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

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Executive Summary

The net transfer of organic matter from the surface to the deep ocean is a major characteristic 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 between 5 – 12 Pg C yr^{-1}. This material can be exported as dissolved or particulate material, 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, but also our inability to accurately represent, or even include, all relevant processes (sometimes for legitimate computational reasons). Predictions will remain uncertain without knowledge and suitable representations of the relevant 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 (in order of importance):

(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 to emerge 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:* Recent work (e.g. Guidi et al., 2016) has revealed an urgent need for integrative studies that connect broad, end-to-end food web characteristics to export and export efficiency. Such studies might be able to identify, novel and as yet unquantified pathways to export and new food web components that regulate or constrain export. Little is known about the effects of alternative physiological or life-history strategies on organic matter export. Studies that quantify Quantifying the effects of mixotrophy, symbioses, or crustacean vs. gelatinous zooplankton-dominated food webs on export were suggested as examples of studies in areas that were thought to be important, but where we currently have little knowledge.

(ii) *Trophic interactions, behaviors, and metabolism of consumers:* Trophic interactions and animal behavior are important controls on organic matter export. Production of sinking fecal pellets by zooplankton and fish plays a key role as these particles often sink rapidly and can have a dramatic effect on export. Consequently, improved understanding and measurement of predator-prey interaction rates and feeding modes is needed. Organisms previously not associated with carbon export such as radiolarians and foraminifera 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. Viruses are extremely abundant and transfer material between particulate and dissolved organic matter pools, thereby affecting the export of these components. The role of jellyfish in consuming and repackaging organic matter, as well their own contribution to export through “jelly-falls” remains poorly quantified, even though recent estimates suggest it is important (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. As a result, our predictive understanding of the fate of organic material has substantial uncertainties. Improved technologies should facilitate investigations into how remineralization and consumption are organized within food webs, and how this varies in space and time. The flux of sinking organic matter generally decreases with depth, but our understanding of the biological processes and organisms responsible for this is lacking. 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, and studies of the effect of vertical migration on export are also needed. Microbes attached to sinking particles excrete extracellular enzymes that solubilize the organic matter allowing the microbes to consume it. The biotic and abiotic factors controlling the relative importance of these processes for export need further study. The export and remineralization of different elements will vary depending on how they affected by different biological communities. For example, 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 organic matter pool and the particulate organic matter pool. 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 through the action of microbially produced ectoenzymes that solubilize particles. Fibrilar macromolecules released by microbes can abiotically form nano- gels that can possibly be incorporated into larger aggregates whilst nano and micro-gels have been hypothesized to be the precursors to transparent exopolymer particles (TEP). We have only a limited understanding of these processes and their consequences for TEP dynamics and the interactions of dissolved and particulate organic matter. Key to understanding these processes is the need for measurements of transformation rates between dissolved and particulate pools.

(ii) *Physical and biological controls on aggregate and TEP dynamics:* Aggregate formation has long been known to be important for export. However, most research on aggregate formation has focused on the physical processes or particle collision and the production of aggregates. Biological processes such as grazing by zooplankton not only remove particulate material, but also produce new particles with different densities and sinking speeds, thereby affecting export in different ways. Microbial processes can produce TEP, thereby potentially enhancing aggregate formation, as well as solubilize and consume particles. Understanding the factors that control the relative importance of the physical and biological processes affecting aggregation and disaggregation of particles, and marine snow formation emerged as an important research priority.

(iii) *Particle composition and sinking speed:* Attempts to develop simple, universal relationships for particle sinking speed have been generally 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: one example being, how does particle composition (e.g., TEP and mineral content) or age affect particle sinking speed?

