



Sensors for ecology

Towards integrated
knowledge of ecosystems



www.cnrs.fr

Edited by Jean-François Le Galliard,
Jean-Marc Guarini and Françoise Gaill

Chapter 1

Integrated observation system for pelagic ecosystems and biogeochemical cycles in the oceans

Lars Stemann, Hervé Claustre, Fabrizio D'Ortenzio

1. Exploring the under-sampled ocean at a time of global changes

Our climate is changing at unprecedented rates, and there is an urgent need to improve the observation at global scales of pelagic ecosystems biodiversity and functioning. The oceans constitute the largest habitats on Earth for a highly diverse and numerous flora and fauna, and play a major role in the carbon cycle and climate. Ocean carbon sources and sinks are controlled by both physical (Sabine et al., 2004) and biological (Volk and Hoffert, 1985) processes that take place at various temporal and spatial scales. Based on global biogeochemical modelling and on the use of paleoproxies from sedimentary archives, the sedimentation of biogenic particulate matter from the euphotic zones of the ocean, a process named biological carbon pump, was shown to contribute significantly to climate variability (Sarmiento and Le Quere, 1996; Volk and Hoffert, 1985). However, the uncertainties in our understanding of the biological pump's functioning in today's oceans remain important. For example, recent reviews about the export of biogenic particles to the deep ocean showed that there is no consensus on the mechanisms controlling its spatial and temporal variability (Boyd and Trull, 2007; Burd et al., 2010). In particular, the roles of zooplankton and bacteria are not well understood.

Large temporal and spatial scales of marine surface production can be studied using satellite data (see III, 3). Alternatively, underwater autonomous floats technology has improved, thus allowing the exploration of the deeper layers of pelagic environments (Claustre et al., 2010b; Johnson

et al., 2009). Run since almost a decade, the international Argo project, which currently has an array of about 3,000 floats deployed in the world ocean, has proven to be an invaluable tool in modern physical oceanography (figure 1). The Argo project provides, on a routine basis and with unprecedented detail, the heat and salt content of the upper kilometre ocean, as well as water mass circulation. In addition, the BIO-Argo research group intends to add biogeochemical sensors to the current floats (Claustre et al., 2010a; 2010b; IOCCG, 2011).

To summarise individual researchers as well as agencies have recognised the fact that autonomous platforms array could provide 3D information not attainable by satellite platforms, where the vertical dimension is missing. Such a platform can also determine near surface properties when cloud cover impedes observations from space. Therefore, it seems useful and timely to coordinate the work of different groups to obtain coherent data sets to determine global patterns of nutrients, plankton and marine particles distribution in the oceans. Until now, studies of the biological pump based on Argo floats have used chemical or physical sensors, and have therefore overlooked the effects of living organisms. This is because available sensors were not adapted to record individual organisms but rather did bulk measurements of their biomasses. Bio-optical and imaging sensors dedicated to the identification and quantification of organisms living in pelagic environments are now being developed (see II, 2). The current limitation of Argo floats shall soon be overcome thanks to the miniaturisation of these sensors, which make them compatible for implementation on the Argo floats.

The abundance and size distribution of plankton and particles are among the relevant variables of pelagic environments that are not measured with standard floats (but see III, 3 for remote sensing techniques). The analysis of the size distribution of planktonic taxa is important because metabolic processes and many ecological traits, including population abundance, growth rate and productivity, spatial niche, trophic, competitive and facilitative relationships between species, are influenced by the body size of the organism (Brown et al., 2004; Gillooly, 2000; 2001; 2002). In addition, most marine organisms are opportunistic feeders and their prey size is limited by the diameter of their mouth. Therefore, predator-prey relationships are, in many marine systems, importantly determined by size (Hansen et al., 1997; Jennings and Warr, 2003). Furthermore, the particle diameter can describe multiple particle properties such as mass and settling speed or flux (Alldredge and Gotschalk, 1988), rate of colonisation by microbes and zooplankton (Kjørboe, 2000; Kjørboe et al., 2002, 2004) and coagulation rate (Jackson, 1990). The rate of biogeochemical activity such as aggregate remineralisation by bacterial activity or zooplankton consumption can also be proportional to the size of

