Towards a transformative understanding of the ocean's biological pump: Priorities for future research

Report on the NSF Biology of the Biological Pump Workshop

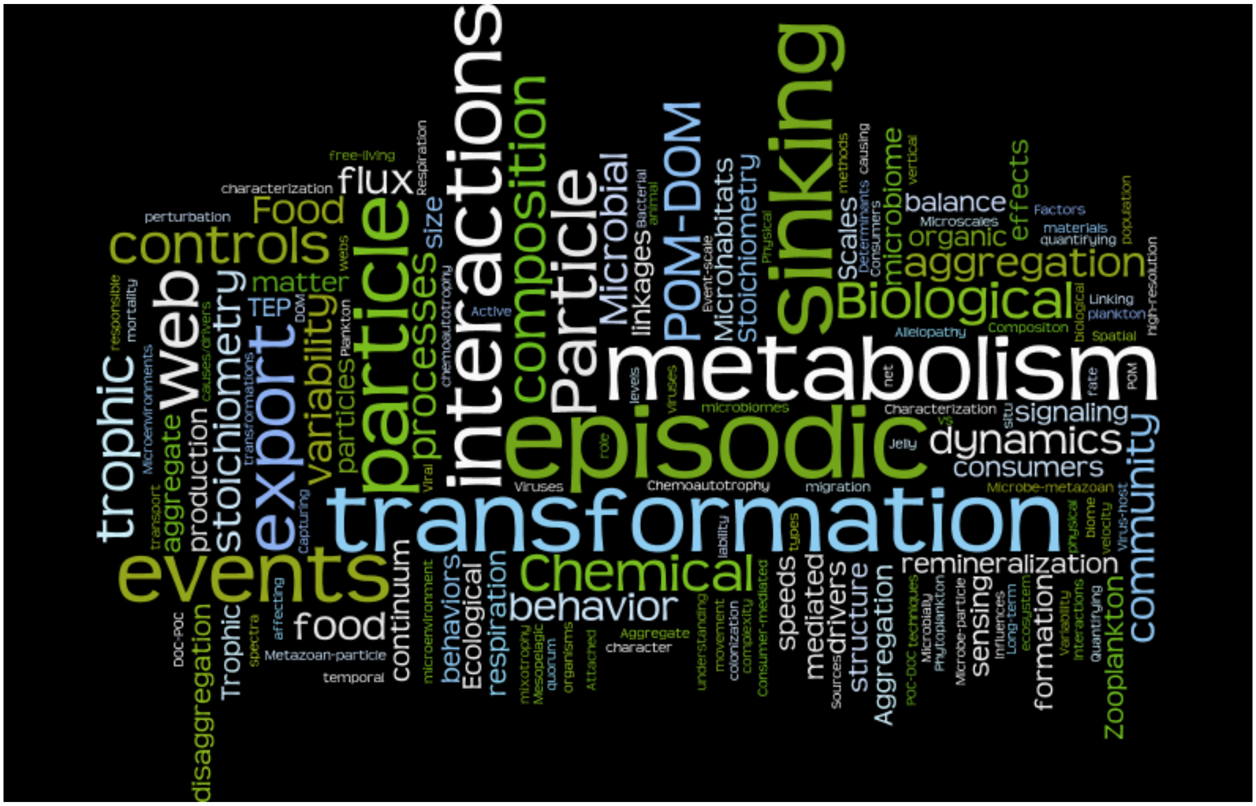


Table of Contents

Towards a transformative understanding of the ocean's biological pump: Priorities for future research

Author List: Adrian Burd (University of Georgia), Alison Buchan (University of Tennessee), Matthew Church (University of Hawai'i), Michael Landry (Scripps Institution of Oceanography), Andrew McDonnell (University of Alaska Fairbanks), Uta Passow (University of California Santa Barbara), Deborah Steinberg (Virginia Institute of Marine Science), Heather Benway (Woods Hole Oceanographic Institution)

Funding for this workshop was provided by the National Science Foundation (NSF). Coordination and logistical support for this workshop was provided by the Ocean Carbon and Biogeochemistry (OCB) Program (www.us-ocb.org)

Recommended citation:
Burd, A.B., A. Buchan, M. Church, M. Landry, A. McDonnell, U. Passow, D. Steinberg, H. Benway. Towards a transformative understanding of the biology of the ocean's biological pump: Priorities for future research. Report of the NSF Biology of the Biological Pump Workshop, February 19–20, 2016 (Hyatt Place New Orleans, New Orleans, LA), 67 pp., DOI:10.1575/1912/8263.

Executive Summary

The net transfer of organic matter from the surface to the deep ocean is a key function of ocean food webs. The combination of biological, physical, and chemical processes that contribute to and control this export is collectively known as the "biological pump", and current estimates of the global magnitude of this export range from 5 – 12 Pg C yr^{-1}. This material can be exported in dissolved or particulate form, and many of the biological processes that regulate the composition, quantity, timing, and distribution of this export are poorly understood or constrained. Export of organic material is of fundamental importance to the biological and chemical functioning of the ocean, supporting deep ocean food webs and controlling the vertical and horizontal segregation of elements throughout the ocean. Remineralization of exported organic matter in the upper mesopelagic zone provides nutrients for surface production, while material exported to depths of 1000 m or more is generally considered to be sequestered — i.e. out of contact with the atmosphere for centuries or longer.

The ability to accurately model a system is a reflection of the degree to which the system is understood. In the case of export, semi-empirical and simple mechanistic models show a wide range of predictive skill. This is, in part, due to the sparseness of available data, which impedes our inability to accurately represent, or even include, all relevant processes (sometimes for legitimate computational reasons). Predictions will remain uncertain without improved understanding and parameterization of key biological processes affecting export.

Participants of the Biology of the Biological Pump Workshop in February 2016 were **charged with producing a prioritized list of research areas that hold the promise of making significant advances in our understanding of the biological processes regulating organic matter export and its consumption in the oceans**. Participants ended up with an ordered list of 10 research priorities, which were further aggregated into three broad research themes:

(i) Food web regulation of export
(ii) The dissolved-particulate continuum
(iii) Variability in space and time

Although presented as three separate themes, there are myriad connections and relationships among them. For example, spatial-temporal variability plays a role in both food web regulation of export and in understanding the dissolved-particulate continuum. Underlying all themes was the concern that, without understanding these processes, we cannot predict how they might respond to global climate change, and consequently how oceanic export might change in the future. Additionally, we recognized that new technological and methodological developments over the last decade have created opportunities for significant advancement in all of these research areas.

Food web regulation of export was both the most important research theme that emerged and the most complex, containing three high-priority research areas: (i) *linking food web complexity* *to export flux; (ii) trophic interactions, behaviors, and metabolism of consumers; (iii) food web controls on production and respiration balance*.

(i) *Linking food web complexity to export flux:* Studies that connect broad, end-to-end food web characteristics to export and export efficiency may be able to identify, novel and as yet unquantified export pathways and new food web components that regulate or constrain export. Studies that quantify the effects of mixotrophy, symbioses, or crustacean vs. gelatinous zooplankton-dominated food webs on export were suggested as examples.

(ii) *Trophic interactions, behaviors, and metabolism of consumers:* Trophic interactions and animal behavior are important controls on organic matter export. Consequently, improved understanding and measurements of predator-prey interactions and feeding modes are needed; for example, the production of sinking fecal pellets by zooplankton and fish. Radiolarians and foraminifera, which are frequently not associated with carbon export, may also play a significant role in the biological pump (e.g. Guidi et al., 2016). Similarly, the role of flux feeders and the mechanisms through which they modify carbon export flux need to be quantified. Poorly constrained trophic interactions such as the role of infectious agents (e.g., viruses, parasitoids) in organic matter export were also identified as a high priority research area. The role of jellyfish in consuming and repackaging organic matter, as well their own contribution to export through “jelly-falls” remains poorly quantified (Lebrato and Jones, 2009).

(iii) *Food web controls on production and respiration balance:* Our understanding of the time and space scales coupling primary production and respiration remains limited by current methodologies and under-sampling. Improved technologies should facilitate investigations into how remineralization and consumption vary in space and time. Zooplankton consume sinking particles, but also re-package organic matter into fast-settling fecal pellets. Vertical migration of zooplankton spatially decouples consumption from fecal pellet production. Microbes attached to sinking particles excrete extracellular enzymes that solubilize the organic matter, allowing the microbes to consume it. Extracellular enzymes are likely to be substrate- and element-specific, resulting in different remineralization length scales and having significant biogeochemical implications.

The dissolved-particulate continuum refers to those biotic and abiotic processes that transfer material between the dissolved and particulate organic matter pools. Dissolved and particulate material follow different export pathways that have different characteristic time and space scales; consequently, improved understanding of the partitioning and flux between these pools is necessary. Three high-priority research areas were highlighted under this theme:

(i) *Dissolved-particulate organic matter continuum and transformations:* Particulate material can be transformed into dissolved material via microbial ectoenzymes that solubilize particles. Fibrillar macromolecules released by microbes can abiotically form nano- gels, microgels and transparent exopolymer particles (TEP), which form larger aggregates. Key to understanding these processes are measurements of transformation rates between the different dissolved and particulate pools.

(ii) *Physical and biological controls on aggregate and TEP dynamics:* Marine snow has long been known to be important for export. However, most research has focused on the physical processes of particle collision and aggregate formation. Biological processes such as production of marine snow via feeding structures or destruction of marine snow via grazing or fragmentation by zooplankton, which affect export in different ways, are less well studied. Microbial processes may also enhance aggregate formation, solubilization, or consumption. Understanding the factors that control the relative importance of the physical and biological processes affecting marine snow formation or destruction emerged as an important research priority.

(iii) *Particle composition and sinking speed:* Attempts to develop simple, universal relationships for particle sinking speed have been unsuccessful, as have been efforts to measure sinking velocity *in situ*. However, sinking velocity determines flux attenuation, and understanding the controls on particle sinking speed was thus felt to be a high-priority research area.

Variability in space and time was the third broad research theme identified at the workshop. Time-series measurements suggest export can occur at different scales, some of which are currently difficult to measure. Two high-priority research areas emerged from discussions of this theme:

(i) *Quantification and biological understanding of episodic events:* Participants identified the spatial and temporal quantification of episodic events as a first-order need. Episodic events like salp blooms, jelly-falls, and resting cyst formation can be associated with physical features such as fronts and eddies, but are generally unpredictable, and resulting flux events are largely missed by conventional sampling methods. An improved understanding of the organisms responsible for these events, including their life cycles and key controls on their distribution is needed.

(ii) *Scales of spatial and temporal variability*: Biological processes that control export occur over a wide range of spatial and temporal scales, and workshop participants identified a strong need to link these biological processes and drivers to improved assessments of the spatial and temporal variability in export. Variability in the biological pump and its drivers is poorly understood at spatial scales ranging from individual microbes and particles to mesoscale physical features, large ocean biomes, and the global biogeochemical patterns that result from this variability. Similarly, a wide range of time scales must be considered, spanning from rapid biological and chemical transformations (on scales of hours or less) to seasonal and interannual variations, the ongoing progression of climate change, and paleoclimatic variations.

Although knowledge of the broad features of the biological pump has improved significantly over the past 25 years, there remain large gaps in our understanding. These gaps are apparent in our inability to balance biogeochemical budgets in the mesopelagic, as well as in the range of model predictions of how the biological pump will respond to changing climate, reflecting a lack or misrepresentation of key processes.

The ideas presented here have the potential to significantly transform our understanding of the biology of the biological pump. New "omics" technologies applied to the DOM-POM continuum are, for the first time, integrating cell physiology and biogeochemistry, thereby allowing cross-scale work relating genomic content and expression with organism phenotypic characteristics and ecosystem functionality. These rapidly evolving technologies increase the power of new trait-based modeling approaches and open a window on organisms and pathways (e.g. viruses, parasites, symbioses, radiolarians, etc.) that have not previously been considered important for the biological pump. The development of theoretical and analytical frameworks such as gel theory, network theory, and stochastic models can cast new light on observations relevant to the biological pump and be used to develop new, testable hypotheses. New methodologies for measuring export and reconciling geochemical and sediment trap estimates will help transform our understanding of the biological pump by providing a solid baseline of reliable observations.

The exciting and transformative ideas presented here provide a roadmap for future research. These ideas can be explored individually, or in association with a larger project that can provide context through additional synoptic and process measurements. For example, coupling investigations of episodic events with the planned NASA EXPORTS project to understand carbon flux pathways will provide novel information on life strategies and food web interactions, provide information for developing stochastic models, and potentially address the fundamental limitations of assuming average or steady-state conditions. Using a program such as EXPORTS to provide contextual information for projects addressing the ideas presented here will have a synergistic effect, creating a whole that is greater than the sum of its parts, and have the greatest chance of making rapid, significant, transformative advances in our understanding of the biology of the biological pump.

1. Introduction and Process

This report summarizes the results of a workshop, *The Biology of the Biological Pump*, held February 19–20, 2016 at the Hyatt Place Hotel in New Orleans. The need for the workshop was stimulated by the forthcoming NASA *EXport* Processes in the Ocean from RemoTe Sensing (*EXPORTS*) field program, which is designed to "develop a predictive understanding of the export and fate of global ocean primary production and its implications for the Earth's carbon cycle in present and future climates" (Siegel et al., 2015). The EXPORTS program is planned as a 5-year program with its first research cruises scheduled to occur in 2018.

The *biological pump* is the term for the collective set of processes that maintain the vertical gradient in dissolved inorganic carbon, including processes such as net organic matter production, its export, and subsequent remineralization (Fig. 1). Many of these processes involve physical (e.g., mixing of dissolved organic matter, gravitational settling of particulate material), chemical (e.g., changes in the solubility of dissolved organic carbon with temperature), and biological (e.g., repackaging of organic matter by grazing) aspects — for example, the formation of large, rapidly settling particles through aggregation involves the physical processes causing particles to collide, the biological production of sticky substances that promote adhesion once particles have collided, and the chemical nature of this stickiness.

This workshop focused on biological processes that substantially affect the functioning of the biological pump, particularly on organisms, processes, and technical and methodological advances that have emerged as potentially important players over the past decade. Workshop participants were charged with identifying and prioritizing research questions concerning

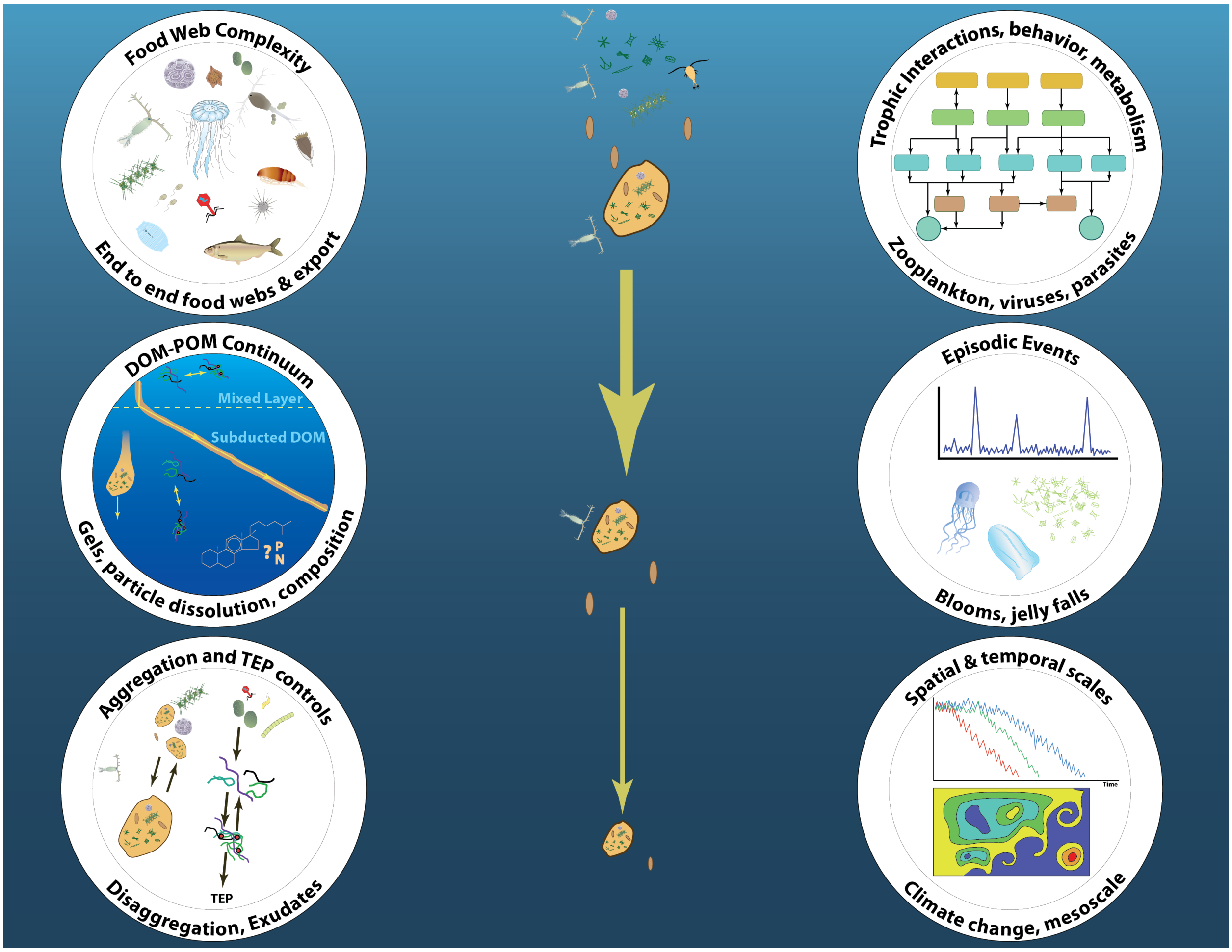


Figure 1. A schematic of the standard view of the biological pump in the center with representations of some of the high priority research areas identified in this report. In the standard view, phytoplankton in surface waters are consumed by zooplankton or form aggregates with other cells and fecal and detrital material. These larger particles sink and are degraded by biological activity as they settle through the water column. Research into foodweb complexity and trophic interactions can identify and quantify new export pathways. Studies of the DOM-POM continuum enable us to map and quantify DOM subduction and composition, as well as the transformations between DOM and POM. Understanding and quantifying the controls on aggregation, disaggregation, and TEP formation will improve predictions of POM export. Studies across spatial and temporal scales will help quantify episodic events and improve predictive modeling skills.

biological processes that have the potential to significantly advance our understanding of the biological pump.

In September 2015, Benway, Burd, and Sieracki invited an organizing committee of eight scientists spanning a range of relevant disciplines and career stages to help with the organization of the workshop:

Heather Benway (Woods Hole Oceanographic Institution)
Alison Buchan (University of Tennessee)
Adrian Burd (University of Georgia)
Matthew Church (University of Hawaii)
Michael Landry (Scripps Institution of Oceanography)
Andrew McDonnell (University of Alaska Fairbanks)
Uta Passow (University of California Santa Barbara)
Deborah Steinberg (Virginia Institute of Marine Science)

This organizing committee developed a list of participants spanning a wide range of career stages and relevant, varied, and complementary expertise (Appendix B); the number of participants was deliberately kept small, and by invitation, to facilitate the task at hand.

To efficiently identify research priorities, we employed the KJ method during the workshop (Appendix A). The KJ method allows groups to quickly reach a consensus on priorities of subjective, qualitative data. The organizing committee initially engaged in a “virtual” KJ session to arrive at five overarching KJ **focus questions** to be explored during the KJ sessions at the workshop. Within small (8-10 people) groups, workshop participants explored each of the following five KJ focus questions:

What would significantly advance our understanding of the following as they pertain to the biological pump and organic matter export?

KJ Focus Q1.	Particle formation in the upper ocean and processes that drive export
KJ Focus Q2.	Mesopelagic flux attenuation and the biological processes that drive it
KJ Focus Q3.	Biogenic material: characteristics, bioreactivity, export, stoichiometry, episodic export events
KJ Focus Q4.	Microbial and viral processes and newly revealed biological pathways
KJ Focus Q5.	Food web, community structure, and trophic interactions.

Each of four groups produced 4–5 top ranked **ideas** for each KJ **focus question**. While there was considerable overlap among the top-ranked ideas from each participant group, a sixth KJ session was required to cull and further prioritize the collective set of ideas that had emerged from the previous KJ exercises. Workshop participants again split into four groups and ranked the collective set of top-ranking ideas from the previous five KJ sessions. Each group presented their overall top three **priorities (**some of which overlapped), in the end yielding ten distinct priorities (Fig. 2).

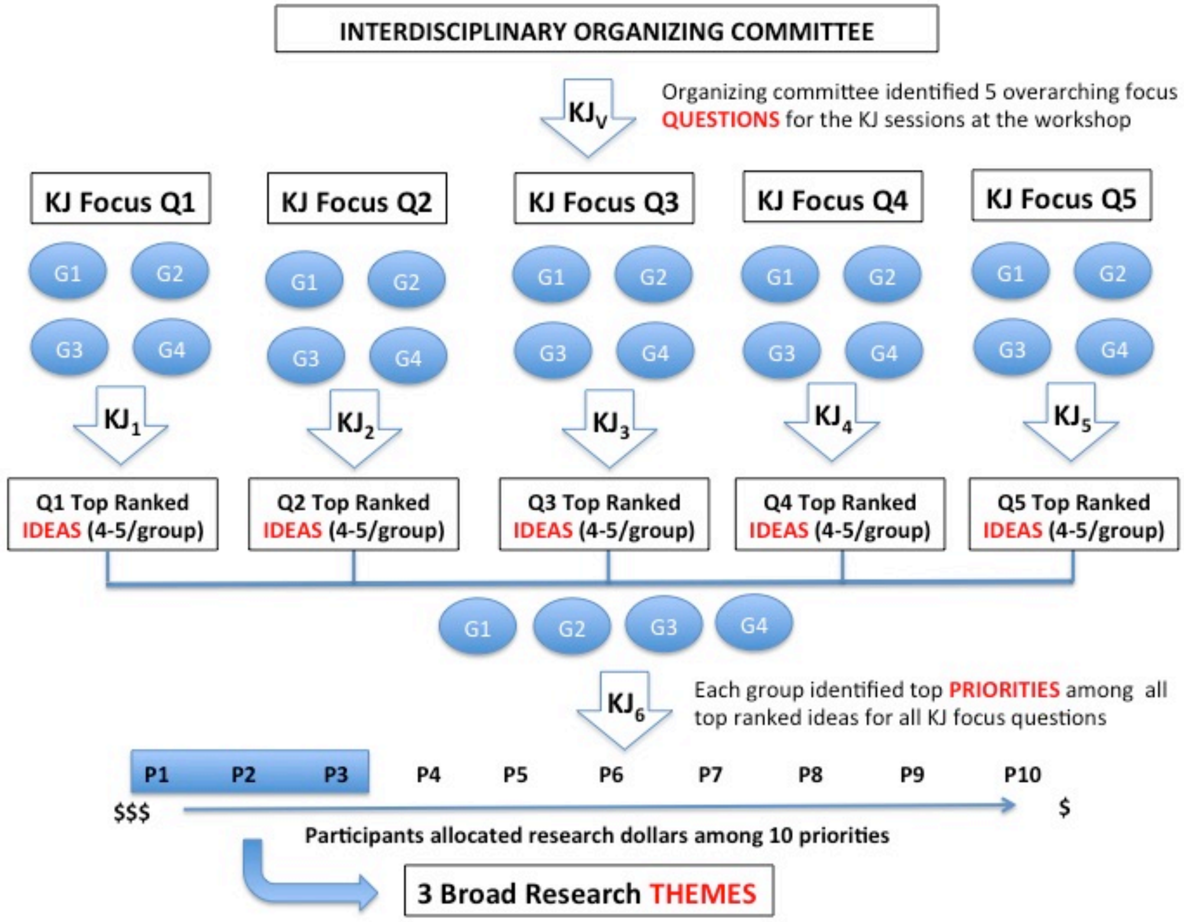


Figure 2. Flow chart demonstrating the use of the KJ technique during the workshop; KJ_v refers to the virtual KJ session that was used by organizing committee members prior to the workshop to identify KJ focus questions. There were five KJ focus questions (listed above) and workshop participants were broken into four groups, the membership of which changed each time to maximize participant interaction. A final KJ session (KJ_6) was used to cull and prioritize the collective set of ideas identified by the four groups for each KJ focus question, which yielded three top priorities for each group, some of which overlapped, yielding a total of 10 priorities. Finally, individual participants were given an allotment of money to invest in the final ten priorities, resulting in the final three research themes.