Variability in space and time was the third broad research theme identified at the workshop. In particular, an understanding and quantification of biological processes leading to episodic events was felt to be a priority research area. Time-series and satellite measurements provide both localized and global views of production and export. However, time-series measurements suggest export can occur at scales 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. This will require creative methodological developments and observational efforts, including integration of remote and autonomous sensing platforms with shipboard sampling and experiments. Although episodic events can be associated with physical features such as fronts and eddies, biologically-driven episodic events (e.g., salp blooms, jelly-falls, resting cyst formation) presumably contribute to organic matter export, but are largely missed using conventional sampling methods. An improved understanding of the organisms responsible for these events, including their life cycles and the associated processes underlying 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 those of 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 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 of this crucial feature of global biogeochemistry. These gaps reveal themselves in our general inability to balance biogeochemical budgets in the mesopelagic, geochemical and sediment trap derived estimates of flux that differ significantly from each other, the lack of accurate models of global carbon export flux and attenuation with depth, and the range of model predictions for how the biological pump will change under a changing climate.

The ideas presented here have the potential to address these issues, go beyond them, and significantly transform our understanding of the biology of the biological pump. For example, 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 (for understanding nano-gel formation from precursor macro-molecules), network theory (for understanding and analyzing large data sets), and stochastic models (for understanding episodic events), to name a few, 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 go a long way to transforming our understanding of the biological pump by providing a solid base of reliable observations that any theory or model will have to agree with, and that observations of other aspects of the biological pump can confidently build upon.