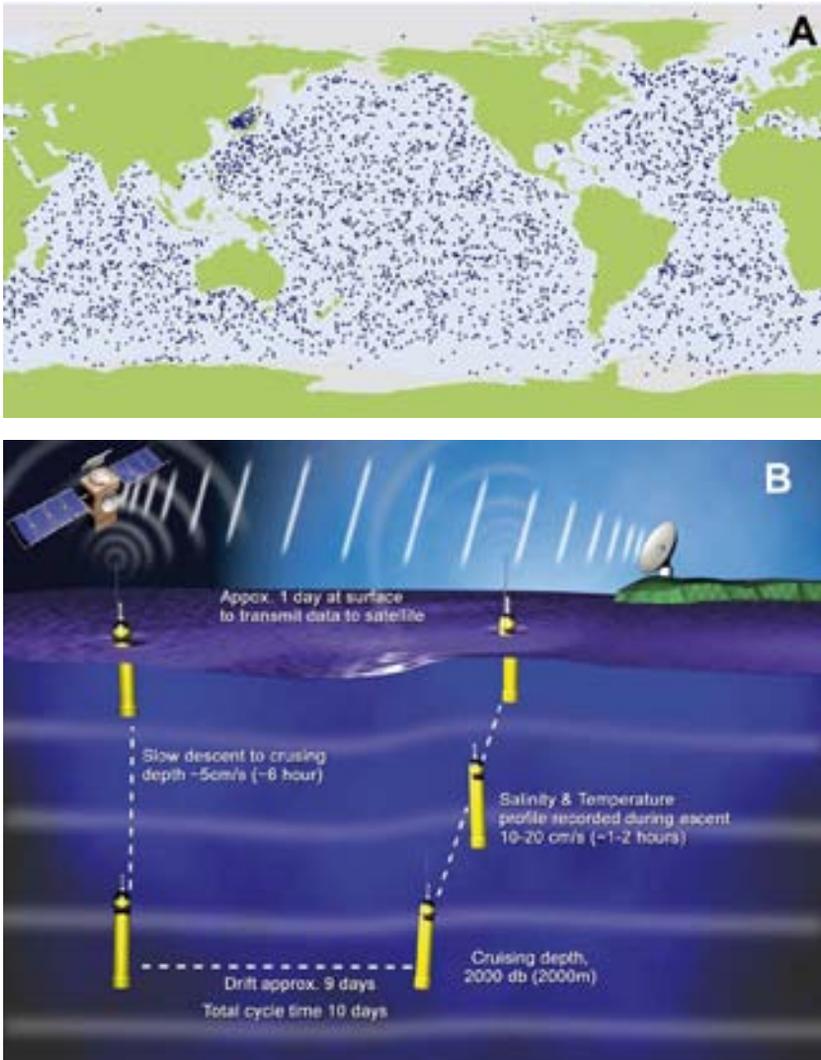


Figure 1: The Argo float is a global array of autonomous floats measuring pressure, temperature and salinity. A. Map showing the location of 3161 Argo floats in the world ocean (in May 2010, <http://www.argo.ucsd.edu/>). B. Schematic operating sequence of an Argo float. See section 2 for a full explanation of the sampling strategy and see figure 2 for an image of the deployment of a Provor float. © Argo, © jcommops.

particles and plankton (Kiørboe and Thygesen, 2001; Ploug and Grossart, 2000). Hence, because size of organisms or particles captures so many aspects of ecosystem functioning, the size distribution of plankton and

particles in a volume of water can be used to synthesise a succession of co-varying traits into a single dimension (Woodward et al., 2005).

Based on autonomous vehicles equipped with bio-optical sensors, pilot projects were launched or are planned for studying the size distribution of pelagic communities at different temporal and spatial scales (Boss et al., 2008; Kortzinger et al., 2004; Niewiadomska et al., 2008). If networks and arrays are implemented from these pilot projects to coordinate the efforts at the international level, a revolution in biological and biogeochemical oceanography will happen. The community will have access to an unprecedented observational array of vertically resolved “biogeochemical” and ecological variables (see next section for details). Developing such an *in situ* automated observation system will constitute an essential step towards a better understanding of biogeochemical cycles and ecosystem dynamics, especially at spatial and temporal scales that have been unexplored until now. Two main outcomes can be expected from a well-designed integrated observation system (Claustre et al., 2010a). The scientific outcomes include a better exploration and an improved understanding of both present state and change and variability in ocean biology and biogeochemistry over a large range of spatial and temporal scales (see figure 1). Associated with this, the reduction of uncertainties in the estimation of biogeochemical fluxes is an obvious target and the assessment of zooplankton resources for higher trophic levels (fish) is also an achievable important goal.

Beside these scientific objectives, the operational and long-term outcomes are the development of sound predictions of ocean biogeochemistry and ecosystem dynamics as well as the delivery of real-time and open-access data to scientists, users and decision makers. It is also expected that reduced uncertainties will result in better policy. The present chapter reviews recent sensor technical developments and scientific results from pilot projects that investigated pelagic ecosystems using autonomous vehicles. It is a synthesis of two recent articles (Claustre et al., 2010b; Stemmann and Boss, 2012). The following sections were set to *i*) describe autonomous vehicles, *ii*) describe miniaturised present and future sensors that can describe habitats (physical and geochemical environment) and plankton communities (phyto and zooplankton), *iii*) suggest framework for data control and quality and *iv*) propose their integration in modelling and observing systems.

2. The various platforms in support of a pelagic autonomous observation system

Autonomous floats spend most of their life drifting at depth where they are stabilised by being neutrally buoyant at the “parking depth” pressure where they have a density equal to the ambient pressure and a compressibility that is less than that of sea water (figure 2A). In the Argo mode, the floats pump fluid into an external bladder at typically 10-day intervals, and rise to the surface for about 6 hours while measuring temperature and salinity. Satellites determine the position of the floats when they surface, and receive the data transmitted by the floats. The bladder then deflates and the float returns to its original density and sinks to drift until the cycle is repeated. The floats can also be configured remotely to another prescribed resting depth. In the Argo array, floats are designed to make about 150 such cycles. With their long lasting capacities (3 years in the Argo array), floats are particularly useful to follow the temporal dynamics of the pelagic ecosystems in large-scale physical structures such as long lasting gyres.

In contrast to floats, gliders can be steered and maintained in particular areas providing the spatial structure for all variables measured by the sensors on-board at relatively slow speed ($30\text{km}\cdot\text{day}^{-1}$ horizontally, see figure 2B). They are suitable platforms for any sustained observational system aimed at monitoring bio-physical coupling at the coastal interface between shelf and open ocean because they can operate at sub- to meso-scale (1km to 100km). The improvements in glider technology were accompanied by the emergence of glider ports or centres. These logistical centres, very often in the proximity of a laboratory, are key to the success of these systems. The development of a “global bio glider network” in the near future will have to rely on a cluster of these local, national or international (e.g. Everyone’s gliding observatories) centres. The endurance (around 4 months) and range (2000km) of gliders constrain the procedure by requiring repetitive deployments, but gliders are already capable to cover large parts of the global ocean. On a longer term and with the continuing improvement of technology (e.g. increasing endurance and range), transoceanic and repeated transects from glider port to glider port will likely become possible. Animal-borne systems (see figure 2C) can nicely complement gliders and floats (Teo et al., 2009). Recently, animal-borne instruments have been designed and implemented to provide *in situ* hydrographic data from parts of the oceans where little or no other data are currently available such as for example the Southern ocean (Bailleul et al., 2010; Roquet et al., 2011). The animal-platform community is only beginning and no continuous deployments is underway (see I, 1 for more details).

