carbon export. “Oceanic plankton, climate and development” TARA OCEANS project with FFEM. Buenos Aires, Argentina, 24-25 February.
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## II. RESEARCH ACTIVITIES

### RESEARCH HIGHLIGHTS (2004 TO 2017)

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Most of my studies rely on the use of the Underwater Vision Profiler (UVP), an instrument to which I contributed to develop during my PhD (Picheral et al., 2010). Since 2007, I published 17 peer-reviewed articles based on data collected with this instrument over the **36 articles (9 as first author and 1 at last and corresponding author)** counting **1011 citations with a h-index of 17** (ISI web of Science), **1675 citations (566 in 2016 only) with a h-index of 20** ([Google Scholar](#)). I gave **20 oral presentations (over 62 contributions)** including **9 as Invited** (3 at internationally established conferences and 6 at international advanced schools). I also contributed to **3 research monographs**.

In 2008, I **led the synthesis of a 3-week multidisciplinary cruise** studying the impact of North Pacific eddies on nitrogen fixers and carbon export (Guidi et al. 2012). Later on, in early 2013, I led the *Tara Polar Circle expedition* (first leg) as the **chief scientist** of 12 researchers for 30 days at Sea.

I got a permanent CNRS research position in late 2013. In 2014 I co-organized a workshop on “*Perspectives on particle flux from observations, measurements, and models*” during the Ocean Science Meeting in Honolulu, USA. This workshop attracted **~90 participants**. In addition, I co-organized a second workshop in 2017 in Villefranche sur Mer, merging oceanographer and computer scientist to advance the link between observations, data, and models. Finally, my involvement in the **Tara Oceans** project since 2011 got me promoted as one of the **coordinators** in 2016. Since 2013, I co-authored and/or led 19 research papers including **5 in Science and 2 in Nature**.

These results recently got me invited as **plenary speaker** at 2 important international conferences:

- [Aquatic Sciences Meeting](#), Hawaii, USA, 26<sup>th</sup> February – 3<sup>rd</sup> March 2017 (~3000 scientists)
- [ICES annual science conference](#), Florida, USA, 18-21<sup>st</sup> September 2017 (~800 scientists)

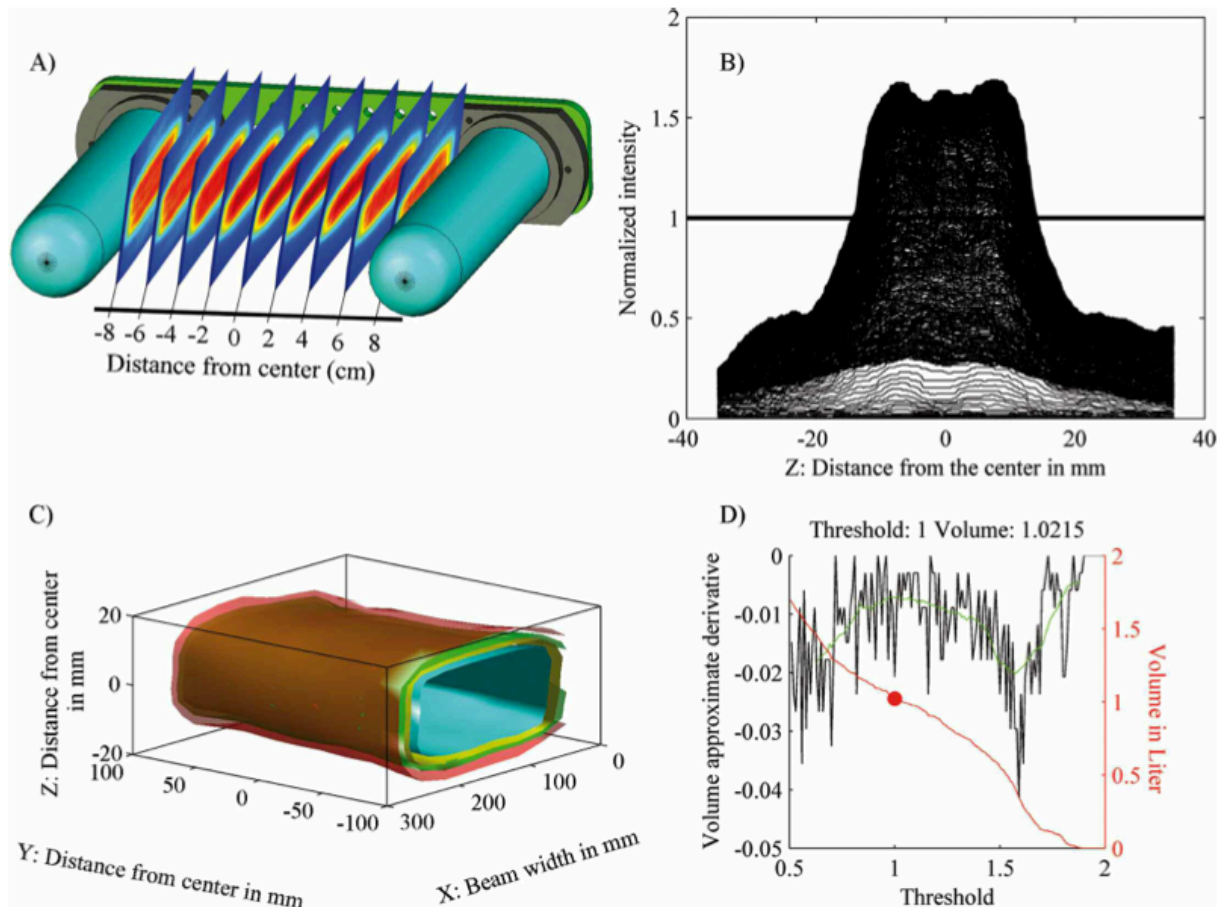
### FROM 2004 TO 2013 (PHD AND POSTDOCS)

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#### 1. INSTRUMENT AND METHOD DEVELOPMENTS

##### a. THE UNDERWATER VISION PROFILER

I started my PhD in November 2004 working on the spatial and temporal variability of the size of particles in the Ocean as seen with the Underwater Vision Profiler (UVP). At the time, the only data available were coming from the UVPs from the 2<sup>nd</sup> and the 4<sup>th</sup> generations. Early on, I realized that there was a need to improve these available prototypes in order to reach a commercialization state and therefore increase the number of users. In particular, we needed to develop methods to standardize the data acquisition and their post treatment so all collected data could be intercomparable. Between 2004 and 2007 (the 3 years of the PhD program), I worked in collaboration with my 2 PhDs advisors (Pr. Gabriel Gorsky and Pr. Lars Stemann) and 1 research engineer (Marc Picheral) in order to develop the 5<sup>th</sup> generation of the UVP, which is the one actually available on shelf from the company “[Hydroptic](#)”. This fruitful collaboration led to an article in 2010 (Picheral et al. 2010) and a book chapter from the CNRS (Stemann et al. 2012a) that described the instrument, its technical characteristics, calibration process (Figure 1), and the methods to calculate the size of particles from their pixels measurements. We also use original data collected during the BOUM cruise in order to illustrate how to use the UVP and what can be learned from measurements of particle size distribution and zooplankton vertical distribution observed at Sea.



**Figure 1:** Reconstruction of the volume of water recorded by the UVP. (A) Repositioning of the 9 images captured in a seawater tank inside the light beam. (B) Light intensity spectrum of the  $-8$  cm image from the center of the light field. The continuous line represents the threshold 1, which is used to calculate the recorded volume. (C) Reconstruction of the recorded volume using different thresholds; threshold 1 in yellow. (D) Estimation of the recorded volume in function of thresholds values in red. The red point indicates the volume for threshold selected for the UVP5. The green curve is the average of the volume approximate derivative (Picheral et al. 2010).

### b. STATISTICAL METHOD DEVELOPMENT

The objective of my PhD was to identify and understand the main processes driving variations of the size distribution of marine particles at the global scale. In order to achieve that goal I had to assemble a database of 25 different oceanographic cruises merging different environmental parameters (temperature, salinity, phytoplankton pigments, transmissometry, etc...). Diving into such a diversity of data is interesting and challenging because of its complexity. Using reductionist approaches is key when one wants to understand such complexity. Most of the available methods used in ecology to analyse these types of data create clusters of observations that then are easier to interpret. In biology, and specifically ecology, datasets are generally highly variable and may contain outliers, which increase the difficulty to identify the number of clusters. During my PhD, in order to cluster profiles of particle size distribution across the Ocean, I developed a new criterion to determine statistically the optimal level of partition in a classification tree. The criterion robustness has been tested against perturbed data (outliers) using an observation or variable with values randomly generated. This method is based on a Monte Carlo simulation and has been named



Random Simulation Test (RST; Guidi et al. 2009a). Following this publication, Nicholls et al. (2010) published a comment on the method highlighting potential weaknesses of the approach. We had the opportunity to reply to this comment, pointing to numerous biases in their analysis (Guidi et al. 2010). Since then, this method has been used across disciplines.

### c. SPECIFIC ALGORITHM: FROM PARTICLE SIZE TO PARTICLE CARBON FLUX

Classical *in-situ* methods (sediment traps and particle-reactive radionuclides) to study and quantify carbon fluxes through the water column are time consuming and costly, limiting the number of observations across the Ocean. Imaging and optical techniques on the other hand are easy to implement but only provide estimates of flux. During my PhD, I developed a UVP specific algorithm that allows estimating particle carbon, nitrogen, and mass fluxes, based on particle size distribution and concentration in the water column. Previous research has shown that the distribution of particle size follows a power law over the  $\mu\text{m}$  to the mm size range (Mccave 1984; Sheldon et al. 1972). This so called Junge-type distribution translates into the following mathematical equation, whose parameters can be retrieved from UVP images:

$$n(d) = ad^k \quad (\text{eq. 1})$$

where  $d$  is the particle diameter, and exponent  $k$  is defined as the slope of the number spectrum when equation (1) is log transformed. This slope is commonly used as a descriptor of the shape of the aggregate size distribution.

The carbon-based particle size approach relies on the assumption that the total carbon flux of particles ( $F$ ) corresponds to the flux spectrum integrated over all particle sizes:

$$F = \int_0^{\infty} n(d).m(d).w(d)dd \quad (\text{eq. 2})$$

where  $n(d)$  is the particle size spectrum, *i.e.*, equation (1), and  $m(d)$  is the mass (here carbon content) of a spherical particle described as:

$$m(d) = \alpha d^3 \quad (\text{eq. 3})$$

where  $\alpha = \pi\rho/6$ ,  $\rho$  is the average density of the particle, and  $w(d)$  is the settling rate calculated using Stokes Law:

$$w(d) = \beta d^2 \quad (\text{eq. 4})$$

where  $\beta = g(\rho - \rho_0)(18\nu\rho_0)^{-1}$ ,  $g$  is the gravitational acceleration,  $\rho_0$  the fluid density, and  $\nu$  the kinematic viscosity.

In addition, mass and settling rates of particles,  $m(d)$  and  $w(d)$ , respectively, are often described as power law functions of their diameter obtained by fitting observed data,  $m(d).w(d) = Ad^b$ . The particles carbon flux can then be estimated using an approximation of equation (2) over a finite number ( $x$ ) of small logarithmic intervals for diameter  $d$  spanning from 250  $\mu\text{m}$  to 1.5 mm (particles <250  $\mu\text{m}$  and >1.5 mm are not considered, consistent with the method presented by Guidi et al., (2008b) such as

$$F = \sum_{i=1}^x n_i A d_i^b \Delta d_i \quad (\text{eq. 5})$$

where  $A=12.5\pm 3.40$  and  $b=3.81 \pm 0.70$  have been estimated using a global dataset that compared particle fluxes in sediment traps and particle size distributions from the UVP images (Table 1).

**Table 1:** Coefficient (A) and exponent (b) and their associated standard deviation (STD) of the empirical relationship between the aggregate size and the related mass, particulate organic carbon (POC), particulate inorganic carbon (PIC) and particulate

organic nitrogen (PON) fluxes determined by minimization of the flux estimations by the Underwater Video Profiler (UVP) and the sediment trap measurements,  $n=118$  (Guidi et al. 2008b)

Fluxes	Symbol	A	STD A	b	STD b	R <sup>2</sup>	P
Generic relationship: $F = Ad^b$							
Mass	$F_m$	109.5	32.6	3.52	0.72	0.70	<0.0001
POC	$F_{poc}$	12.5	3.40	3.81	0.70	0.73	<0.0001
PIC	$F_{pic}$	3.97	1.13	3.60	0.76	0.57	<0.0001
PON	$F_{pon}$	2.02	0.59	3.93	0.82	0.71	<0.0001

I acknowledge that the method to estimate carbon flux from particle size is not perfect. Indeed, carbon flux depends both on size and composition (or density) of particles. Imaging techniques provide information on size but do not inform on particle composition *per se*. Therefore, estimating particle flux based on size assumes that particle composition is similar across the full particle size range. I showed that this assumption is reasonable at the global scale (Guidi et al. 2008b). Indeed, if particle composition was the preponderant factor influencing particle flux (or sinking speed), a significant relationship between particle size and flux would not exist. This global analysis emphasizes that size dominates over composition relative to particle flux at the global scale.