In the final session, workshop participants voted individually on their choices of the top ideas that emerged from the sixth KJ session. This was done by allocating each workshop participant a fixed amount of fake money. Each participant distributed their allotment of money among the priorities, as they deemed appropriate. The ideas that received the most money were selected as the top broad **research themes** (a relative ranking is given for each research theme based on the dollar amounts that arose from this process scaled to a total value of 100).

The initial draft report was written by the organizing committee and then distributed amongst the workshop participants for their comments and input (May 23rd 2016 – June 10th 2016).

Once these suggestions were incorporated, the report was made available to the broader community for their input (July 1st 2016 – August 1st 2016).

In the following sections of the report, the highest priority items as determined using the KJ processes are presented in detail, aggregated under three main research themes. Each section includes a summary of the workshop discussions as well as a selection of specific research questions related to the topics that were raised by the workshop participants.

2. Food web regulation of export

Introduction

Ocean biology plays a central role in regulating the net movement of carbon and bio-elements from the well-lit waters of the upper ocean to the dimly lit or dark waters of the ocean's interior. Although simple depictions of pelagic food webs provide a basic conceptual framework linking plankton community structure to organic matter export, such models generally fail, due to the absence of measurements to parameterize relationships or validate results, to distinguish the contributions of specific biological processes. For example, it remains largely unknown how major loss processes (e.g., viral infection, particle aggregation and sinking, zooplankton consumption) compare to one another or vary in space and time in the ocean. The major food web pathways and biological controls on remineralization and organic matter degradation, which are fundamental to defining flux attenuation and export variability, are comparably unresolved. In addition, we lack basic information on the depth variability of processes and interactions that connect the upper ocean to the mesopelagic realm. Such knowledge gaps need to be filled to develop quantitative models to predict how the ocean's biological pump will respond to subtle or abrupt changes in ocean ecosystems.

Our understanding of the mechanisms underlying food web regulation of elemental fluxes in the oceans is further challenged by new and continuing discoveries that highlight previously unrecognized metabolic flexibility, phylogenetic diversity, and complex interactions among the pelagic biota that drive these processes. Diverse modes of energy and nutrient acquisition, including photoheterotrophy and mixotrophy, are known to be important, but poorly resolved in terms of their net implications for trophic fluxes. In addition, various modes of symbiotic interactions are recognized to facilitate genetic exchanges (e.g., viral infection), catalyze nutrient and energy transfers (e.g., mutualism), and/or serve as loss terms balancing cell growth (e.g., parasitism), but are inadequately incorporated into our understanding of food web function. To date, there have been few efforts to quantify the relative roles and importance of such food web complexities on export rates and efficiencies.

Food Web Regulation of Export was the highest priority research theme that resulted from the final KJ_6 session of the workshop. This research theme comprised the following priorities centered on the role of food webs in controlling the magnitude and efficiency of organic matter export:

- Linking food web complexity to export flux (*13.5, ranked 1st*)
- Trophic interactions, behaviors, and metabolism of consumers (*12.8, ranked joint 2nd*)
- Food web controls on production and respiration (*12.8, ranked joint 2nd*)
- Identifying which organisms control remineralization (*8.7, ranked joint 6th*)
- Ecological causes, drivers, and effects of vertical movement and migration (*8.0, ranked 9th*)

Linking food web complexity to export flux

Workshop participants identified several research areas to advance understanding of food web complexity and export, including the need for integrative studies that connect characteristics of "end-to-end" ocean food webs (food webs extending from viruses to top predators) to export efficiencies. Such studies might, for example, highlight current unknowns in assessing trophic structure and efficiencies leading to key consumers in the biological pump; regional and temporal variability in the fates of primary production; the relative importance of alternate food web pathways leading to export (DOC, aggregation/disaggregation, fecal pellets, vertical migration) and their regulatory nodes and mechanisms; variability in growth efficiencies within the food web, the export contributions of higher-level consumers that are not directly measured by sediment traps or other means (e.g., mass falls of gelatinous zooplankton, carcasses), and the depth dependencies of processes and relationships that link surface waters to the mesopelagic. In addition, workshop participants expressed the need for studies evaluating how or whether variability in biodiversity and food web complexity (from microbes to top predators) impacts productivity and export. The well known biodiversity maxima in open-ocean subtropical oligotrophic regions, where export is typically low (though some estimates using oxygen utilization give similar annual export fluxes to more nutrient-rich regions), would suggest, for example, that diversity or complexity facilitates (or arises from) a more efficient coupling of production-grazing-remineralization processes within the euphotic zone, thereby minimizing export compared to more dynamic high latitude systems. However, the specific contributions of alternate physiological or life history strategies (e.g., mixotrophy, photoheterotrophy, symbioses, grazing or digestion-resistant clones, crustacean-versus gelatinous zooplankton-dominated systems, spatial heterogeneity of microbial communities on particles) are poorly explored in comparative analyses of food web function. On a more practical note, it is also necessary for the advancement of future modeling efforts to establish predictable patterns of food web structure with alternate export pathways and flux regimes, and to ascertain how many ecosystem states, structures, and fluxes are needed to characterize those relationships seasonally and regionally.

Some of the research areas and questions associated with this topic include:

- How is flux regime regulated by food web structure?
- Do changes in community structure alter export pathways in predictable ways?
- How do biodiversity and food web complexity affect export efficiency?
- How does food web structure regulate export mechanisms other than passive particle sinking?

- How many ecosystem states describing food web structure and flux do we need?

Trophic Interactions, behaviors, and metabolism of consumers (zooplankton, viruses, parasites, etc.)

Trophic interactions in planktonic food webs, and the animal behaviors that mediate these interactions, are important controls on the biological pump. Furthermore, consumers drive export through production of sinking fecal pellets and via active transport during vertical migration, and their metabolism plays a key role in recycling of carbon, nitrogen, and other elements. Research into zooplankton feeding modes was highlighted, with detritivory being one mode that requires particular attention. The abundance and behavior of detritivores, as well as their feeding rates, control removal and recycling of sinking detritus. However, experiments to directly measure these rates are limited. Zooplankton behavior and life histories also affect the biological pump. Examples of the former include diel vertical migration and active transport, and of the latter include diapause of some copepod species in the mesopelagic zone, or the asexual reproductive stage of gelatinous zooplankton such as salps that permits rapid formation of a large grazer population. Rates of fecal pellet production (egestion) by different zooplankton species are also required. Finally, rates of grazer mortality (non-predatory and predatory) are needed.

Another area for investigation identified by participants was the role of viruses and infectious agents (e.g., parasitoids) in affecting the biological pump. Viruses are extremely abundant in seawater (10 times or more abundant than prokaryotic cells), infecting both prokaryotes and eukaryotes. There is strong evidence that viruses are actively infecting and lysing their hosts *in situ*, but linking viruses to their hosts is complicated by the lack of culturability of most hosts (and likely viruses). However, recent efforts to develop and apply single-cell, molecular-based approaches to identify host-virus pairs are promising (Brum and Sullivan, 2015). Quantitative measurements in surface seawater reveal that up to a quarter of the photosynthetically fixed carbon in the oceans is shunted to the DOM pool by virus activity. Additionally, the role of viruses in nutrient regeneration, particularly N and Fe, in surface seawaters is being increasingly recognized (Brussaard, et al., 2008). In contrast, little is known of virus influences on primary and secondary consumer populations at ocean depths and this is a critical area for future research. An understanding of the discrete factors that contribute to successful lytic viral infection, including host susceptibility, virus attachment to the host, and host molecular mechanisms that support viral progeny production, is essential to develop quantitative models of the viral role in marine food webs and the biological pump (e.g., demise of a phytoplankton bloom leading to an export event). Of equal importance is gaining an understanding of virus-host dynamics and outcomes during non-lytic (e.g., lysogenic or latent) infections; evidence is emerging that viruses can modulate host physiology during latent infections. In addition, gene-based studies increasingly highlight the relative dominance and diversity of parasitic eukaryotes. These organisms appear highly represented (often upwards of 60-80% of the total eukaryotic gene sequences) throughout the water column, yet we lack basic information on which organisms they infect, how they are transmitted, and their role in altering organic matter flux.

Some of the research areas and questions associated with this topic include:

- What are the trophic interactions influencing phytoplankton-predator interactions?
- How do zooplankton behavior (e.g., diel vertical migration) and life histories (e.g., diapause, asexual reproduction) affect export?
- How do different feeding modes affect export?
- What are abundance, behavior, and feeding rates of detritivores, and how do these factors control removal and recycling of sinking detritus?
- What are rates of fecal pellet production (egestion) by different taxa?
- What role do parasites (viruses, prokaryotes, and eukaryotes) play in plankton mortality, community composition, and partitioning and reactivity of organic matter?
- Which organisms are most susceptible to parasitic infection and how do parasite-mediated exchanges of genetic information influence ecosystem functioning and regulate biodiversity?

Food web controls on production and respiration

The balance between photosynthetically fueled production of organic matter and respiration is termed net community production (NCP). In steady state, export of organic matter (dissolved and particulate) balances NCP, hence, NCP should equal the sum of vertical and horizontal fluxes of organic matter out of the upper ocean. Evaluating the mechanisms underlying “tipping points” in the balance between production and respiration are fundamental to our ability to predict and model spatial and temporal variability of export (Karl and Church, 2014). Over the past decade, there have been a number of important advances in our ability to measure rates of photosynthetic production, including several non-incubation-dependent methodologies and sensor-based measurements from autonomous sampling platforms (gliders, profiling floats, moorings). Such measurements include ratios of oxygen (O_2) to inert gases (e.g.*,* O_2:Ar or O_2:N_2), oxygen isotope determinations ($\Delta^{17}O$), and evaluating *in situ* changes in dissolved O_2 concentrations. These approaches have enabled robust, higher-frequency quantification of NCP and gross productivity, and have provided new insights into observed differences among methods. However, progress on developing methodologies for direct quantification of respiration has lagged, as have approaches to define the major pathways for organic matter production (e.g., dissolved versus particulate matter). As a result, complete understanding of processes that couple or decouple organic matter production and respiration, and the fate of this organic matter remain lacking. Moreover, the time and space scales appropriate for balancing export and NCP remain unclear; for example, sediment trap-derived sinking organic matter fluxes are often 2- to 4-fold lower than simultaneous estimates of NCP (Emerson, 2014). Such results may reflect underestimation of trap-derived vertical fluxes due to the contributions from dissolved organic matter (Carlson et al., 2004), spatial heterogeneity in export (subduction features), episodic export events (e.g. salp or jelly falls), and migratory losses not measured by traps, as well as poor trapping efficiencies of sediment traps or spatiotemporal decoupling of NCP and export. In addition, many of the methodologies for constraining NCP rely on measurements of O_2 and hence require conversion to carbon using poorly constrained stoichiometric ratios.

Ubiquitous meso- and submesoscale physical dynamics appear to decouple production, respiration, and export over short time and space scales and the impact of such high-frequency (episodic to seasonal scale) decoupling between upper ocean production and respiration on consumer production and metabolism remains largely unknown. Similarly, we currently lack information on the complexity and organization of remineralization and consumption processes that occur at small spatial scales (<1 meter), including patterns of succession in microbial colonization of particles, rates of and controls on enzymatic degradation of organic matter, and how the stoichiometry and energy content of available substrates influence consumer metabolism. Hence, examining temporal and spatial scales coupling productivity, respiration, organic matter remineralization, and export remain first order research priorities, as does research focusing on how organic matter export couples the biology of upper ocean to the physiology and metabolism of organisms in the ocean's interior waters. Episodic or event-scale export of organic matter reflects high-frequency decoupling in production and respiration. Such dynamics can be promoted by temporal variability in production, for example through episodic nutrient delivery to the euphotic zone via physical or biological processes; alternatively, such dynamics may reflect variations in consumer metabolism or community structure. Capturing these complex physical and biological dynamics requires integration of remote and autonomous observational tools with shipboard and laboratory experimental approaches that identify mechanisms and processes.

The workshop also highlighted the need for better integration of research linking food web ecology to biogeochemistry, in particular identifying gaps in our current understanding of the relationships between trophic transfer efficiencies, respiration, and export. There is limited information on the metabolic efficiencies of ocean plankton and how changes in food web structure and biodiversity might influence that efficiency and ultimately, export. Conceptually, the prevailing notion is that shorter food webs should channel a larger proportion of energy and material to top predators and fuel greater export than relatively inefficient food webs containing numerous trophic linkages. However, this overly simplistic view does not include trophodynamically complicated processes such as mixotrophy, whereby organisms have the capacity to consume organic matter for nutrition and energy, and also actively consume inorganic nutrients (including carbon) and obtaining energy from sunlight or oxidation of reduced inorganic substrates (Zubkov et al., 2008). Similarly, 'omics-enabled methodologies have revealed diverse and abundant chemoautotrophic microbes in the sea, particularly in the energy-poor meso- and bathypelagic waters. The metabolism and physiology of these organisms remains largely unknown, including only limited information on the types of substrates utilized to fuel their nutritional and energetic demands. Similarly, there is limited information to evaluate the extent to which the activities of these organisms control the vertical attenuation of organic matter and remineralization, and the extent to which these organisms interact with and depend on the suite of consumer organisms in the interior waters of the ocean.

Some of the research needs and questions associated with this topic include:

- What are the biological and physical tipping points that drive net ecosystem metabolism?
- What role do symbioses (i.e., parasitism, mutualism) and mixotrophy play in net ecosystem metabolism?
- How do meso- and submesoscale physical processes influence the coupling between production, respiration, and export in the upper ocean, and how does episodic restructuring of the upper ocean biology influence mid-water consumer physiology and metabolism?
- Coupled measurements of production and respiration across multiple scales
- What substrates fuel chemoautotrophy and how do these metabolisms influence organic matter attenuation?

Identifying which organisms control remineralization

A key topic that emerged during the workshop was the understanding of biological processes affecting the attenuation of sinking particles with depth. Mesopelagic zooplankton may modify the sinking particle flux by ingesting sinking POC and remineralizing it to CO_2, 'repackaging' it into fecal pellets with different sinking rates and organic content (Wilson et al., 2008), or fragmenting sinking POC into smaller, non- or more slowly sinking particles (Goldthwait et al., 2004). Bacteria secrete exoenzymes that solubilize and transform POC into DOC, which is remineralized to CO_2, and that also leads to particle fragmentation. The relative importance of these processes and the extent to which the supply of organic matter to depth can satisfy zooplankton and bacteria metabolic requirements needs further study (Steinberg et al., 2008; Giering et al., 2014). Two of the areas workshop participants prioritized as requiring research included ecology of gelatinous zooplankton and bacterial remineralization.

Highlighted areas for research on gelatinous zooplankton (or 'jellies') were considerably broader than remineralization per se, and included the role of gelatinous filter feeders (e.g., salps, appendicularians) in consuming and repackaging suspended or sinking particles into rapidly sinking fecal pellets, affecting attenuation. Data on gelatinous zooplankton community structure are needed, especially in the mesopelagic zone. Trophic interactions between gelatinous zooplankton and other organisms also need investigation, such as identifying key predators of gelatinous zooplankton, the role of gelatinous zooplankton as hosts for parasites, and interactions between jellies and microbes (e.g., production of mucus or DOM by jellies that support bacterial production). The fate of large bloom-forming gelatinous zooplankton and the role of these relatively large zooplankton in export were also questioned.

A number of studies show that bacterial remineralization alone could be responsible for the attenuation in sinking POC with depth (Herndl and Reinthaler, 2013). However, several remaining uncertainties that affect these estimates that were highlighted at the workshop, including bacterial growth efficiencies, new approaches to measurements of microbial production and respiration, and rates of enzymatic degradation. Bacterial colonization of particles and the need for whole community respiration measurements were also noted, as were the need for better constraint on the stoichiometry of bioreactive components of particulate and dissolved organic matter. Finally, the need for studies integrating quantification of organic matter decomposition and nutrient remineralization with functional diversity of microbes that catalyze specific degradation processes was highlighted.

Some of the research areas and questions associated with this topic include:

- What is the relative importance of the different processes by which bacteria and zooplankton affect attenuation of sinking particles in the mesopelagic zone?
- What is the role of gelatinous filter feeders in controlling export?
- What are the trophic interactions between gelatinous zooplankton and other organisms (including predators and parasites, and interactions between jellies and microbes)?
- Rates of microbial remineralization and organic matter degradation
- Methodologies for measuring microbial respiration and quantifying microbial growth efficiencies, and identification of processes regulating growth efficiencies
- Mechanistic studies linking biodiversity to material export

Ecological causes, drivers, and effects of vertical movement and migration

Diel vertically migrating zooplankton and fish play an integral role in the biological pump by feeding in the surface waters at night, and metabolizing this ingested particulate organic matter in the mesopelagic zone during the day (e.g., through respiration of CO_2, excretion of both dissolved inorganic and organic matter, and egestion of POM as fecal pellets at depth). Seasonal or “ontogenetic” vertical migrations are also particularly important in active transport in higher latitude regions. Export by vertical migration is commonly referred to as “active transport” to distinguish this process from the passive sinking of POM. A number of research areas needed to advance our understanding of active transport by diel and seasonal vertical migration of zooplankton and fish were identified by workshop participants. These include studies of species composition and biomass of migrators, the spatial variability of active transport and the degree to which migrating zooplankton act as a “vertical shunt”, and exported organic matter not measured by sediment traps. Studies addressing active transport by mesopelagic fishes (myctophids and others) are very limited (Davison et al., 2013) and will be required to understand the relative magnitude of zooplankton vs. fish active transport, and even more broadly the overall contribution of these higher trophic levels to export via the biological pump. For example, a recent study estimates that active flux by vertically migrating mesopelagic fish may account for as much as 70% of the vertical flux near the ocean floor near the Mid-Atlantic Ridge (Hudson et al., 2014). The influence of fish predation on zooplankton vertical migration and distribution was also noted, as rates of mortality of diel vertically migrating zooplankton at depth is still largely unknown.

Some of the research areas and questions associated with this topic include:

- What is, and what controls, the species composition, vertical distribution, biomass of migrators, the spatial variability of active transport by diel and ontogenetic vertical migrations?
- What is the contribution of mesopelagic fishes to active transport, and how does this compare to zooplankton?
- What are the rates and causes of mortality at depth of migrating zooplankton?

3. The Dissolved-Particulate Continuum

Introduction

Marine organic matter (OM) exists in a size continuum ranging from colloidal fibrils, through gel particles up to hundreds of microns long, to large marine snow particles (Verdugo et al., 2004). The distinction between dissolved organic matter (DOM) and particulate organic matter (POM) is operationally defined and depends on the pore size of the filters used to separate the two pools. Both pools contribute to the biological pump though their fates may differ appreciably — e.g., particles may aggregate, be consumed by animals, and sink. Exudation by phytoplankton, viral lysis, or zooplankton feeding releases fresh DOM into the marine environment.

Our understanding of the biological and abiotic processes influencing organic matter transformation, distribution, and fate in the ocean is in its infancy, largely because of the complexity of these interacting processes and the complexity of organic matter composition. The methodological challenges of characterizing marine organic matter that exists at very low concentrations and in the presence of high salt content adds further complexity.

The cycling of organic matter, especially the formation of gel-particles and their role in carbon cycling, and more broadly the rates of transformation between particulate and dissolved phases are largely unconstrained. However, the importance of gel-particles such as TEP for aggregation and gravitational sinking of organic matter is generally acknowledged. This was recognized by the workshop participants, and organic matter cycling was identified as a key area for future research needs.

Dissolved-Particulate Continuum was the second most important research theme that resulted from the final KJ_6 session of the workshop. This research theme comprised the following topics:

- *DOM-POM continuum and transformations (10.0, ranked 5th)*;
- *Physical and biological controls on aggregate and TEP dynamics (8.7, ranked joint 6th)*
- *Particle composition and sinking (8.3, ranked 8th).*

DOM-POM continuum and transformations

One of the central issues of the *DOM-POM continuum and transformations* concerns the formation of gel-particles (nano-gels, micro-gels, TEP, CSP: Comassie Stainable Particles) from macro-molecules, which are produced by a variety of organisms (Passow, 2002). What conditions lead to the exudation of these substances and what are their functions? What characterizes macromolecules that form gel particles, and when and by whom are they produced and released into the water? Which biotic and abiotic factors determine the formation rate of gel-particles from such macromolecules and the equilibrium between gel particles and dissolved precursors? The relationship between the pool of transparent exopolymer particles (TEP) and Coomassie stainable particles (CSP), which are polysaccharide- and protein-rich particles, respectively, is also unknown, although differences in their dynamics suggest that both differ in many aspects. There is also uncertainty regarding which fraction of the marine DOM pool is included in the gel-particle-precursors continuum. Are these elusive gel-substances important mostly because they are essential for aggregation and gravitational settling flux of solid particles, or do they themselves contribute significant amounts of organic carbon? An understanding of the formation mechanisms of gel-particles is required to predict their role in the marine carbon cycle.

Another key issue discussed within this first subtopic was the question of how much DOM is subducted in different regions of the ocean. Sinking particles contribute to the sequestration of carbon (i.e., its removal from the atmosphere on timescales of centuries to millennia) only if they sink rapidly enough to transport organic matter below the mesopelagic zone before being recycled. The bioavailability of organic matter is a crucial constraint on this. For example, organic matter recalcitrant to one microbial community may become available when exposed to another. This means that subducted DOM may be utilized rapidly at depth, even if it has remained in the surface layer for months. DOM that is recalcitrant on a timescale of 100 years should be considered sequestered, regardless of its depth distribution. An interesting new hypothesis, *the microbial carbon shunt* (Jiao et al., 2010) predicts an increase in the average age of the recalcitrant DOM in the ocean. Although it is important, this hypothesis is challenging to test because the oceanic recalcitrant DOM pool is very large compared to potential changes.

Many participants highlighted the need to characterize marine organic matter (OM), with the goal to relate specific characteristics to function, fate and behavior. It was suggested that marine organic matter needs to be described in terms of its:

(i) chemical and molecular composition,
(ii) bioavailability and lability (e.g., photolysis),
(iii) physical characteristics (e.g., dissolved, single particle or aggregate and associated properties like size, density, porosity and sinking velocity or buoyancy),
(iv) ability to interact with other particles (e.g., reactivity, stickiness, surfactant properties, potential for absorption), and
(v) microenvironment in the case of aggregates (e.g., micro-gradients).

The potential fate of organic matter depends not only on its own characteristics, but also on external factors such as microbial transformation of the material, O_2 concentrations, etc. Biological factors such as viruses, parasites, and symbiotic relationships all potentially play a role in determining the fate of organic matter by altering the export pathway taken by organic matter (e.g., viral lysing of bacterial cells) or affecting the behavior of organisms. However, to date we have only a vague idea of what those roles might be, and understand less about their drivers and their overall importance to organic matter export. Complicating factors include possible relationships between particle type and composition (e.g., presence or absence of minerals) and microbial degradation and zooplankton grazing. These relationships indicate the strong relationship between the POM-DOM continuum, food web structure, and spatial-temporal variability.

Rates of transformation between particulate and dissolved organic matter remain largely unconstrained. These rates are tied to the rates of production and consumption of both particulate and dissolved organic matter, which will change as both pools become less labile over time and with depth in the oceans. New and emerging ‘omics tools can provide insight into the biological processes that consume and transform POM and DOM.

Suggested research areas for this topic include:

- TEP, CSP, and micro-gel formation, consumption, and remineralization.
- Quantifying and mapping subduction of DOM and DOM export in general
- Understanding the formation and roles of exopolysaccharides and exudates
- Understanding the transformations between dissolved and particulate organic matter
- The relevance of gel formation to the DOM-POM continuum and export

Physical and biological controls on aggregate and TEP dynamics

Aggregation of small, slowly settling particles into larger, rapidly sinking ones has long been recognized as a key process in organic matter export from the surface ocean. Questions involving the dynamics of aggregation/disaggregation and the biological controls on these processes consistently arose during the KJ-sessions.

We have a basic understanding of the physical processes (Brownian motion, fluid shear, differential sedimentation) that bring particles together to form aggregates. However, we lack a similar understanding of the processes that break up particles (Burd and Jackson, 2009). We know that fluid motions, including small-scale turbulence, can break apart particles, as can swimming organisms, but we often lack a fundamental understanding of these fluid motions *in situ* and how these processes affect particle size distributions and fluxes as well as the ability to model them accurately.