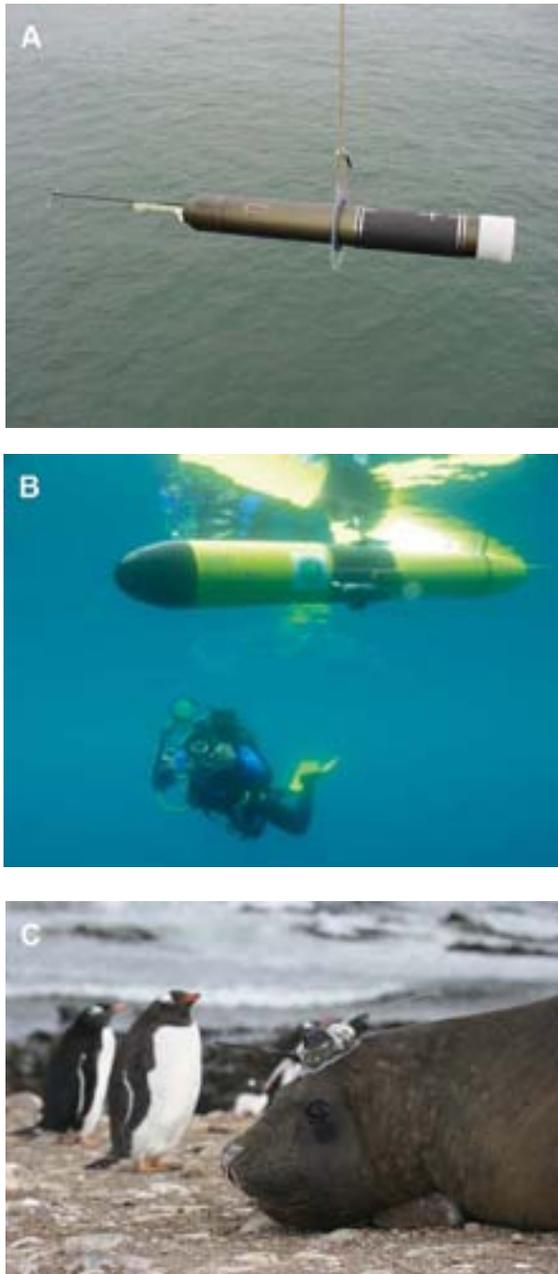


Figure 2: Three platforms used to study the pelagic environment. A. PROVOR float about to be immersed in the ocean for a three years journey (© Ifremer). B. Glider (© DR). C. Elephant seal equipped with sensors glued at on the top of his head (©C. Guinet/CNRS).

3. Relevant pelagic ecosystem variables at global scales

3.1. *Monitoring the pelagic habitats with core physical and geochemical variables*

The broad-scale global array of temperature and salinity profiling floats, known as Argo, has already grown to be a major component of the ocean observing system. The final array of 3,000 floats now provides 100,000 temperature/salinity (T/S) profiles and velocity measurements per year distributed over the global oceans at an average 3-degree spacing (figure 1). Floats cycle at a 2,000m depth every 10 days, with 3-4 year lifetimes for individual instruments. All Argo data are publically available in near real-time via the global data assembly centers (GDACs) after an automated quality control (QC), and in scientifically quality controlled form, delayed mode data, *via* the GDACs within six months of collection. Hence, basic physical data about the salinity and temperature of the pelagic habitat are readily available. In addition to these physical sensors, geochemical sensors are now being developed and deployed on Argo floats. Oxygen sensors are currently being installed on floats for multi-year periods with little or no drift in sensor response (Kortzinger et al., 2004; Riser and Johnson, 2008). As for June 2009, more than 200 floats have been deployed with oxygen sensors, with about 150 currently active (Johnson et al., 2009). Nitrate sensors based on direct optical detection are now also deployed on floats, and they operate for more than 500 days (Johnson and Coletti, 2002). Detection limits are on the order of 0.5 to 1 μ M. Although not sufficient to measure euphotic zone nitrate concentrations in many regions, these sensors can resolve annual cycles in mesotrophic, bloom-forming regions. Measurements with gas tension devices (McNeil et al., 2006) can be combined with oxygen concentrations to determine the partial pressure of molecular nitrogen (N_2) in seawater. Finally, prototype pCO_2 sensors were tested on floats but several technical problems (long time constants of sensors) have to be solved before their operational use. Yet, major improvements in the pCO_2 sensors can be expected in the near future.

Bio-optical sensor technologies have also been refined so that they can now be deployed on autonomous platforms (Bishop and Wood, 2009; Boss et al., 2008). Particle load is the main driver of water turbidity or transparency in the open ocean. Turbidity can be quantified by the measurement of the backscattering coefficient using a backscattering metre, while transparency is measured by the particle attenuation coefficient using a transmissometer. In open ocean waters, particulate organic carbon (POC) is the main source of particles, and both optical measurements can be converted to a concentration of POC with reasonable

accuracy (Bishop and Wood, 2009). The long-term deployment of bio-optical sensors is possible on Argo floats because these platforms spend much of their time deep down in cold and dark waters. Consequently, biofouling is less of an issue than when sensors are permanently fixed in the upper ocean, for example, on moorings, or on benthic surfaces (see III, 1).