This method, used to estimate carbon flux based on particle size distribution and concentration, has been reported in more than 60 articles since its first application. The use of the UVP to measure particle size and to derive carbon flux has been well embraced by the community for the past 10 years as highlighted by the number of UVPs sold by “[Hydroptic](#)” that manufactures them. In spite of its relatively recent development, this method has been well accepted in the field of oceanography/biogeochemistry as shown by the body of literature using it or citing it (see the example of references below).

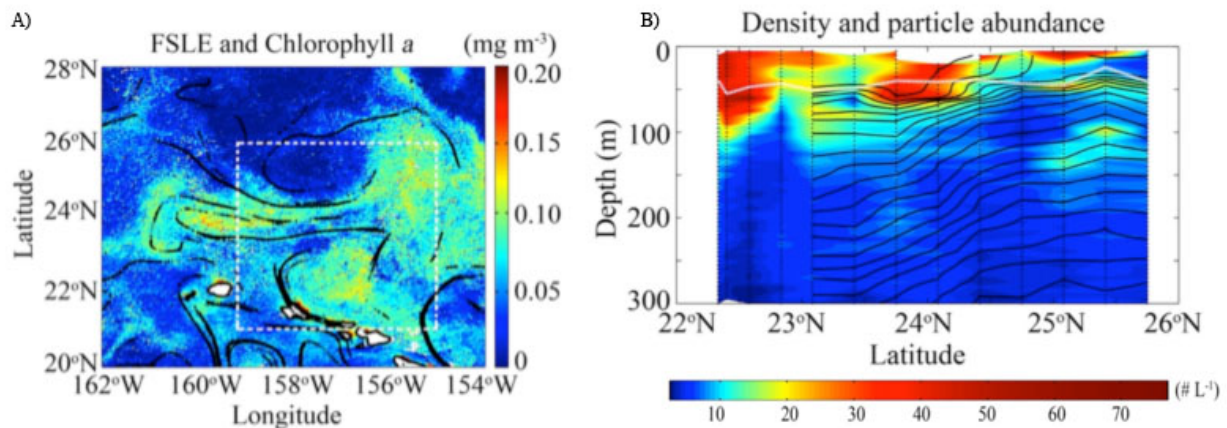
#### **Examples of citations of Guidi et al 2008 from ISI Web-of-Science:**

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## 2. CARBON FLUX SPATIAL VARIABILITY

### a. SUB-MESOSCALE SPATIAL VARIABILITY

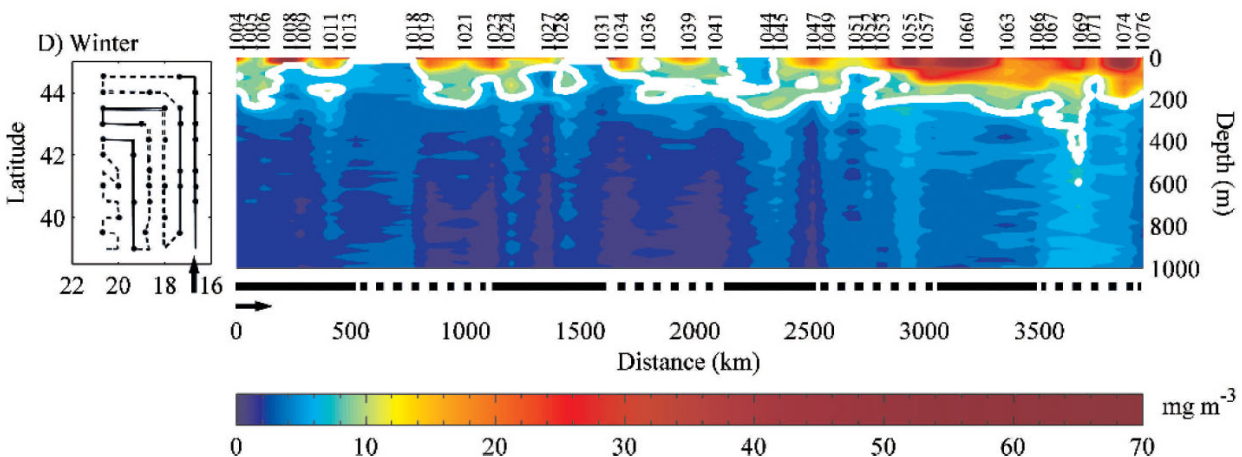


**Figure 2:** A) Finite-size Lyapunov exponents (FSLE) maxima superimposed on chlorophyll *a* from MODIS (8-day composite centered on the 5<sup>th</sup> of August 2008) representing the location of stretching. White dashed rectangles delimit the area studied during the OPEREX cruise. B) Large particle (>100  $\mu\text{m}$ ) abundance from the UVP with the mixed layer depth represented by the white dashed line. The black contour lines represent the density field showing particle accumulation on isopycnals (Guidi et al. 2012).

Because it's much easier to measure particle size than directly measuring flux, the use of a relationship between particle size distribution and carbon flux allow improving the spatial resolution of carbon flux estimates. In that context, I've been involved is the OPEREX cruise out of the coast of Hawai'i

in 2008 to study the impact of sub-mesoscale filaments on the carbon export spatial variability in this area. In the North Pacific Subtropical Gyre, the regular occurrence of summer phytoplankton blooms contributes to marine ecosystem productivity and the annual carbon export. The mechanisms underlying the formation, maintenance, and decay of these blooms remain largely unknown; nitrogen fixation, episodic vertical mixing of nutrients, and meso- (<100 km) and submesoscale (<10 km) physical processes are all hypothesized to contribute to bloom dynamics. In addition, zones of convergence in the ocean's surface layers are known to generate downwelling and/or converging currents that affect plankton distributions. It has been difficult to quantify the importance of these convergence zones in the export flux of particulate organic carbon (POC) in the open ocean. During the OPEREX cruise we use two high-resolution ocean transects across a pair of mesoscale eddies in the vicinity of Station ALOHA (22°45'N, 158°00'W) to show that horizontal turbulent stirring may have been a dominant control on the spatial distribution of the nitrogen fixing cyanobacterium *Trichodesmium spp.* Our observations of particle size distributions along the two transects showed that stretching by the mesoscale eddy field produced submesoscale features that mediated POC export *via* frontogenetically generated downwelling currents (Figure 2). This study highlights the need to combine high-resolution biogeochemical and physical data sets to understand the links between planktons (here *Trichodesmium spp.*) surface distribution and POC export in the NPSG at the submesoscale level.

#### b. MESOSCALE SPATIAL VARIABILITY

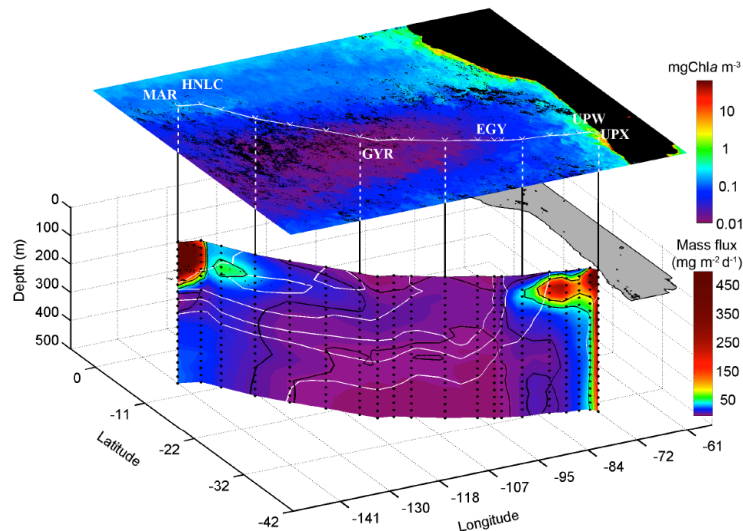


**Figure 3:** Vertical distribution of aggregates in winter along the ship tracks. The station numbers where the UVP was deployed are given above the section. The color scale emphasizes variability at the lower end of the concentration range. The ship track is given on the left. The continuous and dotted lines are repeated under the section plot. The arrows point to the start of the track (Guidi et al. 2007).

The Programme Ocean Multidisciplinaire Meso Echelle (POMME) research cruises were organized off the Iberian Peninsula and the Azores Islands in winter, spring, and summer 2001, an area dominated by mesoscale and submesoscale hydrodynamics. The cruise is a good example of the importance of using imaging/optical sensor, in addition to classical sediment traps, in order to capture the potential mesoscale patterns of carbon fluxes. During that program we observed that in the 0–200m layer, aggregates were most abundant in spring and lowest during summer and winter. In the deeper layers (down to 1000m), the seasonal pattern was different, with concentrations highest in spring and summer, and lowest in winter. The seasonal change in the abundance of aggregates in the upper 1,000 m was consistent with changes in the composition and intensity of the particulate flux recorded in sediment traps and with seasonal changes in the surface phytoplankton community. In an area dominated by eddies, surface accumulation of aggregates and export down to 1000 m occur at mesoscale distances (<100 km). The occurrence of a rich aggregate

layer (Figure 3) may be related to mesoscale activity in water flow that drives nutrient inputs, phytoplankton production, and the formation of large aggregates. Such spatially constrained zones of massive export may be typical of frontal open-sea systems.

### c. REGIONAL / BASIN-SCALE SPATIAL VARIABILITY



**Figure 4:** Flux (in total mass) of particles estimated from size measurements of every individual particle recorded during the vertical deployment of the UVP. Only data from 0–500 m are shown for better visualisation of the upper water column structures. Isohalines are in white (Guidi et al. 2008a).

Finally, not only interesting at the submeso- or meso-scale level, the UVP is also useful to look at regional patterns of carbon flux. Here I present results obtained with the UVP during the BIOSOPE cruise in the southeastern Pacific. During the cruise, I was able to compare particle fluxes estimated based on particle size distribution and measurements of fluxes in sediment traps. The use of the UVP allowed interpolating between flux measurements with sediment traps. We could show that the South Pacific Gyre exported about  $2 \text{ mg m}^{-2} \text{ d}^{-1}$ . On the western end of the BIOSOPE section the standing stock of particles in the surface layer was high but the export between 150 and 250m was low. Below this layer (between 300 and 400m) the flux values increased which is counterintuitive because of the idea of exponential decrease of flux with depth (Martin et al., 1987). In addition, even though the surface concentration of particles near the Chilean coast was high, 95% of the matter was disaggregated, remineralized or advected in the upper kilometer. These results suggest that the carbon export to deep waters and remineralization are spatially heterogeneous and related to the different biotic and abiotic factors at the scale of the South Eastern Pacific (Guidi et al. 2008a). Today, the UVP is involved in international programs as one of the core instruments to map particle distribution across different ocean basins. This important advancement is the result of our effort to show the capability of the imaging sensor in estimating fluxes at a resolution that no other instrument could achieve.

### 3. CARBON FLUX AND PHYTOPLANKTON COMMUNITY COMPOSITION

The previous sections described the research that I've been doing in order to develop an instrument and specific statistical methods to allow fast imaging estimates of particle fluxes in the water column. Most of the above results are descriptive and do not provide a lot of information on the processes that are driving the observed spatial variations. While we discussed the role of physical mechanisms driving the carbon export variability, we barely considered the role of the biology as a potential source of variation.

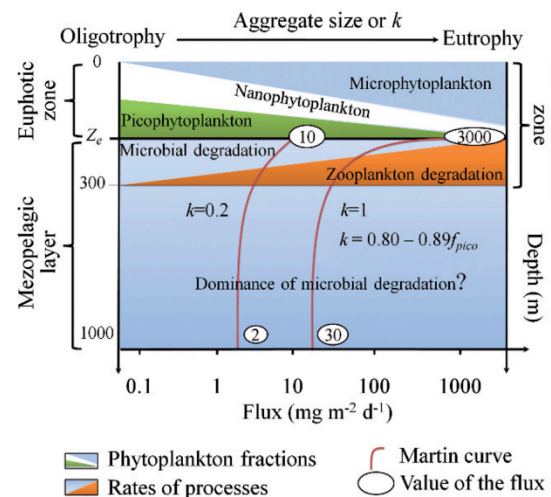
**Figure 5:** Schematic representation of the different processes that affect the size distribution and decrease in the flux of particles in oceans. The width of the different surfaces in the zone of intense remineralization represents the relative importance of phytoplankton fractions or processes rates, and  $k$  is the value of the exponent of the Martin's power relationship. The equation corresponds to the calculation of this exponent from the size structure of phytoplankton (Guidi et al. 2009b).