Most research on aggregation has focused on the physical processes leading to particle collisions, but biological aggregation (e.g., fecal pellet production, discarded mucus feeding structure) is also important and we do not understand what controls the relative importance of these process types. Grazing by zooplankton aggregates small food particles into larger, faster settling fecal pellets, with the sinking rate dependent on the species of zooplankton among other factors. Discarded feeding structure, such as larvacean houses, can also be thought of as aggregation agents, and in some regions can contribute as much as 50% of the POC reaching the sea floor. The contribution of these biological aggregation processes to the biological pump will change with community structure and, possibly with climate change; for example, fecal pellet fluxes have been found to be negatively correlated with indices of climate variability (Wilson et al., 2008).

New and evolving technologies present opportunities for significantly advancing our understanding of aggregation processes. Imaging systems — conventional camera, laser, and holographic (Stemmann and Boss, 2012; Jackson et al., 2015)— and ROVs provide sources of new, detailed information about the types and sizes of particles that contribute to the biological pump. In addition, they can potentially address questions about the interaction between organisms and particles in the water column, providing insight into particle transformation processes. Most flux attenuation typically occurs within 50–100 m of the euphotic zone. However, processes of particle aggregation, transformation, and destruction are not separated by depth but instead they co-occur and the relative magnitude of their rates changes with depth. Consequently, these processes cannot be studied in isolation from each other.

The biological drivers and controls of particle stickiness represented a consistent sub-theme. The high stickiness of TEP make them an essential ingredient of the particle aggregation process, as well as the disaggregation process; more cohesive particles are less likely to break apart. However, stickiness is not necessarily constant, and our understanding of the biological processes (e.g., organism physiology, species producing TEP) and chemical and physical properties (salinity, pH, trace metal concentration) that control stickiness is in its infancy. Even though it is acknowledged that TEP is important for particle aggregation, its specific role remains unclear. For example, does TEP enhance aggregation through its stickiness alone, or does it add to the number of particles present and thereby increase collision frequencies?

Heterotrophic bacteria are known to produce, utilize or alter TEP, separately or in concert with autotrophs (Simon et al., 2002). However, results from these individual studies often appear contradictory, emphasizing that a general framework for the role of bacteria in regulating stickiness or TEP production, and their net effect on aggregation, is lacking. For example, it is unclear if the TEP matrix of aging aggregates is degraded, thus leading to the disintegration of aggregates, or whether the bacterial activity increases the cohesiveness of aggregates, thus stabilizing them with age. Aggregates are considered hot spots of activity, with complex communities developing; the need to understand these micro-ecosystems and their impact on flux was raised both within this topic and within the topic focusing on food webs. For example, do flagellates control bacteria within aggregates?

Models of particle aggregation generally represent only the physical processes that bring particles together and vary in complexity depending on the number of size classes they depict. Participants thought that both physical and biological processes of aggregation and disaggregation need to be included in models so as to improve predictions of POM export from surface waters and its utilization as it sinks through the water column.

Research topics and questions that were highlighted as important in this area included:

- Mechanisms and relative roles of particle aggregation and disaggregation
- What regulates particle stickiness?
- How does TEP facilitate particle aggregation?
- What is the contribution of bacteria to TEP production?
- Does bacterial activity increase or decrease particle aggregation?
- Understanding biological vs. physical controls on aggregation

Particle composition and sinking

Particle sinking velocity is a crucial factor determining POM export in the ocean. At a hypothetical constant degradation rate, sinking velocity (e.g., time in the water column before reaching sequestration depth) determines the fraction of carbon sequestered (Passow and Carlson, 2012). Sinking velocity of a spherical marine aggregate depends to a large degree on its size, but also on its excess density and porosity. However, *in situ* large marine aggregates are rarely spherical and little is known about *in situ* sinking velocities. Does sinking velocity of aggregates change with depth and age, and if so, how? Typical sinking velocities of aggregates at depth are often cited to be on the order of 100 m d^{-1}, but for some particles can be an order of magnitude higher. Futhermore, ascending marine snow particles have also been observed, but very little is known about the mechanisms leading to their formation or how frequently they occur. Clearly, a better understanding of sinking velocities of aggregates as a function of their composition and size is needed, along with an understanding of how various decomposition processes alter particle density.

In general, we have been unable to find a universal relationship between particle sinking rate and particle size, indicating that other factors also play a strong role. Particle composition (and hence excess density) is an obvious factor, but currently there is only limited evidence that TEP content can decrease sinking velocities, whereas mineral content may either decrease or increase sinking velocity, depending on how it affects particle size and excess density. If composition does play a significant role, then as particles age and their composition changes (e.g., through microbial degradation), then it is likely that their sinking velocity (and hence particle flux) will also change.

Sinking velocities also determine the rates at which sinking particles interact with organisms in the surrounding water column. Rapidly sinking particles (hundreds of meters per day) can reach the seafloor relatively intact and not heavily degraded, indicating that sinking velocity may affect grazing efficiency and the connection between the surface, mesopelagic, and bathypelagic food webs.

Research areas that were highlighted under this heading included:

- Size distribution of sinking particles

- Quantifying and understanding the role of the TEP fraction within sinking aggregates
- Relationship between elemental stoichiometry and particle sinking speed.
- Do particle size-sinking rate relationships hold across particle types?
- How do particle composition and interactions with organisms relate to particle density, sinking speed, and fate?

4. Variability in Space and Time

Introduction

The strength, efficiency, and nature of the ocean's biological pump are known to exhibit large variability over a range of spatial and temporal scales. This variability is driven by a combination of physical, biological, and chemical processes. Advances in remote sensing capability and modeling have increased our understanding of the physical drivers of variability, but our understanding of the biological drivers remains poor. Understanding this variability and what drives it is critical to assessing the biological pump's impact on the air-sea balance of carbon dioxide and our understanding of local to global biogeochemical cycling. Despite its importance, our understanding of the organic matter export and sequestration is largely based on a limited collection of heterogeneous studies conducted at specific times and locations. In comparison to our ability to monitor the state of ocean temperature and salinity with ARGO floats, mooring arrays, and satellites, methodological limitations make it difficult to capture the variability of biological processes that occur on scales of micrometers to ocean basins. In particular, we have a very poor understanding of episodic export events, their frequency, magnitude, ecological attributes and triggers, as well as their integrated effect over larger spatial and temporal scales.

Variability in Space and Time was the third high-priority research theme that resulted from the final KJ_6 session of the workshop. This research theme comprised the following topics:

- Episodic Events– quantification and biological understanding (*12.4, ranked 4th*)
- Scales of Spatial and Temporal Variability (*4.6, ranked 10th*)

Episodic Events

Workshop participants identified episodic biological events and their associated transfer of organic matter to depth as a priority research area. Measurements of vertical organic matter flux in the oceans have provided generalized descriptions of annual patterns of flux and processes underlying these patterns. However, time series measurements often provide serendipitous evidence for strong episodic pulses of sinking particulate organic matter and mass deposition events of phytodetritus or the carcasses of gelatinous zooplankton. Such events imply decoupling in biological processes that produce and consume organic matter, but often it is difficult to disentangle whether such events result from decreased consumption or accelerated production. For example, high flux events could be triggered by compositional shifts in phytoplankton taxa or size, or could result from changes in the structure and metabolic demands of the mid-water consumer community. The underlying triggers for these mechanisms are likely to be very different. Schools of fish or swarms of zooplankton can also accelerate the local fluxes of particulate matter to depth in a highly heterogeneous manner through the production of fecal pellets

Most existing observational systems are not well suited to studying event-scale dynamics that, by their very nature, are short-lived and presently unpredictable. Therefore, methodological developments and improved observational efforts are required to capture these transient features of the biological pump. Most information on episodic fluxes in the water column are either purely serendipitous, or come from long-term time series. Some regions of the ocean are known to support seasonally high populations of gelatinous zooplankton, but we have little knowledge of the global distribution of such regions. Similarly, shifts in phytoplankton composition (e.g., proportional increases in the biomass of diatoms) can result in episodic to seasonal-scale increases in export. In some cases, these upper ocean compositional shifts can be subtle, without large perturbation to upper ocean biomass, and hence such features can escape detection by remote sensing.

Understanding processes underlying episodic export events requires an integrated biological, geochemical, and physical observational approach. At the meso- and submesoscale, triggers of export could include subduction or mixing of organic matter out of the euphotic zone, or upwelling/downwelling of isopycnal surfaces. Such physical processes can alter vertical supply of nutrients or displace isolume surfaces, resulting in spatiotemporal imbalances in organic matter production and consumption. Alternatively, atmospheric deposition of nutrients or supply of nitrogen to the upper ocean via nitrogen fixation can also result in episodic export. Hence, there is need for studies identifying the time scales over which perturbations to upper ocean physics and biology are linked to event-scale removal of material to the deep sea.

The remineralization rate of exported organic matter helps determine the length of time the organic material is sequestered in the oceans. Episodic events can inject large quantities of fresh organic matter into the deep ocean. For example, typical sinking speeds of particulate organic material are on the order of 100 – 150 m d^{-1}, but salp carcasses and fecal pellets can sink at speeds in excess of 1000 m d^{-1}. Consequently, this material can arrive at the deep benthos in a relatively fresh (i.e. unaltered) state, affecting deep ocean ecosystems. Understanding the compositional nature (e.g., stoichiometry, mineral content, taxonomic and genetic identity of organisms) of material sinking in episodic events can help us better understand why the material escapes degradation, how its input alters deep-ocean ecosystems, and how event-scale processes impact ocean carbon sequestration.

Traditionally, our understanding and estimates of organic matter export are largely based on sediment trap data, radiotracer information, or are modeled derivations from satellite surface chlorophyll estimates. New approaches for measuring net community production are increasingly being used to constrain estimates of export. Scaling these observations to obtain regional and global estimates of organic matter export will neglect, or potentially underestimate the contribution of episodic events which can be inherently non-linear. Therefore, in addition to new methodological developments and observational efforts, modeling exercises and sensitivity studies will be required to scale up limited observations and assess the integrated importance of such episodic processes. Moreover, numerous independent approaches indicate that sediment trap-derived fluxes underestimate organic matter export, particularly during high-flux periods. Given the dependence of global carbon models on the vertical attenuation of organic carbon flux in the ocean, there is a pressing need to develop new observational tools that capture spatiotemporal variability in the magnitude of flux and remineralization length scales associated with flux events.

Episodic export events can be driven by both physical and biological processes. Recent advances in submesoscale modeling have improved our understanding of the physical drivers. The biological drivers of episodic export events, however, remain poorly understood and need more research attention. Many different food web components may be involved in initiating large pulses of exported dissolved and particulate organic matter. In addition, interactions between different ecosystem components may be important in determining the timing and intensity of such pulses. For example, one open question is what role do viruses or other parasitoids play in the initiation of phytodetrital export events? Similarly, it remains unclear whether or how such events influence the metabolism of organisms living in the ocean's interior waters. Efforts are needed to identify the ecological traits that promote strong episodic fluxes of organic matter into deeper waters, the organisms involved (e.g., fish, gelatinous zooplankton, diatoms, diazotrophs), and to characterize the different types of episodic events (e.g., jelly fall events, fecal pellet flux events) that occur.

Some of the specific research questions and areas that repeatedly arose concerning this topic include:

- Capturing and quantifying the frequency and intensity of episodic export events and estimating their importance on a global scale
- How do episodic export events structure ecosystems throughout the water column and what ecosystem traits or characteristics lend themselves to episodic flux events?
- The development of models that describe episodic events — modeling was seen as useful tool to examine biological processes affecting organic matter export across all time and space scales
- What are the contributions of fecal material versus dead and living organisms to flux events, and how do these contributions vary in time and space?
- How biologically reactive is organic matter associated with these events, and how/why does it escape consumption?
- How will climate change affect the spatial and temporal distributions of episodic events?
- What are the biological drivers of episodic events?

Scales of Spatial and Temporal Variability

Export of organic matter from the surface ocean occurs over a wide range of spatial and temporal scales and workshop participants identified the need to quantify and understand the variability of the biological pump across all relevant spatial and temporal scales. Physical processes such as the formation of fronts and eddies are well known to induce meso- and submesoscale spatial and temporal variability in export flux (e.g., Omand et al., 2015). The biologically driven processes that lead to export span many orders of magnitude in scale from particle aggregation and organic matter remineralization (microns to centimeters, and times scales of seconds to hours) to near-basin-scale blooms (10s of kilometers, weeks).

Factors affecting the spatial and temporal scales pertinent to biological process that drive export of organic matter are not always well understood. This is partly because of the challenges in making observations on the relevant scales, and also that these processes are inherently coupled to other processes occurring at different scales. For example, aggregation depends on the stickiness of particles (Burd and Jackson, 2009), which is in turn a function of community composition (e.g., Kiørboe and Hansen, 1993). Export of organic matter from the upper ocean should be balanced by import of material (e.g., nutrients) over appropriate time and space scales. However, the physical (e.g., mixing or upwelling) and biological (e.g., nitrogen fixation, vertical migration) processes that supply nutrients to the upper ocean can vary independently over a range of time and space scales. Similarly, there is little known about variability in processes that transform organic matter in the ocean. For example, the quantitative role of viruses in the transformation of particulate material to dissolved organic matter, which may have different modes and scales of export, remains largely unknown. Consequently, multi-scale observational studies will be necessary to assess the magnitude of variability that exists at spatial scales ranging from microns to ocean basins. Dominant modes of variability in export must be linked with the physical, chemical, and biological drivers that influence them.

Understanding the scales of both temporal and spatial variability of organic matter export will help improve regional and global estimates of export, and how climate change might influence them. As with episodic events, a better quantitative understanding of spatial and temporal variability in export (and the biological processes affecting it) will provide more accurate scaling of local observations of export to regional and global estimates. Similarly, modeling exercises have revealed that the regional distributions of particulate matter fluxes and remineralization rates are key determinants in the sequestration efficiency of the biological pump, yet the current observational evidence does not allow us to adequately map these regional patterns and assess how they vary with time. These relationships become important in understanding how changes in climate and ocean food webs may impact the patterns and strength of the biological pump, and how those changes can result in biological, biogeochemical, and climate feedbacks throughout the earth system.

Some of the research areas associated with this include:

- How does climate change affect the spatial and temporal variability of organic matter export?
- How do scales of physical process such as mixing affect species interactions (e.g., grazer-phytoplankton interactions) and how are these reflected in scales of organic matter export?

- How temporally and spatially variable is export and what combinations of tools are best suited to capture that variability?
- What are the spatial and temporal scales relevant to gelatinous zooplankton and their effect on export?
- How does climate change affect exudation and what are the ramifications for export of organic matter?

5. Conclusions

The biological pump is controlled by a variety of biological, chemical, and physical processes. Consequently, a predictive understanding of the biological pump requires an interdisciplinary approach spanning a range of temporal and spatial scales. The participants of this workshop were charged with developing research priorities on the biology of the biological pump, but were always acutely aware of the intimate links to relevant chemical and physical processes and the interactions between them. This is evident in the three broad research themes and the specific research areas that emerged.

Our understanding of the biological pump and its drivers has improved dramatically over the past 20 to 30 years through a combination of field programs at multiple scales, combined with smaller-scale, focused process research, and modeling. However, new observational and data analysis techniques, combined with increased spatial and temporal coverage, have led to the realization that previously unrecognized or under-appreciated biological processes and pathways may be, or may become important — examples include the role of gelatinous zooplankton, the production of gels, and the role of viruses and parasitoids. It is important to understand the drivers of these processes and pathways so that, if needed, accurate yet simplified models suitable for global simulations can be developed from observations and more complex, process-based models.

The broad themes and research areas presented here provide guidelines for what the community feels are research areas that have the highest potential for significantly advancing our understanding of the biology of the biological pump. Some of these ideas (e.g., creation and consumption of gels) might best be studied using focused, potentially interdisciplinary research that can explore the details of individual processes. Such research can, for example, produce a detailed understanding of a given mechanism suitable for the development of complex, processes-based models. Other ideas (e.g., linking food web complexity to export, or studies of episodic events) will benefit from data on competing pathways and are best implemented within large-scale field campaigns. Without such additional data, imbalances in budgets cannot be resolved and have to be attributed to a combination of unmeasured processes. Consequently, we believe that successful biological pump research will involve both coordination among research groups as well as the implementation of integrated studies operating at multiple spatial and temporal scales.

References

Brum JR, Sullivan MB, 2015. Rising to the challenge: accelerated pace of discovery transforms marine virology. *Nature Reviews Microbiology,* 13:147–159.

Brussaard CPD, Wilhelm SW, Thingstad F, Weinbauer MG, Bratbak G, Heldal M, Kimmance SA, Middelboe M, Nagasaki K, Paul JH, Schroeder DC, Suttle CA, Vaque D, Wommack KE, 2008. Global-scale processes with a nanoscale drive: the role of marine viruses. *ISME J*ournal, 26: 575–578.

Burd AB, Jackson GA, 2009. Particle aggregation. *Annual Review of Marine Science*, 1:65–90.

Carlson CA, Giovannoni SJ, Hansell DA, Goldberg SJ, Parsons R, Vergin K, 2004. Interactions between DOC, microbial processes, and community structure in the meopalegic zone of the northwestern Sargasso Sea. *Limnology and Oceanography*, 49:1073–1083.

Davison PC, Checkley DM, Koslow JA, Barlow J, 2013. Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. *Progress in Oceanography,* 116:14–30.

Emerson S, 2014. Annual net community production and the biological carbon flux in the ocean. *Global Biogeochemical Cycles*, 28:14–28.

Hudson JM, Steinberg DK, Sutton TT, Graves JE, Latour RJ, 2014. Myctophid feeding ecology and carbon transport along the northern Mid-Atlantic Ridge. *Deep-Sea Research I,* 93:104–116.

Giering SLC, Sanders R, Lampitt RS, Anderson TR, Tamburini C, Boutrif M, Zubkov MV, Marsay CM, Henson SA, Saw K, Cook K, Mayor DJ, 2014. Reconciliation of the carbon budget in the ocean's twilight zone, *Nature,* 507:480–483.

Goldthwait S, Yen J, Brown J, Alldredge A, 2004. Quantification of marine snow fragmentation by swimming euphausiids. *Limnology and Oceanography*, 49:940–952.

Guidi L, Chaffron S, Bittner L, Eveillard D, Larhlimi A, and others, 2016. Plankton networks driving carbon export in the oligotrophic ocean. *Nature,* 532:465–470.

Herndl GJ, Reinthaler T, 2013. Microbial control of the dark end of the biological pump. *Nature Geoscience*, 6:718-724, doi:10.1038/ngeo1921.

Jackson GA, Checkley DM, Dagg M, 2015. Settling of particles in the upper 100 m of the ocean detected with autonomous profiling floats off California. *Deep-Sea Research I,* 99:75–86.

Jiao N, Herndl GJ, Hansell DA, Benner R, Kattner G, Wilhelm SW, Kirchman DL, Weinbauer MG, Luo T, Chen F, Azam F, 2010. Microbial production of recalcitrant dissolved organic matter: long-term carbon storage in the global ocean. *Nature Reviews Microbiology,* 8:593–599.

Karl DM, Church MJ, 2014. Microbial oceanography and the Hawaii Ocean Time-series programme. *Nature Reviews Microbiology,* 12:699–713.

Kiørboe T, Hansen JLS, 1993. Phytoplankton aggregate formation: Observations of patterns and mechanisms of cell sticking and the significance of exopolymeric material. *Journal of Plankton Research,* 15(9):993-1018, DOI: 10.1093/plankt/15.9.993.

Lebrato M, Jones DOB, 2009. Mass deposition event of *Pyrosoma atlanticum* carcasses off Ivory Coast (West Africa). *Limnology and Oceanography*, 54:1179–1209.

Omand MM, D'Asaro EA, Lee CM, Perry MJ, Briggs N, Cetinić I, Mahadevan A, 2015. Eddy-driven subduction exports particulate organic carbon from the spring bloom. *Science*, 348:222-225, DOI: 10.1126/science.1260062.

Passow U, 2002. Transparent exopolymer particles (TEP) in aquatic environments. *Progress in Oceanography*, 55:287–333.

Passow U, Carlson, C., 2012. The Biological Pump in a High CO_2 World. *Marine Ecology Progress Series*, 470:249–271.

Siegel DA, Buesseler KO, Behrenfeld MJ, Benitez-Nelson CR, Boss E, Brzezinski MA, Burd A, Carlson CA, D'Asaro EA, Doney SC, Perry MJ, Stanley RHR, Steinberg DK, 2015. Prediction of the Export and Fate of Global Ocean Net Primary Production: The EXPORTS Science Plan. *Frontiers in Marine Science*, http://dx.doi.org/10.3389/fmars.2016.00022

Simon M, Grossart HP, Schweitzer B, Ploug H, 2002. Microbial ecology of organic aggregates in aquatic ecosystems. *Aquatic Microbial Ecology,* 28:175–211.

Steinberg DK, Van Mooy BAS, Buesseler KO, Boyd PW, Kobari T, Karl DM, 2008. Bacterial vs. zooplankton control of sinking particle flux in the ocean's twilight zone. *Limnology and Oceanography*, 53:1327–1336.

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*, 4:263–290.

Verdugo P, Alldredge AL, Azam F, Kirchman D, Passow U, Santschi P, 2004. The oceanic gel phase: a bridge in the DOM-POM continuum. *Marine Chemistry,* 92:67–85.

Wilson SE, Steinberg DK, Buesseler KO, 2008. Changes in fecal pellet characteristics with depth as indicators of zooplankton repackaging of particles in the mesopelagic zone of the subtropical and subarctic North Pacific Ocean, *Deep Sea Research Part II: Topical Studies in Oceanography*, *55*:1636–1647.

Zubkov MV, Tarran GA, 2008. High bacterivory by the smallest phytoplankton in the North Atlantic Ocean. *Nature,* 455:224–226.

Appendix A: The KJ Technique

The KJ technique was developed by the Japanese anthropologist Jiro Kawakita for analyzing and ranking large quantities of disparate information. As a group activity, the KJ-technique allows for rapidly arriving at a consensus choice of priorities. The advantages of the technique are that it minimizes the potential for a few individuals to monopolize the conversation and allows the group to work both creatively and critically in a productive fashion. Although the technique is typically used in managerial or design-based settings, its original use was in organizing and prioritizing ideas developed from large bodies of information; this made it a good choice for the workshop. One of the interesting characteristics of the KJ-technique is that, in general, different groups of individuals tend to independently arrive at similar priorities for the same problem.

Workshop participants were divided into four groups, with group composition changing for each KJ focus question. At any one time, all four groups considered the same focus question (see Workshop schedule, Appendix C). The expectations were that each group would arrive at broadly similar priorities, but if they didn't, the diversity of ideas that emerged would be beneficial. Four KJ facilitators (Paula Bontempi, Lisa Clough, Mike Sieracki, Cynthia Suchman) were chosen (one for each group) to lead each group through the KJ sessions.

Within in each focus question, the sequence of the KJ technique was broken down into the following steps:

Step1: Brainstorming (quiet activity, minimal discussion) — approximately 10 minutes during which participants wrote ideas on yellow sticky notes
Step 2: Grouping of similar Ideas (quiet activity, minimal discussion) — approximately 5 minutes, during which the yellow sticky notes were sorted into similar groups
Step 3: Assign Names to Groups (quiet activity, minimal discussion) — approximately 5 minutes during which overarching names were given to each group using different colored sticky notes
Step 4: Vote for the top three groups (quiet activity, minimal discussion) — approximately 10 minutes during which each participant individually ranked the groups
Step 5: Rank the most important groups (group activity with discussion) — 30 minutes during which overall ranking was conducted and groups could be merged, split or changed

At the conclusion of each KJ session, all participants gathered and one individual from each group reported out on the outcomes of their KJ session. These were recorded (Appendix D) and used for the final prioritizing session.