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

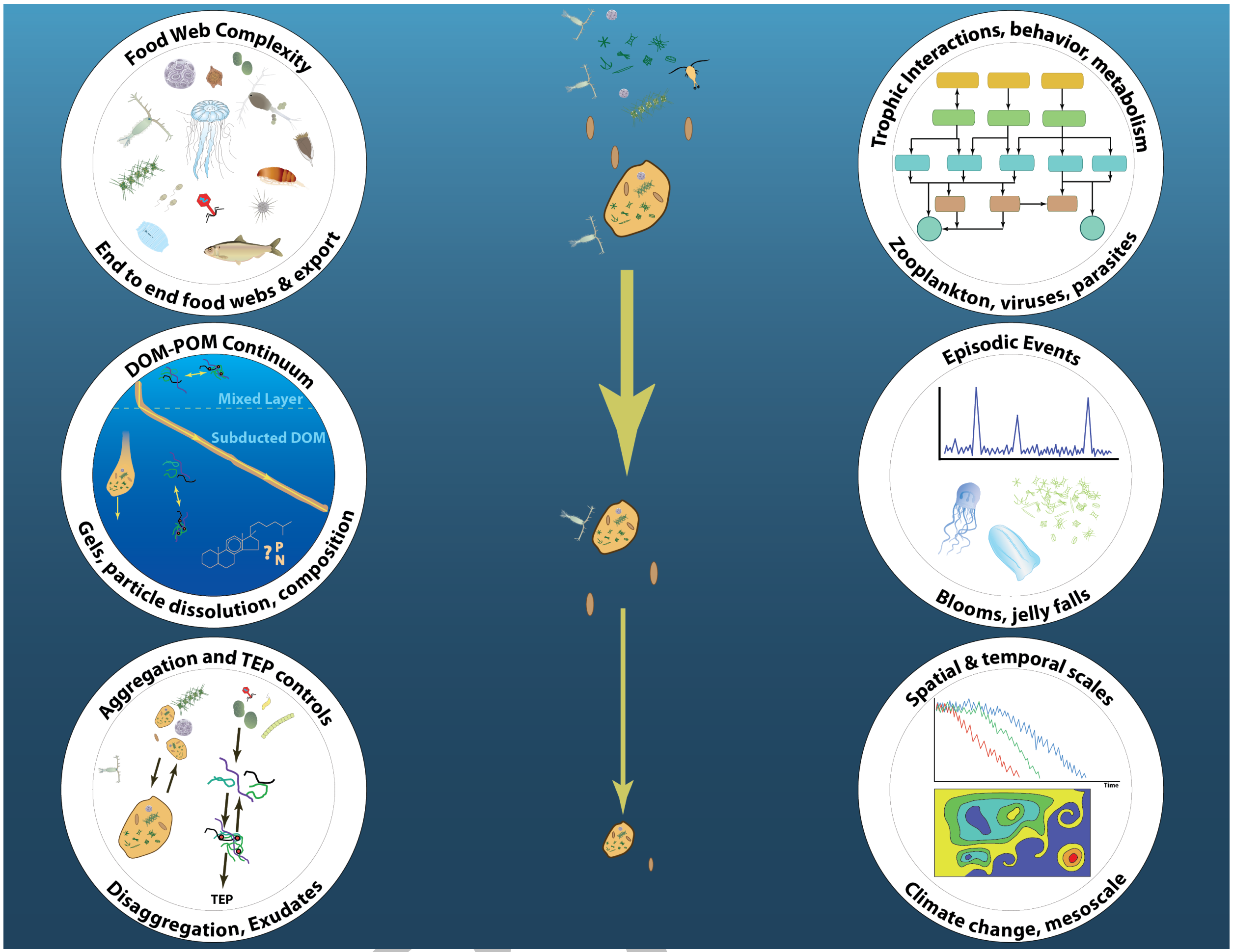

Figure 1. A schematic of the standard view of the biological pump in the center with representations of some of the high priority research areas identified in this report. In the standard view, phytoplankton in surface waters are consumed by zooplankton or form aggregates with other cells and fecal and detrital material. These larger particles sink and are degraded by biological activity as the settle through the water column. Research into food-web complexity and trophic interactions can identify and quantify new export pathways. Studies into the DOM-POM continuum map and quantify DOM subduction and composition, and the transformations between DOM and POM. Understanding and quantifying the controls on aggregation, disaggregation, and TEP formation will improve predictions of POM export. Studies on 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 covering 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 10 distinct priorities (Fig. 2).

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).