Here I present an important result published in 2009 that discuss the role of the phytoplankton community composition and structure in carbon export and remineralization. In order to better understand the role of the community, and not the one of single species, in carbon export in the Ocean, I used a database of 410 vertical profiles of size distributions of large particles ( $>100 \mu\text{m}$ ) from the surface to 1000m in the Atlantic, Indian, and Pacific Oceans and in the Mediterranean Sea. I merged this database with 193 associated profiles of temperature, salinity, and high-performance liquid chromatography (HPLC)-resolved pigments, which I used to characterize the size structure of the phytoplankton community. After clustering analysis (see methods above) I could identify six clusters of vertical profiles of size distributions of particles. Each cluster was characterized by the size distribution of its particles in the mesopelagic layer and the change of the particle-size distribution with depth. Clusters with large particles in the mesopelagic layer corresponded to surface waters dominated by microphytoplankton, and those with small particles corresponded to surface waters dominated by picophytoplankton. Principal-component regression analysis showed that 68% of the variance of the particle flux at 400m was explained by the size structure of the phytoplankton community and integrated chlorophyll *a* in the euphotic zone. I found that remineralization (here defined as the exponent of the Martin's power relationship) varies between 0.2 and 1.0 in the world ocean, and I provided an empirical relationship to derive this exponent from the size structure of phytoplankton biomass in the euphotic zone (Figure 5). Since then, modelers have used that relationship to obtain a realistic description of the downward particle flux instead of using a constant exponential.

#### 4. SYNTHESIS (2004 TO 2013)

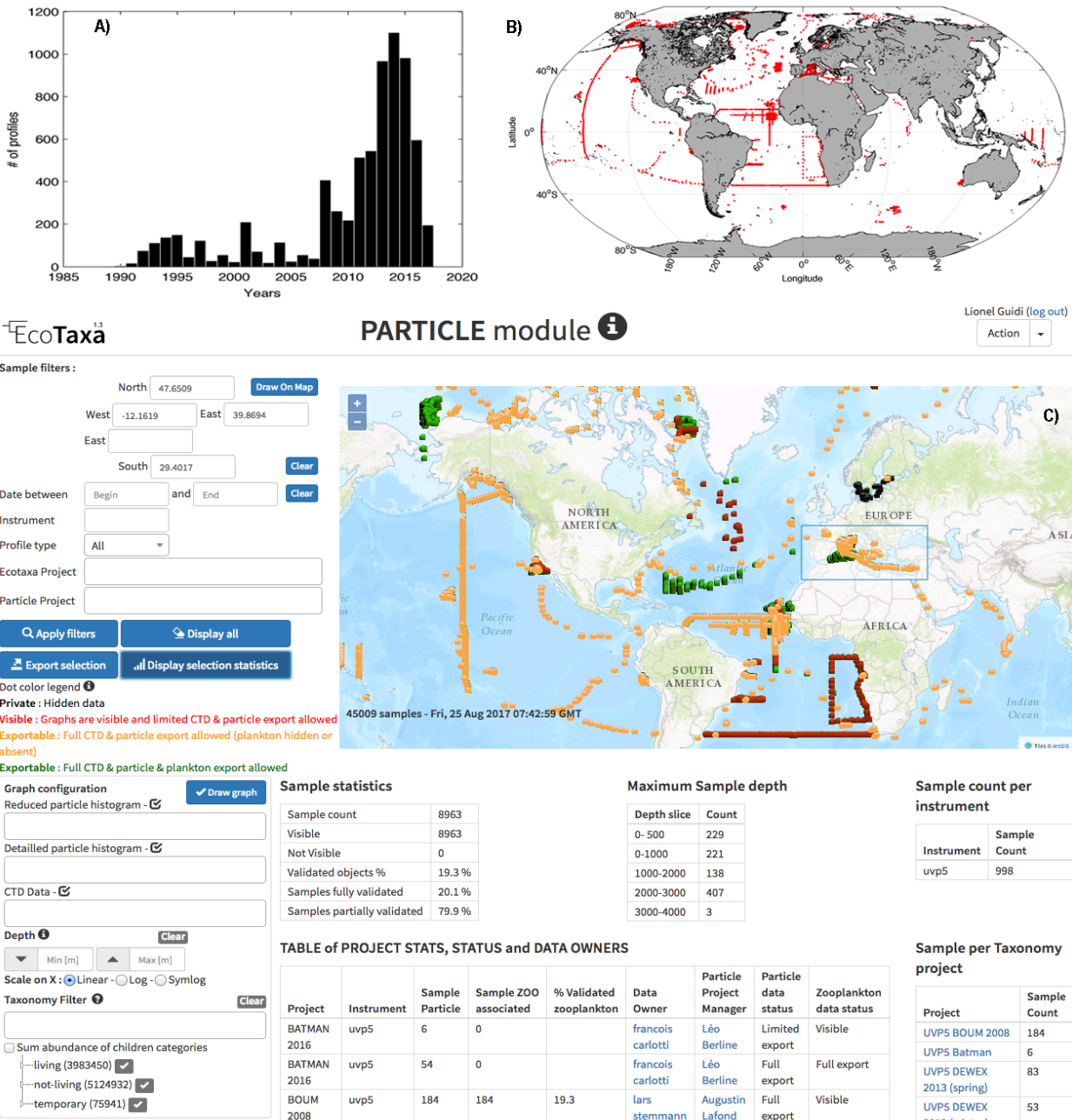
Results presented above correspond to the highlights of the research that I have done, or contributed to, during my PhD and Post-doctoral research. Overall, I had published 17 papers (see the full list of the scientific contributions) in diverse topic but with main interest focused on the study of the biological carbon pump. I contributed to both instrument and statistical development to improve our understanding of particle size distribution and dynamic in the Ocean. These methods have led to a better appreciation of the variation of the particle flux from the submeso- to the basin-scale. Because we developed better tools to observe these variations, we could study physical mechanisms driving these observed patterns. In addition, I started to develop approaches coupling physical and biological observations with particle size distribution to untangle their respective contributions to carbon export. One major result of this period relies on the understanding that community composition is a key component of variations of carbon export (Guidi et al. 2009b). This first conclusion will be the main motivation for the research that I have conducted since then.

#### FROM 2013 TO 2017 (SINCE THE CR2 POSITION AT THE CNRS)



## 1. TOOL DEVELOPMENT

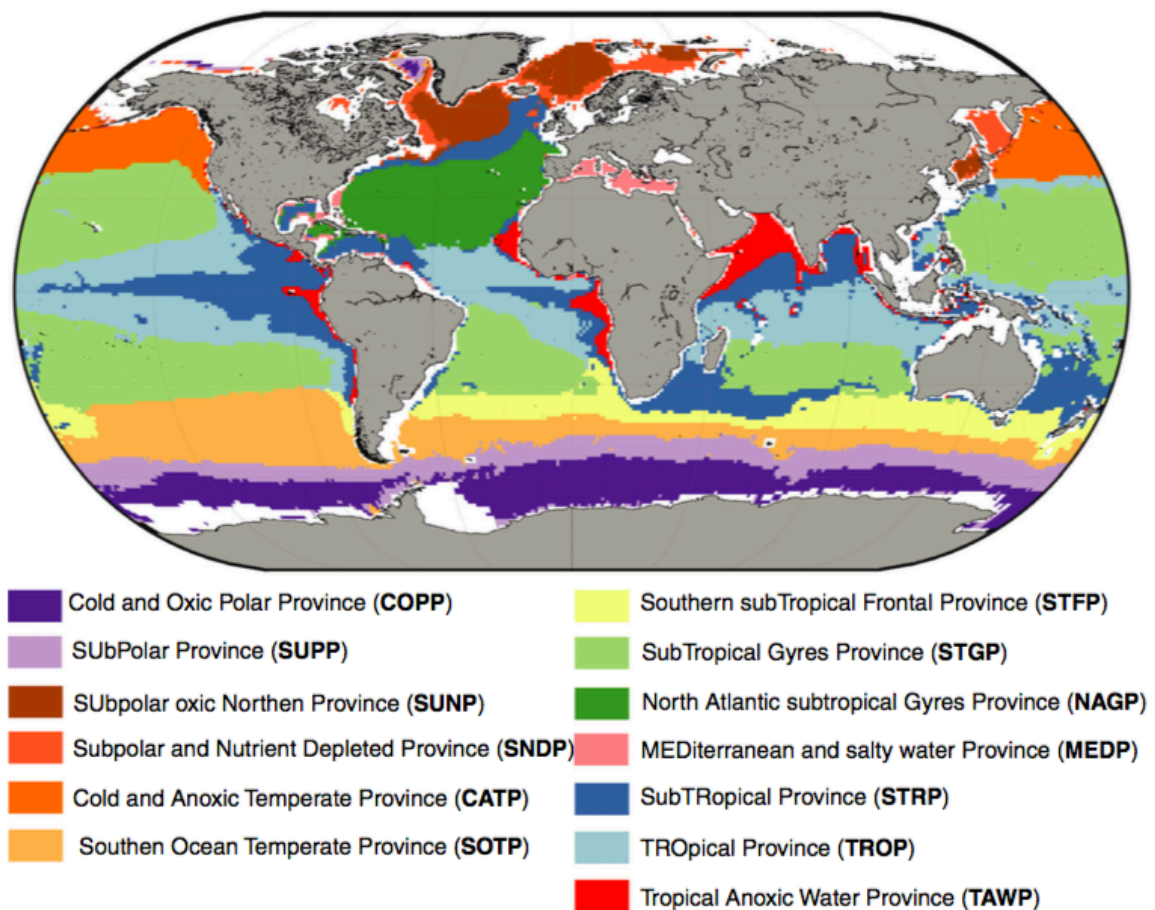
### a. A WEB SERVICE FOR UVP AND OTHER PARTICULES DATA



**Figure 6:** Current status of the UVP database. A) Total number of UVP profiles collected per year between 1990 and today. B) Global distribution of these collected profiles. C) Particle Module of the ECOTAXA web application that allow loading, pre-processing, and sharing data collected with the UVPs. This software also allows uploading complementary data associated to particle profiles such as CTDs. Finally, ECOTAXA is the web application to sort UVP zooplankton images in taxonomic categories. Therefore particle profiles are directly linked to these data as well. Overall, this new web application is a tool that will help scientists to explore the global particle database and link profiles to their environmental conditions.

Since 2004, the database of UVP profiles evolved from few hundred to more than 6 thousands profiles in 2017 (Figure 6A, B). In addition, the recent H2020 funded project (BRIDGE) will lead to a new low cost and low wait imaging sensor, called OCTOPUS and based on the UVP technology, that will be mounted on gliders and floats. This new instrumentation will lead to an exponential increase of profiles collected across the globe by different users. Because of this fast growing database, the need to develop a user-friendly web interface (Figure 6C) to gather profiles, allowing first efficient quality control, facilitating standardization of the data processing, and finally allowing easy data sharing, become evident. To achieve that goal we developed the Particle module of the ECOTAXA software that centralized all UVP data and facilitate their preliminary analysis before release. In addition collaboration among UVP users are facilitated with this web application. This tool is in its Beta-testing version but will be released in the coming months.

#### *b. DEFINING MESOPELAGIC BIOGEOCHEMICAL PROVINCES*



**Figure 7:** Map of the Mesopelagic BioGeoChemical Provinces (MBGCP). Names, annotations and corresponding colours of each MBGCP are provided. Geographical cells represented in white are areas where the methodology is not performed either because no data were available or the bathymetry was too shallow to retrieve the mesopelagic layer

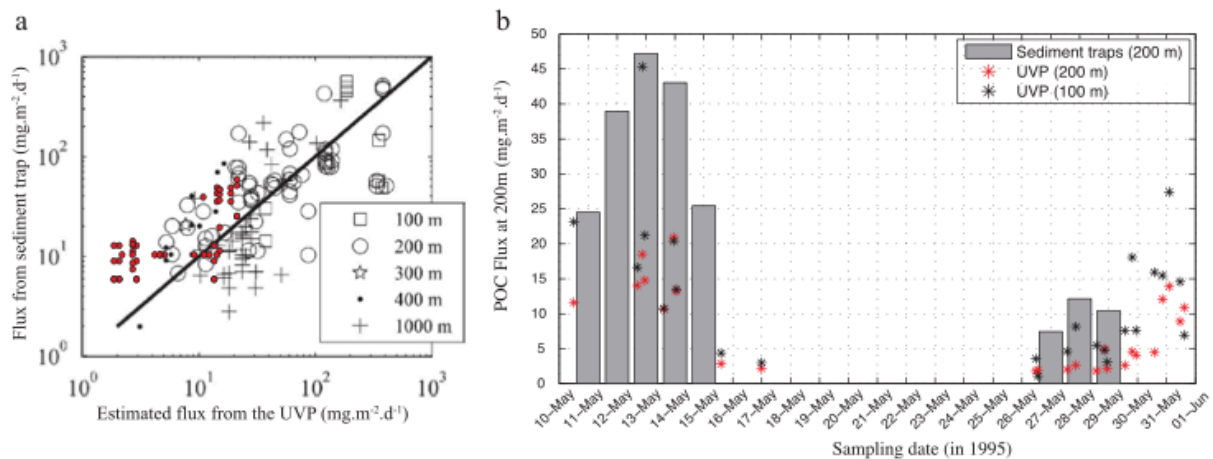
Following the biogeographical approach implemented by Longhurst for the epipelagic layer, we proposed to identify a biogeochemical 3-D partition for the mesopelagic layer (Reygondeau et al. 2017). The resulting partition is based on the most comprehensive environmental climatology available to date (temperature, salinity, dissolved oxygen concentration, nutrients concentration and carbon fluxes), which is both spatially and vertically resolved. We showed that the vertical division of the pelagic zone varies and, hence, is not



constant throughout the global ocean. A latitudinal gradient was found between the epipelagic–mesopelagic and mesopelagic– bathypelagic vertical limits. Second, the mesopelagic layer is shown here to be composed of 13 distinguishable Biogeochemical Provinces (Figure 7). Each province shows a distinct range of environmental conditions and characteristic. These deep environmental biotopes and their vertical boundaries on a global scale, which can be used as a geographical and ecological framework for conservation biology, ecosystem-based management and for the design of oceanographic investigations.