3.2. Monitoring the plankton communities

The BIO-Argo community has already implemented multispectral optical sensors to estimate chlorophyll-a as a proxy for phytoplankton biomass. It can be measured by fluorescence, and miniature fluorescence sensors are now available to equip a variety of platforms (e.g. gliders, floats, animals). When converting chlorophyll-a data into biomass data, one must however take into account the issues of variable pigment to carbon ratios and variable fluorescence to chlorophyll concentration ratios, which are caused by non photochemical quenching, changes in species composition, and changes in temperature. Chlorophyll fluorescence and light scattering (proxy for POC) in the upper 1000m were measured in the North Atlantic for three years (Boss et al., 2008). In the future, coccolithophorids carbonate shells might be detected from the background of nano-sized phytoplankton cells by their specific optical birefringence properties (Guay and Bishop, 2002).

Much less work has been carried out to characterise the zooplankton, which constitutes a major trophic level of pelagic ecosystems. Checkley et al. (2008) combined a sounding oceanographic lagrangian observer float with a laser optical plankton counter (LOPC) and a fluorometer to make an autonomous biological profiler, the SOLOPC. The instrument senses plankton and other particles over a size range of 100 μ m to 1cm in profiles to 300m in depth and sends data ashore via satellite. Objects sensed by the LOPC include aggregates and zooplankton, the larger of which can be distinguished from one another by their transparency. The instrument was deployed during several weeks in the Californian current system (Checkley et al., 2008). In the future, these imaging systems will make monitoring particles and zooplankton at the same time possible (see II, 2).

Acoustic sensors from gliders (Davis et al., 2008) or from floats were also used to detect plankton and non living particles (Jaffe et al., 2007). But the interpretation of acoustic backscatter at a single frequency is complicated by several factors. Marked spatial changes in intensity of acoustic backscatter do not necessarily imply changes in zooplankton or fish biomasses, as differences in body size, species composition, elastic properties of the animals, or orientation, can also markedly influence

acoustic signals (Roberts and Jaffe, 2007; 2008). These instruments have not yet been deployed over long periods of time but we expect that a strong development and wide use of these instruments will be seen the next decade.

The use of flow cytometry for plankton organisms smaller than about 20 μ m (pico and nano-size range) provides an alternate way to automatically obtain taxonomic information in this size range (Olson and Sosik, 2007). Molecular sensors are also now being developed for coastal observatories to remotely detect marine microbes and small invertebrate (Scholin et al., 2009). *In situ* flow cytometers and molecular sensors represent a promising avenue in this respect, although their size and energy consumption prevent them, for the moment, from being part of an operational open ocean observation system, for which long term autonomy and cost efficient sensors are important.

3.3. *From observations to predictions using modelling framework*

Building a global observation system to describe and predict the functioning of the pelagic ecosystem requires a stepwise approach with regional-scale, pilot projects. Pilot studies that combine *in situ* sensors deployed on long-endurance platforms with satellite sensors, ship cruises, and data assimilation of biogeochemical-ecological models must be carried on to obtain a proof of the concept. In particular, data assimilation into different types of models is essential to interpret spatial and temporal variability, and to convert the sum of local measurements into quantitative rate estimates over large regions of the ocean.

For more than two decades, pelagic ecosystem modeling has focused on the role and functioning of ecosystem components described as “boxes”. In these box models, the marine ecosystem is divided into several dynamic compartments. The first models of marine ecosystems dynamics contained only one variable, the phytoplankton (Fleming, 1939; Riley and Bumpus, 1946), but models including three variables – nutrient, phytoplankton, zooplankton – were quickly developed (Riley et al., 1949). Thereafter, the development of computers enabled the number of variables to increase up to seven by adding bacteria, particulate and dissolved detritus and ammonia as a second source of nutriment (Fasham et al., 1990). This latter model became a standard for the subsequent development of biogeochemical models, including the development of biogeochemical models with up to 11 compartments (Aumont et al., 2003; Le Quere et al., 2005) or models involving a greater number of phytoplankton types from which merging communities can be extracted (Follows et al., 2007). Despite these improvements, little attention has been paid