Appendix B: Participants

NAME	AFFILIATION AND EMAIL	RESEARCH INTERESTS
William Balch	Bigelow Laboratory for Ocean Sciences	Coccolithophores, satellite ocean color, bio-optics
Andrew Barton	Geophysical Fluid Dynamics Laboratory, Princeton.	Microbial physiology, ecology, climate variability & feedbacks on biogeochemical cycles, trait based approaches
Heather Benway	Woods Hole Oceanographic Institution **Organizing committee**	Carbon cycle, climate change, paleoceanography
Daniele Bianchi	University of California Los Angeles	Biophysical interactions, oxygen minimum zones, vertical migration
Alexander Bochdansky	Old Dominion University	Microbial ecology, deep-sea microbial communities, marine particles
Paula Bontempi	NASA Program Manager, Ocean Biology & Biogeochemistry **KJ Facilitator**	Phytoplankton, bio-optics, remote sensing
Alison Buchan	University of Tennessee, Knoxville **Organizing committee**	Microbial molecular biology/ecology, viruses in heterotrophic bacteria
Adrian Burd	University of Georgia **Organizing committee**	Particle flux and transformation, process modeling
Craig Carlson	University of California, Santa Barbara	Dissolved organic carbon, microbial ecology, carbon export
David Caron	University of Southern California	Microbial diversity, ecology, physiology, biogeography
Matt Church	University of Hawai'i **Organizing committee**	Microbial organisms, biogeochemical cycling
Lisa Clough	NSF, Head of Ocean Section **KJ Facilitator**	Benthic organisms and ecosystems, animal-sediment interactions
Robert Condon	University of North Carolina, Wilmington	Role of jellyfish in biogeochemical cycles, zooplankton community structure and carbon export
Peter Davison	Farallon Institute	Fish, carbon export

Colleen Durkin	Moss Landing Marine Lab	Phytoplankton, carbon export
Kyle Edwards	University of Hawai'i	Phytoplankton functional traits, community structure
Meg Estapa	Skidmore College	Transformation and export of particulate material, remote sensing, optical sensors
Lionel Guidi	Observatoire Océanologique de Villefranche-sur-Mer, France	Particle size distributions, carbon export, remote sensing, particle transport
Ryan Hechinger	Scripps Institution of Oceanography	Ecology of parasites, effects on ecosystem structure and function
George Jackson	Texas A&M University	Coagulation, particle dynamics, small-scale processes, mesopelagic processes
Julie Kellner	NSF Program Director, Biological Oceanography	Marine ecology, marine ecosystem management
Richard Lampitt	National Oceanography Center, Southampton, UK	Particle flux, sediment traps, carbon export
Mike Landry	Scripps Institution of Oceanography Organizing committee	Micro- and mesozooplankton, community ecology, physical-biological coupling
Ricardo Letelier	Oregon State University	Phytoplankton ecology, biogeochemical processes, remote sensing
Xavier Mari	Institut Méditerranéen d'Océanologie, France	TEP, particle size and flux, black carbon
Andrew McDonnell	University of Alaska, Fairbanks Organizing committee	Marine particles and flux, sediment traps, optics
William Miller	NSF Program Director, Chemical Oceanography	Fluxes of trace gases and their significance to global warming, biogeochemical feedbacks, and climate change
Uta Passow	University of California, Santa Barbara Organizing committee	Biological pump, TEP, ocean acidification, marine particles
Helle Ploug	University of Gothenburg, Sweden	Particle transport, remineralization, aggregate and colony formation, small-scale processes
Astrid Schnetzer	North Carolina State University	Protistan and zooplankton ecology and biogeochemical cycling

Mike Sieracki	NSF Program Manager, Biological Oceanography **KJ Facilitator**	Microbial ecology, planktonic ecosystems, community & trophic structure
Heidi Sosik	Woods Hole Oceanographic Institution	Phytoplankton ecology, remote sensing, optics
Deborah Steinberg	Virginia Institute of Marine Science **Organizing committee**	Zooplankton ecology and physiology, nutrient cycling
Grieg Steward	University of Hawai'i	Marine microbial ecology, eukaryotic viruses
Diane Stoecker	UMCES-Horn Point Lab	Planktonic protists, microzooplankton, mixotrophy
Mike Stukel	Florida State University	Plankton trophic dynamics, particle flux, trophic and ecosystem models
Cynthia Suchman	NSF Program Director, Biological Oceanography **KJ Facilitator**	Zooplankton, medusa, marine policy
Ann Tarrant	Woods Hole Oceanographic Institution	Copepod physiology and life stages, molecular tools to examine stressor response and adaptation of marine organisms
Ben Twining	Bigelow Laboratory for Ocean Sciences	Trophic transfer, recycling

Appendix C. Workshop Agenda

NSF Biology of the Biological Pump Workshop
February 19-20, 2016 (Hyatt Place New Orleans, New Orleans, LA)

WORKSHOP AGENDA

THURSDAY, FEBRUARY 18, 2016

6:30-8:00 PM	KJ Technique facilitator training (KJ facilitators and workshop organizing committee members)

FRIDAY, FEBRUARY 19, 2016

7:30 AM	Breakfast (Meeting room)
8:00 AM	Welcome (Adrian Burd, Univ. Georgia)
8:10 AM	Biological Pump Research Initiatives (Adrian Burd, Univ. Georgia, Debbie Steinberg, VIMS, Michael Sieracki, NSF)

PLENARY SESSION (25-min. presentations, 5 mins. for questions)

8:30 AM	Biological Pump Overview (Adrian Burd, Univ. Georgia)
9:00 AM	New Instrumentation (Andrew McDonnell, Univ. Alaska, Fairbanks)
9:30 AM	New Biological Processes (Michael Landry, Scripps Oceanographic Inst.)
10:00 AM	Break
10:30 AM	Aggregation and Marine Snow (Uta Passow, Univ. California, Santa Barbara)
11:00 AM	Quantification of Export (Matthew Church, Univ. Hawaii)
11:30 AM	Group Discussion
12:00 PM	Lunch (Hotel Atrium, 3rd floor)

KJ FOCUS GROUP SESSIONS (Groups will change for each KJ Focus Area, please see back of your name tag for your group assignments)

1:30 PM	Presentation on the KJ Method (Adrian Burd, Univ. Georgia)
2:00 PM	KJ Focus Area 1: *Particle formation in the upper ocean and processes that drive export* (All groups)
3:00 PM	Report back and discussion on Focus Area 1 (~5 mins./group)

3:30 PM Break

4:00 PM KJ Focus Area 2: *Mesopelagic flux attenuation and the biological processes that drive it* (All groups)

5:00 PM Report back and discussion on Focus Area 2 (~5 mins./group)

5:30 PM Check-in by KJ facilitators

6:00 PM Adjourn for the day

7:00 PM Group Dinner at Cochon Restaurant (930 Tchoupitoulas Street, New Orleans, 2nd floor)

SATURDAY, FEBRUARY 20, 2016

7:30 AM Breakfast (Meeting room)

8:00 AM Morning kickoff

KJ FOCUS GROUP SESSIONS (Groups will change for each KJ Focus Area, please see back of your name tag for your group assignments)

8:15 AM KJ Focus Area 3: *Particles: Characteristics, bioreactivity, export, stoichiometry, episodic export events* (All groups)

9:15 AM Report back and discussion on Focus Area 3 (~5 mins./group)

9:45 AM Break

10:15 AM KJ Focus Area 4: *Microbial and viral processes and newly revealed biological pathways* (All groups)

11:15 AM Report back and discussion on Focus Area 4 (~5 mins./group)

11:45 AM Lunch (Hotel Atrium, 3rd floor)

1:00 PM KJ Focus Area 5: *Food web, community structure, and trophic interactions* (All groups)

2:00 PM Report back and discussion on Focus Area 5 (~5 mins./group)

2:30 PM Break

2:45 PM Introduce final group exercise

3:00 PM KJ Final: *Funding priorities* (All groups) - Small group discussions to prioritize (with research dollars) collective group outcomes of five KJ focus areas (10 mins./focus area)

4:00 PM	Groups report back in plenary on funding priority exercise
4:30 PM	Final discussion
5:00 PM	Adjourn meeting (workshop organizers meet to discuss next steps)

Funding for this workshop was provided by the National Science Foundation (NSF).
Coordination and logistical support for this workshop was provided by the Ocean Carbon and Biogeochemistry (OCB) Program (www.us-ocb.org)

Appendix D. Community Feedback

The report from this workshop was released to the broader oceanographic community for comment between June 29th 2016 and August 1st 2016. The community was informed of this through the OCB and GEOTRACES email lists, on the front page of the OCB website, and at various workshops (e.g. OCB summer workshop and the joint OCB/GEOTRACES workshop on internal trace metal cycling). The report was made available for download through the OCB webpage. We would like to sincerely thank all those who spent time reading the report and providing thoughtful and insightful comments. The received written comments and responses (in italics) are listed below.

COMMENT 1

I already skimmed this report and think it's pretty good. If I were writing it, I would stress that we know almost nothing about sinking speeds of natural particles and that means that we have to guess at or use proxies for residence times etc. To understand the pump, we need rates and the primary rate is sinking speed and we have almost no idea. I think this is one of the Holy Grails of marine science; maybe we could have an X-prize for it after we get a stable pH meter? I've scratched my head for 35 years and have not figured out how to do it so I guess I have to leave it to the next generation.

Response: *We agree strongly with this comment and our lack of predictive understanding of particle sinking velocities was a topic that was recognized frequently by the workshop participants and appears in several places in the report, as well as its own section (p. 23). Some efforts are currently being made to develop devices that estimate sinking velocity in situ.*

COMMENT 2

I think it would be helpful to know the precise physics measurements, microstructure, etc. needed to help your aggregate dynamics simulations. The white paper seems very general.

Response: *The workshop participants were charged with developing a set of high-level scientific research priorities for the* ***biology*** *of the biological pump, however, participants recognized that biology is influenced by numerous physical and chemical processes. Thus, the report emphasizes the biological processes affecting aggregate dynamics, but also acknowledges that this is a highly interdisciplinary research area and recognizes the importance of relevant physical processes.*

COMMENT 3

I've read the report, "Towards a transformative understanding of the ocean's biological pump…" and am writing with some comments. I thought the report gave a good summary of processes, excluding photoautotrophy, that influence euphotic zone NCP and export of dissolved and particulate organic C (which I'll refer to as "export"). I found the report to be interesting and exhaustive. It certainly deals with a fundamental issue in ocean biogeochemistry.

Granted that it's always easy to be critical of a report like this, I did feel that there were a number of limitations. First, photosynthesis (and autotrophic carbon fluxes generally) obviously play a major role in determining export, but these were essentially ignored in the report. For example, more is written about the workings of the KJ method than about photosynthesis and its influence on ocean carbon fluxes. I guess the response to this comment would be that the report did not intend to address this topic. In this case, it would be helpful to align the name and the goals to what the report was actually intended to address.

Response: *We agree that photosynthesis is a highly important process for understanding the biological pump. This topic could have been a major focus, and is implicit in the discussion in the section on Food web Controls of Production and Respiration (p. 15–17). However, photosynthesis did not explicitly end up in the final list and, whilst important, was not considered as one of the most important research areas at this time. That being said, processes regulating primary production and NCP are important and do occur in several places in the detailed topic list from the KJ1 session (Particle formation in the upper ocean and processes that drive export).*

Second, surely there is enough information about ocean carbon fluxes to provide a context for future studies. For example, Emerson, Quay and others have shown that annual NCP is about 1-4 moles m^{-2} yr^{-1} over most of the ocean, and that annual net/gross carbon production is about 10-30%. One would think that this broad picture, together with the underlying specific observations, would give some guidance to aspects of physical and heterotrophic processes that are most important for regulating export.

Response: *This is an important point that highlights some of the unresolved issues of determining the relevant spatial and temporal scales of different export estimates. We have examples where one process or another is important locally, or for a certain time, but it remains unclear how important such a processes is on average or on global scales (e.g. the role of gelatinous zooplankton). This makes it hard to match individual processes to average global estimates. However, the comment raises an important, and as yet unanswered biogeochemical question. Many of the large scale estimates such as those mentioned above rely on measurements of bulk products such as oxygen. The estimates for annual NCP that are derived this way often conflict with those determined using sediment traps and satellite algorithms. However, sediment traps do provide actual samples that can be used to determine the properties of sinking material. The difference between these methods is troublesome — even if sediment traps are incorrect, one is left with the question of what parts of the sinking flus are they missing and how can we determine its properties? These different processes and measurement techniques have different relevant space and time scales. The discrepancy in methodologies was recognized by workshop participants, and this is reflected somewhat in the discussion on p.15 of the report.*

I have 3 other general comments. First, the report identifies some priorities, but does not look for “sweet spots” where we can make the most rapid progress in characterizing ocean carbon fluxes. For example, oligotrophic regions make up maybe half the surface ocean, and (as stated above) have export fluxes similar to waters with much higher nutrient concentrations (the contrary statement on p. 13 is incorrect). We have some guesses about the N source for phytoplankton in these regions, but no compelling evidence. This topic might be a question on which we could make good progress in the coming years. A successful investigation would then inform us about controls on N fluxes, and ultimately C fluxes, over a very broad area of the oceans. I don't want to focus on this aspect of biogeochemistry; my broader point is that priorities need to be shaped by opportunities as well as how basic the scientific question is.

Response: *There is a discrepancy between estimates of flux obtained from biogeochemical measurements and other techniques (see discussion below). This is likely a result of different techniques measuring processes that operate on different scales. We are basing our statement on p. 13 on results from Henson et al. (Global Biogeochemical Cycles, 26, GB1028, doi:10.1029/2011GB004099), among others. In the report, we do acknowledge the different results obtained by different techniques (p. 15) and suggest that coupled measurements across multiple scales are needed to resolve these differences.*

We would argue that the report does indeed identify research areas where rapid progress can be made, and these are the 10 key topics listed under each theme; e.g. episodic events (p. 24), controls on TEP dynamics (p. 21). The KJ method is designed to come to a consensus about priorities, and we believe it was successful at doing so. However, we also recognize that it aggregates topics into broader themes. We have tried to counter that by incorporating bulleted lists of research questions that were considered important (determined by the number of individual votes they received) and these might be considered as "sweet spots" for those themes.

Second, a process level understanding of ocean carbon fluxes needs to be achieved in the context of the mass balance of carbon. As far as I know, Meg Estapa is the only invitee whose main research focus is the carbon balance. The report acknowledges that flux studies of the biological pump have been successful, but doesn't include other people who've done this work (including for example Ken Buesseler, Rachel Stanley, Steve Emerson, Paul Quay, Masha Prokopenko, Nicolas Cassar, Roberta Hamme, David Kadko, and I could include a lot more names here).

Response: *The emphasis of the workshop was on the* ***biology*** *of the biological pump rather than on a more general biogeochemical approach. To this end, invited participants generally had expertise that was more concentrated on biological processes. However, the organizing committee recognized the importance of having participants that could represent a biogeochemical point of view as well and several participants had been involved in projects of that nature. However, we do appreciate that a consequence of this is that the priorities arrived at were strongly biological.*

Finally, the invite list seems to exclude data analysts and modelers who have deduced carbon fluxes. For example, Amala Mahadevan, Dennis McGillicuddy, and Marina Levy have looked at the expression of spatial and temporal variability on local carbon fluxes, and their work might provide a new window for accessing this variability. My thinking is that spatial and temporal variability might be registered in the small-scale variability of mixed layer properties (concentration properties) that could be measured at high resolution. The guidance of a model might allow this concentration variability to be used for deducing temporal and spatial variability in the underlying carbon fluxes.

Response: *The workshop participants recognized the importance of variability on a wide range of spatial and temporal scales. We agree that physical processes leading to micro-layers and meso-scale features will be important, but the emphasis of the workshop was to develop a set of priorities related to the **biology** of the biological pump. We recognize the importance of physical processes in influencing the relevant biological processes (see e.g. p.15), and these must be a part of any interdisciplinary study on these aspects of the biological pump. This is one reason why some of the topics highlighted here would benefit from being part of a larger, comprehensive project (like EXPORTS) that would provide additional data.*

Overall, I think that the report will be useful to those of us interested in ocean biogeochemistry topics that complement the topics discussed in the report. It will also provide useful background to NSF program managers. It might stimulate thinking and the development of good ideas. I do think it is too narrow to provide guidance about what research will best advance our understanding of carbon fluxes associated with the biological pump.

Response: *Again, we emphasize the fact that is mentioned on p.4 of the report that this workshop was held to provide guidance on research into the biology of the biological pump. All participants recognized the importance of the physical, chemical, and geological components of the biological pump, and they are discussed (to a limited degree) in the report.*

COMMENT 4

This is a very well written summary of our workshop in New Orleans that in my opinion accurately reflects the priorities we identified collectively for future research. What I don't see in here is a suggested road map forward.

Response: *We have included a concluding section to the report that includes suggestions for such a road map.*

Is the intention of this white paper to inspire research on topics related to EXPORTS? If there is sufficient buy-in from the community, is the NSF planning to set aside funds for research related to the biological pump? Will submissions that are related to the priorities stated in the white paper be given priority for funding? What will be the format in which we will disseminate information contained in the white paper to the broader community of biological/chemical/physical oceanographers? Is the goal to have a solicitation for proposals? What are the approximate time lines for action involved? EXPORTS will begin very soon (given our 6-months application cycles), so any coordination between EXPORTS and NSF-funded research should commence as soon as possible. I assume that the NSF will provide all these details (call for proposal etc) later but I think there should be some mention about the proposed process going forward in this document as well (even if they are just suggestions, and not written in stone of course).

Response: *These issues are all important, but they were beyond the remit of this workshop. The workshop was held in order to arrive at a list of scientific priorities for research into biological processes affecting the biological pump.*

COMMENT 5

The report is well written and comprehensive, though I feel that a few key subjects have not received the attention they deserve, or are missing. Below my comments. Feel free to do with them as you wish:

Turbulence - small scale fluid motion is key to many processes affecting particles formation, destruction and biological contact rates at small scales (as well as chemical gradients) and vary by order of magnitudes in time and space in the upper ocean (affected, for example, by waves, wind driven shear, shear instabilities in the bottom of the ML, stratification). It is a very difficult subject that, to date, have eluded quantification from space based satellites.

W/o better understanding of how turbulence varies in time and space I am afraid we will not be able to constrain many of the basic processes affecting export.

Response: *Research into small-scale turbulence and its effects on zooplankton behavior and zooplankton-particle interactions has attracted considerable attention in recent years. Less attention has been paid to the role of small-scale turbulence in particle-particle interactions. Small-scale turbulence was implicit in the discussion on Physical Controls on Aggregate and TEP Dynamics (p.21), specifically: "We have a basic understanding of the physical processes (Brownian motion, fluid shear, differential sedimentation) that bring particles together to form aggregates. However, we lack a similar understanding of the processes that break up particles (Burd and Jackson, 2009). We know that fluid motions can break apart particles, as can swimming organisms, but we lack a mechanistic understanding of how these processes affect particle size distributions and fluxes as well as the ability to model them accurately." However, we have modified the third sentence to read "We know that fluid motions, including small-scale turbulence, can break apart particles, as can swimming organisms, but we often lack a fundamental understanding of these fluid motions in situ and how these affect particle size distributions and fluxes; we also lack the ability to model them accurately."*

Processes affecting particle packaging (not just density) are critical to understand processes occurring within aggregate (micro-environments having different chemistry compared to ambient water) and their mechanical properties (e.g. ability to withstand shear rather than breaking). The document addresses packaging mostly as affecting only density.

Response: *We agree that the effect of particle packaging is important for the reasons stated. This was mentioned in item (iii) on p.20 ("[Organic matter needs to be described in terms of its] physical characteristics, e.g. dissolved, single particle or aggregate and associated properties* *like size, density,* ***porosity****, and sinking velocity (or buoyancy)”).*

Methods to constrain NPP (e.g. C14) still involve high uncertainties. Most recent advances are in constraining NCP.

Response: *Yes, we agree that methods constraining NPP, or flux for that matter, involve high uncertainties. Using a multitude of approaches to simultaneously measure these parameters, will allow a direct comparison between different methods and may resolve some of the uncertainties. This is one of the strong points of the EXPORTS plan.*

Flux attenuation (p. 17) and vertical gradients in DIC (p. 8) are simple consequences of the processes controlling the biological pump.
To better understand flux attenuation (or export), processes affecting sinking velocity (density, size, packaging) as well as concentration of POM need to be constrained.

Response: *We agree with this comment, particularly with our inability to predict particle settling velocities. The report contains a section detailing the role of settling velocity (p. 23) and some of the processes affecting it. Discussions of processes affecting the concentration of POM occur throughout the report, particularly in Chapter 2 (e.g., the roles of food web complexity, trophic interactions, food web constraints on production etc.). See also answer to question 3.*

I think that approaching the biological pump as a multifaceted problem where a holistic approach to field measurements and modeling as well as laboratory and targeted process studies to elucidate specific facet are necessary to make significant headway. This requires a significant investment in a large, coordinated multidisciplinary program, something the US community has not done in a while. Recommending it here would be great.

Response: *We agree that an ideal approach to tackling many of these scientific questions is through a “coordinated, multidisciplinary program”, and we argue for the benefits for such an approach on page 8. Potentially EXPORTS could become such a program. However, the remit of the workshop was not to argue for a specific program or project, but rather to develop a range of scientific questions that could make significant progress in understanding the role that biological processes play in the biological pump.*

Atmospheric deposition of particles can also play a role we currently do not understand. Worth mentioning.

Response: *This is a complex topic as atmospheric deposition of particles affects a myriad of processes related to the biological pump. These include, but are not limited to how iron in particles affect primary production, and the role that atmospherically deposited particles play in ballasting sinking marine particles, affecting their sinking speeds and remineralization rates. Addition of particles likely also increases aggregation rates. Regardless, we agree that these topics are important, and they did arise through the KJ method employed during the workshop (e.g. KJ1 column 1, “allocthonous input”, KJ3 column 2, “OM chemistry, ocean and atmosphere* *influences", and KJ4 column 1, "Atmospheric Input"). However, these issues did not explicitly make it to the final group selection, becoming subsumed into other topics such as Episodic Events (p.25). While the role of atmospheric deposition of particles is a significant one, there remains considerable uncertainty in even quantifying this deposition — e.g. current global estimates of modeled inputs of iron to the oceans vary over 2 orders of magnitude (A. Tagliabue, OCB Newsletter, Vol. 9, No. 2, Summer 2016).*

Issue of tightly coupled vs. not tightly coupled ecosystems (e.g. due to perturbations such a storm) is worth mentioning.

Response: *This is an insightful comment and highlights the problem of studying coupled phenomena that occur on multiple spatial and temporal scales; similar and related comments were made by other commentators (e.g. Comment 6). As such, this comment is related to the research theme "Variability in Space and Time" (p. 24–27). Field campaigns that operate on short timescales (weeks) may not be long enough to capture these decoupled events. To study these events and processes requires integrated field campaigns (presumably using a combination of observations from ships, satellite remote sensing, and autonomous vehicles) designed to look at multiple spatial and temporal scales.*

Particle can break from the shear generated by their own sinking (wrt 4th paragraph in p. 21). This, some of my colleagues believe (e.g. Paul Hill), is what limits aggregate size.

Response: *We agree that the role of particle break up is poorly understood for marine particles. This disaggregation can occur through zooplankton-particle interactions, and also through particle-fluid interactions. It remains unclear which process dominates under given situations. In addition, the mechanics and consequences of particle break up are not at all constrained. For example, does a particle break up into a few, similarly sized particles or into a large number of particles covering a wide range of sizes? More fundamental work needs to be done on particle disaggregation — e.g. we are aware of only one paper that estimates the strength of marine snow. The importance of disaggregation and our lack of predictive understanding of disaggregation processes was recognized by the workshop participants in their final choice of topics and consequently it is mentioned in several places in the report as an area of important study (e.g. Physical and Biological Controls on Aggregate and TEP Dynamics", p.21).*

I would add to 'TEP and micro-gel formation' also their destruction (consumption, remineralization etc').

Response: *This was the intent behind our discussion of DOM-POM transformations (p. 19–21), but gel consumption and remineralization was not explicitly mentioned. We have altered the text of that section to include this.*

COMMENT 6

I'm reading over the NSF white paper on the bio pump and thinking about whether or not to comment. I thought I'd write to you and see if what I've been thinking was already thought through.

When I read the document it captures many salient points about factors and relationships that control export from surface water ecosystems ranging from food web dynamics to sub mesoscale physics. All great stuff. However, most of the text involves descriptions of interactions or processes acting within a given food web structure such as aggregation, migration, respiration, etc that affect export. A missing piece is a goal to understand how a given food web structure, particle size spectrum, zooplankton community, etc come to be. If we understood the export associated with many ecosystem states our understanding of export would remain poor if we did not understand the conditions (physical, chemical, biological) that give rise to that ecosystem state. Plankton dynamics are fast enough that - to use EXPORTS wording- a given 'state of the biological pump' is transient lasting days to maybe weeks depending on the system. We re really talking about a continuum of states and interactions that evolve over time in an inter-related fashion. Understanding the drivers that cause 'states' to wax and wane are as important as understanding what happens within a given 'state'.