## 2. THE BIOLOGICAL CARBON PUMP SPATIAL VARIABILITY

### a. BASIN-SCALE: CASE STUDY OF THE MEDITERRANEAN SEA



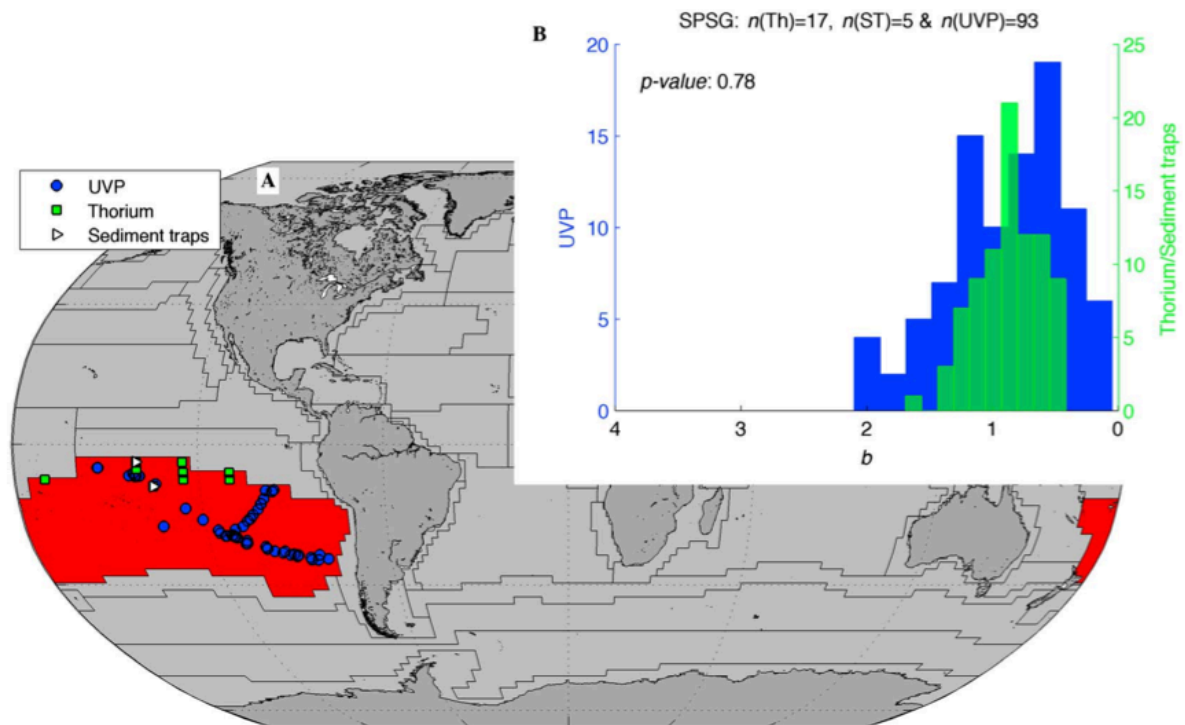
**Figure 8:** Cross-comparison of fluxes measured with sediment traps vs UVP fluxes estimates at the DYFAMED station (red dots) obtained during a 3 weeks cruise (DYNAPROC) superimposed to the global dataset available from the literature (black dots). (b) Time-series of POC flux at 200m based on daily averaged sediment traps measurements and UVP's POC flux estimates at 100 and 200 m during the DYNAPROC cruise (Ramondenc et al. 2016).

In the research presented above (between 2004 and 2013), the spatial variability of particle size distribution and carbon flux was mainly investigated using UVP data. Only few sediment trap data were available to crossvalidate our observations. While several methods have been developed to measure directly or indirectly carbon flux (moored and drifting sediment traps, particle-reactive radionuclides, optical and imaging proxies), none of them are perfect and they all have specific biases. Because there is no perfect method to study these fluxes, I have been trying to analyse local, regional, or global patterns, merging several methods (Figure 8) in order to get a more robust picture of fluxes spatial variations and potential drivers. In that context we gathered a database of all available POC data collected from drifting sediment trap and Underwater Vision Profiler data collected in the framework of the SESAME EU FP6 project in the Mediterranean Sea (INSU PROOF database, 1991–2011). We then used this database to assess carbon export at the scale of the Mediterranean Sea (Ramondenc et al. 2016). We observed that particle size, POC export, and the contribution of microphytoplankton to the phytoplankton community structure, all decreased following the west to east net primary production gradient. On the other hand, no clear longitudinal gradient was found regarding particle composition (C/N ratio or lipid content). The above longitudinal patterns were also observed at the seasonal scale from spring to summer in the northwestern subbasin. These observations suggest that particle size rather than organic matter composition controls fluxes of POC in the Mediterranean Sea. In addition, in that study, the comparison between POC and dissolved organic carbon (DOC) fluxes in the Mediterranean Sea highlighted the different time-scale of physical vertical mechanisms driving their export. Indeed, DOC supply to deeper layers can be one order of magnitude larger than particle carbon flux but occurs in pulses when stratification breaks due to (i) deep-

water formation, or (ii) winter mixing. In contrast, the vertical export of POC occurs throughout the year bringing weak, but almost continuous, energy to meso- and bathypelagic organisms. Merging different methods allowed to better understand the dynamic of carbon export in the Mediterranean Sea and to identify specific processes related to different forms of exported carbon.

#### ***b. GLOCAL SCALE: FIRST REGIONALIZATION OF REMINERALIZATION***

Most the POC sinking through the water column is remineralized during its downward transit, and modest changes in remineralization have substantial feedback on atmospheric CO<sub>2</sub> concentrations. The POC flux decreases exponentially with depth as aggregates are fragmented, decomposed, and remineralized through respiration, and the carbon released in the water column above the depth of sequestration returns to the atmosphere. It has been shown that a modest change in remineralization can have a substantial impact on atmospheric *p*CO<sub>2</sub>; *e.g.*, a deepening of the *e*-folding depth (*i.e.*, the depth at which 63% of POC sinking from the surface waters is remineralized) by as little as ~20m could lead to a decrease in atmospheric *p*CO<sub>2</sub> of 10 to 30 ppm, *i.e.*, ~3 to 9% of the present atmospheric *p*CO<sub>2</sub> (Kwon et al. 2009). Furthermore, although POC remineralization is known to vary spatially in the oceans, most global biogeochemical models that compute ocean carbon sequestration from sinking POC assume that remineralization is spatially uniform because its variability among ocean regions has not been adequately quantified. Hence, quantifying the ocean-wide variability of POC remineralization is of high priority to climate research but sediment trap data are too scarce to allow an appropriate estimation of its spatial variability. Here, in order to provide a first regionalized estimate of remineralization (here the exponent of the Martin's power relationship) based on the Longhurst's provinces, I combined flux estimates based on the UVP particle size distribution, with flux estimates using the particle-reactive radionuclides disequilibrium between <sup>238</sup>U and <sup>234</sup>Th, and a global database of deep moored sediment trap flux measurements (Figure 9). Merging sediment trap data with particle radionuclides I could calculate a set of potential remineralization values *per* Longhurst's provinces (Guidi et al. 2015). In addition, I could calculate a similar set of values based on the UVP data and therefore compare each others (Figure 9). In that research paper we obtained the first regionalized estimates of remineralization in biogeochemical provinces, where these estimates range between -50 and +100% of the 0.81 commonly used globally uniform remineralization value. We applied the regionalized values to satellite-derived estimates of upper ocean POC export to calculate regionalized and ocean-wide deep carbon fluxes and sequestration. The resulting value of global organic carbon sequestration at 2000m is calculated to be 0.33 Pg C yr<sup>-1</sup>, and 0.72 Pg C yr<sup>-1</sup> at the depth of the top of the permanent pycnocline, which is up to 3 times higher than the value resulting from the commonly used approach based on uniform remineralization and constant sequestration depth. Finally, we also have shown a strong statistical relationship at the global scale between remineralization and the satellite-derived size structure of the phytoplankton assemblage in surface waters. Overall, the wide regional variability in remineralization, and its correlation to the phytoplankton community structure, stresses the importance of using spatially variable values of organic carbon remineralization parameters to estimate or model the feedback of ocean carbon remineralization on atmospheric carbon.



**Figure 9:** A) Example of locations of  $^{234}\text{Th}/^{238}\text{U}$  disequilibrium data, deep sediment traps deployments, and UVP profiles in the South Pacific Subtropical Gyre (SPSG). B) Resulting distributions of the exponent of the Martin's power relationship calculated using UVP profiles and with  $^{234}\text{Th}/^{238}\text{U}$  combined with deep sediment traps. The two distributions belonged to the same statistical population (Mann-Whitney U test,  $p$ -value > 0.05).

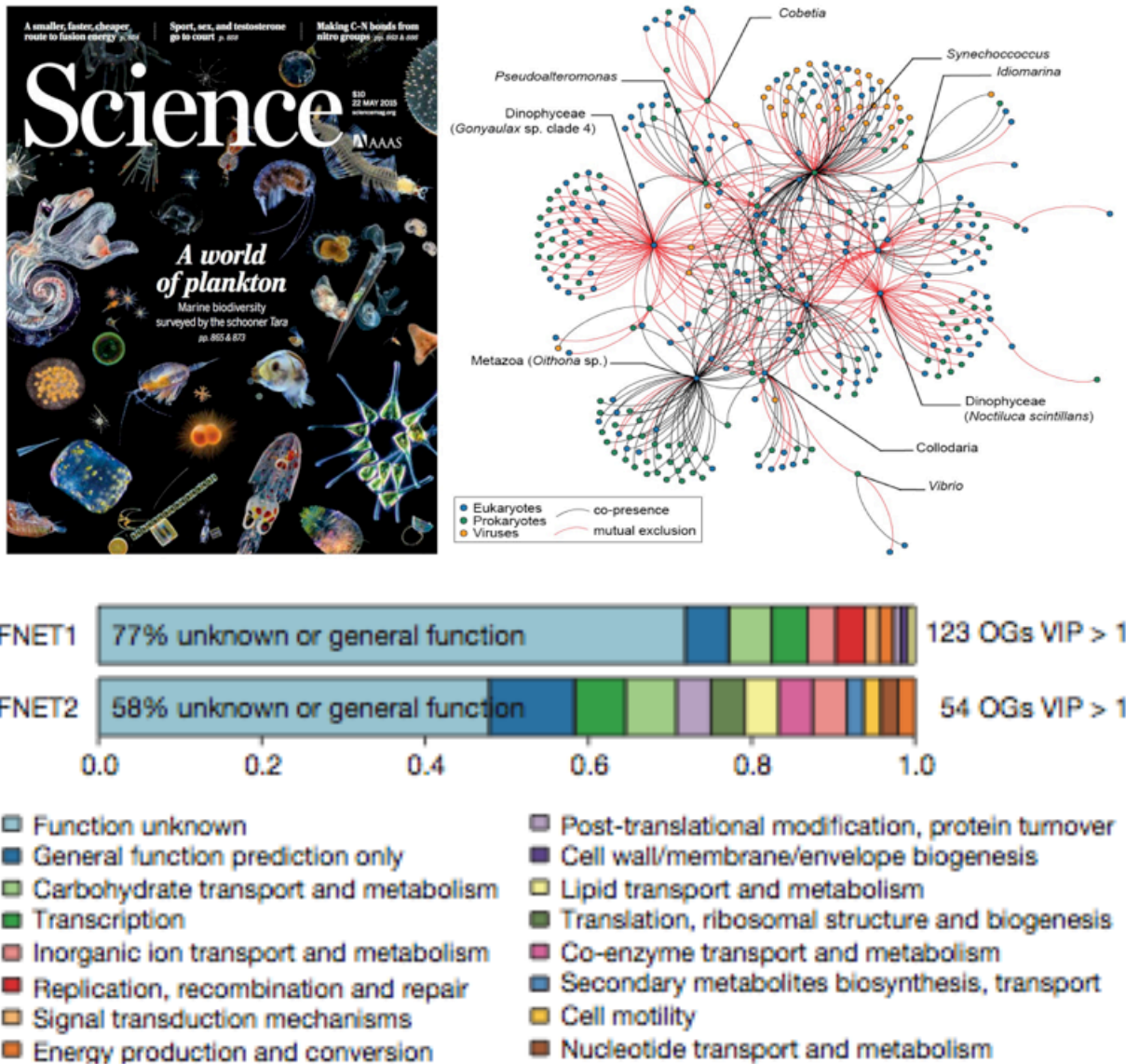
### 3. INCLUDING -OMICS TO STUDY THE BIOLOGICAL CARBON PUMP

#### a. COMMUNITY STRUCTURE AND CARBON EXPORT

A large number of studies have shown that the strength of the biological pump is directly correlated to the abundance of certain plankton species or phytoplankton community structure (Guidi et al. 2015; Guidi et al. 2009b). However, the structure of the whole community (virus to large eukaryotes) involved in carbon export has remained poorly understood. The *Tara* Oceans expedition (2009-2013) is the largest DNA sequencing effort ever done for the ocean revealing around 40 million genes, the vast majority of which are new to science, thus hinting towards a much broader biodiversity of plankton (from viruses to eukaryotes) than previously known (Brum et al. 2015; De Vargas et al. 2015; Sunagawa et al. 2015; Figure 9, left panel). Thanks to network analysis, these data also allowed to predict how these diverse planktonic organisms interact (Lima-Mendez et al. 2015; Figure 9, left panel). These resources provided a unique opportunity to look at the biological pump integrating its entire biological complexity, describing the first 'planktonic social network' (Figure 10, right panel) associated with carbon export in the oligotrophic ocean (Guidi et al. 2016).