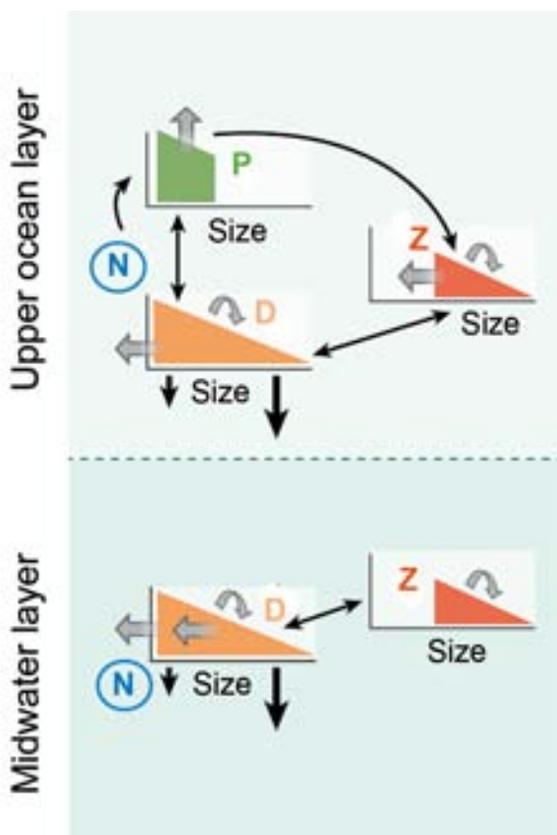


Figure 3: Conceptual scheme showing how data from the new generations of sensors can be integrated into improved models of the pelagic ecosystems. Improved models include coupled dynamics of nutrients (blue ellipse), size-structured populations of phytoplankton (P, green symbols) and zooplankton (Z, dark orange symbols) and a size-structured pool of detritus (D, orange symbols) in the upper ocean layer and the midwater layer. Black arrows represent the flow of mass from one compartment to the other. The flow of mass of detritus due to physical processes (mixing and particle settling) from the upper to the midwater layer depends on the size of detritus. Grey arrows represent mass transfer between the size classes within the same group. In the future, detritus and some zooplankton groups detected using imaging systems may be replaced by a size-based description. However, not all compartments may be described with size when size is less important for bio-geochemical processes or less variable. This is particularly true for the phytoplankton because these species don't prey on each other or they have very specific functions (N_2 fixators, calcifiers) and several zooplankton taxa (tunicates, jellyfish). Crustaceans may be good candidate for a size based description because they share many metabolic pathways and life cycle dynamics. The proposed model should be simple enough to be included in 3D biogeochemical models. Only vertical processes are represented here and land-oceans transports or benthic-pelagic coupling are not represented.

to zooplankton because of the complexity of this group and the small number of global data sets (Carlotti and Poggiale, 2010). The zooplankton is often represented as a closure variable with fixed rates in compartment models while their dynamic trophic interactions with the phytoplankton may be important to understand the ecosystem dynamics. Robust models relating climate change to fish production require also an adequate description of the zooplanktonic intermediaries between phytoplankton and fish in end-to-end models. Therefore, acquisition of *in situ* data is needed for testing mechanistic end-to-end models and optimising the balance between fidelity and simplicity in the zooplankton component.

At the same time, the deeper ocean (below the mixed layer) was treated as a black box because of the lack of data. In particular, the description of particle sinking to the deep oceans still mostly relies on exponential or power law functions (Armstrong et al., 2002; Betzer et al., 1984; Martin et al., 1987; Suess, 1980). However, marine particle fluxes display strong regional and temporal variability in response to production regimes and their seasonality. The relationship between surface ocean ecosystem structure and variability is not captured by these simplified approaches.

A recent model (Gehlen et al., 2006; Kriest and Evans, 2000) provides an interesting alternative suitable for global scale applications (figure 3). It relies on the explicit parameterisation of particle interactions (aggregation/disaggregation) where particle number and size are state variables. The sinking speed is computed as a function of particle size distribution. This approach relies however on simplifying assumptions that have not been fully validated by comparing with data on particle dynamics. For instance, the description of the particle size spectrum by a constant exponent contradicts observations where variability with depth of the latter was reported (Guidi et al., 2009). This variability most likely reflects the impact of zooplankton feeding and microbial degradation on particle size spectra (Stemmann et al., 2004a; 2004b). In this case, measuring organisms and particles size distribution would also lead to general improvement of the description and dynamics of zooplankton in models.

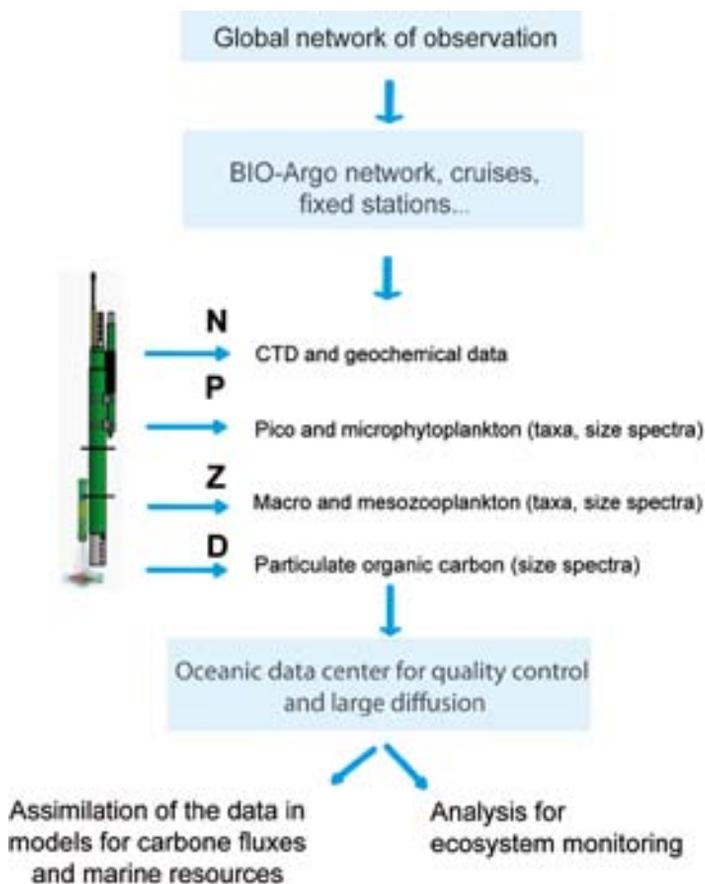


Figure 4: Schematic representation of the outcomes of a future array of oceanic floats equipped with biological sensors to measure various pelagic ecosystems components as well as standard physical and chemical sensors. In the future, the nutrient(N)-phytoplankton(P)-zooplankton(Z)-detritus(D) conceptual scheme of most biogeochemical models will be quantified by the observation of new ecosystem components.

4. The key to success: agreed procedures, data management and distribution

In principle, the different observational approaches from ships, satellites, or autonomous vectors can be regarded as stand-alone initiatives with their own rationales, objectives, analysis tools and synthesis products. In fact, this was the path followed previously, even though many scientists are often involved in more than one approach. Overcoming the separa-

tion between the different observational approaches is a major objective for the scientific community for the next decade.