Maybe this is all semantics but this document and EXPORTS start with 'a given structure/state' and look at what drives export in that situation. For EXPORTS that was a decision to reign in the scope of the project. For the NSF document a broader perspective may be warranted.

Does this make sense? I don't feel that I've explained myself well. One way to look at it is to ask the question if you were to write a model to describe the annual export cycle in a region what would you use to predict the sequence of 'states' and their evolution over time in that area.

Response: *This is a very insightful comment and is related to both the content of this report and the EXPORTS project. In the report (p.13) we discuss the need to develop "predictable patterns of food web structure with alternate export pathways and flux regimes, and to ascertain how many ecosystem states, structures, and fluxes are needed to characterize those relationships seasonally and regionally." Later (p.26) we state that it is important to understand the ecosystem traits or characteristics that lend themselves to episodic events. We believe that both these statements are moving in the direction described in the above comment. In particular, the research areas listed under "Linking food web complexity to export flux" (p.13) reinforce this. There was considerable discussion by workshop participants about these larger questions of how food webs with different export regimes arise, so we agree that is an important research area that will involve a close interaction between field observations, theory, and simulation. In particular, deployment of autonomous vehicles before, during, and after a process-based cruise may give sufficient information to understand how given plankton communities, particle size spectrum, and food web structure come into being. In many ways this is related to comments 9 and 10 about model complexity.*

COMMENT 7

Having been involved in EXPORTS but not this meeting, I was pleased to read the level of scientific discussion and break down into your 3 research themes on food webs, the dissolved-particulate continuum, and variability. In fact it was surprising last week at our GEOTRACES meeting, how much overlap there was in the discussion there of controls on particle-reactive trace elements and isotopes, and the ideas and processes put forth in your BBP workshop report.

My comment today, is to support what is written, including to argue that if you want to title this report “Towards a transformative understanding…”, that word “transformative” implies sampling of multiple biological pump pathways at the same time. As just one example, zooplankton can attenuate PC flux by breaking up particles, making DOM (or not) and in the process, respiring DIC, repackaging and changing sinking rates and pellet reactivity, and actively transporting PC via migration on daily and seasonal time scales. If you just studied one of these pathways very carefully, you would still not be able to predict how zooplankton would impact the magnitude and efficiency of the biological pump.

Taken further, we need to bring in microbial processes and geochemical properties of what in the BBP report is called the “continuum” of dissolved, colloidal and particulate materials. Likewise, without understanding the physical processes down to submeso-scales that both initiate, isolate and dilute/subduct production and loss of DOM/POM, we can’t understand mechanisms that create the variability that is the 3rd theme here in your report.

To keep this short- we shouldn’t use the work transformative lightly. I think we do have an opportunity with larger multi-disciplinary programs like EXPORTS to make transformative progress. OCE already in their programs of BO, CO and PO have individually and at times jointly sponsored over the last several decades, excellent work on the biological pump. Now it is time to combine efforts across OCE disciplines and across agencies, as already noted at the end of your executive summary, to make the transformative understanding that your report articulates.

Thanks to you and your group for articulating the exciting science and key questions related to understanding the oceans biological pump.

Response: *We agree strongly with the comment that sampling multiple biological pump pathways at the same time is a key to rapidly moving our understanding of the biological pump forward. In the conclusions of our report we state that it will be important for there to be both focused and detailed research work, with strong coordination between research teams, as well as larger scale programs. We too are strongly encouraged by the convergence of ideas and focus being demonstrated between different components of the oceanographic community.*

COMMENT 8

As a participant in the February workshop in New Orleans, I can attest to the “bottom-up” nature of the K-J process that was used to generate the ideas in this draft, “Biology of the Biological Pump” white paper. What I find most compelling is the degree of overlap between it and the motivations and central questions of the proposed NASA EXPORTS program. This high degree of overlap exists in spite of the fact that EXPORTS could be interpreted as having been designed “from the top down” by a 13-person writing team (but of course with many more individuals commenting, reviewing, and drafting a possible implementation). Both documents underscore the importance of the ocean's biological pump, our requirement for better predictive models of its current and future functioning, and the need for more research on contributing processes if we are to have any hope of improving our models. However, only the EXPORTS document currently talks much about the requirement for coordinated, multi-group studies to tackle some of the central science questions.

Below, I highlight two (of the many) instances that I find compelling where the Biology of the Biological Pump (BBP) white paper has articulated scientific questions that are also central to EXPORTS. Both examples also illustrate the need for integrated, multidisciplinary studies.

Linking food web complexity to export flux. The BBP working group identified a number of areas where a more detailed understanding of food web pathways would help us refine our ability to predict export. Urgently required are "*integrative studies that connect broad, end-to-end food web characteristics to export and export efficiency*." These end-to-end studies, needed to link processes such as symbiosis, mixotrophy, feeding modes, and zooplankton-dominated foodwebs of different types to the amount and type of exported organic matter, fit centrally within the study framework that is required to answer Science Question 1 of the EXPORTS program: How do upper ocean ecosystem characteristics determine the vertical transfer of organic matter from the well-lit surface ocean?

Quantification and biological understanding of episodic events. The BBP group also ranked highly the need to better understand the biological controls and triggers of export events that operate over short spatial and temporal scales. The white paper states that *an integrated biological, geochemical, and physical observational approach* is required to quantify these kinds of fluxes, which may be triggered by certain ecological traits and/or organisms, and which may be of different types depending on the organisms involved. Similarly, EXPORTS science questions 1D and 2D consider the importance of physical and biological variability to export *("How do physical and ecological processes act together to export organic matter from the surface ocean?"* and *"*How does variability in environmental and/or ecosystem features define the relative importance of process that regulate the transfer efficiency of organic matter to depth?"). Sampling at multiple, nested spatial and temporal scales – critical for quantifying the importance of episodic export events – is a central part of the EXPORTS science plan.

In both of the examples above the BBP document, perhaps reflecting its origins in the K-J method, breaks down research targets into much more detail than do the EXPORTS documents, which spend more time discussing how comprehensive, end-to-end studies might actually be coordinated and implemented. If anything, I would recommend that the Biology of the Biological Pump white paper briefly discuss the importance of coordination among research groups, and the need for mechanisms to fund and carry out the **integrated studies at multiple scales** that we will need to make progress towards the scientific goals that have been identified.

Response: *We have added a closing statement to the report that incorporates these comments.*

COMMENT 9

General Comments:

The group responsible for developing this report has provided an exhaustive assessment of the state of knowledge, and lack of knowledge. They have well articulated and identified priority uncertainties, with food web structure and associated export mechanisms and controls at the top of the list. These are important questions that must be answered before we can hope to make the biological pump a predictable process.

Having said that, I do not see many of the priority questions as being a good fit for the EXPORTS program (presumably that was not the primary goal of the report). EXPORTS will experience a relatively small number of export and NCP events, as well as a small number of mechanisms and variables relative to the long list identified as representing the full range observed in nature (as listed in the BioPump report). I see a need for separate process studies, wrapped around time-series studies, to observe the many conditions sought in the report. Again, EXPORTS will experience but a fraction of the conditions sought by the BioPump report. A few processes/controls identified here could be addressed in the EXPORTS program, but those proposals need to be well rationalized as being particularly suitable for Lagrangian study, as in EXPORTS. I suggest that a line running from the tropics, through the subtropics, and into the subarctic, occupied in time-series mode, would answer many of the priority questions posed. That way the scientists will observe variability in foodweb structure, in export efficiency, in ecosystem states, etc., all embedded in seasonality and interannual variability.

Response: *We agree that multiple large-scale projects could be designed around the ideas arising from the workshop. However, designing such a program was beyond the remit given the workshop participants. Given that, we do discuss (p. 8 and in the concluding statement) the advantages of incorporating these research ideas into a larger program.*

Some of the foci, such as assessing the role of meso- and submesoscale processes similarly cannot be addressed readily in either EXPORTS or the meridional section I suggested; scientists who study the role of eddies, for example, target and follow those eddies to learn about them. The same will be true for spatial-related questions posed in this report; those need to be targeted in order to understand them.

Response: *We believe that the EXPORTS Plan includes use of autonomous assets which can potentially be in the water for up to a year at each of the planned sites, providing some information on meso- and submesoscale processes. This discussion was, however, not part of the workshop focus.*

Specific Comments:

What is the real global annual rate of export production? The stated uncertainty is far too wide now (given as 5-12 PgC/yr in the report). I do not believe that we are so far from the truth on this total number. If we are, then the federal agencies will be putting good money after bad should they support more work on the biopump; we certainly know more than the stated uncertainty suggests. That uncertainty reflects very poorly on our community; it does not say to me, “send funds so we can wrap this up”, but rather the opposite.

Response: *The factor of 2–2.5 uncertainty in global export production stated on p. 4 is possibly a conservative estimate. For example, a recent study (Laufkotter et al., Biogeosciences, 13:4023–4027, 2016) gives published estimates of global export production obtained from observation ranging from 4.0 to 12.9 Pg C* y^{-1}*. Estimates of ANCP at specific locations differs from satellite based estimates by a factor of 3 and measured ANCP values show little variability in the open ocean whereas models and satellite estimates vary with latitude by a factor of 2 or more (Emerson, Global Biogeochemical Cycles, 28:14–28, 2014). We would argue that a factor of 2 uncertainty in current global estimates of export production is probably realistic.*

Attention needs to go beyond the “The Biology of the Biological Pump”, by including the physical controls/processes at work. Biology does not act in isolation, so studying it that way will provide the requisite outcome.

Response: *We agree that we need to understand the inter-relationships between the physical, chemical, and biological processes is crucial for a good understanding. Although, the participants were charged specifically with examining the biology of the biological pump, the importance of relevant physical and chemical processes was recognized and brought to the fore when relevant. We feel that this is reflected in our report — e.g. mesoscale physical processes are mentioned, as are small-scale physical processes affecting particle aggregation and disaggregation.*

“Participants identified the spatial and temporal quantification of episodic events as a first-order need.” Understanding the controls on episodic export events is more important than quantification of those events. Quantification is easier than understanding; we’ve done that since the JGOFS days, but controls are still poorly understood.

Response: *We agree with these excellent comments that we feel reinforce the views of the workshop participants. The episodic events discussed in the report are intense events on short time scales, such as salp blooms and jelly falls, rather than phytoplankton blooms. The effects that these episodic events have on the biological pump have only been observed fortuitously. In these cases, their impact has been profound — e.g. a salp bloom at the Bermuda Atlantic Time Series station resulted in a pulse of POC flux to the sea-floor equivalent to a that for a typical year. The importance of such events on a global scale has not been assessed. For that reason, the workshop participants felt that attempts to quantify such events would be useful. Understanding the controls on episodic events was also felt to be important, and we feel this is reflected in the third and sixth paragraphs of the section on Episodic Events (p. 24–26).*

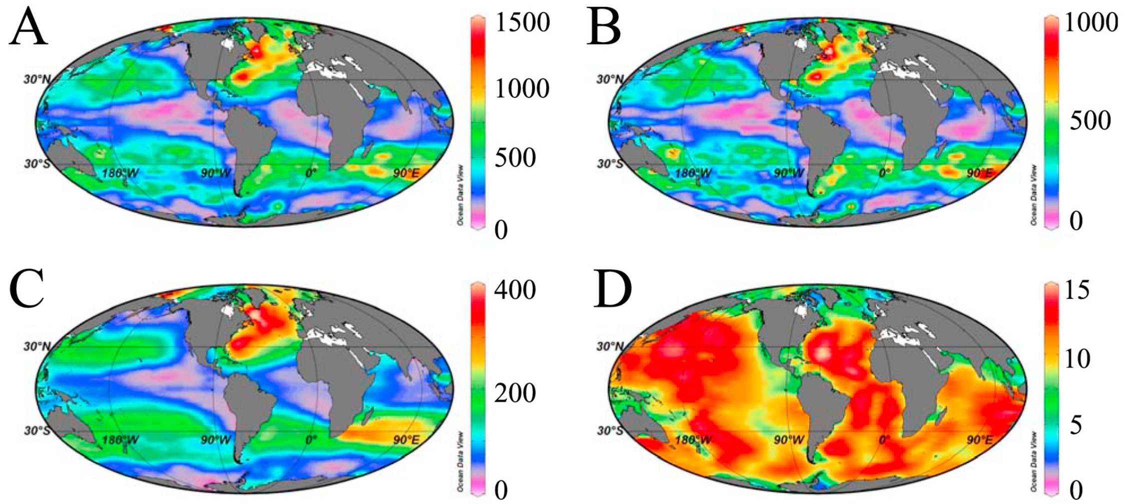
Relative to the statement: “An improved understanding of the organisms responsible for these events, including their life cycles and the associated processes underlying their distribution is needed.” As note above, more than biology controls export, episodic events, etc. The full spectrum of controls needs assessment.

Response: *We agree, and these are discussed in the second paragraph on p.25.*

Relative to the statement: "To date, there have been few efforts to quantify the relative roles and importance of such food web complexities on export rates and efficiencies." The complexities described include "Diverse modes of energy and nutrient acquisition, including photoheterotrophy and mixotrophy, are known to be important, but poorly resolved in terms of their net implications for trophic fluxes. In addition, various modes of symbiotic interactions are recognized to facilitate genetic exchanges (e.g., viral infection), catalyze nutrient and energy transfers (e.g., mutualism), and/or serve as loss terms balancing cell growth (e.g., parasitism), but are inadequately incorporated into our understanding of food web function." I wonder if this complexity, presently not understood or described, actually has a direct role in controlling the biological pump. Is the biological pump simple rather than complex, such that it is simply controlled by new nutrient input and exhaustion, and most efficient when enacted by well-ballasted organisms, or is the full complexity described in the report necessarily understood (e.g., genetic exchanges, mutualism, parasitic infections, etc.) before the pump can be said to be predictable and model-able? In other words, how simply can the system be described in order to model it and predict it? Is the fundamental control on the biological pump hidden in its great complexity (as I read this report to suggest), or is a simple attribute of the system the fundamental control? I'd hate to see complexity be the outcome since I know how hard/impossible it will be for us to overcome it; we need to find the easiest path for understanding the biological pump. If too many aspects of the whole system are made extremely complex and detailed in our approach to them, we'll not be much further ahead in whole system understanding. To what extent can the system remain a black box, yet still be predictable?

Response: *This is an excellent comment, and as scientists we constantly tread the line between striving for a simple understanding of a system, and the danger of making it too simple. Simple models require assumptions as to what is and what is not important for the question at hand. The danger being that such assumptions may miss something that is important, or that may become important in the future. In this regard we think that the last sentence in the above comment and the approach suggested in the comment 10 are insightful: we agree that both simple and more complicated models should be pursued so that we can make a more informed determination of how simple the "black box can be, yet still be predictable".*

Relative to the statement: "The contribution to the biological pump from the downward transport of non-sinking carbon via subduction is largely unconstrained, both globally and regionally." This is not entirely true. Following is the global distribution of DOM consumption at depths >130 m, mostly exported by subduction, from Hansell et al (2012). As Cindy Lee noted at the OCB workshop recently, we know much more than these reports/assessments suggest we do.



Caption: Water column integrated rates of DOC removal (mmol C m-2 yr-1 at >130 m). (a) Total DOC (sum of semi-labile, semi-refractory, and refractory fractions). (b) Semi-labile DOC. (c) Semi-refractory DOC. (d) Refractory DOC. This is Figure 5 in Hansell et al. 2012.

Response: *The statement in the report that is referred to has been corrected. We also think that this comment is important and very relevant to understanding the purpose of the workshop and this report. We agree that we do know a great deal about the biological pump, its drivers and the processes affecting it. However, the role of this workshop and report was to determine where our current understanding is still lacking and to provide a set of priorities for future research. Again, we stress that the main emphasis was the biology of the biological pump, and we fully recognize that there remain important problems in chemical and physical oceanography that are relevant to the biological pump (some of these are explicitly mentioned in this report). Consequently, this report was not meant to be a comprehensive review of our current understanding of the biological pump, but rather a document focusing on these exciting new areas of research that have the potential to enhance our predictive understanding of the biological pump.*

COMMENT 10

Some broad comments on the OCB white paper on ocean's biological carbon pump.

- Firstly, I think this is a tremendously important area of research and encourage NSF to support it.
- An enormous variety of different possible processes and variables that may affect export or remineralisation are mentioned. Is it possible to prioritise these in any way? As just one example, is determining the effect of zooplankton diel vertical migration more important to understanding export flux than symbiontes? Although I agree generally with the 3 big questions identified in the white paper (these are indeed the 'critical gaps' which the authors set out to define), my perspective is including all possible processes gives the impression that the problem is so complex as to be almost unsolvable (which might prompt NSF to think they shouldn't try?).

Response: *The intent of the report was to provide NSF with a prioritized set of research areas related to the biology of the biological pump. The participants recognized that there were some topics for which a quantitative estimate of their importance is likely to be available in the near future (e.g. the role of vertical migration), this is not the case for others (e.g. the role of parasites or jelly falls). In these latter cases, a first order question would be to develop first estimates of their importance globally and regionally. The concern is that, without studying these various processes and understanding how they might change in importance with climate change, it is impossible to know if they are or will become an important component of the biological pump. A good example of this is the role of gelatinous zooplankton (e.g. salp blooms and jelly falls). In the few cases they have been observed they have been shown to be locally important components of the biological pump, but their episodic nature makes global estimates of their importance very difficult without further study.*

Our concern is not that the "problem is too complex to solve", but rather that we need to determine what are important controlling factors for the biological pump, and (perhaps more crucially) what processes might become important in the future. To determine this needs some assessment of these processes under current conditions.

On a related note, is the intention to ultimately enable improved models to predict changes in the pump in a changing climate? (I think so). In that case, an identification of the processes that truly matter in the context of global climate models is important. It's impossible (and undesirable) to include everything in a global climate model, and from that perspective the only things that matter are how much carbon is exported and where (what depth) is it remineralised. The details of how these things occur is not needed. Complex process models can (and have been) developed to explore certain aspects of the pump. Likely both approaches are necessary here - a point worth making explicitly in the paper perhaps.

Response: *This is an insightful comment, and is similar to ones made in comment 9. The commentator here provides a path forward. We agree that actively pursuing both complex, process-based models and simpler global models is the best approach to rapidly assess the importance of many of the processes discussed in the report. If observations and complex process based models show the current and future importance of a given process, the models and observations can be used to help develop simpler formulations that can be incorporated into global models.*

- The observation that exploitation of autonomous technologies will be needed to address some of the critical gaps (in particular the spatial and temporal variability of export and remineralisation) is absolutely correct. My perspective however is that these are likely to provide more information on the 'broad brush' aspects, e.g. episodic variability in remineralisation length scale, than on specific processes. And that's fine - we desperately need that information. But a touch of pragmatism in what we are likely to realistically be able to measure is needed.

Response: *We agree with this statement. However, with increasing technology (especially with* *advances in miniaturization), there is the tantalizing prospect of being able to explore specific processes.*

COMMENT 11
In general, I think the group did a nice job pulling together unknown aspects of our understanding of the biological pump. My primary comment is that the executive summary (pages 4 - 8) is disjointed and redundant. I realize that the topics and key points are all interconnected, but the summary feels like the output of a series of lists with no editing rather than an overarching summary. Perhaps the summary can be shortened to only list the main points, without so many examples which end up overlapping in a manner that makes the division between sections confusing.

Response: *We agree with these good suggestion and we have edited the executive summary and added a summary statement.*

The later parts describing each key point are clear and easy to follow.

Some examples:
from the summary, I am not clear on how food web complexity (section i) differs from the trophic interactions described under (ii). Is the *complexity* of the food web the key point in (i), and if so, what is meant by that? Or, is it the presence of the food web itself that is the key component?

Or, why talk about jellyfish consuming and repackaging in section (ii), but zooplankton doing the same thing in section (iii)?
Otherwise, well done.

Response: *This is a good comment and reflects the highly interconnected and interdisciplinary nature of work on the biological pump. It is, as mentioned in the comment, the food web itself and how its structure and function gives rise to different export and flux attenuation regimes. Our aim is to show that overall complexity of the food web (e.g. it's topology) can have an effect on export, but so can the specific interactions between trophic levels. Similarly, we wanted to make a distinction between the role of jellyfish on the biological pump and that of zooplankton such as copepods which has been more studied.*

COMMENT 12
I think you have done a great job on this document and presenting it to the community at these two back-to back meetings. My only comment is that you should view these two experiments as a template to be utilized by other nations, and should have a description of supporting infrastructure embedded into the document. This includes infrastructure for standards and intercalibration, data management and development of guidelines for best practices.
You already have a wealth of expertise in the chemical side of EXPORTS with folks like Ken Buesseler already involved in GEOTRACES and CLIVAR. But getting the biologists on board is trickier. There are a variety of reasons for this. Rate measurements are harder to intercompare

than chemical analyses, and molecular biology tools evolve so fast they are a moving target. But it is worth giving this some careful consideration. It will greatly expand the long range impact of your document. I think I have an OCB scoping report from a workshop in 2010 "The molecular biology of biogeochemistry" that addressed some of these issues. I'll look for it over the weekend.

Response: *We agree wholeheartedly with this comment. Inter-comparison (of field and experimental methods and of models) is crucial, particularly when working on such an interdisciplinary problem. The goal of this workshop was to suggest worthwhile topics to fund, but it is important to realize that if this next step occurs, inter-calibration will have to be addressed. This Is mentioned briefly in the report in regards to measurements of net community production (p. 15), but agree with the comment that inter-calibration should be more common-place. We have also added the following statement to the report conclusion (p.27), based heavily on the wording in comment 8: "Consequently, we believe that successful biological pump research will involve both coordination among research groups as well as the implementation of integrated studies operating at multiple spatial and temporal scales." Inter-calibration of methods and models would be an integral part of the "coordination among research groups".*

COMMENT 13

I applaud the workshop leaders and participants in defining research priorities that are aimed at increasing our biological /mechanistic understanding of the Biological Carbon Pump. These priorities go far beyond a 'simple' geochemical view of element fluxes and flux attenuation. This white paper is a milestone, and I believe that the title 'towards a transformative understanding' is certainly very fitting. A few comments below:

This white paper outlines important insights stemming from a consensus exercise, thus by design it is a list of priorities that emerged from the group's work. However, I think there are a few gaps that could be considered and added to the document. It is exciting to see that food web control of the biological carbon pump takes on such a prominent role, but the importance of phytoplankton primary production (or growth rates) and its community composition could be made more clear. While implicit in 'food web control', the composition of phytoplankton prey determines the composition of its grazers, and vice versa, and can be crucial in determining the 'fate' of primary production. Thus, a broader range of grazers, not only those that act in active export, but also those that act on the recycling of primary production in the euphotic zone (micro-grazers) should be considered. Linking community composition in the euphotic zone with the organisms responsible for particulate flux is crucial and can only be made if the euphotic zone community, both in terms of composition and activity, is known. Genomic techniques have a great potential in clarifying the linkages between the ecology of the euphotic water column and particle export.

Response: *We agree that it is crucial to know and understand the factors affecting community composition in the euphotic zone in order to understand and predict the export of material into the ocean interior. This is implicit in the section on "Food Web Regulation of Export", in particular in discussions of the different pathways that become available with different* *community compositions. This comment is also germane to understanding the characteristics of food webs that lead to export events.*

Executive summary is too long in my view with 4.5 pages. It is redundant in the level of detail with the later sections, and thus potentially confusing to the reader. The sequence of topics seems to be a bit inconsistent with the later sections. This section should be shortened to two pages. I like the final paragraph of that section, and wonder if some of that content could be picked up again in a concluding paragraph (see below).

Response: *We have edited the executive summary and added a set of conclusions to the report.*

Also, some final editing is required of the document, for example the section "Identifying which organisms control remineralization", p. 17, has a lot of passive sentences strung together, and some sentences don't make sense.

Response: *We have edited this section so that hopefully it reads better.*

The document ends relatively abruptly, maybe concluding paragraph could be used to reiterate the consensus approach used to identify the research priorities and to put a forward looking spin on the document.