In that research article we showed that specific plankton communities, from the surface and deep chlorophyll *a* maximum, correlate with carbon export at 150m 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 (up to 89% for the viral genes) of the variability in carbon export in these regions. These findings can be used as a basis to include biological complexity and guide experimental work designed to inform climate modelling of

the global carbon cycle. Such analyses, scaling from genes to ecosystems, may open the way to the development of a new conceptual and methodological framework to better understand the mechanisms underpinning key ecological processes.



**Figure 10:** The left panel is the cover of the special issue of Science featuring the 5 research articles I co-authored. The right panel presents the “plankton social network” related to the carbon export in the oligotrophic ocean and published as an article in Nature (Guidi et al. 2016). The bottom panel highlights key bacterial functional categories associated with carbon export at 150 m at global scale. It’s also worth noting that a co-author on a letter in the same issue of Nature that focuses on the global distribution of radiolarian that were identified as a key group in the carbon export network (Biard et al. 2016)

### b. SPECIES VS FUNCTIONS

Based on the above, I contributed to a review article published in Nature Geoscience in 2017, in which we assessed the role of diatom diversity on the biological carbon pump from past to future climate scenarios. Indeed Diatoms sustain the marine food web and contribute to the export of carbon from the surface ocean to depth. They account for about 40% of marine primary productivity and particulate carbon

exported to depth as part of the biological pump. Diatoms have long been known to be abundant in turbulent, nutrient-rich waters, but observations and simulations indicate that they are dominant also in meso- and submesoscale structures such as fronts and filaments, and in the deep chlorophyll maximum. Diatoms vary widely in size, morphology and elemental composition, all of which control the quality, quantity and sinking speed of biogenic matter to depth. In particular, their silica shells provide ballast to marine snow and faecal pellets, and can help transport carbon to both the mesopelagic layer and deep ocean.



**Figure 11:** Diatom lineages and their role in net primary production (NPP) and carbon export (Ce) as revealed by high-throughput DNA datasets. Regression-based modelling was used to study correlations between meta-barcoding data and environmental parameters. A heatmap highlights groups of lineages, which are the best statistical predictors of CE and/or NPP in

the oligotrophic low-latitude oceans. The blue and green groups show a significant positive correlation to NPP and CE, whereas the red group is only contributing to CE. Such analysis highlights the potential contribution of specific lineages to different aspects of the biological carbon pump

In this paper (Tréguer et al. 2017) we showed that the extent to which diatoms contribute to the export of carbon varies by diatom type (Figure 11), with carbon transfer modulated by the Si/C ratio of diatom cells, the thickness of the shells and their life strategies; for instance, the tendency to form aggregates or resting spores. Model simulations project a decline in the contribution of diatoms to primary production everywhere outside of the Southern Ocean. We argue that we need to understand changes in diatom diversity, life cycle and plankton interactions in a warmer and more acidic ocean in much more detail to fully assess any changes in their contribution to the biological pump.

#### 4. SYNTHESIS

These above results represent a small fraction of the total production during my past 4 years as a CR2 researcher at the CNRS. However decided to highlight them because they correspond to the most remarkable outcomes of the past research. In particular, I contributed to and/or led 7 papers published in Science and Nature in 2015 and 2016, as part of one of the *Tara* ocean coordinator. During that research, I had the opportunity to create collaborations with researchers with very different background (biology, evolution, computer sciences, etc...), which contributed to increase my creativity and the multidisciplinary research that I'm trying to do. The MEGALODOM project, funded by the Mission pour l'Interdisciplinarité from the CNRS, is one of the outcomes of these collaborations. Finally, in 2016, I applied to an ERC – Consolidator Grant that was very well evaluated but unfortunately not funded. I'm presenting this project (CARBOMICS) in the following section and will take benefits from the reviews to improve it and resubmit in 2019.

### III. RESEARCH PROJECT

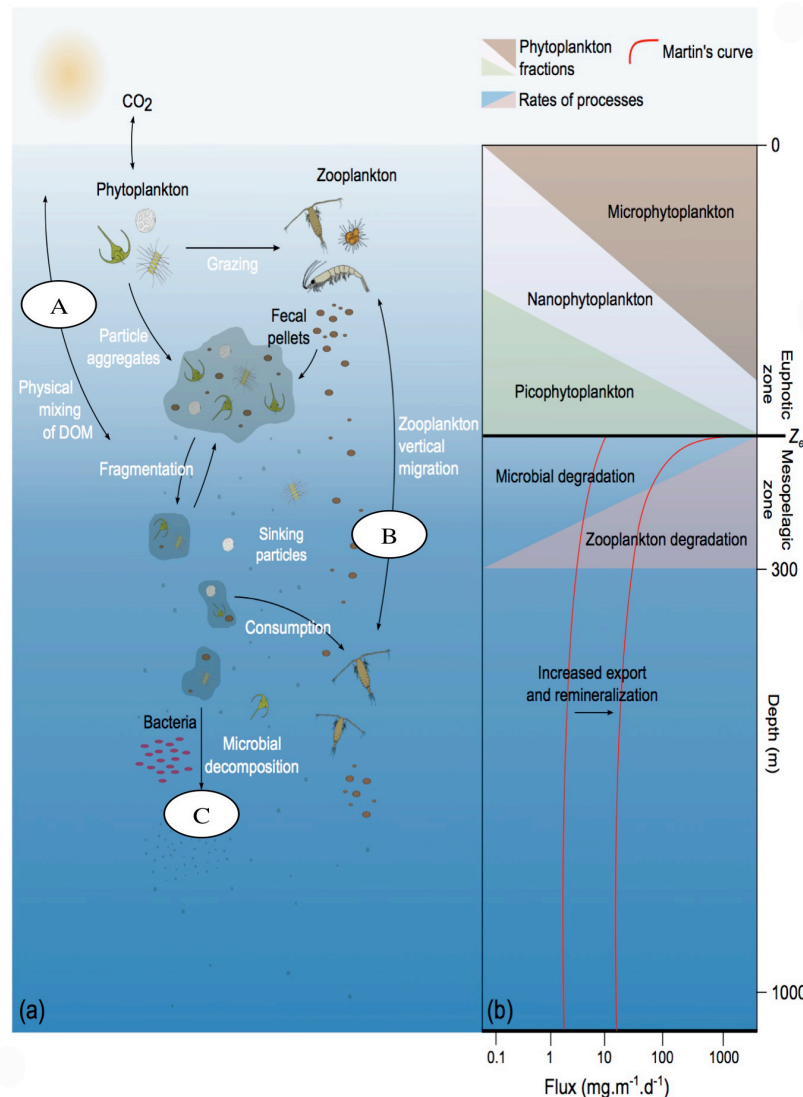
#### STATE-OF-THE-ART AND OBJECTIVES

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##### 1. GENERAL CONTEXT

In the context of our changing climate the future evolution of the **Ocean Carbon Pumps** and related ecosystem remains uncertain because of poorly constrained processes. This concept of ocean carbon pumps was proposed early on by *Volk and Hoffert* (1985) to explain the vertical gradient of CO<sub>2</sub> that exists in the World Ocean. In their paper, they defined three vertical ocean pumps, corresponding to different forms of carbon in the marine environment: the *solubility pump* for dissolved inorganic carbon, the *carbonate pump* for particulate inorganic carbon, and the *soft-tissue* pump (also called organic carbon pump, but more generally biological carbon pump) for particulate organic. Recently, the *microbial* carbon pump was added to the system (Jiao et al. 2010), which compared to the other pumps, sequesters carbon in refractory dissolved organic carbon at all depth. **CARBOMICS focuses on the organic component of the Biological Carbon Pump (BCP)**. The (BCP) is exporting ~5-12 PgC yr<sup>-1</sup> from the surface to the mesopelagic layer from which ~0.2 PgC yr<sup>-1</sup> is stored in sediment for millennia (IPCC, WG1-Chapter 6; Ciais et al. 2013) maintaining the vertical gradient of carbon in the ocean, contributing to the functioning of the solubility pump. Although this is a small fraction of the total removed carbon by the ocean (2 PgC yr<sup>-1</sup>), changes in the BCP strength could dramatically exacerbate or dampen changes in our climate (Kwon et al. 2009). Surprisingly, we currently do not know whether the ocean will continue to take up carbon at the same pace, how long the exported carbon will remain isolated from the atmosphere, and how the biological

pump will respond to climate change (Passow and Carlson 2012). **These major unknowns led the international scientific community to agree that it is urgent to better characterize the dynamics of the BCP** (Burd et al. 2016). Among others, NASA is launching an intensive Field Campaign Project (EXPORTS; 2017-2021; Siegel et al. 2016) to quantify the state of the BCP in the North Pacific and North Atlantic (<http://exports.oceancolor.ucsb.edu>). Multiple other countries are joining in the effort (COMICS-UK, SEAPUMP-Germany, FLUXES-Spain).



**Figure 11:** Representation of the biological carbon pump and processes regulating the flux of particles in the ocean. CO<sub>2</sub> fixed during photosynthesis by phytoplankton in the upper ocean can be transported / exported to depth via 3 major processes, (A) physical mixing, (B) active transport by zooplankton migration and (C) passive sinking of particles produced at the surface. The particle flux decreases with depth as aggregates are fragmented, decomposed and remineralized returning carbon to the atmosphere. This decrease is ideally modeled by the “Martin curve”. Particle size, form, and composition all affect sinking and remineralization rates (Benoiston et al., (2017) modified from (a) Buesseler et al., (2007a) and (b) Guidi et al., (2009b).

On a global scale the **BCP** is powered by three closely related processes: **particle production, their export to the bottom of the ocean, and their remineralization.** Knowledge of the amount of particles produced at the surface by plankton is insufficient to estimate the particle export to depth. In addition, it was suggested that **plankton community structure and interactions** plays a major role in the efficiency of the BCP (Guidi et al. 2016; and Figure 10).

However, spatial and temporal variability of the BCP is still largely unknown both because of the lack data in the deep ocean (Burd et al. 2010) and the lack of studies that connect the ecosystem complexity (diversity and function from viruses to large eukaryotes, and species interactions) to export and export efficiency (Burd et al. 2016).

## 2. EMERGING NEW TECHNOLOGIES

Over the past 30 years, direct and indirect approaches have been developed to study and quantify carbon fluxes through the water column. Direct approaches are based on **sediment traps**, both mooring and drifting, that have been widely deployed over the global Ocean to measure carbon and other nutrients fluxes at various depths. Although, these instruments are efficient to collect sinking particles, they are well known to integrate fluxes and to be biased by lateral advection, making estimations of the spatial and temporal variability of the BCP particularly difficult (Buesseler et al. 2007a). Indirect approaches include the use of naturally occurring **particle-reactive radionuclides** such as disequilibrium between  $^{238}\text{U}$  and  $^{234}\text{Th}$  (Buesseler et al. 2006; Cochran and Masque 2003) or more recently between  $^{210}\text{Pb}$  and  $^{210}\text{Po}$  (Le Moigne et al. 2013). In order to quantify elemental export fluxes, these indirect methods need to determine the ratio of carbon to  $^{234}\text{Th}$  or  $^{210}\text{Po}$  in sinking particles that are usually collected with *in-situ* pumps. This approach is not without biases as *in-situ* pumps may cause rupture of aggregates (Gardner et al. 2003) and the adsorption of dissolved matter onto the membranes filters (Zhou et al. 2016) both disturbing the size structure of particles and their elemental concentrations. In addition, indirect approaches to estimate carbon fluxes using **optical** (Briggs et al. 2011; Estapa et al. 2013) or **imaging sensors** (Guidi et al. 2008b) also emerged over the last 10 years providing opportunities to study the spatial and temporal variability of the BCP. However these methods are based on particles properties (light attenuation, backscattering, particle size) therefore providing biased absolute values of carbon fluxes. Because none of the above methods used individually is perfect when it comes to study the BCP and its variability, it's important to use multiple instruments/sensors/proxies simultaneously to better apprehend this complex chain of processes (Guidi et al. 2008b; Guidi et al. 2015; Ramondenc et al. 2016). For example, the Underwater Vision Profiler (UVP; Picheral et al. 2010) allow fast measurements of *in-situ* particle size distribution (PSD; 100  $\mu\text{m}$  to few mm) and concentration. These parameters used simultaneously with conventional sediment trap measurements of particle flux led to the first global relationship between PSD and carbon flux (Guidi et al. 2008b). Since then, this relationship has been used in more than 60 studies (i.e Iversen et al. 2010; Jouandet et al. 2011)

In parallel, next generation sequencing techniques have been developed, providing an unprecedented level of biological, ecological, and evolutionary information from the human gut microbiota to marine microbial oceanography. Notably, molecular and genomic techniques applied to ocean sciences appeared as a revolution for the study its biogeochemistry (Delong 2009; Delong and Karl 2005; Doney et al. 2004; Worden et al. 2015). Indeed, newly available **high throughput sequencing** data gave access to the biology of the ocean **from gene to the ecosystem level**. For example, this new source of biological information demonstrated their potential in the context of the **Tara oceans expeditions (2009-2013)**. This expedition was the largest DNA sequencing effort ever done for the ocean revealing around 40 million genes, the vast majority of which are new to science, thus hinting towards a much broader biodiversity of plankton (from viruses to eukaryotes) than previously known (Brum et al. 2015; De Vargas et al. 2015; Sunagawa et al. 2015). Thanks to novel methods of computational modeling, these data also allowed to predict how these diverse planktonic organisms interact (Lima-Mendez et al. 2015). Used together, these resources (biodiversity and planktonic interactions) provided a unique opportunity to look at the biological carbon pump integrating its entire biological complexity, describing the first 'planktonic social network' associated with carbon export in the oligotrophic ocean (Guidi et al. 2016).