The technology for observing key oceanic biogeochemistry and ecosystem variables has progressively matured to the point where it is now amenable to a global dissemination (figure 4). Additionally, data sources will be much more diverse than today, going essentially from ship-based data acquisition to an increased contribution of data acquired through remotely operated platforms. Within a few years, our community will thus acquire tremendous amounts of biological data in addition to the standard physical and chemical data. An integrated observation system will be operationally useful and scientifically relevant if and only if this huge data acquisition effort is supported by an efficient data management system, able to meet both basic scientific and operational goals. Indeed, the success in implementing these new cost effective technologies in our observation strategy will heavily rely on our capacity to make all data easily available.

Nevertheless, such data management system is still to be designed and implemented. The important criteria that preclude this implementation are, notably, the availability of real-time quality-controlled (QC) data for operational applications and the production of delayed-model QC data required for climate-related studies. In some ways, these prerequisites are orthogonal to the historic habits or constraint in relation with biological data management. First of all, with the exception of satellite data, biologists were not used to the management of very large datasets because most biological data acquisition was done during discrete measurements performed from ship-based platforms. Secondly, there are generally some hurdles to make biological data publically available. While efforts in this direction are underway, much remains to be done and the community has to consider this aspect of data management as a priority. Finally, and in relation with the preceding point, the biological oceanographer community is even less used to the constraints involved in the production and distribution of data in near-to-real-time. A technological evolution is thus required in the way we manage data to guarantee public access and to deliver real-time data and products, when required. This likely represents the most challenging issue for our community, at least as challenging as the required technological developments themselves.

Authors' references

Lars Stemann, Hervé Claustre, Fabrizio D'Ortenzio:
Université Pierre et Marie Curie, Laboratoire d'Océanographie de Villefranche, UPMC-CNRS UMR 7093, Villefranche-sur-Mer, France.

Corresponding author: Lars Stemann, stemmann@obs-vlfr.fr

Aknowledgement

This work is a synthesis of two recent articles (Claustre et al., 2010b; Stemmann and Boss, 2012). Authors were supported by funding from 7th European Framework Program (Research Infrastructure JERICO and GROOM projects). Lars Stemmann is supported by the CNRS/UPMC Chaire on Biodiversity and Functioning of Pelagic Ecosystems.

References

- Allredge A. L., Gotschalk C., 1988. *In situ* settling behavior of marine snow. *Limnology and Oceanography*, 33, pp. 339-351.
- Armstrong R. A., Lee C., Hedges J. I., Honjo S., Wakeham S. G., 2001. A new, mechanistic model for organic carbon fluxes in the ocean based on the quantitative association of POC with ballast minerals. *Deep Sea Research Part II: Topical Studies in Oceanography*, 49, pp. 219-236.
- Aumont O., Maier-Reimer E., Blain S., Monfray P., 2003. An ecosystem model of the global ocean including Fe, Si, P colimitations. *Global Biogeochemical Cycles*, 17, pp. 1060-1083.
- Bailleul F., Authier M., Ducatez S., Roquet F., Charrassin J. B., Cherel Y., Guinet C., 2010. Looking at the unseen: combining animal bio-logging and stable isotopes to reveal a shift in the ecological niche of a deep diving predator. *Ecography*, 33, pp. 709-719.
- Betzer P. R., Showers W. J., Laws E. A., Winn C. D., Ditullio G. R., Kroopnick P. M., 1984. Primary productivity and particle fluxes on a transect of the Equator at 153°W in the Pacific Ocean. *Deep Sea Research Part I: Oceanographic Research Papers*, 31, pp. 1-11.
- Bishop J. K. B., Wood T. J., 2009. Year-round observations of carbon biomass and flux variability in the Southern Ocean. *Global Biogeochemical Cycles*, 23, pp. 1-12.
- Boss E., Swift D., Taylor L., Brickley P., Zaneveld R., Riser S., Perry M. J., Strutton P. G., 2008. Observations of pigment and particle distributions in the western North Atlantic from an autonomous float and ocean color satellite. *Limnology and Oceanography*, 53, pp. 2112-2122.
- Boyd P. W., Trull T. W., 2007. Understanding the export of biogenic particles in oceanic waters: is there consensus? *Progress in Oceanography*, 72, pp. 276-312.
- Brown J. H., Gillooly J. F., Allen A. P., Savage V. M., West G. B., 2004. Toward a metabolic theory of ecology. *Ecology*, 85, pp. 1771-1789.
- Burd A. B., Hansell D. A., Steinberg D. K., Anderson T. R., Aristegui J., Baltar F., Beupré S. R., Buesseler K. O., DeHairs F., Jackson G. A., Kadko D. C., Koppelman R., Lampitt R. S., Nagata T., Reinthaler T., Robinson C., Robison B. H., Tamburini C., Tanaka T., 2010. Assessing the apparent