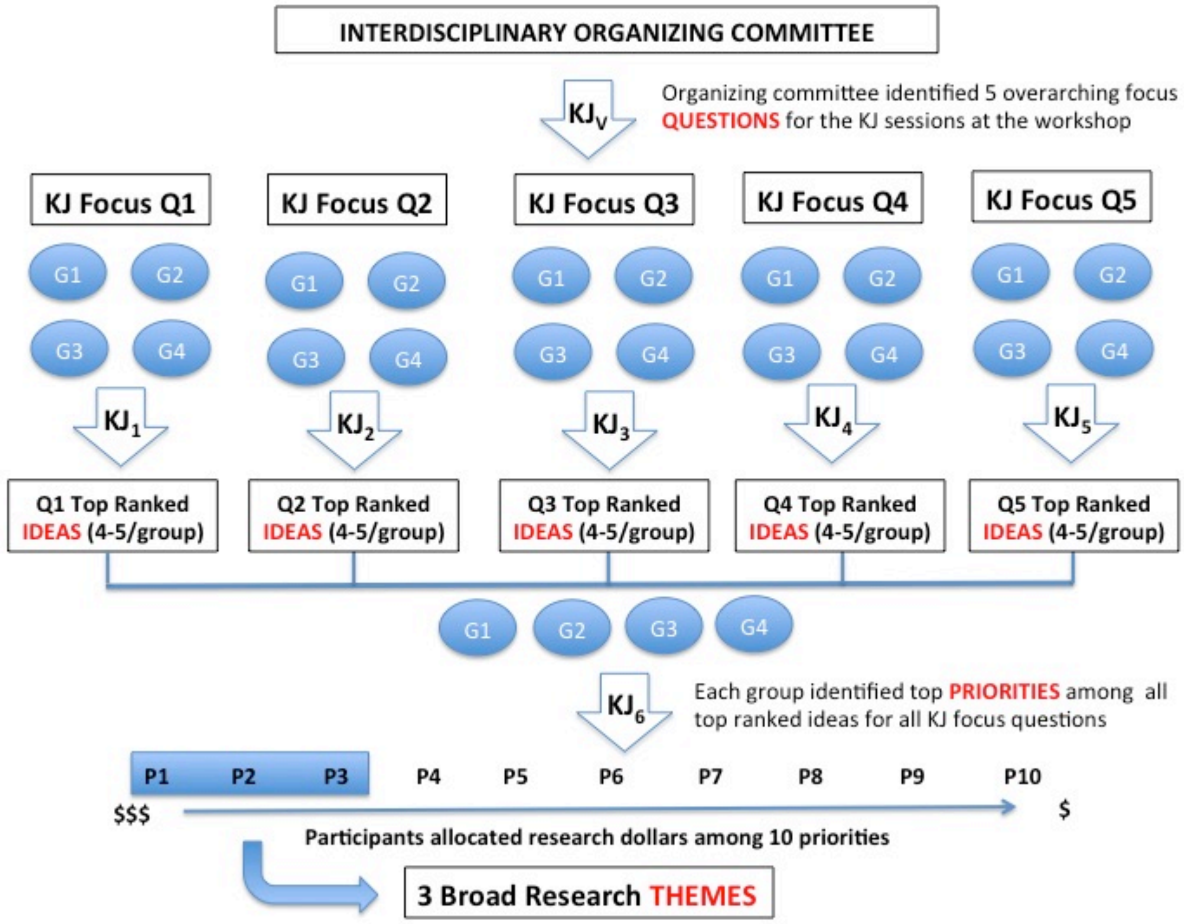

Figure 2. Flow chart demonstrating the use of the KJ technique during the workshop; KJ_v refers to the virtual KJ session that was used by organizing committee members prior to the workshop to identify KJ focus questions. There were five KJ focus questions (listed above) and workshop participants were 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 3 top priorities for each group (for a total of 12 priorities). Finally, individual participants were given an allotment of money to invest in the final 12 priorities, resulting in the final three research themes.

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 8 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 raised by the workshop participants and related to that topic.

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 into 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, 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 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, 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 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 seawaters 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 in 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, 2013). Such results may reflect underestimation of vertical flux based on sediment traps due to the importance of dissolved organic matter (Carlson et al., 2004), spatial heterogeneity in export (subduction features), animal falls and migratory losses not measured by traps, poor trapping efficiencies of sediment traps, or spatiotemporal decoupling in 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 or particles, rates of and controls on enzymatic degradation of organic matter, and how the stoichiometry and energy content of available substrates influences 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 simple view does not include trophodynamically complicated processes such as mixotrophy, whereby organisms will consume organic matter for nutrition and energy, and also actively consuming inorganic nutrients (including carbon) and obtaining energy from harvesting of sunlight or oxidation of reduced inorganic substrates (Zubkov and Tarran, 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 in 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 slower-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 requires 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 fast 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 what animals prey on gelatinous zooplankton, the role of gelatinous zooplankton as hosts for parasites, and interactions between jellies and microbes (i.e., production of mucus or DOM by jellies supporting 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, there are uncertainties remaining that affect these estimates that were highlighted in 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”, exporting 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 compared to fish active transport, and even more broadly the overall contribution of these higher trophic levels to export via the biological pump. 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. However, 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 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. It is furthermore uncertain 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. The contribution to the biological pump from the downward transport of non-sinking carbon via subduction is largely unconstrained, both globally and regionally (Passow and Carlson, 2012). 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 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 suggestions addressed 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 (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 help cast a light on biological processes that consume and transform POM and DOM.

Suggested research areas for this topic include:

- TEP and micro-gel formation
- 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 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.

Most research on aggregation has concentrated 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, though 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 leading to the disintegration of aggregates, or whether the bacterial activity increase the cohesiveness of aggregates, 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 depths are often cited to be of the order of 100 m d^{-1}, but for some particles can be an order of magnitude higher. What is more, 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 piecemeal knowledge 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 (for example, 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?
- Relationships between phytoplankton taxa and particle composition 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 in 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, for example 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 of 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 fresh 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 from the 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 allowed advances in 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 felt that there is a 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 (micron to cm scales) to near-basin scale blooms (10s of km, 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?

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* Journal, 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 2013. Annual net community production and the biological carbon flux in the ocean. *Global Biogeochemical Cycles*, 28:14–28.

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.

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*, 15:993-1018.

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

Omand M, 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.

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 D, Buesseler K, Behrenfeld M, Benitez-Nelson C, Boss E, Brzezinski M, Burd A, Carlson C, D'Asaro E, Doney S, Perry MJ, Stanley R, Steinberg D, 2015. EXport Processes in the Ocean from RemoTe Sensing (EXPORTS): A Science Plan for a NASA Field Campaign.

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 University	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 A. 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
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)

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 zones
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: KJ3: 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 conribútions
- 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