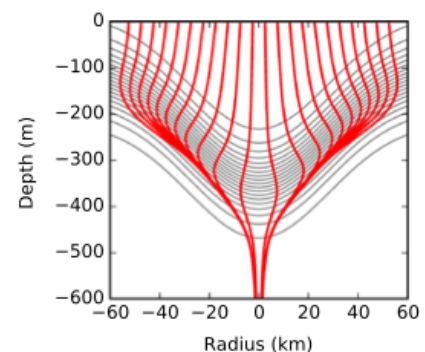
Based on these new technologies, it appears timely to propose a transformative view of the BCP combining cutting edge **imaging sensors** and **genomics approaches** to simultaneously measure particles in the ocean and better understand who is making and degrading them, therefore influencing the BCP.

### 3. THE BCP SPATIAL VARIABILITY



The scales of variability of the BCP, including blooms/production, carbon export events, and remineralization processes determine the appropriate vertical, horizontal, and temporal sampling resolution necessary to capture the signal. Mesoscale eddies are known to cover 1/6 of the world ocean (Chelton et al. 2011) and to be important contributors to spatiotemporal variability of upper ocean biology and biogeochemistry (Benitez-Nelson et al. 2007; Boyd et al. 2007; Boyd et al. 2000; Mahadevan and Archer 2000; Mcgillicuddy et al. 2007; Mcgillicuddy et al. 2003; Waite et al. 2016a; Waite et al. 2016b). In general, physical mechanisms such as frontogenesis, geostrophic adjustment, ageostrophic flow can lead to higher particle concentrations in areas of low productivity, promoting the formation of aggregates, and increasing the local efficiency of the biological pump (Figure 12). Anticyclonic eddies generate a convergence of surface water toward their center due to Ekman transport (Klein and Lapeyre 2009). However, high vorticity occurs on their edges, potentially generating larger particles by aggregation, therefore enhancing particle export. Similar patterns were found in several eddies in the North Pacific Subtropical Gyre (Guidi et al. 2012), in the oligotrophic western North Pacific Ocean (Shih et al. 2015), in the northern South China Sea (Zhou et al. 2013) or in the Western Mediterranean Sea (Gorsky et al. 2002; Ramondenc et al. 2016).

**Figure 12:** Modeled particle trajectories using a simple model of eddy spin-down predicting that ageostrophic flow concentrate particles in the eddy center, increasing the local efficiency of the BCP. Particle trajectories with sinking rate of 5 m d<sup>-1</sup> (in red) plotted against ageostrophic velocity. Grey contours show the density field, which is assumed to be rotationally symmetric (modified from Waite et al. 2016b).



There are increasing evidences that the BCP is highly influenced by surface physical mesoscale processes. **However, there is still no clear link between the plankton community composition and interactions in the surface layer of the ocean, and the vertical transfer of carbon through sinking particles at the meso/sub-mesoscale level.** Indeed, traditional tools to measure particle flux, such as sediment traps, are not adequate to capture fine spatial and temporal variability of the flux. Combining traditional approaches with autonomous platforms, like gliders/floats, and new imaging instruments, like the UVP, would provide a new picture of the BCP dynamic and allow addressing relevant processes at scales that couldn't be sampled previously.

I will exploit **new technologies to study the spatial and temporal variability of the BCP** in a dynamic environment and relate this variability to the surface ecosystem structure.

To summarize, **CARBOMICS** propose an innovative, multiscale, multidisciplinary approach of the BCP from **gene to the ecosystem** level in order to understand processes controlling the BCP focusing on the following central and unresolved question:

**What is the impact the ecosystem complexity (diversity and function from viruses to large eukaryotes, species interactions, and ocean dynamic) on the BCP?**

To address this question CARBOMICS will be articulated around 2 research objectives:

- I. Understand how changes in plankton communities and particle properties impact the BCP?
- II. Understand how mesoscale physical and biological activity (~100 km) impacts the spatial and temporal variability of the BCP?

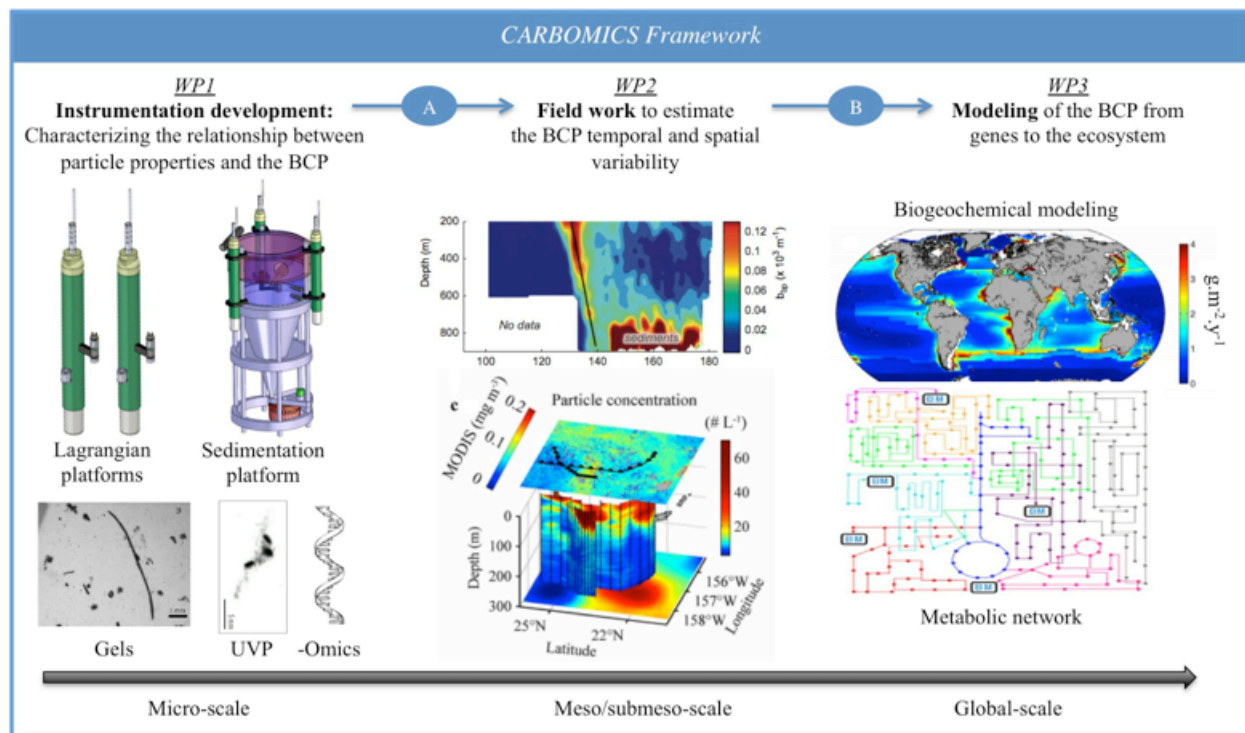
To respond to the above objectives, I propose the following approach divided in 3 Work Packages (WP).

WP1) **Instrumentation development:** Characterizing the relationship between, plankton communities, particle properties and the BCP.

WP2) **Field programs:** Characterizing fine-scale spatial and temporal variability of the BCP

WP3) **Modeling (from genes to ecosystem):** Integrating newly available high-throughput sequencing data with the above observations to better understand the complexity of the biological component of the ecosystem and relate this to the BCP functioning across scales.

## METHODOLOGY



**Figure 13.** CARBOMICS framework. WP1 corresponds to the instrumentation development phase (sedimentation and lagrangian platforms). Images show examples of aggregates seen with the UVP and collected in sediment traps with gels. Particles will be analyzed both by imaging and –omics approaches. WP2 (top) represents an example of a time-series of “particles” as seen with a backscatter sensor mounted on floats (Briggs et al. 2011). WP2 (bottom) represents an example of a submesoscale study of carbon export in the North Pacific where the UVP was used to map aggregate distribution. WP3 shows a hypothetical representation of future maps of BCP (here carbon sequestration) as one of the outcomes of CARBOMICS using both biogeochemical and metabolic network modeling. A) The use of the lagrangian platform developed in WP1 will allow tracking the BCP over time with floats as never done before. The use of the sedimentation platform developed in WP1 will allow parameterizing particles sinking speed and map carbon flux at the mesoscale level using particle size distribution acquired with the UVP deployed from ships. B) Knowledge gained from WP2 will be used to improve the representation of sinking aggregates in biogeochemical models and develop new metabolic network modeling of the BCP.

The originality of **CARBOMICS** relies on its **multiscale / multidisciplinary** integrative approach to study and understand mechanisms driving the BCP. The 3 following WPs of CARBOMICS will lead to a better understanding of mechanisms driving the BCP from the micro-scale through the mesoscale leading to a major breakthrough in carbon-cycle research (Figure 13). CARBOMICS will benefit from the existing UVP database (more than 6000 profiles of particle size distribution) for a parameterization of sinking particulate matter and from the high throughput sequencing data collected during the *Tara* ocean

expeditions (including *Tara Oceans*, *Tara Polar Circle*, and the upcoming data from *Tara Pacific*). CARBOMICS will significantly advance our understanding of the BCP by **(WP1)** providing new **instrumentations** to simultaneously measure particle size distributions, sinking speed, and bacterial activity, **(WP2) participating to field programs** to study processes affecting the spatial and temporal variability of the BCP, **(WP3) bringing systems ecology to the oceanography** leading to a biogeochemical and metabolic modeling of the BCP.

## 1. INSTRUMENTATION DEVELOPMENTS

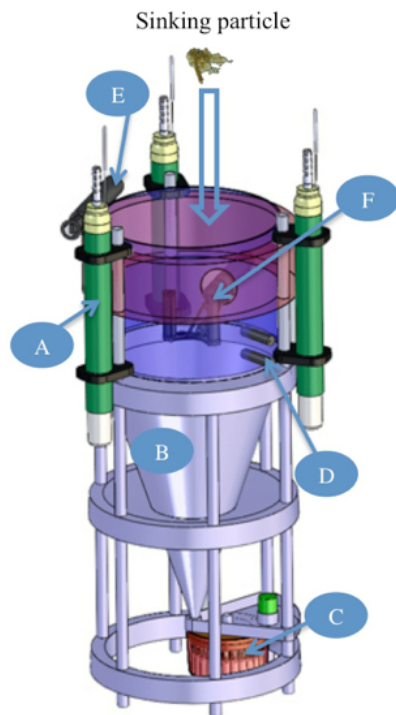
### a. BACKGROUND

Sinking marine particles are responsible for a significant fraction of the sinking carbon in the ocean (Buesseler et al. 2007b) and thus play an critical role in the BCP. Important efforts have been made to understand how sinking aggregates are formed in surface layers, sink through the water column and are consumed during their path to the bottom (Boyd and Trull 2007; Turner 2015). In particular, sinking speed variations have been attributed to particle size (Alldredge and Gotschalk 1988; Guidi et al. 2008b; Jouandet et al. 2011), composition, and density (Francois et al. 2002; Mcdonnell and Buesseler 2010). **However, there is still an intense debate in the oceanographic community to see if observed variations in sinking velocity of particles are primarily due their size or composition.** In addition, still very little is known on the plankton community (from viruses to large eukaryotes) that is making and using particles as they sink, therefore changing their properties. Overall, sinking speed is a critical variable in some biogeochemical models using a mechanistic approach of carbon export, but very little is known on its variability, increasing climate models uncertainties. Here I propose **(1)** to develop a new platform to characterize the sinking speed of particles and simultaneously study plankton communities that are making and using them, **(2)** to merge cutting edge autonomous platforms with imaging sensors, to track the BCP over time.