- imbalance between geochemical and biochemical indicators of meso- and bathypelagic biological activity: what is wrong with present calculations of carbon budgets? *Deep Sea Research Part II: Topical Studies in Oceanography*, 57, pp. 1557-1571.
- Carlotti F., Poggiale J. C., 2010. Towards methodological approaches to implement the zooplankton component in “end to end” food-web models. *Progress in Oceanography*, 84, pp. 20-38.
- Checkley D. M., Davis R. E., Herman A. W., Jackson G. A., Beanlands B., Regier L. A., 2008. Assessing plankton and other particles in situ with the SOLOPC. *Limnology and Oceanography*, 53, pp. 2123-2136.
- Claustre H., Antoine D., Boehme L., Boss E., D’Ortenzio F., Fanton d’Andon O., Guinet C., Gruber N., Handegard N. O., Hood M., Johnson K., Körtzinger A., Lampitt R., LeTraon P.-Y., Lequéré C., Lewis M., Perry M.-J., Platt T., Roemmich D., Sathyendranath S., Testor P., Send U., Yoder J., 2010a. Guidelines towards an integrated ocean observation system for ecosystems and biogeochemical cycles, in: Hall J., Harrison D. E., Stammer D. (Eds.), *Proceedings of OceanObs’09: Sustained Ocean Observations and Information for Society*. ESA Publication WPP-306.
- Claustre H., Bishop J., Boss E., Bernard S., Berthon J.-F., Coatanoan C., Johnson K., Lotiker A., Ulloa O., Perry M. J., D’Ortenzio F., Fanton d’Andon O., Uitz J., 2010b. Bio-optical profiling floats as new observational tools for biogeochemical and ecosystem studies: Potential synergies with ocean color remote sensing, in: Hall J., Harrison D. E., Stammer D., (Eds.), *Proceedings of OceanObs’09: Sustained Ocean Observations and Information for Society*. ESA Publication WPP-306.
- Davis R. E., Ohman M. D., Rudnick D. L., Sherman J. T., Hodges B., 2008. Glider surveillance of physics and biology in the southern California Current System. *Limnology and Oceanography*, 53, pp. 2151-2168.
- Fasham M. J. R., Duclow H. W., Mckelvie S. M., 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *Journal of Marine Research*, 48, pp. 591-639.
- Fleming R. H., 1939. The control of diatom populations by grazing. *Journal du Conseil International pour l’Exploration de la Mer*, 14, pp. 210-227.
- Follows M. J., Dutkiewicz S., Grant S., Chisholm S. W., 2007. Emergent biogeography of microbial communities in a model ocean. *Science*, 315, pp. 1843-1846.
- Gehlen M., Bopp L., Ernprin N., Aumont O., Heinze C., Raguencau O., 2006. Reconciling surface ocean productivity, export fluxes and sediment composition in a global biogeochemical ocean model. *Biogeosciences*, 3, pp. 521-537.
- Gillooly J. F., 2000. Effect of body size and temperature on generation time in zooplankton. *Journal of Plankton Research*, 22, pp. 241-251.
- Gillooly J. F., Brown J. H., West G. B., Savage V. M., Charnov E. L., 2001. Effects of size and temperature on metabolic rate. *Science*, 293, pp. 2248-2251.

- Gillooly J. F., Charnov E. L., West G. B., Savage V. M., Brown J. H., 2002. Effects of size and temperature on developmental time. *Nature*, 417, pp. 70-73.
- Guay C. K. H., Bishop J. K. B., 2002. A rapid birefringence method for measuring suspended CaCO₃ concentrations in seawater. *Deep Sea Research Part I: Oceanographic Research Papers*, 49, pp. 197-210.
- Guidi L., Stemann L., Jackson G. A., Ibanez F., Claustre H., Legendre L., Picheral M., Gorsky G., 2009. Effects of phytoplankton community on production, size and export of large aggregates: A world-ocean analysis. *Limnology and Oceanography*, 54, pp. 1951-1963.
- Hansen P. J., Bjornsen P. K., Hansen B. W., 1997. Zooplankton grazing and growth – Scaling within the 2-2,000 micrometer body size range. *Limnology and Oceanography*, 42, pp. 687-704.
- IOCCG, 2011. Bio-Optical Sensors on Argo Floats, in: Claustre H. (Ed.), Reports of the International Ocean-Colour Coordinating Group, No. 11. IOCCG, Dartmouth, Canada.
- Jackson G. A., 1990. A model of the formation of marine algal flocs by physical coagulation processes. *Deep Sea Research Part I: Oceanographic Research Papers*, 37, pp. 1197-1211.
- Jaffe J. S., Glatts R., Schurgers C., Mirza D., Franks P. J. S., Roberts P., Simonet F., 2007. AUE: An autonomous float for monitoring the upper water column. *Oceans 2007 – Europe*, Vols 1-3, pp. 1392-1395.
- Jennings S., Warr K. J., 2003. Smaller predator-prey body size ratios in longer food chains. *Proceedings of the Royal Society of London B*, 270, pp. 1413-1417.
- Johnson K. S., Berelson W. M., Boss E., Chase Z., Claustre H., Emerson S. R., Gruber N., Kortzinger A., Perry M. J., Riser S. C., 2009. Observing biogeochemical cycles at global scales with profiling floats and gliders: Prospects for a global array. *Oceanography*, 22, pp. 216-225.
- Johnson K. S., Coletti L. J., 2002. *In situ* ultraviolet spectrophotometry for high resolution and long-term monitoring of nitrate, bromide and bisulfide in the ocean. *Deep Sea Research Part I: Oceanographic Research Papers*, 49, pp. 1291-1305.
- Kjørboe T., 2000. Colonization of marine snow aggregates by invertebrate zooplankton: abundance, scaling, and possible role. *Limnology and Oceanography*, 45, pp. 479-484.
- Kjørboe T., Grossart H. P., Ploug H., Tang K., 2002. Mechanisms and rates of bacterial colonization of sinking aggregates. *Applied and Environmental Microbiology*, 68, pp. 3996-4006.
- Kjørboe T., Grossart H. P., Ploug H., Tang K., Auer B., 2004. Particle-associated flagellates: swimming patterns, colonization rates, and grazing on attached bacteria. *Aquatic Microbial Ecology*, 35, pp. 141-152.
- Kjørboe T., Thygesen U. H., 2001. Fluid motion and solute distribution around sinking aggregates. – Implications for remote detection by colonizing zooplankters. *Marine Ecology Progress Series*, 211, pp. 15-25.