Response: *We have added a concluding statement to the report.*

COMMENT 14

I have read the Biology of the Biological Pump (BBP) workshop report while preparing the draft EXPORTS Implementation Plan for public comment (see http://cce.nasa.gov/ocean_biology_biogeochemistry/exports). Although there are many similarities between the two plans, there is one important difference that I would like to highlight. EXPORTS aims at developing a **predictive understanding** of the biological pump consistent with NASA's objectives for quantifying, remotely monitoring and predicting changes to ocean ecosystems and their impacts on the global carbon cycle; while the BBP workshop report aims at a **transformative understanding** of the ocean's biological pump, consistent with NSF's role in facilitating basic research in ocean sciences. To achieve the requisite predictive understandings, EXPORTS needs to observe and understand the dominant processes regulating the export and fate of ocean net primary production (NPP) as well as collect the observations needed to parameterize them. However, many if not all of the issues outlined in the BBP workshop report can be conducted in near-isolation from other and progress will be made. EXPORTS' need for the simultaneous quantification of the dominant NPP export and fate pathways is what in my opinion fundamentally separates the two research plans from each other.

The three research themes identified in the BBP workshop report map well to the export pathways and science questions in the EXPORTS science plan. In fact, nearly all of the measurements and experimental work needed to obtain the transformative understandings suggested in the BBP plan will be conducted in EXPORTS. For example, I am very excited about the subtheme in the BBP workshop report on *Scales of Spatial and Temporal Variability* as this issue has an important bearing on how we link point measurements of stocks and fluxes to the satellite pixel or numerical grid scales needed to parameterize coupled ecosystem / carbon cycle processes. In previous work (Estapa et al. 2015, GBC), we have hypothesized that the processes creating sinking aggregates would be more prevalent where near surface water masses converge thereby increasing particle coagulation rates while elevated net community production (NCP) rates would occur where these surface waters diverge and the upwelling of new nutrients fuel elevated NCP. Hence a spatial segregation of regions of particle formation and particle export should be expected and regulated by the submesoscale physics of the upper ocean. This submesoscale decoupling particle formation and export is a fundamental issue that we have little understanding about beyond what is afforded by numerical modeling. Along another line, we know very little about the dynamics or even the distributions of organisms that compose the ocean food webs. Based upon typical abundances, spatial separations between individuals of the same species as well as potentially interacting species are often many meters to a several 10's of meters apart from each other. Yet the interactions among these organisms control the ecosystem processes that impact the ocean's carbon cycle and we do not know how these interactions occur. And we know even less about these interactions in the twilight zone...

The Goal Plan in the EXPORTS Implementation Plan outlines a strategy for collecting the observations needed for investigators to address these critical issues. Instrumented profiling packages towed behind the survey research vessel will collect video imagery that can be used to elucidate the distributions of sinking aggregates and zooplankton along with physical and optical measurements needed to understand the distributions of phytoplankton, nutrients, suspended particles and physical oceanographic variables. These measurements will be supplemented by autonomous, long-term observations of physical and optical measurements from an array of underwater robots. Further, biogeochemical fluxes will be sampled spatially from the survey research vessel, providing spatial context for the rate and process measurements and experiments conducted by the process ship. Together the EXPORTS Goal Plan measurements will be used to answer the EXPORTS science questions and provide an open data set for future researchers to investigate a myriad of science questions (many listed in the BBP workshop report) that I think will transform the ocean sciences.

As I'm sure you've been told, the ocean sciences community is ready for the challenge of conducting a comprehensive study of the ocean's biological pump. Frankly, the achievement of a predictive understanding of the biological pump is **the** transformative problem of our time that the ocean sciences can solve with critical societal benefits. The problem has something for nearly everyone in the marine sciences – from genomics to submesoscale physics with everything in between. And we have new tools at our disposal - from interdisciplinary ocean robots and next generation sequencing to data-driven, high-resolution numerical models and a comprehensive suite of satellite-derived observables. For many, many reasons, the time do this is now…

Response: *We agree that there are many complementary scientific questions and connections* *between EXPORTS and those research priorities highlighted in this report. As we state in our conclusions, there are many synergistic benefits to undertaking research into these priorities in conjunction with a larger program. The principal benefit being that additional pathways and processes are being measured so that budget mismatches are less likely to occur.*

COMMENT 15

One of our BGC guys sent this to me.. I attach an article highlighting a key issue… vertical migration of mesopelagic fish on transport.. If the references are correct 70 % of the organic carbon reaching depth is mediated by this mechanism… this seems to be under or not recognized in this document…

Response: *We have added this to the text of the document on p. 18 under the section on vertical migration.*

COMMENT 16

I wanted to express my excitement about the "bio pump: priorities for future research'' pdf. I am particularly excited about the DOM-POM paragraph. Although CSP are mentioned on page 19, I think that this part of the document focuses a bit too much on TEP dynamics. CSP can also be measured quiet easily now using the spectrophotometrical method proposed by Cisternas-Novoa et at. (2015). I am currently testing their method to visualize TEP and CSP using a FlowCAM. Anyway I think we should give CSP more attention also because they can be at times more abundant than TEP (Long and Azam, 1996). As you also point out in the document, the role of bacteria in the formation and fate of TEP (and CSP) is not well constrained thus more research is needed in that direction. For instance, I have yet to come across a study that directly measures bacterial degradation of (micro- and macro-)gels. It seems to be widely accepted that TEP and CSP represent hotspots for bacteria; I might be wrong but I could think of several reasons why surface water bacteria do not want to be attached to/embedded in a gel-like matrix like TEP and CSP.
Thank you for putting this document together!

Response: *We agree with these comments that more research is needed on CSP (Comassie Stainable Particles) and possibly other organic abiotic particles that are not detritus. We also agree with the comments about bacterial degradation of gel particles. We have slightly edited the relevant sections of the report to make these aspects more explicit.*

COMMENT 17

I really appreciated the presentations on this workshop and the resulting white paper during this past week's OCB workshop (and thank you for all the work of organizing the workshop and making it available remotely via the webcast!). I have now read through the white paper and wanted to share some comments.

Overall, I think this effort to identify important research priorities in studying the ocean's biological pump is important and timely. I think the white paper does a good job of pointing attention towards understudied biological processes that could play an important role in determining the strength and efficiency of export from the surface as well as the ultimate fate of exported material by influencing the the depth where sinking organic material is remineralized.

However, though I understand that this workshop focused explicitly on biological processes, I think it is an oversight for this document to not to more explicitly mention the interplay between biological and physical processes in determining the ultimate fate of exported material, including the time scale over which export sequesters carbon from the atmosphere. This seemed particularly relevant under the theme of "variability in space and time," which focused on episodic export events, but not variability in timescales of sequestration (as discussed in DeVries et al., 2012) or on seasonal/potentially episodic processes of net heterotrophy or ventilation.

Time series measurements, identified in the document as important to capture episodic export pulses, also play an important role in determining the fate of exported material on annual to multi-annual time scales. This has historically not been well observed in the ocean, but a number of studies (e.g. Bushinsky et al., 2015; Fassbender et al., 2016; Kortzinger et al., 2008; Palevsky et al., 2016; Quay et al., 2012) have shown that much of export from the stratified summertime mixed layer is subsequently respired and ventilated back to the atmosphere, either by remineralization below the mixed layer that is ventilated during winter mixing or by wintertime net heterotrophy.

I understand that the scope of the original workshop was more narrowly focused on biological processes and didn't include people with expertise focused on the interaction with physical processes, but I think it would serve the community better to at least acknowledge the importance of physical processes that were not explicitly considered for this document but remain important to understanding the biological pump. I worry that since the title of the document says that this white paper represents "priorities for future research" on the biological pump without specifying that these are only the biological process-focused priorities, it could lead to future neglect of physical processes that are also important to the rate and efficiency of the biological pump. I obviously don't expect you to add new sections to the document on this subject, but I would like to see the importance of physical processes more clearly acknowledged as important but outside the scope of the workshop and the document.

References:

Bushinsky, S. M., and S. Emerson (2015), Marine biological production from in situ oxygen measurements on a profiling float in the subarctic Pacific Ocean, *Glob. Biogeochem. Cycles*, *29*, doi:10.1002/2015GB005251.

DeVries, T., F. Primeau, and C. Deutsch (2012), The sequestration efficiency of the biological pump, *Geophys. Res. Lett.*, *39*, L13601, doi:10.1029/2012GL051963.

Fassbender, A. J., C. L. Sabine, and M. F. Cronin (2016), Net community production and calcification from 7 years of NOAA Station Papa Mooring measurements, *Glob. Biogeochem. Cycles*, *30*, doi:10.1002/2015GB005205.

Körtzinger, A., U. Send, R. S. Lampitt, S. Hartman, D. W. R. Wallace, J. Karstensen, M. G. Villagarcia, O. Llinás, and M. D. DeGrandpre (2008), The seasonal pCO2 cycle at 49°N/16.5°W in the northeastern Atlantic Ocean and what it tells us about biological productivity, *J. Geophys. Res.*, *113*, C04020, doi:10.1029/2007JC004347.

Palevsky, H. I., P. D. Quay, D. E. Lockwood, and D. P. Nicholson (2016), The annual cycle of gross primary production, net community production, and export efficiency across the North Pacific Ocean, *Glob. Biogeochem. Cycles*, *30*, doi:10.1002/2015GB005318.

Quay, P., J. Stutsman, and T. Steinhoff (2012), Primary production and carbon export rates across the subpolar N. Atlantic Ocean basin based on triple oxygen isotope and dissolved O 2 and Ar gas measurements, *Glob. Biogeochem. Cycles*, *26*, GB2003, doi:10.1029/2010GB004003.

Response: *This is an excellent comment which demonstrates clearly the interdisciplinary nature of research on the biological pump. We agree that physical processes play crucial roles in determining the fate of sinking material and the efficiency of the biological pump. These processes act at multiple spatial and temporal scales and include, but are not limited to, the physics of particle-particle interactions (e.g. fluid shear and turbulence), subduction of particulate and dissolved material, and the effects of mesoscale and sub-mesoscale processes.*

The workshop participants recognized the importance of physical processes and this is reflected in the detailed output from the KJ sessions (Appendix E). Some of these topics are mentioned throughout the main text of the report, but as the commentator appreciates, the emphasis of the workshop was the biology of the biological pump. We have also tried to make this clear by amending the title page to include the phrase "Report on the NSF Biology of the Biological Pump Workshop".

Finally a very minor comment: the Emerson GBC paper cited on page 15 is from 2014, not 2013.

Response: This has been corrected.

I appreciate the opportunity to provide feedback on this document, as well as the considerable work that has clearly gone in to it so far. Please let me know if you have any questions.

COMMENT 18

Thank you for distributing the NSF report on the Biological Pump. Here are some comments I would like to make. I strongly encourage the community and the NSF to address the need for new measurements and new understanding of carbon export in the deep ocean.

I am a physical-biogeochemical oceanographer currently working on modeling the ocean carbon cycle. My interest in the ocean carbon cycle stems primarily from the fact that the ocean is a major sink of anthropogenic emissions of CO2 and therefore controls critically the Earth's climate response to this forcing. Although, we know quite well the magnitude of the ocean sink, the flux of CO2 at the surface of the ocean, we know little about how this carbon is transported within the ocean and specifically how it is sequestered at depth, below 100m all the way to the ocean bottom.

The biological pump, the export of organic matter from the surface to the deep ocean, is one major pathway of carbon sequestration in the ocean, the other being physical transport (mixing and advection). The physical mechanisms are understood but not well measured. Argo floats together with satellite altimetry have advanced our quantitative understanding but do not provide input on mesoscale and submesoscale processes in the subsurface ocean that can only be measured in situ, possibly with submersibles and other autonomous vehicles.

Response: *We agree that more detailed measurements on relevant scales are needed to improve our predictive understanding of how processes acting on mesoscales and sub-mesoscales affect the biological pump. We hope that the use of autonomous vehicles as part of the EXPORTS program will provide some of these measurements.*

While physical transport and mixing control the decadal-century scale of carbon export in the ocean, the relative role of physically vs biologically-biogeochemically mediated export at higher frequencies (daily to interannual) is unknown. Modeling at these scales (high spatial and temporal resolution) provides only conjectural evidence. And this is where the NSF report offers critical input to the community: **what are the processes that need to be studied to improve our understanding and quantification of carbon export at the high frequency temporal and spatial domain.**

Response: *We strongly agree that there is a need to both quantify (on both regional and global scales) and understand many of the biological processes discussed in this report. To take just one example, the contribution of salps to carbon export remains both unconstrained and poorly understood. The few cases where observations are available have revealed that salp blooms can result in one year's worth of local export flux reaching the ocean floor over the span of days to weeks. The biogeochemical and physical factors leading to salp blooms also need to be explored.*

Additionally, advancing our knowledge of the biological pump is not only important for Earth's climate because of carbon sequestration. The biological pump (together with physical circulation) is critical in setting the distributions of nutrients in the mesopelagic ocean, which ultimately, through upwelling and vertical mixing, determine the distributions in the upper ocean and hence the biodiversity and ecology of the surface ocean, at scales that vary from interannual to decadal and from local to basin wide effects. The carbonate pump which is an important part of the biological export controls the rates of acidification in the world's oceans.

Response: *Again, we agree strongly with this comment. Modeling studies tend to predict larger and more intense oxygen minimum zones, largely because they use simple algorithms for sinking and remineralization of organic matter that yield more intense remineralization than actually occurs (e.g. Moore, JK et al., Journal of Climate 26:9291–9312, 2013). We hope that the suggestions in this report will stimulate process studies that lead to more accurate* *representations of these processes in biogeochemical models.*

It is unclear whether in the near future we will be able to reduce the uncertainties in physical ocean circulation processes in the subsurface ocean (below ~100m) so it becomes critical to constrain the biological pump from the biology/biogeochemistry side. This is why priority research highlighted in this NSF report needs to be undertaken as soon as possible and will truly transform our understanding of export, ocean's efficiency in taking up CO2 and biodiversity changes on longer time scales.

Response: *We agree with the commentator.*

Appendix E. Results from the KJ Sessions

The following pages contain tables of the results from each KJ session. These were preserved because it was recognized that the KJ technique, by its very nature, aggregates ideas and so some degree of granularity and detail is lost. Our motivation for including these tables here is to preserve these detailed ideas as examples of what types of focused research was considered by the workshop participants to be important.

KJ1: Particle formation in the upper ocean and processes that drive export

Particle/Dissolved Interactions
Relevance of gel formation, DOM-POM continuum
DOM-POM transitions

Conditions influencing sinking — Particle Composition — Sinking
Nutrient limitation & cell buoyancy
Relationship between nutrient limitation/status & aggregation
Factors influencing ballast formation (silica, CaCO3 etc)
Particle size/growth/sinking velocity
Conditions (physiology/nutrients) that lead to export events
Size, density, sinking
Evolution of particle buoyancy

Food web processes — Growth & consumption — Euphotic zone trophic sinks — Zooplankton community structure
Zooplankton production
Contribution of dead animals vs feces/detritus
Mesozooplankton/microzooplankton grazing
Zooplankton community structure (taxonomy) and fecal pellet production
Recycling via microzooplankton
Food web efficiency to fecal pellets
Grazing by DVM predators

Depth Variation
Particle standing stock attenuation in euphotic zone
What is the depth variation of particle formation?

Viruses — Lysis
Do viruses affect particle formation and export?
Importance of viruses?
Does cell lysis increase or decrease export?

Relevant scales — Environmental Variability
What drives spatio-temporal variability?
What is the spatial and temporal variability of these processes?
What is the global significance of episodic events?

Aggregation — Controls on aggregation — TEP — Stickiness
What is the contribution of coagulation vs food web?
Aggregation/disaggregation
Relationship between phytoplankton physiology and aggregation?
Physical vs biological controls on aggregation?
Does bacterial activity increase or decrease aggregation?
TEP production
Contribution of bacteria to TEP production
What regulates particle stickiness?
How does TEP facilitate particle formation?
Relevance of Sverdrupian light/mixing dynamics

Measurement of export
How much of downward particle flux is really export?
Particles at which depth do we consider exported?

Allocthonous Input
Role of atmospheric particles?

Phytoplankton production structure
Magnitude of primary production
Phytoplankton production
Biomass, concentration
What do observations tell us about community composition?

Nutrient effects on aggregation
Nutrient limitation and cell buoyancy
Nutrient flux
Micro nutrient limitation

Relative role of drivers
Mainly physical or biological?
Environmental triggers of intentional sinking?

Community Composition
Community Composition
Who are the key players?
What is the role of ecosystem structure in driving export?

Viruses — Role of viruses — Role of infectious agents — *Parasitism and particle formation*
Viral lysis
Viral lysis rates
What is the role of parasitoids in particle formation?
Factors that influence virus–phytoplankton interactions.

Detritivores — Biological degradation — Detritivores Fluxers or Anti-fluxers?
How extensive is top-down control on particle detritivores?
Do predators regulate particle degraders?
Do parasites regulate particle degraders?
What is the role of detritivores in particle flux?

Grazers — Zooplankton — *Zooplankton behavior and metabolism* — Grazers as drivers of export
Fecal matter formation (rate)
Zooplankton feeding modes
Factors that influence phytoplankton-predator interactions
Vertical migration of detritivores
Diel Vertical Migrators abundance/biomass
Abundance and behavior of detritivores
Are salps present?
Zooplankton behavior and life histories
Egestion by zooplankton
Grazer mortality (identity)
Grazer mortality (rates, taxonomic distribution, which grazers)

DOM-POM transformations — Size and composition of organic matter
Transformations between DOC and POC
Factors stimulating DOM to POC transfer
Contributions of plankton to POC pool
How big are the particles?
C/N uptake ratio >> C/N ratio biomass implies delta percent PER

Size and structure of phytoplankton — Phytoplankton size spectra — Size and compostion of phytoplankton — Phytoplankton community structure
Phytoplankton chemical composition
Regulation of community structure of primary producers
Size spectrum of primary producers
Nutrient enrichment vs aerosol deposition
How big are cells?

TEP — *TEP Stickiness* — Role of TEP — Factors affecting particle adhesion
Differential TEP production rate vs biomass production, percentage TEP in aggregates
Impacts of photodegradation on components of aggregates
Role of stickiness for aggregate structure and sinking characteristics.
TEP production
TEP, factors that influence its production
How sticky are particles?
Interaction between plankton and sticky stuff
Parameters affecting stickiness
Rates of TEP formation

Turbulent motions at small scales, effects on particles — *Turbulence* — Particles, mixing, and turbulence
Aggregation of phytoplankton
Rates of particle sinking in a turbulent fluid
Turbulence and aggregation
Mixing and turbulence affecting particle distributions and aggregation/disaggregation

Ballast — Skeletons and their role
Ballasting by biominerals
Ballast vs non-ballast:

Density Aggregates
Upward flux and retention time in surface waters

Mesoscale physics — Water column physics — Submesoscale physical motions — *Ocean Physics*
Subduction or springtime mixed layer shoaling
Chemical vs physical processes
Convergence along fronts

Production and respiration
What is a biologically useful way to separate out surface/euphotic zone from deeper?
How does DOM & POM stoichiometry relate to particle export?
Dependence on mineralization
What is the role of production vs. respiration in mediating carbon export?
Rates of primary production & respiration.
Defining respiration to get at NCP
Non-Redfield stoichiometry

Nutrients — Nutrient Supply
Nutrient utilization
Availabillity of nutrients
Source of material available to build particles

Ballast
Role of mineral ballast
What drives absolute flux vs what affects flux efficiency

TEP
How does TEP affect aggregation production?
TEP
Algal community structure and TEP production
Bacteria, TEP

Particle Biome
Do viruses affect export?
Viruses
Distinguishing living particles from detritus/dead particles
What ecological traits are associated with high density/fast sinking?
Are there marine snow "fingerprints" that are linked to source and export?
Linking species composition to particle size and composition
Predicting export from assemblages
Do marine snow biomes relate to export efficiency (use of genomics and geochemistry?)
Relative importance of picoplankton

Variability — Export variability — Vertical export
Spatial and temporal distributions of export fluxes
What controls episodic export?
What is the fate of gelatinous zooplankton biomass?
Episodic Events
What conditions select for episodic flux events?
What controls aggregate export downward?

Aggregate dynamics
Controls on stickiness
Particle stickiness
Aggregation and disaggregation
What organismal traits promote aggregation?
Processes controlling aggregation
What controls aggregate size (disaggregation?)
Mesoscale/submesoscale physics as an aggregation control
What is vertical structure of aggregate production & consumption
How important are aggregates moving within the euphotic zone?
Where do aggregates form vertically?
Measures of particle density, concentration, and size

Food webs — Animal feeding and flux — Interactions between & within trophic levels
Diel vertcal migration
Who eats aggregates?
Does fecal pellet flux decrease flux relative to aggregates?
What controls the relative importance of microbes & zooplankton feeding on particles?
What roles do fish & higher trophic levels play in particle export?
What is the role of gelatinous zooplankton in particle export?
Mixotrophy
Clearer understanding of predator and prey interactions.
What controls aggregate feeding rates?

Particle fate
What is the role of UV photolysis on POC formation and DOM ?
What controls microbial degradation of POM and DOM?
What organic compounds dissolve from fecal pellets?

Climate Change
What are synergistic responses to climate change?
What are the climate divers of zooplankton communities?
Changing ocean
What are the natural vs anthropogenic drivers of particle formation?
Where is export/particle formation changing most rapidly?
What are the short vs long term time scales of DOM pools?

Stoichiometry —Chemical composition of particles —Nitrogen
Chemical character of sinking POM
Elemental stoichiometry of nutrient supply
Stoichiometry of particles
What effect does stoichiometry on phytoplankton export?
What effect does stoichiometry on respiration?
What effect does stoichiometry have on fecal pellet production?

Primary production — Balance of new and export production — N measures of the biological pump — N fixation and new producion
DON and NH4 release from N2 fixers
New production -> NCP -> export connections
Fate of nitrate assimilation, fate of N2 fixation
New production = neet CO2 sequestration: N2 fixation and nitrate as drivers for the C pump
Which are the N sources for Synec? N released by N2 fixers.

Life History
What effect does life history of copepods have on export?
Life cycle stage of organisms
What effect does life history of rhizaria (forams, radiolaria) have on export?

Food web — zooplankton dynamics — food web diversity & biology — community structure
Changing role of certain functional groups across ocean regions
Minimum number of ecosystem types which should be explored to generate an adequate global synthesis
Bacteria–zooplankton interactions in the euphotic zone
What aspects of community structure are relevant?
Zooplankton functional groups
Predactor–prey interactions
Trophic efficiency
How to track new production in zooplankton vs microbial food webs?
Synergy between prokaryotes and zooplankton?
Link between plankton community structure and particle formation rate and its chemical composition
Influence os phytoplankton diversity
Number of processing steps between particle formation and sinking particles
Biomass, species composition, diel and seasonal vertical migrators
Key influential species?

Microbial signatures of particle colonization — Microscale cell-cell and cell-particle interactions — Omics — Microbiology
Particle associated omics measurements (genomics to proteomics)
Bacterial colonization of aggregates
Microscale environments
Role of cell-cell interactions and signalling molecules
Chemical transformation signatures of aggregates as they sink
Gene epxression associated with marine snow/ particle formation
Bacterial-zooplankton interactions (zooplankton tracking aggregates from hydrolysate trails)

Where to quantiy particles
Define depth of export flux vs sequestration flux

Aggregation — Sticking — Stickiness — Coagulation
Aggregation rates
What makes TEP sticky
Where in water column are aggregates most pronounced?
Relating stickiness to community composition
Aggregate/particle formation in deep chlorophyl maxima (not seen by remote sensing)

Phytoplankton diversity and size — Size spectra — Size and sinking speeds
What effect does ingestion of bacteria by phytoplankton (mixotrophy) have on primary production and export?
Phytoplankton diversity
Are size-sinking relationships predictive across particle types?
In situ sinking velocities of marine snow as functions of depth, size and composition
What effect does photosynthesis in micro-zoo (mixotrophy) have on particle size distributions?
Relationships between particle size structure and stoichiometry
What are mechanisms for export in Synechococcus dominated areas?
Retrieval of particle spectra and size structure from remote sensing
Phytoplankton size spectra
Link between particle size, density and sinking speed
Relationship between zooplankton and fish size structure and particle size spectra.
Sinking rates of particles from whole size spectrum
Mineral ballasting.

Environmental drivers — Integration of biological measures with other perspectives — biological physical coupling
Mechanistic understanding
What effect does upper ocean temperature have on export efficiency?
Quantify both biological and physical export pathways at the same time.