### b. Task 1: DEVELOPMENT OF A SEDIMENTATION PLATFORM MERGING SEDIMENT TRAPS, IMAGING AND OPTICAL SENSORS, AND META-OMICS MEASUREMENTS

Particle production, their active transport or passive sinking, and their remineralization directly mediate the BCP. Better understanding and constraining processes (biological and physical) affecting particles properties (size and composition) is key when studying this chain of processes. While particle size is fairly well constrained with imaging/optical instruments, very little is known on biological/microbial processes affecting them (Fontanez et al. 2015; Grossart and Ploug 2001; Simon et al. 2014; Simon et al. 2002). **Here, I propose to develop a new platform (Figure 14) that will allow simultaneous measurements of particle size, sinking speed, and microbial functional activity that lead to their transformation.** The following briefly described experimental setup will allow to first test the platform and get preliminary results before field deployments.

In order to estimate size and sinking speed of *in-situ* particles, I will develop a new platform, inspired from the non-commercially available PELAGRA - Sediment Trap from the National Oceanography Centre, in Southampton. Once developed, I will perform a “test” sedimentation experiment in the Bay of Villefranche-sur-Mer. This “sedimentation platform” will include a **UVP** [Box 1] that is a light-weight (<30 kg, details in *Picheral et al., 2010*) image-collecting detector. In its normal configuration, the UVP is looking downward not using full advantage of its light system. By changing the orientation of the UVP to horizontal, it will be possible to identify, size, and track individual particles as they fall through the plane of observation. This will allow establishing empirical *in-situ* relationships between particle size, shape and composition, and settling rate in the size range observable by the UVP (100  $\mu\text{m}$  – 2 cm).



**Figure 14:** Scheme of the sedimentation platform to simultaneously estimate the contribution of size and composition to particle settling speed. **A)** Float hydraulic pump technology allowing depth adjustment of the platform. **B)** Sediment trap like system (example PPS5) that will allow collection of particles through settling. **C)** Rotating poisoned, lived, or filed up with polyacrylamide gel cups to collect particle without alteration of shape and allowing various analysis. **D)** Two backscatter sensors, one outside and one inside to monitor particle loads. **E)** LISST to measure the particle size distribution of small particles ( $\sim 2 \mu\text{m}$  to  $200 \mu\text{m}$ ) outside of the range of the UVP. **F)** The UVP to monitor the size distribution of large sinking particles ( $\sim 100 \mu\text{m}$  to few mm) and measure their sinking speed. This scheme presents the general idea of the platform but it will evolve depending on the engineering constrained provided by the research engineer hired through CARBOMICS.

In addition to the UVP, a **LISST-200X** (Laser *In Situ* Scattering and Transmissometry, Sequoia Scientific, Inc.; Box1) will be deployed within the system, sizing particle ( $\sim 2 \mu\text{m}$  to  $200 \mu\text{m}$ ) outside of the range of the UVP and providing information on the water particle load. Also **2 backscatter sensors** [Box 1] will be associated to the platform (in and out) to monitor differences in water particle content inside and outside the settling experiment device. Furthermore particle fluxes will be analyzed during these experiments, using rotating **poisoned, lived, or filed up with polyacrylamide gel** sediment traps allowing retrieval of aggregates. Using the gel will simultaneously provide information on particle flux, particle size distribution, shape, porosity, and composition that will be compared to the size distribution from the UVP. A well-known caveat of sedimentation experiments is introduced by convection/vertical motion. Convection will be estimated by tracking small “neutrally” buoyant particles, on UVP images, in order to remove any potential upward water movement from settling speed estimates. Finally, the UVP will be placed in a cylinder to avoid advection. PSD and settling speed will be acquired several hours every day over a 3-week period in order to get statistical representative data.

#### **Box 1:** Key instruments specifications

- **The UVP** is a relatively light-weight ( $<30 \text{ kg}$ ) image-collecting optical detector that can be deployed to depths of 6000 m. It contains an intelligent camera, optics, pressure and angle sensors, acquisition and piloting board, Internet switch, hard drive and dedicated electronic power boards. The light source is a red LED strobe synchronized with a full frame Vision camera positioned perpendicular to the light slab and only illuminated and recording particles in dark background. The short flash duration allows a rapid lowering speed (up to  $1.5 \text{ m}\cdot\text{s}^{-1}$ ) without the deterioration of image quality. Processing of images is automated and made by the system during the recovery. The objects in each image are detected and enumerated automatically by custom-developed software. The software also monitors data from up to 8 analogue sensors and sends them to the camera with the pressure to interface them with the images in real time. The main functions of the UVP are to 1) quantify and determine the size of the large particulate matter stock (aggregates and free-living plankton), and 2) identify and quantify the large and fragile zooplankton species [Picheral et al., 2010].

- **The LISST 200X** measures the near-forward angular scattering distribution between  $0.1\text{-}20^\circ$  at  $670 \text{ nm}$ , which is a region of scattering that is strongly influenced by particle size. Using Mie scattering theory, the LISST estimates a particle size distribution based on an inversion of the shape (angular pattern) of forward

scattering, and the concentration of particles based on the magnitude of scattering that reaches the detector. It also measures beam transmission at an acceptance angle of  $0.03^\circ$ , which is an indicator of bulk particle concentration and has been strongly related to particulate organic carbon in previous studies (Stramski et al. 2008).

- **Backscatter sensors** output a factory-calibrated volume scattering coefficient  $\beta$ , which is then used to calculate the particulate backscatter  $bbp$  as described in the Wetlabs ECOBB2FLS Manual ([www.wetlabs.com](http://www.wetlabs.com)). Mean diameter of suspended particles will also be inferred from high-resolution time series of  $bbp$  according to Briggs et al., (2013).

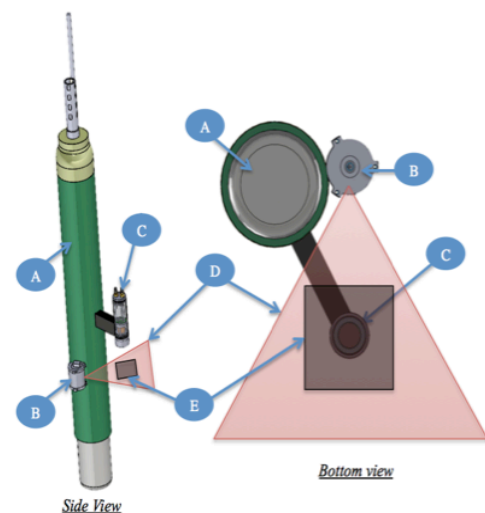
- **The remA sensor** is composed by one downwelling irradiance sensor (OCR 504: 380, 410 and 490nm + PAR) and one ECO3 sensor (Chlorophyll-a fluorescence, Colored Dissolved Organic Matter and particle backscattering coefficients at 700nm).

(2) In order to better understand biological processes that lead to transformation of sinking particles, I will simultaneously perform a complementary experiment using a **meta-omics** (*MetaB: metabarcoding, MetaG: metagenomic, MetaT: metatranscriptomic*) approach to reveal the composition and structure of “plankton” communities on aggregates collected by the sediment traps. Meta-omics analysis involves next-generation sequencing techniques for whole DNA and/or RNA of genetic material isolated from environmental samples providing an exhaustive (and potentially unbiased / less biased) sampling from a mixed planktonic assemblage (Brum et al. 2015; De Vargas et al. 2015; Fontanez et al. 2015; Simon et al. 2014; Sunagawa et al. 2015). Environmental RNA and DNA communities (*free-living* and *particle-attached*) will be extracted, quantified and sent to an independent company for high-throughput sequencing. **Overall, this experiment will highly improve our understanding of the relationship between particle size, composition, sinking rate, and microbial community and activities in the studied system (i.e. the link between biogeochemical cycles and biodiversity).** Although observations of sinking particles in the open Ocean may not exactly replicate the one of the Bay of Villefranche-sur-mer, this experiment will provide valuable insight into the effects of plankton and bacterial communities, aggregate composition and morphology on sinking rates of natural particles.

### c. TASK 2: A LAGRANGIAN PLATFORM TO TRACK THE BCP OVER TIME (IMAGING-BIOGEOCHEMICAL-ARGO FLOATS)

**Figure 15:** Scheme of the lagrangian floats that I will develop through CARBOMICS to track the BCP over time. **A)** Float hydraulic pump technology **B)** Lighting source **C)** Intelligent camera that will size particles in-situ **D)** Collimated light field generated by the lighting source. **E)** Subpart of the lighted field where particles are sized and counted. B and C correspond to the OCTOPUS sensor.

The main mission of Biogeochemical-ARGO program is to contribute to the development of a bio-optical and biogeochemical component within the ARGO program (<http://biogeochemical-argo.org>). Profiling **Biogeochemical-ARGO floats**, in addition to a Seabird CTD, can be equipped with a remA sensor [Box 1], an Aanderaa oxygen optode and a SUNA nitrate concentration sensor allowing to measure (Oxygen, Nitrate, Chlorophyll a, CDOM, backscattering for suspended particles, downwelling irradiance). As part of a EU-H2020 BRIDGE project (<http://www.bridges-h2020.eu/>), I



am contributing to the development of a new imaging sensor named OCTOPUS. This sensor will be low-weight, low-energy, and low-cost with characteristics similar to the UVP therefore compatible with floats requirements. OCTOPUS prototype is schedule for early 2018. I propose to use this opportunity to develop **6 Imaging-Biogeochemical-ARGO floats** mounting OCTOPUS on Biogeochemical-Argo (Figure 15 to be able to track the BCP between 0 and 1000 m in a lagrangian mode. These floats will be deployed as part of field programs both in the North Atlantic and in the Mediterranean Sea (WP2)

#### *d. RISK ASSESSMENT*

All sensors, except OCTOPUS, used in the WP1 are already on shelf, however integrating them on 2 different platforms (task 1 and 2), require expertise and engineering time. In addition, I will devocate time to secure funding for a 4-year full time research engineer position as well as 60,000€ for subcontracting in order to insure successful developments. Marc Picheral, an experienced research engineer from the LOV in charge of the development of OCTOPUS, will dedicate some of his time to CARBOMICS in order to oversee the engineering work and facilitate knowledge transfer to the research engineer hired for CARBOMICS.

## *2. FIELD PROGRAMS*

### *a. BACKGROUND*

Mesoscale (~100 km) eddies cover 1/6 of the world ocean (Chelton et al. 2011) and mesoscale and submesoscale (~10 km) physical processes have been shown to be important contributors to spatiotemporal variability in upper ocean biogeochemistry and hydrography (Benitez-Nelson et al. 2007; Guidi et al. 2012; Mcgillcuddy et al. 2007; Omand et al. 2015; Villar et al. 2015). In addition, submesoscale frontal structures, which appear to be ubiquitous throughout the upper ocean, may be important in supplying nutrient to the upper ocean (Calil and Richards 2010). High-resolution satellite imagery also shows that meso- and submeso-scale features can account for 50% of the horizontal variance in ocean color (Lima et al. 2002). In contrast, **very little is known about their impact on the deeper layers such as the mesopelagic realm and in particular on the spatial and temporal variability of the BCP**. Here I propose to use the instrumentation developed in WP1 to contribute to field programs, using cruises opportunities **(1)** in the North Atlantic and **(2)** in the Mediterranean Sea in order to compare the 2 systems. I will study both the spatial and temporal variability of the BCP that will be related to compositions and interactions of surface plankton communities.

### *b. TASK 1: FIELD PROGRAM IN THE NORTH ATLANTIC*

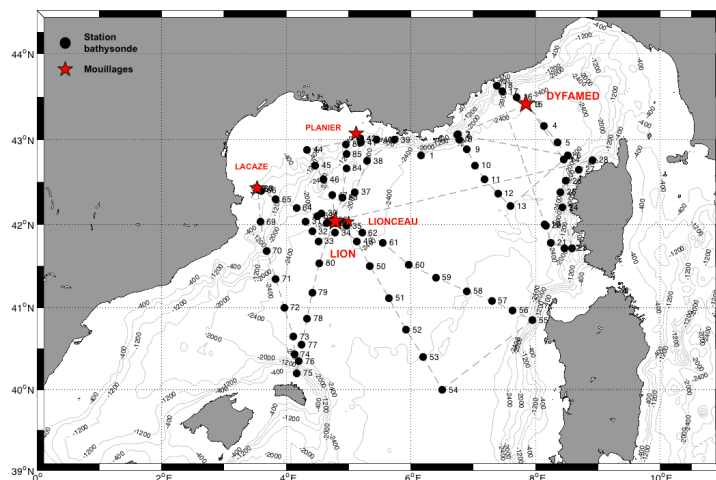
The North Atlantic represents one of the most productive spring phytoplankton bloom of the world's ocean, starting first within the European basin in March and propagating northwards within the sub-polar region in April and May (Henson et al. 2009). This strong bloom generates an important pulse of sinking material which accounts up to 18% of the global biological carbon pump (Sanders et al. 2014). As a consequence, the North Atlantic has been identified as an efficient ocean to export carbon to depth (Buesseler and Boyd 2009; Guidi et al. 2015). However this ocean is also strongly under the influence of mesoscale eddies, impacting the spatial variability of the BCP (Guidi et al. 2007). Furthermore, fixed sediment trap data demonstrated that export events are not necessarily recurrent over years indicating that the BCP in the North Atlantic is also variable in time (Lampitt et al. 2010).