- Kortzinger A., Schimanski J., Send U., Wallace D., 2004. The ocean takes a deep breath. *Science*, 306, pp. 1337-1337.
- Kriest I., Evans G. T., 2000. A vertically resolved model for phytoplankton aggregation. *Proceedings of the Indian Academy of Sciences, Earth and Planetary Sciences*, 109, pp. 453-469.
- Le Quere C., Harrison S. P., Prentice I. C., Buitenhuis E. T., Aumont O., Bopp L., Claustre H., Da Cunha L. C., Geider R., Giraud X., Klaas C., Kohfeld K. E., Legendre L., Manizza M., Platt T., Rivkin R. B., Sathyendranath S., Uitz J., Watson A. J., Wolf-Gladrow D., 2005. Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. *Global Change Biology*, 11, pp. 2016-2040.
- Martin J. H., Knauer G. A., Karl D. M., Broenkow W. W., 1987. VERTEX: Carbon cycling in the Northeast Pacific. *Deep Sea Research Part I: Oceanographic Research Papers*, 34, pp. 267-285.
- McNeil C., D'Asaro E., Johnson B., Horn M. I., 2006. A gas tension device with response times of minutes. *Journal of Atmospheric and Oceanic Technology*, 23, pp. 1539-1558.
- Niewiadomska K., Claustre H., Prieur L., d'Ortenzio F., 2008. Submesoscale physical-biogeochemical coupling across the Ligurian Current (northwestern Mediterranean) using a bio-optical glider. *Limnology and Oceanography*, 53, pp. 2210-2225.
- Olson R. J., Sosik H. M., 2007. A submersible imaging-in-flow instrument to analyze nano-and microplankton: imaging FlowCytobot. *Limnology and Oceanography: Methods*, 5, pp. 195-203.
- Ploug H., Grossart H. P., 2000. Bacterial growth and grazing on diatom aggregates: respiratory carbon turnover as a function of aggregate size and sinking velocity. *Limnology and Oceanography*, 45, pp. 1467-1475.
- Riley G. A., Bumpus D. F., 1946. Phytoplankton-zooplankton relationships on Georges Bank. *Journal of Marine Research*, 6, pp. 33-47.
- Riley G. A., Stommel H., Bumpus D. F., 1949. Quantitative ecology of the plankton of the western North Atlantic. *Bulletin of the Bingham Oceanographic collection*, 12, pp. 1-169.
- Riser S. C., Johnson K. S., 2008. Net production of oxygen in the subtropical ocean. *Nature*, 451, pp. 323-325.
- Roberts P. L. D., Jaffe J. S., 2007. Multiple angle acoustic classification of zooplankton. *Journal of the Acoustical Society of America*, 121, pp. 2060-2070.
- Roberts P. L. D., Jaffe J. S., 2008. Classification of live, untethered zooplankton from observations of multiple-angle acoustic scatter. *Journal of the Acoustical Society of America*, 124, pp. 796-802.
- Roquet F., Charrassin J. B., Marchand S., Boehme L., Fedak M., Reverdin G., Guinet C., 2011. Delayed-mode calibration of hydrographic data obtained from animal-borne satellite relay data loggers. *Journal of Atmospheric and Oceanic Technology*, 28, pp. 787-801.

- Sabine C. L., Feely R. A., Gruber N., Key R. M., Lee K., Bullister J. L., Wanninkhof R., Wong C. S., Wallace D. W. R., Tilbrook B., Millero F. J., Peng T. H., Kozyr A., Ono T., Rios A. F., 2004. The oceanic sink for anthropogenic CO₂. *Science*, 305, pp. 367-371.
- Sarmiento J. L., Le Quere C., 1996. Oceanic carbon dioxide uptake in a model of century-scale global warming. *Science*, 274, pp. 1346-1350.
- Scholin C., Doucette G., Jensen S., Roman B., Pargett D., Marin R., Preston C., Jones W., Feldman J., Everlove C., Harris A., Alvarado N., Massion E., Birch J., Greenfield D., Vrijenhoek R., Mikulski C., Jones K., 2009. Remote detection of marine microbes, small invertebrates, harmful algae, and biotoxins using the environmental sample processor (ESP). *Oceanography*, 22 pp. 158-167.
- Stemmann L., Boss E., 2012. Plankton and particle size and packaging: from determining optical properties to driving the biological pump. *Annual Review of Marine Science*, 4, in press.
- Stemmann L., Jackson G. A., Gorsky G., 2004a. A vertical model of particle size distributions and fluxes in the midwater column that includes biological and physical processes – Part II: application to a three year survey in the NW Mediterranean Sea. *Deep Sea Research Part I: Oceanographic Research Papers*, 51, pp. 885-908.
- Stemmann L., Jackson G. A., Ianson D., 2004b. A vertical model of particle size distributions and fluxes in the midwater column that includes biological and physical processes – Part I: model formulation. *Deep Sea Research Part I: Oceanographic Research Papers*, 51, pp. 865-884.
- Suess E., 1980. Particulate organic-carbon flux in the oceans – surface productivity and oxygen utilization. *Nature*, 288, pp. 260-263.
- Teo S. L. H., Kudela R. M., Rais A., Perle C., Costa D. P., Block B. A., 2009. Estimating chlorophyll profiles from electronic tags deployed on pelagic animals. *Aquatic Biology*, 5, pp. 195-207.
- Volk T., Hoffert M. I., 1985. Ocean carbon pumps: analysis of relative strengths and efficiencies in ocean-driven atmospheric CO₂ changes, in: Sundquist E. T., Broecker W. S. (Eds.), *The carbon cycle and atmospheric CO₂: Natural variations archean to present*. *Geophysical monography series*, pp. 99-110.
- Woodward G., Ebenman B., Ernmerson M., Montoya J. M., Olesen J. M., Valido A., Warren P. H., 2005. Body size in ecological networks. *Trends in Ecology and Evolution*, 20, pp. 402-409.