Fecal pellets — zooplankton waste — Higher trophic level impacts — Role of feces and carcasses
Particle/pellet production by micronekton at different depths
Importance of fish feces
Role of dead jellies for flux
Fecel pellet production
How does diet (phytoplankton vs microzooplankton) affect fecel pellet production by copepods and export

Zooplankton effects — Protozoan vs mesozooplankton
How does intraguild predation affect respiration and export?
What effect does grazing by dinoflagellates have on export of diatoms in fecal pellets?
Grazing rates of zooplankton (micro and meso)
In situ depth profiles of feces and zooplankton to get at production and loss

Types of marine snow — types of sinking material
Marine snow originating from pteropod webs
Formation of detrital snow via viruses, parasites, and cell death
Relative influence or importance of aggregate vs fecal pellet vs organismal export
Foraminifera and radiolarian marine snow
Effect of forams and radiolaria on primary production and export?
Percentage contributions of different types of marine snow.

Episodic events — Space and time variability
What environmental variables should be measured continuously in order to provide temporal context for fixed duration observations?
Overall flux of episodic events compared to seasonal flux
Episodic events driven by mesoscale and sub-mesoscale processes
What factors generate episodic export events?
Variability in the export pathways out of the surface
Regional variability in processes driving export
Temporal variability
Temporal scales of NPP and export
Temporal varibility in processes driving export

KJ2: Mesopelagic flux attenuation and processes that drive it

Chemical signalling
Chemical sensing of particles
Chemical signalling
Chemical signalling and trails

Flux methods — Methods and conversion factors
Flux by proxy (I,e, optics, Delta O2) Need good conversion factors
Cross calibrate optical and trap estimates of flux
Accurate methods to measure export flux

Flux attenuation of carbon pools
Particle aggregation and disaggregation processes
Flux attenuation of DOC, POC, PIC
Need both POC and DOC flux and attenuation

Chemoautotrophy — Microbial metabolism
Quantify and characterize chemolithotrophy
Availability of electrons (O2, NO3 etc)
Rates of bacterial growth (heterotrophy/autotrophy)

Consumption of particles by zooplankton — trophic interactions and consumer-mediated transformations
Zooplankton behavior
Zooplankton feeding modes
Flux feeders
Chemical sensing of particles
Rates of consumption of sinking particles by zooplankton
Cell removal processes (gravity, lysis, death)
Particle formation at depth
Bacteria-zooplankton interactions
Trophic complexity
Diel vertical migrations
Zooplankton vertical migration
Macrozoo vs microzoo grazing
Quantifying microbial consumption relative to higher trophic levels
Characterization of mesopelagic redident community
Properties of resident mesopelagic zooplankton and fish communities that undergo DVM
Impacts of higher trophic levels

Respiration— Respiration and metabolism
Fish behavior and metabolism/respiration
Community respiration
Respiration vs solubilization of particles
Temperature
Direct measurement of respiration
Respiration on aggregates and sinking velocity
Rates of metabolism (respiration, enzyme production) by bacteria
Rates of metabolism (respiration, excretion) by zooplankton and fish
Depth variation of particle composition and respiration
Controls on microbial metabolism
Mesopelagic respiration

Deep Export
Extremely deep export (abyssal particle fluxes)

Spatial variability — Scales
Advection and mesoscale physics
Scales of coupling between upper ocean and mesopelagic.

Depth dependent stoichiometry and lability — Chemical characterization/Stoichiometry of DOM and POM
Organic matter stoichiometry
DOM reactivity
How much variability in digestibility/lability
Stoichiometry of sinking material
Depth variation of particle stoichiometry and respiration
Availability (lability) of DOM to resident microbial community
Transformation of organic matter (POM ad DOM) as it moves through the water column

Ballast — Ballast controls
Ballast as a determinate of sinking rate
Mineral ballasting
Dust (Fe) ballast and N2 fixation

Particle transformations — Particle size and composition changes
Particle size spectra variations with depth
Repackaging
Phytoplankton community composition in overlying euphotic zone
Depth dependent particle size
Aggregation-disaggregation processes
New particle formation in the mesopelagic
Particle composition
Mechanisms of transformation of sinking particles into smaller non-sinking particles and vice versa.

Particle degradation — Microbial particle degradation
Enzymatic activity (ecto and exo) on sinking POM
Change in microbial community on sinking particles
Particle solubilization to DOC
Particle-attached bacteria and remineralization
Particle microenvironments
fecel pellet coagulation
Growth efficiencies of mesopelagic food web trophic levels
Microbial community structure on particle vs free-living
Particle specific bacterial communities
Particle scale metgenomics and metaproteomics
Hydrolysis vs. remineralization on particles
Rates of remineralization of sinking particles by microbes
Vertical structure of heterotrophic bacteria from lower EZ to upper MZ

Physical effects on vertical flux
Mesoscale variability
Regional features: Oligotrophic vs High production

Scales of spatial variability
Lateral advection
Debris funnels, overlap in time and space, when and where did that particle come from?
Role of episodic flux events
Is there a relationship between the magnitude variation of lux and its attenuation at one location?

Active transport (all taxa)
Zooplankton community and DVM
Zooplankton vertical shunt
Ontogentic vertical migration

Zooplankton vertical transport
Vertical movement: Vinogradov's ladder
Vertical changes in active/passive transport ratio

Sinking Velocity
Sinking velicoty and its drivers
Upward rising particles

Flux attenuation vs microbial metabolism — Microbial assemblage on sinking particles — Bacterial C demand — Microbial community — Microbial processes
What is the fate of marine snow infauna
Archaea vs bacteria, which dominates metabolically
Microbial food webs, bacteria–protists–viruses
How important is microbial colonization on fate of flux?
How do microbe properties couple to particle flux (archaea vs bacteria, motile vs non-motile)
How does vertical flux drive non-particulate microbial community
Respiration rates
Microbial respiration of sinking particles
Microbial respiration
Microscale heterogeneity (particle-ambient)
Bacteria and archaea growth efficiencies
Genomics, organism and metabolism
How do zooplankton and microbes segregate vertically?
Chemotrophy, chemolithotrophy

Particle quality
Food quality vs depth
Different lability of cellular moieties

Enzyme activities — extracellular enzyme hydrolysis
Hydrolytic enzymes
Bacterial enzyme activities and demands

Solubilization
POM -> DOM solubilization
Solubilization of particles by bacteria

Standing stock vs flux
Optical particle attenuation (standing stock) vs sediment trap data (flux)
How much do changes in the flux affect particle standing stock?
Residence times of particles and aggregates

Physical vertical transport
Entrainment/detrainment of DOM and POM
Vertical mixing of DOM and POM

Properties of sinking particles — Export from EZ
Community composition of euphotic zone — quality of sinking particles
Particle size distributions
Repackaging particle acceleration
Consumption, respiration, transformation, repackaging

Flux attenuation by zooplankton — Metazoan consumption
What is the relative importance of different groups of detritivores feeding on sinking particles
Detrital food chain vs consumption of vertical migrators
What categories of flux feeders are required?
Zooplankton grazing in mesopelagic
Zooplankton-particle interactions
Mesopelagic zooplankton/nekton feeding
Zooplankton grazing on mesopelagic particles
Carnivory at depth
Zooplankton consumption of microbes
Flux feeders
Coprophagy
Coprorhexy
Can mesopelagic animals feed on flux?

Metazoan Remineraliztion — Animal carbon demand — Animal metabolism
Zooplankton metabolic demands
Metaolc rates of metazoa — carbon demands

Sub-oxic processes
Deoxygenation
Role of oxygen concentration
Effect of OMZ
Particles as chemical microenvironments/reactors

Existential view of the mesopelagic world (a bone for the modelers)
Empirical vs "fundamental" models

Aggregation-disaggregation
Is aggregation important below the euphotic zone
Aggregation disaggregation mecahnisms
Aggregate fate
Reaggregation and entrainment of ballast
Disaggregation of particles
Physical disaggregation

Mesopelagic food webs — Trophic interactions
Effects of multiple trophic transfers on respiration and attenuation
Trophic interactions in the deep euphotic zone
Trophic cascades (impact the degree of flux attenuation?)
What role, if any, do fish play?
Squid and fish in the mesopealgic and top down control
Flux attenuation as a function of food web structure
Parasites, viruses
Role of parasitism on particle degradation
Effects of parasitism in protists and zooplankton on flux attenuation
Spatial variability in particle degradation/consumption and community structure

Geography
What are the boundaries of the mesopelagic?

Amelioration of flux — Counter flux — Flux attenuation
Amelioration of flux attenuation by chemosynthesis
Primary production in the deep Chl max
Martin's curve no appropriate?
Upward particle flux

Consumers of sinking particles — Consumption — Particle eaters
What/who are the main consumers of particles?
Zooplankton vs bacteria
Details of consumee-particle interactions
How much sinking stuff do detritivores eat?
Zooplankton grazing rates (taxa, group specific)
Marine snow as a hotspot of biological activity

Vertical Migration
Active migration
Zooplankton vertical migration

Particle composition and type — Sinking rate — Direct particle specific flux measurements — Particle sinking spectra
Effect of particle composition
Which particles are actually sinking?
What rate do particles sink at?
In situ sinking velocities
Sinking velocity as a function of particle type
Mineral ballasting
Elemental composition of particles

Spatial variability of consumers and particles
Marine snow particle size distribution with depth in concert with zooplankton taxa distribution
Simultaneous determination of zooplankton distributions + grazing + defecation rates on a taxa (group) specific level

Role of turbulence
Turbulence: does it still matter?

Balance of aggregation/disaggregation
How does marine snow aggregate once it sinks?
Aggregation vs fragmentation
Fecal pellet depth distributions

Particle breakdown — Aggregate processes
Disaggregation by zooplankton
Particle disaggregation by swimming animals
Zooplankton rate of fragmentation of particles

DOM–POM continuum — Aggregation disaggregation processes —
Chemical particle dissolution
DOM to POM (and reverse) processes

Cyanobacterial resistance — Cyanobacteria
Do cyanobacteria stay alive and/or grow on particles in the mesopelagic?
Are cyanobacteria resitant to digestion?
Heterotrophy among cyanobacteria and amelioration of flux attenuation

Bacteria and Remineralization
Enzymatic degradative rate
Rates of remineralization
Bacterial colonization
Community respiration
and several unreadable

Particle input — Boundary conditions
Importance of particle input (details of source) to mesopelagic flux attenuation
Taxa specific fecal pellet production rates

Repackaging
Particle repackaging by particle eaters
Repackaging of particles
Repackaging of sinking particles

Metabolic Demands
Mortality at depth
Supporting metabolic demands of mesopelagic community

Metabolic processes — physical/chemical factors controlling metabolic rates — Processes of O2 minimum zo
O2 minimum zones
Extent and intensity of oxygen minimum zones
Anamox processes
Temperature dependence of respiration
Different rates of respiration with depth

Import and export flux — Particle production at depth — Particle formation in the mesopelagic
What are the physical drivers of aggregate formation
Importance of particle formation at depth
TEP production at depth
Source of small sinking particles at depth
Connections between the euphotic zone and mesopelagic

Time and space scales
Climate drivers in the mesopelagic
Short vs long term processes in the mesopelagic

Microbe-particle interactions — mesopelagic metabolism
DOM absorption onto sinking particles
Using technology to measure rate processes
Bacterial diversity and their detection of organics
Microbial metabolism of POM and DOM
Particle turnover rates
Respiration by particle attached microbes
Respiration by free living microbes
Microbial and viral dynamics
Attached microbes to organisms
Balance between solubilization and absorption
Microbial solubilization and utilization
Chemical transformations between POM and DOM

Particle sinking speeds
Fragmentation of sinking aggregates due to shear
Drivers of particle sinking speed
Particle residence times
Sinking speeds of particles relative to degradation
Dynamics between large particle pool and small particle pool
Density gradients
Gas bubble production within aggregates
Sinking rates of aggregates vs fecal pellets
Shifts between sinking vs suspended particles

Vertical migration
Vertical migration
What controls DVM to different depths
Grazing and migration
DVM community composition
Role of DVM in "biogenic mixing"

Zooplankton behavior and trophic linkages — Grazing
What controls DVM to different depths
Zooplankton repackaging of sinking particles
DVM community composition
Grazing my mesopelagic zooplankton
Sloppy feeding by zooplankton
Trophic fate (micro and mesozoop)
Mesopelagic food webs

Chemical composition of POM and DOM
Particle composition
Quantification of carcasses
Change in aggregate porosity
Chemical composition of particles
DOM compounds produced by zooplankton
Degree of pre-processing in surface ocean (lability of sinking organic matter)
Diversity and composition of DOM and POM
Ballast materials
Chemical transformations between POM and DOM and vice versa

Physical Biological Interactions
POC organism interactions
Modeling flux attenuation
Zooplankton disaggregation

KJ3: IKJ3: Particles — Characteristics, bioreactivity, export, stoichiometry, episodic export events

Spatial Variability in Export — Episodicity of export & production due to physical motions
Bloom subduction does to shoaling mixed layer
Covariance of vertical mixing and organic matter production
Submesoscale physical motions driving convergence and particle aggregation
Mesoscale upwelling of nutrients driving production and episodic export

Effect of larger environment
How do low O2 environments affect particle fate?

Particle heterogeneity
Oxygen gradients inside particles
Small scale gradients

Microbial metabolism
Microbial activities
Mapping microbial physiology onto substrate utilization (specificity)
Digestibility of bacterial and protisan taxa

Sediment traps
Validation of methods to measure export

Temporal variability — Time scales for export — Temporal couplling/decoupling oe export/production
What controls export on scales of hours, days, weeks, years
How do rates of export vary in space and time
Time lag between OM production and (episodic) export events

Triggers of export — Aggreggation events
Aggregation cues or triggers
Physical reactivity surface-active properties and links to episodic events
Particle aggregation at the end of a bloom

Reactivity gradients, under anthropogenic pressure

Solubilization
How much DOC export involves release from particles?
POM <-> DOM transformations

Particle composition and sinking — Sinking Sinking Rates
Do size sinking rate relationships hold across particle types.
How important is particle composition to fate?
Physiological health of phytoplankton and sinking rates
Size distribution of sinking particles
Relationships between phytoplankton taxa and particle density
Elemental stoichiometry and sinking speed
TEP fraction within aggreggates

Consumers, particle formation and export — Episodic trophic interactions
What is the role of parasitism in driving/regulating episodic export
Bloom termination due to viral lysis/parasite infection
Particle aggregation driven by cell lysis/ TEP production
What is the role of predation in regulating episodic export events

Consumer interaction with OM — Consumer interactions with particles
How do different consumer influence particle size distributions and their export
Match/mismatch between elemental stoichiometry of particles and consumer demand
Quantifying organisms catalyzing remineralization (relative roles of microbes vs animals)

Bioavailability
Definition of bioavailable/refactory
Bioavailability of organic matter
Relative lability of different classes of organic matter

Biogenic matter composition — Evolution of elemental ratios — Stoichiometry
Particle evolution (chemical and biological)
Evolution of elemental (CNP) ratios during aging
CNP ratios of exported OM
C:N ratio of uptake by primary producers
Quality of POM (CN ratios etc)
Stoichiometry of oranic matter remineralization
Taxa specific differences in stoichiometry
Particle source (marine snow, fecal etc.)

Physical interactions aerosol OM — Supply side ontrol of particle formation
Aerosol nutrient (N, Fe) input driving episodic production/export
Impact of aerosol deposition on episodic events
Quantification of nutrient supply fueling export

Aggregation Adsorpition — OM-OM Interactions
Tendency to interact with other organic matter

Composition & spatio-temporal variability in biogenic matter — Composistion and lability — Lability and recalcitrance
Lability/recalcitrance before being respired by bacteria
DOC/POC turnover rates
Lability of DOM
Natural vs anthropogenic climate drivers
Short vs long term environmental stressors on biogenic matter
Bioreactivity of biogenic matter and how it changes with depth and time
Mineral and organic protection of OM
Recalcitrance
Changes in bioavailability of particulate carbon with depth
Changes in chemical composition with time, depth, succession
Shifts in ectoenzyme profiles on particles with depth
Variations in comsumability across phytoplankton
Ambient influence on OM reactivity: Temp, salinty, pH, Omega(aragonite), Omega(calcite)

Particle biome
Factors driving colonization of particles by microbes
Biological succession on particles
Living organisms inside particles (bacteria, phytoplankton, protists)

Chemical composition and stoichiometry — Biota controls on stoichiometry
Elemental composition
Chemical/compound specfic composition of biogenic matter
Effect of C, N, P. Si, and carbonate ratios on sinking
Biogenic mineral content
Relationship between particle composition and size
Stoichiometry of DOM
Chemical structure of DOM
Importance of non-Redfield stoichiometry for export
Effects of biology on chemical composition, stoichiometry, and particle stickiness
Stoichiometry of animal metabolism on sinking particles

Physical propertie of particles — sinking
Physical strength of particulate material
Relative magnitude of export of siinking particulate material vs advection of dissolved matter
Density, shape and sinking speed
sinking velocity
Evolution of particle buoyancy

Sources of biogenic matter
Role of lifecycle of rhizaria on formation/dissolution of particles at depth
Exopolymer production by mesopelagic zooplantkon/microzooplankton
Organismal source of biogenic matter

Factors causing episodic events — biological drivers of episodic export events
Importance of jelly falls to annual export
What ecological traits promote episodic events?
Importance of viral infection of phytoplankton blooms to export

Jelly plankton export and trophic interactions — zooplankton and nekton as sources of biogenic matter
Gelatinous zooplanton community structure
Nekton-plankton trophic linkages
Jelly falls
Jelly-microbial interactions/rates/processes
Importance of jelly falls to annual export

OM chemistry, ocean & atmosphere influences — Source-sink dynamics of biogenic matter between atmosphere and ocean
Biogenic matter as antioxidants to climate stressors
Iodine and cycling & linkages to biogenic matter
Photolysis of OM
Volatilization of OM
Composition of DOM excreta from zooplankton
Ocean atmosphere interactions
Atmospheric deposition

In situ method development
In situ methods development

Biogenic matter as anti-oxidants
Biogenic matter as anti-oxidants to climate stressors

OM transformations — Molecular OM characteriation —
Lability studies
DOC composition and reactivity
Diagenetic character of organic matter POM and DOM
Hydrolysis
Fraction of DOC that is labile
Solubilization of POC to DOC
Partitioning of primary production between POM and DOM
Molecular transformation & their effects on properties of organisms
OM dissolution
Particulate <-> Dissolved transformations
DOM characterization

Sinking velocities — What influences sinking speeds?
Controls of sinking speed
Role of fast sinking particles (fish falls)
Particle size-dependent properties (velocity etc.)
Unique behavior of different sinking particle types
Relative contribution of different types of sinking particles to export

Fecal pellet export — role of fish
Do schools of coastal pelagic fish contribute to export with their consumption, dense schools and patchiness
Fate of fish poop; does it hit the bottom?
Fecal pellets

Biogenic matter characterization
Is biogenic matter different during episodic export events?
Association of bioreactivity with eddy fields
Does POM:DOM of export change with season?
Factors driving remineralization of ballast materials (opal, PIC)
Biogenic ballast minerals
Effects of inorganic dust input on export?

Community composition — Taxonomy and export
Which key taxonomic groups contribute most to C export (absolute flux)
Coccolithophores
Diatoms
Phytoplankton community structure
Which key taxonomic groups contribute most to export efficiency

Capturing and quantifying episodic events
Observations of frequency of episoduc events
Modeling episoduc events (only way to addresss all space and time scales)
Episodic events structuring ecosystems
Is material which generates an episodic event more or less labile

POM size spectra — Particle size —
Marine snow
Effect of molecular characteristics on aggregate structure
Spatial resolution of plankton and size spectrum
Particle size spectra
Properties and roles of nano-gels
Aggregation/disaggregation processes

Microbial respiration and remineralization — Particle respiration and metabolism
Different labilities of different particle types
POM remineralization vs solubilization
Microbially mediated remineralization
Respiration
Accurate estimates of respiration
Bacterial growth efficiency

Microbial communities on aggregates — Particle microbial interactions — Particle microbiome
What microbial pathways are active as organic matter become recalcitrant?
Microbial genome, transcriptome, proteome for attached vs free-living populations
Particle microbiome
Particle scale genomics & transcriptomics
Particle colonization by bacteria
Trophic level interactions on particles of different composition
Understand the variability of microbial community function and structure over depth

Methods validation and calibration
Primary production — which methods work?
In situ visualization techniques

Microbial community effects — Microbial metabolism
Microbial community on marine snow
Particle biome: microbial community and degradation
Chemotrophy
Microbial colonization and food webs
Microbial microhabitats

Cllimate change impacts
Effects of ocean acidification

Bioavailability of organic matter — changes in bioavailability
Changes in DOM bioavailability as a function of bacteria populations
Bioavailability
DOM bioavailability
What is bioreactivity exactly?

POM <-> DOM Transformations
How much DOM is subducted and where?
Particle-dissolved continuum
TEP and microgel production
Lability of DOM
DOM export
Labile vs refactory DOM
DOM <-> POM continuum
DOM concentration vs Pom concentration
Exopolysaccharides and exudates

Microbial transformations — microbial dynamics
Microbial metabolic pathways: e.g. chemoautotrophy
Bacterial secondary production and respiration comparison
Microbial transformations
Microbial metabolism and remineralizatoin
How does temperature impact vital rates (e.g. reminalization)
Contribution of symbiotic associations
What conditions/organisms faciliate degradation of refactory organic matter

Temporal variability — event scale processes — Episodic events
What is the relative importance of export events at global scales; local vs global
Small scale variability
Biology behind episodic flux events
Climate driven changes in exudation and effects on particle export/events
Magnitudes of different episodic events;
Role of gelatinous plankton
Temporal spatial variability
Ocean physics drives episodic export events
Quantifying episodic events
What species are doing episodic events
Patterns (spatial/temporal) of episodic flux events
Drivers of episodic flux evetns
Types of episodic flux events

Poopology — Consumption & repackaging — Animal impacts on particles — Particle transformations
Fecal pellet degradation
Trophic up and downgrading
Consumption/repackaging
Repackaging in deep euphotic zone
Quality of organic matter for consumption
What is the variability of food quality in the mesopelagic?
Zooplankton mediated particle transformations
Differential digestibility

Aggregation disaggregation
Aggregation disaggregation

Particle sinking velocity — ballasting effect
Minerals (biogenic and lithogenic) as ballast
Sinking rates and particle density
What keeps particles suspended in the surface ocean?
Distribution of sinking rates with partilcle characteristics
Packaging and sinking velocity
Ballast formation
Inorganic constituents, ballast
Buoyancy regulation by planktong
Ballast,TEP content, sinking velocity
Mineral ballasting
Particle composition
Particle composition determines sinking velocity

Living vs Dead
Organisms vs detritus
Live vs. dead inventories

Benthic-pelagic coupling
Benthic-pelagic coupling

Particle characterisitcs — Particle size spectra and characterization —
Particle size ditributions
What drives export? Size vs composition
Particle size spectra
What do particles look like? Size, shape, density etc.
Particle shape and surface areas vs volume
Particle size spectra
Density and size measurements
How have particle characteristics changed in "anthropocene"/modern era

Plankton community structure — Plankton dynamics — Nutrient limitation & community dynamics —
Community structure composition
Effect of phytoplankton community structure
Plankton community structure
Phytoplankton bloom dynamics
Nutrient limitation
Nutrient/micronutrient regulation
Community adaptation to limitation

Stoichiometry
DOM stochiometry
Stoichiometry
C, N, P, Fe measurements
What is the stoichiometry in particles?
Contribution of N2 fixation to particle quality/stiochiometry
What promotes deviation from Redfield in exported particles?
High carbon organics
Particle stoichiometry at a range of depths

KJ 4: Microbial and viral processes and newly revealed biological pathways

Effects of microbies on aggregation, solubiliztion, mineralizarion — Microbe particle interactions
- Microbial composition and its role in particle solubilization
- Changes in aggregate cohesiveness due to bacterial activity
- Microbial marine snow formation
- Effect of grazing on bacterial activity on particles
- Biological formation of marine snow: new pathways
- The importance of microbial motility
- Aging of aggregates
- Is the physical activity of protozoa relevant for particle disaggregation

Microhabitats
- Microbe-microplastic interactions
- Microenvironmental habitats for unique biogeochemical transformations
- Microbial microhabitats

Effects of Ocean acidification
- Influence of ocean acidification on microbial activity

Microbe, metazoan
- Balance between viral and metazoan controls on bacteria
- Synergy between microbes and zooplankton
- Attached microbe communities to jellies

Vertical migration
- Diel vertical migration
- Vertical migration in phytoplankton (assuming they are microbes)

Mixotrophy
- Mixotrophy
- Mixotrophic bactivory

Chemoautotrophy
- Mesopelagic DIC fixation
- Chemoautotrophy promotes sinking flux
- Chemosynthetic bacteria associated with particles? Effect on particle composition and size?