For the above reasons, an international field program, led by the French community, is currently being developed in this region **targeting mesoscale eddies close to the Porcupine Abyssal Plain (PAP) fixed-point sustained observatory**. This particular location has been selected for logistical motivations

and to leverage collaborations with NASA-EXPORTS and the UK-COMICS field programs. The long history of observations, regional coverage, and already deployed floats and sediment traps near this station will contextualize the proposed study. The following four themes will be tackled by this field campaign (1) Characterization of the physical dynamic of the studied region (2) Quantity and quality of the organic matter (OM) produced in surface waters related to the structure and dynamics of the primary producers (3) Identifying the role of size and composition (mineral ballasts) on the OM exported towards the meso- and upper bathypelagic layer (4) Linking the structure and dynamics of the microbial and zooplankton communities leading to remineralization of the OM in the meso- and upper bathypelagic layer. Instrumentations developed in WP1 (sedimentation and lagrangian platforms) will be deployed during this field program in order to bring insights on the role of the structure of the ecosystems, as well as on the size and composition of particles, on the BCP variability. Here, as part of CARBOMICS, I propose the following activities:

- a Mapping of particle size distribution over entire sampled area using the UVP deployed from the ship and mounted on the rosette frame
- b Deployment of the sedimentation platform in the center of the selected mesoscale eddy in order to characterize the relationship between particle size, composition, and sinking speed. This relationship will be then propagated to data collected in (a)
- c Deployment of 3 Imaging-Biogeochemical-ARGO floats to track the evolution of the BCP over the lifetime of the floats. The 3 floats will be deployed at the center, on the edge and outside of the selected mesoscale eddy. This task will benefit from the expertise and the involvement of the LOV in the Biogeochemical-ARGO program.

### c. TASK 2: FIELD PROGRAM IN THE MEDITERRANEAN SEA



**Figure 16:** Overall annual sampling strategy of the MOOSE project. Black dots represent Hydrological casts with seawater sampling for oxygen, dissolved inorganic carbon, nutrients, pigments. The UVP is deployed at each station. Red stars correspond to long-term monitoring stations including the DYFAMED station.

The Mediterranean Sea pelagic ecosystems are mainly limited by inorganic nitrogen and phosphorus available for bacteria and planktonic growth (Berland et al. 1980; Krom et al. 1991; Thingstad and Rassoulzadegan 1995). This characteristic results in a

trophic status varying from oligotrophic to ultra-oligotrophic from the Western to the Eastern basins (Moutin and Raimbault 2002), leading to particle size, particulate organic carbon export, and the contribution of microphytoplankton to the phytoplankton community structure, all decreased following this latitudinal gradient (Ramondenc et al. 2016). In addition, the above general pattern at the scale of the Mediterranean basin is locally modified by meso- to submeso-scale local structures (Ramondenc et al. 2016; Stemmann et al. 2008). Because of these characteristics and marked “trophic” differences with the North Atlantic Ocean, this enclosed Sea is a perfect study site for comparison of the BCP based on 2 contrasted systems.

The MOOSE program is a CNRS-INSU initiative for building an efficient integrated observation network in the North Western Mediterranean Sea (Figure 16) in order to observe its long-term evolution in the context of climate change and anthropogenic forcing.

In particular MOOSE provide ideal platforms to develop and test new sensors in order to acquire new parameters useful to observe marine ecosystem changes. In this context, MOOSE aims to a multi-disciplinary observing system in the North Western Mediterranean Sea. Here I propose to benefit from this project to deploy instruments developed in CARBOMICS (WP1) performing the following activities:

- a Deployment of the sedimentation platform at the DYFAMED station to characterize the relationship between particle size, composition, and sinking speed. This relationship will be then propagated to UVP data collected during the MOOSE annual surveys.
- b Deployment of 3 Imaging-Biogeochemical-ARGO floats at the DYFAMED station to track the evolution of the BCP over lifetime of the floats in the NW Mediterranean Sea.

#### d. RISK ASSESSMENT

The field strategy developed in WP2 is based on cruise opportunities. **The field program in the North Atlantic** partly relies on ship-time that has been requested to the French government (project APERO in preparation). However, if this grant is not funded, this will not directly impact CARBOMICS as several other opportunities will be available in the same region. Indeed, station PAP is a long-term monitoring station (<http://projects.noc.ac.uk/pap>) and I will be able to leverage my current collaborations (including researchers from the National Oceanography Center; NOC) to deploy instruments at this station. In addition, the American NASA-EXPORTS program is planned in the same region, providing additional opportunities for CARBOMICS. Ship-time for the **Mediterranean field program** is already secured through the MOOSE project (<http://www.moose-network.fr/>).

### 3. MODELING OF THE BCP FROM GENES TO THE ECOSYSTEM LEVEL

#### a. BACKGROUND

As presented above, **reminerzalization** and **sinking speed** of particles are important mechanisms impacting the BCP. Today, most studies attempting to describe the efficiency of the BCP use simple relationships modeling the attenuation of carbon flux with depth with a power law functions (Martin et al. 1987) or exponential functions (Suess 1980). In parallel, mechanistic modeling (1D model or 3D regional/global) is used to perform quantitative budgets of carbon (Giering et al. 2014) and to study the interplay between ocean dynamics and ocean biogeochemistry such as the lateral transport of organic material, subduction, elemental fluxes. Several factors such as the “ballast effect” (Armstrong et al. 2002; Dunne et al. 2005; Lombard et al. 2013), the ecosystem structure and composition (Boyd and Newton 1997; Guidi et al. 2016), temperature (Marsay et al. 2015; Matsumoto 2007), and the bacterial activity (Grossart and Ploug 2001) have been proposed to explain the variability of remineralization. However most of these processes are poorly constrained which explained why they are omitted in current biogeochemical models. In particular, despite its potentially critical role on the BCP, microbial diversity is only, at most, crudely represented in models and its impact is limited to the magnitude of the biological production and to the physical characteristics of the organic matter (size of the particles/aggregates) (Guidi et al. 2016). **Here I propose to improve the representation of sinking aggregates in biogeochemical models and develop new metabolic network modeling of the BCP using a microbial systems ecology approach.** These modeling approaches will go one step further in the mechanistic understanding of this process by considering particle size distributions and meta-omics knowledge. In order to achieve that goal, data collected during the field programs (WP2) will be merged and analyzed in the framework of the environmental-omics dataset from *Tara-Oceans* expeditions.

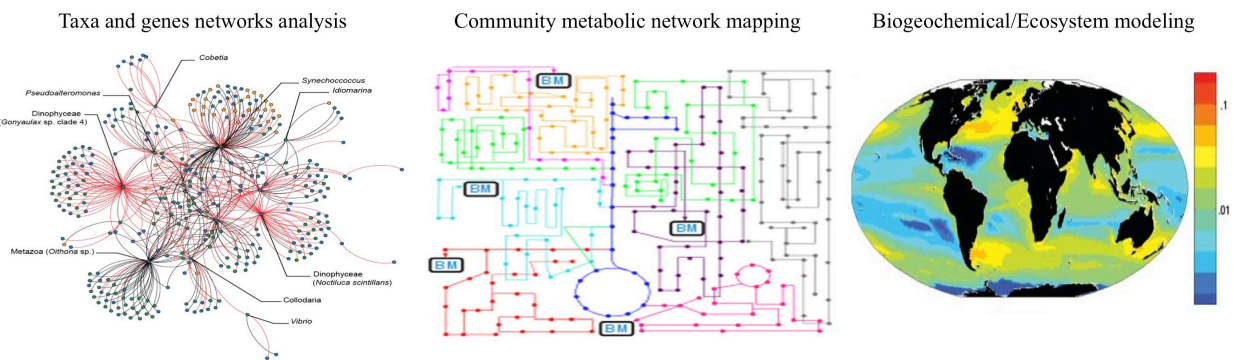


### b. TASK 1: BIOGEOCHEMICAL MODELING

The “Darwin project” model developed at MIT couples marine biogeochemical, ecosystem and physical modules, and captures the size and functional phytoplankton diversity (e.g. Dutkiewicz et al. 2012; Follows et al. 2007; Ward et al. 2012). The model ocean biogeochemistry includes explicit representation of cycles of carbon, oxygen, nitrogen, phosphorus, silicon, iron and alkalinity where inorganic, organic living and detrital forms of these elements are transported by the physical framework. The biogeochemical and biological tracers interact through the formation, transformation and remineralization of organic matter. Excretion and mortality transfer living organic material into sinking particulate and dissolved organic detritus, which are respired back to inorganic form. **However, though sinking of particulate matter is explicitly represented, the model to date has only crudely resolved export of organic matter.** Improving the parameterization of export is planned as part of this proposal. I will use the data collected through CARBOMICS and the UVP database for a parameterization of sinking particulate matter of the “Darwin project” model such as to better capture the global patterns and relationships between the plankton size distribution and the export fluxes. I will perform the following tasks:

- Propose a better parameterization of particle sinking speed, based on both the overlying community structure and the size distribution of detrital matter (linked to WP1 and WP2).
- Investigate how best to incorporate the spatial variability of the export fluxes (linked to WP2) in the global framework of “Darwin project” model.

### c. TASK 2: METABOLIC NETWORK MODELING



**Figure 17:** Models that will benefit from CARBOMICS. The **left panel** corresponds taxa/genes interaction networks (Guidi et al. 2016). The **middle panel** represents metabolic networks at the scale of the community (Erdrich et al. 2015). The **right panel** represents biogeochemical/ecosystems models (Follows et al. 2007). The overall figure is inspired and modified from Karsenti et al., (2011)

One of the main challenge in modeling marine ecosystems and biogeochemical cycles is to represent diversity, community structure and interactions, and how its spatial and temporal variations can be linked to nutrient distribution and carbon fluxes. Newly available meta-omics data have revealed that there is much greater diversity (from viruses to eukaryotes) than previously thought (Brum et al. 2015; De Vargas et al. 2015; Sunagawa et al. 2015) and that interactions are of primary importance when studying their link to the biogeochemistry of the ocean (Guidi et al. 2016; Lima-Mendez et al. 2015). This diversity is currently addressed in ocean biogeochemistry models by resolving the ecosystem size structure (*i.e.* multiple size classes of phytoplankton and zooplankton) or, using “functional groups” where groups are defined based on their biogeochemical functions (Le Quéré et al. 2005). In contrast, the “Darwin project” model (Follows et al. 2007) is initialized with a diverse plankton community, representing many functional types. The model let the fittest “organism” grow while the other decline to very low abundance or extinction. This framework allows to “self-select” a community structure based on its environmental characteristics

however using physiological but no metabolic information. This approach, extended to metabolic processes could lead to a new class of models that allow community structure to emerge and evolve in response to changing environmental conditions (Hood et al. 2007).

The BCP encompasses a chain of processes situated at the interface between biology, chemistry, and physics. The latest technological developments in high throughput sequencing and imaging techniques, allow studying the BCP from genes to entire ecosystem, and from the micro- to the global scale. High-throughput sequencing and functional genomics methods are revolutionizing the fields of environmental microbiology and microbial ecology, and are reshaping our view of microbial ecosystems. Computational biology advances enabling the description of environmental genomes and their expression *in-situ* have accompanied these new technologies.

In that context, modeling marine ecosystems is facing the great challenge of incorporating this – omics “complexity” to improve our understanding of the ocean biogeochemistry. In order to do so, we may need to change the way “interactions” (Figure 17) are currently represented in biogeochemical models (Hood et al. 2007). **CARBOMICS will fully take benefit of these advances advocating for a new modeling of the BCP that integrate meta-omics knowledge.** I propose the following approach:

- a From a gene relative abundance dataset (linked to WP1, WP2, and *Tara Oceans*), I will emphasize set of genes that are closely present (MetaG) or expressed (MetaT) on distinct samples and related to the BCP.
- b Since some of these genes encode for enzymes, the next step of the modeling will seek for these genes. Considering that these genes encode for **metabolic reactions**, the whole set of reactions will be linked within a **metabolic network** that link reactions when a product is a substrate of another.
- c This reconstruction will be based on **MetaPathways computational method**.

#### d. RISK ASSESSMENT

This modeling WP proposes 2 different approaches of the BCP. Task 1 relies on a better parameterization of particle sinking speed in biogeochemical models, more precisely the “Darwin project” model developed at MIT, which is low risk/high payoff” and based on the development of the sedimentation platform. On the other hand, task 2 is exploratory, based on metabolic modeling at the scale of the community, instead physiological status of “key” organisms, in order to represent the BCP. While this task is risky, it has the potential to dramatically transform the way we represent organisms in biogeochemical models. Based on my past experience, working at the interface between biology, physics, and computer science, I have acquired all tools and competences, in order to succeed and overcome this challenge.

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