Symbiosis
- Symbioses
- Gut microbie interactions

Fish
- Export from fishes
- Fish respiration is higher than we thought

Remineralization
- Rates of remineralization
- Enzymatic activitiesassociated with particles, Diffusion of enzymes into water column
- Microbe respiration in the mesopelagic
- Remineralization

Parasites and parasitoids
- Parasitism as an indicator of high flux?
- Parasite-host secificity
- Role of parasites
- Pathogenic microbes -> linkages to the onset of episodic events

Plankton community structure
- Viral impacts on plankton community structure
- Co-occurrence patterns (community structure)
- Bloom termination (e.g. role of viruses)

Atmospheric input
- Atmospheric deposition of particles with attached microbes

Respiration — Controls on microbial growt efficiency — Respiration vs growth efficiency
- How does microbial espiration relate to stoichiometry
- Microbes as a shunt of energy
- Priming effect — uptake of refractory compounds

Non-bacterial microbiota
- Role of archaea
- Are non-bacterial microbiota significant in material transformation?

Viruses
- Role of viral lysis
- Viral lysis of non-microbes
- Viruses
- Role of OM after viral lysis
- Rates of viral infection
- Short term (minute to hour) microbe-viral interactions
- how do viruses affect microbial remineralization activity
- Viral infections as a marine snow formation pathway
- Microbe-virus coevolution
- Fate of lysed cellular material

Role of exudates
- Exudation vs lysis – role for marine snow formation
- Exudate composition as a determinant of aggregates characteristics
- Exudation of DOM by microbes

Allelopathy
- Effect of phytoplankton allelochemicals on microbial activity on particles
- Allelopathic defenses: bug-on-bug violence

Grazing
- Microzooplankton grazing
- Deep euphotic zone grazing and recycling

High resolution techniques — omics
- New techniques (nanosims etc. genomics)
- Particle vs free living metagenomics and proteomics

Microbial competition
- Microbial competition for substrates
- Species specific microbial interactions (predation, parastitism, mutualism)
- Secondary metabolites
- Quantification of material exchange via symbioses

Particle microbiome
- Particle microbiome
- Change in microbial community structure, proteome and transcriptome as organic matter is chemically transformed
- Bacterial community structure
- What is the microbial composition related to BCP

Exopolymers
- Ecto and Exoenzyme production and activity

Viral dynamics and interactions
- Virus-host relationships
- Role of viruses in determining microbial community structure
- Adpative genes via viral infection
- Viruses constraining export?
- Viral termination of blooms
- Resting stage formation vs export

Controls on viral lysis and OM transformations
- Triggers of lysogeny
- Viral DOM
- Controls on viral lysogeny vs lytic phase
- Role of viral lysis on altering lability of DOM/POM
- Viral lysis increase or decrease export?

Effects of particle composition on remineralization
- How does stoichiometry influence microbial community composition and vice versa
- Map specificity in microbial metabolism to oraganic matter substrates
- Particle aging and composition changes (stoichiometry, energy content)
- Synergistic degradation of POM by different microbes
- Identify biological processes decoupling remineralization and production(space and time)
- Different remineralization of different phytoplankton taxa

Mixotrophy
- Importance of mixotrophy (photoheterotrophy)

Chemoautotrophy
- Magnitude and pathways of chemolithotrophy
- Quantify chemoautotrophic production and energy demand
- Chemoautotrophy
- Sulphur based metabolism

Particle transformations
- Microgel formation and sinking
- Microbial controls on organic matter transformation (i.e. persistence vs bioavailability)
- PIC dissolution and sinking speed
- TEP/stickiness/aggregation
- Organic cycling within fecal pellets
- DOC uptake into POC

Microbial community structure changes
- Microbial community structure with depth
- Free living vs particle attached microbial interactions
- Foraminiferal flux feeders in the deep
- Microbial transport by sinking particles
- What is the link between microbial carbon pump and biological carbon pump

Ocean acidification
- OA effects on biology and export

Trace metals — Microbes and nutrient dynamics
- Quantify biological sources and sinks of N
- Nutrient dynamics within aggregates in eh euphtoic zone
- *Something about trace metals (yellow sticker was covered up)*

Bacteriall growth efficiency
- Bacterial growth efficiency
- Rates of respiration

Particle microenvironments
- Microenvironment formation and characterization
- Aggregates as microhabitats
- Nanogels and microbial substrates
- Oxygen gradients within particles and aggregates
- Chemical microenvironments
- Internal particle heterogeneity (microbial niches)

Bacterial colonization of particles — Quorum sensing
- Qurorum sensing
- Bacterial quorum sensing
- Qurorum sensing
- How do microbes find and colonize particles
- Processes leading to particle colonization by bacteria/archaea
- Microbial-viral hotspots on particles

Microbial food web — Microbial food web effects
- Protist grazing and export
- Protozoan comsumption of diatoms and other microplankton
- Predation by microbial predators
- Microbial loop — food web integration
- Microbial food webs and consumers
- Impacts of mixotrophy
- Parasite interactions

Microbial C pump — Microbial C utilization efficiency — Microbial C utilization
- Utilization thresholds
- Microbial utilization of deep DOM
- Microbial C pump
- Labile-recalcitrant

Quorum sensing — Chemical sensing
- Quorum sensing
- Microbial quorum sensing to degrade sinking particles
- Chemotaxis

Enzyme effects
- Hydrolytic enzyme production
- Exoenzymes

Microscale variability — Microhabitats and communities — Microbial heterogeneity on small scale
- Particle microbiomes and associated transformations
- Microbial associations
- Microbial microhabitats
- Microscale patchiness

Chemotrophy
- Inputs of organic material from deep chemoautotrophic communities
- Chemotrophy
- Chemoautotrophy
- Anaerobic metabolic strategies

Symbioses
- Symbiosis mediated transformations

Nitrification
- Impacts of nitrification

TEP dynamics — POM-DOM interconversion processes — POM-DOM transformations
- Role of viral lysis in aggregation disaggregation
- Virus-TEP production and stickiness
- Viral mediated production of DOM
- TEP production by organisms
- DOC productoin utilization
- POM-DOM transformations

Viral processes — Virus mortality— Viral and parasite interactions
- Virus-TEP production, stickiness
- Cell death/mortality
- Viral bloom termination
- Non-lytic viral interactions
- Viral shunt
- Cell death/mortality
- Methods for detecting lysed cell populations remotely
- Viral shunt (DOM production)
- Parasite interactions
- Defence strategies against infection

Phytoplankton resting stages
- Phytoplankton resting spore formation and potential contribution to flux
- Cyst and resting stage formation in phytoplankton

Gelatinous zooplankton
- Effects of filter feeding gelatinous organisms
- Gelatinous zooplankton and export

Physical and chemical controls on metabolic rates — effect of temperature and oxygen
- Temperature and oxygen sensitivity of microbial processes in a changing ocean

Meatzoan mediated export — large animals
- Large metazoan contributions (whale, fish etc.)

Vertical migration
- Vertical migration

Saprotrophy
- Eukaryotic decomposers (saprotrophy)

Picoplankton and export
- Role of picoplankton in export

Vertical controls and trophic interactions — Microbial food web
- Evolution of functional diversity within a functional group
- What controls the vertical distribution of microbial taxa
- Phylotypic selection
- Prevalence of vertical migration among phytoplankton
- What control vertical distribution of free-living vs. particle attached microbes
- How do flagellates control microbial concentration on particles
- C demand (metabolism) of flagellates and ciliates in the mesopelagic
- Spatial variability of active transport

Mcrobiomes — Microenvironments
- Characterization of microbiomes on particles and animals
- Linkages between microbes and metazoans
- Sinking particles and animals as microbiomes
- Microenvironments on or inside particles and if they enable different metabolisms

Viruses as repackagers of nutrients — DOM production by viruses and bacteria
- Viral controls of DOM production
- Viruses as sources of labile DOM
- TEP production by bacteria
- What fraction of POM comsumed on a particle vs released in the water column

Microbial particle remineralization
- Mechanistic understanding of microbial transformation of OM
- Better quantification and understanding of enzyme dynamics
- Variability of enzyme activites with depth
- Microbial transformation and particle composition
- Microbial controls on particle buoyancy
- Rates of microbial remineralization of sinking POM and DOM in the mesopelagic
- Microbial transformations that alter nutrient pools (inorganic <-> organic)
- How much remineralization occurs on intact falling particles vs broken up bits
- Role of microbial utilization of advected DOM

Phytoplankton ecology and physiology
- Phytoplankton that can become heterotrophic or use different metabolisms in the dark
- Bacteria-phytoplankton symbioses
- Physiological diversity among phytoplankton
- Survival strategies or physiological changes at deep/dark depths
- Does mixotrophy really promote export?

Bacterial sensing and interactions — Factors that contribute to microbial colonization and transformation of particles
- Info-chemical signalling between organisms
- Colonization pathways
- Microbe-microbe interactions on particles
- Microbial cell-cell sensing and communication

N cycling
- Magnitude and variability of N fixatoin
- Magnitude of euphotic zone nitrification

Chemotrophy
- Microbial chemosynthesis and new production at depth
- Importance of chemoautotrophy as C source in mesopelagic

Anearobic processes
- OMZ - anaerobic processes

Contributions of viruses that are hard to count
- Contributions of single sranded NA viruses

Lysogenic infections
- Lysogenic effects: Virus influences on host physiology (before lysis)

Biomineralization
- Variability in the precipitation of biominerals among organisms/species
- The role of silicon in cyanobacteria and its influence on export

Viruses and aggregates — quantifying viral impacts — Viruses causing aggregation
- Relative contributions of lysis to respiration vs C export
- Whether viral lysis leads to export through aggregates or not
- Impact of viral shunt vs stickiness of lysed material
- Role of viruses in aggregation
- Do viruses enhance or dampen episodic events

Role of viruses — Role of aggregates in viral infection
- Evolution of viral density within aggregates
- Aggregates: source or sink of viruses
- How do viral dynamics change on particle vs free living?
- Aggregate consumption, vector of virus infection for consumers
- Aggregate structure as infection site for bacterial community

Microbial structure and particle composition — Bacterial community structure
- Microscale structure of microbial communities
- Changes in microbial community functional capabilities with particle age
- Microbial succession and transformation of OM (temporal)

Virus-host dynamics —
- Virus host specificity
- Varying role of parasitoids across bacterial functional groups
- Role of parasitoids in lysing heterotrophic bacteria
- Quantification of viral production/host lysis
- Viral controls on demise of phytoplankton blooms
- Virus-host population dynamics
- What are causes/rates of viral dynamics

KJ5: Food web, community structure and trophic interactions

Chemical signalling — the role of chemicals in community interactions
Chemicals as signals and chemicals as defence
Anto-predation mechanisms
Chemical signalling between different trophic levels

Influences on food webs and pathways — relating metablism and flux
Relating biogenic matter consumption and specific pathways mediating transformations
Mechanisms causing statistical links between certain foodwebs and flux
Methods for identifying trophic linkages
Deciphering contributions of individuals within microbial consortia
Cascading biochemical pathways

Community composition and export
Links between diversity in the surface and export
Vertical changes in species composition

Phytoplankton community structure — Phytoplankton size and composition effects on export
Size structure of phytoplankton community
Phytoplankton community structure
Phytoplankton community composition effects on aggregate formation and sinking rates
Phytoplankton community structure and mineral ballasting
Phytoplankton structure and rate and extent of consumption

Physical and chemical controls on community structure — Determinants of community structure — Abiotic influences
Role of oxygen as determinant of community structure
Role of inorganic nutrient availability as determinant of community structure
Biogeographic species shifts under changing clinate

Role of patchiness — spatial variablity
Increasing spatial patchiness at higher trophic levels
Role of patchiness in encounter rate

Flux feeding — role of different zooplankton types
Flux feeding in mesopelagic
Flux feeders
Zooplankton community ffect on chemical composition, sinking rates of fecal pellets
Role of radiolarians

Microhabitats
Do fecal pellets serve a micro-refugia for specific communities
Food webs on particles
Microhabitats and small scale variability
Microbial succession on particles
Role of patchiness in encounter rates

Allometry, Size distribution — Particle organism size effects
How are small things exported
Particle size distribution
Influence of organism size and particle size on export
Size selectivity of mesozooplankton grazing
Allometric plankton models
Relationship between specific phytoplankton derived particles and sinking speeds

Variability over time — Periodicity of trophic interactions
Periodicity of trophic interactions (seasonaly, monthly, daily)
Seasonal timing shifts in changing climate

DOM and POM Production — DOM production through trophic interactions
Predator-prey/host-virus interactions and aggregates vs DOM production
Procution of DOM and POM by zooplankton and utilization by bacteria

Symbiosis
Symbiosis
Parasitism

Top down controls
Top-down grazing pressure
Removal of large predators by humans
Importance of fishes in the surface and at depth for export

Rethinking the microbial loop
Extent to which mixotrophy leads to export
Is the traditional dichotomy in biochemical role of protozoans and mesozooplankton real?
Relative importance of phytoplankton -> zooplankton and phyto -> protozoa -> zooplankton pathways
Microbial loop

Mesozooplankton mortality
Do most zooplankton get eaten or die and sink?
Role of mortality at depth for active transport by vertical migrators

Material transfer rate measurements

Zooplankton particle dynamics
Role of zooplankton in disaggregation
Particle colonizing zooplankton
Contents of fecal pellets
Immigration and emigration of community members on particles with depth

Resource utilization models — grazing dynamics
Diet characterization of mesopelagic metazoa (zooplankton, fish)
Preferential grazing on certain species
Species specific predator prey relationships
Predator prey relationships
Ecological guilds
Size selectivity of mesozooplankton grazers
Functional responses
Numerical response models
Deep euphotic zone imbalance between growth and grazing
Characterize assimilation efficiency of mesopelagic animals
Microbial predators (euks)
Lower thresholds for resource utilization
Role of grazing vs aggregation in export

Microzooplankton grazing
Do flagellates control microbial populations on aggregates
Mixotrophy
Microzooplankton grazing
Protozoan grazing

Phenology
Drivers of species succession
Synchronization of life cycles

Competition — Allelopathy
Allelopathy and its importance to plankton community structure
Competition and niche partitioning

Virus food web interactions
how do viruses structure plankton communities
Do viruses control microbial populations on particles
Viral lysis

Symbiosis
Symbiotic relationships
Symbiosis

Reproductive processes
Reproductive phenology
Egg production (zoo and fish)
Spawning phenology
Controls on recruitment (fish)

Microbial gene transfer
Marine snow hot spots for gene transfer

Trophic cascades
Top-down trophic cascades
Trophic cascades -> biological pump

Bioaggregate dynamics — depth related processes
What phytoplankton species preferentially aggregate?
how important is aggregation for detrital removal throughout the water column
What controls microbial taxa shift with depth
Depth-related changes in active/passive flux ratio

Particles
What is the fate of broken particles in the water column

Fish poop
How much do fish poop?
Do surface fishes contribute to export flux via fast sinking feces? E.g. episodic events from passing schools of sardines

Human impacts
Effects of overfishing, defaunation on marine communities
Do human impacts (fishing etc.) on ecosystems matter for biopump?

Food web structure — Role of higher trophic levels — Meso-and macrozooplankton consumption
Food web short cuts
Size structuring of food webs
Any role foe whales, seals, seabirds, penguins etc. in biopump
Trophic interactions as a function of temperature
Defining high trophic level functional types
Modeling higher trophic levels (micronekton, fish)

Linking food web processes to global C models

Phyto- vs zooplankton contributions to export
Does zooplankton feeding and fecal pellet production decrease or increase flux?
Contributions of differenti sized plankton to POC vs DOC

Deep Consumers
Feeders at depth
Where is zooplankton feeding on sinking particles most important
What zooplankton feed on aggregates
How do zooplanton find and feed on sinking particles
What do deep-living jellies eat
Does detrital material fuel food webs of large animals in bathypelagic ? Does it escape the microbial loop?
Mesopelagic community composition
Pealgic feeding by demersal fauna at shelf-break

Diel vertical migration — Migrations — Diel Vertical migration interactions
Relative magnitude of zooplankton/fish active transport
Characterizing diel vertical migrations: Who, where and how much
Influence of fish predation on zooplankton vertical migration and distributions
Spatial variability of active transport

Diversity
Does diversity of species matter to biological pump
Observing/characterizing species ecotypes

New Methods — Acoustic methods
Can strength of the biopump be measured by benthic respiration
Improving acoustic estimates of biomass/composition/location

Drivers of patterns of plankton community structure
remote sensing of phytoplankton size structure
Plankton size spectra

Ocean physics and climate
Climate -> biopump -> community structure
Mesoscale (eddies) and submesoscale (fronts, filaments) physics set community structure and distributions

Food web controls on aggregation — Aggregation pathway
Aggregation as a shunt of the microbial loop
Food web controls on aggregate vs fecal pellet export
When and where does zooplankton feeding enhance export
Does each aggregates have a unique community structure or do all aggregates have the same
Food web controls on aggregation
Aggregation induced transfer of pathogens
Microbial controls on aggregate chemistry (bioavailabillity and stoichiometry)

DVM controls and impacts
Does parasitism influence DVM
DVM and jellies biogenic mixing
What is the "true" distribution of resident and DVM organisms
Do zooplankton take up DOM

Zooplankton behavior
Effects of zooplankton behavior and life histories

Quorum Sensing
Quorum Sensing

Gut biota metabolism
Internal microbiome

Climate effects
Climate (human and natural) drivers in the mesopelagic

Food web structure and BP — Variability in trophic networks
How do allelochmics influence trophic interactions

Balancing production and respiration — Net ecosystem metabolism — Autotrophy vs respiration — Microbiota and community respiration
Particle Microbiome interactions
Microbial foodweb interactions
Fates of primary production
Metabolism of zooplankton as it relates to food source
Autotrophy/heterotrophy tipping points
Budgets that balance sources and sinks
remineralization/recycling
Community respiration
Is trophic transfer of energy related to carbon export
Balancing production and respiration
Bacterial growth efficiency
Alternate pathways
Bacteria/phytoplankton competition for nutrients

Food web structure and BP — Variability in trophic networks
How do allelochmics influence trophic interactions
Does community structure depend on algal source (phytoplankton bloom spp) of aggregates
Resolving contributions/fate of functional groups
Quantification of deepwater food webs and community structure
Vertical structure of metagenome, transcriptome, proteome
Trophic networks
Changes in community structure with depth and aggregate age
Regional temporal variability relating to biological C pump

Methods development
Insitu methods development

Metabolic theory and allometry — Inverse allometry
Explaining trophic interactions
Inverse allometry (small eating big)
Protozoan grazing on diatoms/microzooplankton

Depth varibiabiility integrating euphotic and mesopelagic
Role of small organisms (non-diatoms) in export
Control mechanisms, populations, export
Varibility with depth, mixed layer, lower euphotic, mesopelagic
Deep water food web effects on export
Export efficiency mediated by food web interactions
Connection beytween surface community structure and export

Rheological properties of seawater
Changes in viscoelastic properties of seawater controlling trophic interactions

Microbial communities on metazoa

POM <-> DOM
Food web controls on POM vs DOM export
POM<->DOM transformations
biological controls in transforming organic matter lability: labile-> recalcitrant, POM <-> DOM
Change in attached vs free living microbiome as organic matter is transformed

Episodic events
Longevity of episodic events
Episodic blooms events
Causes of ecosystem episodic events affecting export

Parasites — Role of parasitism in the biological pump
role of parasitoids/parasites
Parasites and commensals of gelatinous plankton and higher trophic level organisms
Does parasite increased trophic transmission alter energy flows in pelagic foodweb
Parasite controls on export
Contribution of parasites to respiration of C in mesopelagic
Do parasites structure zooplankton community
How much energuy flows to parasites
Do parasites influence DVM?
What is the role of parasitoids and virsues in structuring phytoplankton community
Are parasitoids common in zooplankton

Microbial interactions
Microbial metazoan interactions: integrated food web flows
Synergy between microbiota and zooplankton

Mixotrophy
Mixotrophy vs classical auto and heterotrophic contributions
Mixotrophuc interactions
Mixotrophy

Viruses — virus ecology
Viral shunt and controls on organic matter export
Controls on triggering viral lysogeny to lytic phase
Viral adaptive genes

Indicartors of community structure
what are the indicators of community strutcure for export
Impacts of community structure and trophic interactions within aggregates for the strutcure fo free communities
What are the metric of community structure that are most important for BCP
Does temperature influence community strutcure
Nutrient limitation and controls of phytoplankton community structure

Role of larger consumers — Metazoa —
How are fish related to carbon export processes
Metazoan consumption and behavior
Role of higher trophic levesl for export
Repackaging and consumption by fish

Symbioses
Symbioses
Symbioses in the mesopelagic

Ecology of gelatinous zooplankton — Jelly
Jellies
Fate of jellies
Gelatinous filter feeders and repackaging
What eats a gelatinous zooplankter
Gelatinous organisms as hosts for parasites commensals
Jelly-microbe interactions
Gelatinous zooplankton community structure
Jellies and DVM biogenic mixing
Role of large zooplankton like salps for export
Adaptation of the gelatinous bodyplan
How much PP is converted in gelatinous biomass

Role of complexity and diversity — Food web complexity — Linking food web structure to sinking flux
End-to-end community structure
How can food web structure be paired with flux regime
Do changes in community structure alter pathways in predictable ways?
How does biodiversity influence productivity
Food web complexity and export efficiency
How does foodweb structure determine flux of non-sinking organic matter
How many different food web "types" are needed over a year to determine a site?
How many ecosystem states describing foodweb structure and flux do we need
Which food webs increase flux on non-sinking matter?
Heterogeneity in microbial communities
Growth efficiencies within food web

Food web interaction — Predicting flux from community
Which functional groupings best describe simplified food web structures
Predicting flux/export from community structure
Which food webs typically promote flux by sinking particles
Export from simple vs complex food webs
Contribution of particle eating meatzoans to flux attenuation
Which food webs are responsible for high flux attenuation
Which type of trophic interactions promote flux
How does food web structure determine flux by gravitational sinking

Chemical signalling
How specific is chemical signalling to particle colnization and consumption

Higher trophic levels — ecosystem controls — Food web inteeractions
Competition
Top-down control vs bottom-up
Are there cascading effects of higher trophic leels in the mesopelagic
Bottom up vs top down control
Do higher trophic levels matter?
Predation
Allelopathy
Is export driven by well-defended prey

Phenology
Changing phenology and export
Life cycle changes
Match-mismatch (pp/zp) and particle export

Material transport through food webs
How do changes (in time and space) in food webs influence organic matter reactivity
Tracing particulate material (labile and refractory) through foodwebs

Temporal scales — small scales — episodic foodweb dynamics — spatiotemporal variability
Spatial and temporal varibility
What triggers episodic imbalances between growth and removal
Mixing and non steady-state growth
How do nutrient input events ramify through foodwebs
Small scale processes with global impact?
Mixing and chaos affect species interactions

Climate impact
Impact of climate driven community shifts on export

Gelatinous zooplankton
Role of gelatinous zooplankton in export
Role of gelatinous zooplankton
What is the role of gelatinous zooplankton
What is the magnitude of gelatinous zooplankton contribution to particle export

Roles of different consumers
Mesozooplankton vs microzooplankton
Contributions of different taxa/groups to remineralization (macrozoop/microzoop/bacteria)
How trophic interactions affect particle size distribution and composition
How do different modes of feeding influence particle stoichiometry/composition

Mixotrophy
Quantification of mixotrophy for nutrient and energy flow
Mixotrophy
Does mixitrophy make a difference in magnitude of export
Does mixotrophy enhance export

Different microbial communities
What proportion of microbial food webs are particle-localized

Parasitoid conributions
Quantification of parasitoid abundance and modes of reproduction
Role of viruses

Role of individual components of food webs
Contribution of picoplankton to export
Molts, carcasses importance for flux
Role of diapause (lipid pump, microbial environment etc.)

Significance of upward flux
Deep sea community contributions to upward particle flux