Notes from the Twilight Zone

A US-JGOFS Workshop

San Antonio, TX, U.S.A.

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Introduction

These are notes that were taken by me (Adrian Burd) during the workshop. As such they represent an idiosyncratic view of what occurred and what was said and retain some of the feeling of a set of notes in that "language sometimes abbreviated". They should be viewed as an aide memoir rather than a verbatim record. I hope that I've not misrepresented anyone's remarks, left anyone out or misattributed comments. If anyone notices such egregious errors, please get in touch with me and I'll correct them, that way all participants will have a reasonably accurate record of what was said and what occurred. Note that more detail for some of the talks can be found on the Workshop website: http://usjgofs.whoi.edu/mzweb/midwater.html .

The notes are structured around the talks and topic discussions. Talks are given according to speaker and which of the four topics (Particles, Bacteria, Zooplankton, Models) they fitted in. Discussions that followed each talk are included along with attributions by initials (in a few cases the discussion moved so fast it I was unable to figure out who said what – if anyone notices omissions please let me know). Notes on the discussions that followed each of the half-day of talks are also included. At the end, I've included notes on the last day of discussions as well as some useful references that people have given me.

Overview

George Jackson

- Vertical organic matter flux decreases with depth − this is what we want to explain.

- Most of the decrease occurs in the upper 1000 m

- Present descriptions of remineralization are regression-based and do not include biological processes.

- Estimates of integrated respiration can satisfy both the bacterial demand and the zooplankton demand separately. So both of these communities can account for the change of flux separately. This is indicative of our state of understanding of the system.

- Particle dynamics is important: particle size and mass determine particle sinking speeds. Also accounts for non-biological mechanisms for bringing particles together.

- There currently exist different models: Banse (for Panama Basin), Grant (zooplankton), Armstrong et al. (ballast − particle composition controls degradation), Dadou, Jackson & Burd.

- Animals recycle different components of detritus differently; c.f. Nick Fisher's work on rates of assimilation for material within cells vs. material on cell wall.

- Zooplankton biomass and metabolism decreases with depth (Childress)

- Not only particulate, but also dissolved material is exported.

- But, we do know something which can constrain what is occurring: for example we know something about the radio-isotope signature and changes of particle composition and age (Druffel); we also know something about calcium carbonate

dissolution which can also say something about the biology (Milliman et al).

- There are lots of different pieces of the puzzle that need to be brought together. For example, what is the relative importance of bacteria and zooplankton in altering the particle flux? How does seasonality change things? What about changes in species composition in midwater communities? Which zooplankton are the vertical migrators? How do zooplankton feed in these regions? What controls the bacterial population? What effect do bacteria have on particles? How much metabolism is fuelled by DOC?

RN: What about attached vs. free-living bacteria? Free-living bacteria are responsible for most of the respiration.

GAJ: But attached bacteria are the ones that degrade the particles, so they must be providing material for the free-living bacteria to consume?

WB: Particles are not just carbon.

GAJ: Carbon is one of the elements we're interested in determining mineralization and for providing a resource for deep-water communities.

RJ: Look at the carbon cycle: processes that send nutrients back to the surface waters accelerate primary production by recycling. Thus one can think of biology as recycling and stimulating primary production, whereas physics is responsible for the interception of falling material (*i.e.,* falling primary production).

GAJ: What are the timescales for the various processes involved?

Particles

Avan Antia (Particle Flux Overview)

- There are regional differences in depth profiles of mineralization − based on annually averaged sediment trap data from a variety of stations in the Atlantic (mostly N. Atlantic) (Antia et al. 2001).

- Export ratios (percentage of primary production leaving a specified depth horizon) shows considerable variation in the upper 2000 m, but significant constancy at 3000 m where export ratios are 1.5-2%. This indicates that the Twilight Zone (TZ) can intercept widely varying amount of primary production.

- Regions that exhibit a steady annual flux tend to have lower export ratios than those regions where the flux is pulsed.

- There is a relationship between sequestration flux and winter mixed layer depth. (NEED TO DEFINE SEQUESTRATION FLUX)Sequestration flux is greatest at low latitudes where the winter mixed layer depth is the shallow. This is the case, even though the biological pump efficiency (measured using rain rates i.e., POC:PIC) is higher at larger latitudes (Antia et al., 2001). So the location of the winter mixed layer in some way determines the relative mineralization of organic and inorganic carbon. Climate driven changes in the depth of the winter mixed layer will alter POC:PIC ratios of sequestration fluxes in ways that are not directly related to changes in nutrient inputs.

- Particle size distributions change with depth and with time. There is an increase in

large particles just before a spring bloom (this may be a way for particles to rapidly transit the TZ without being affected since the particle sinking rates will be greater and so they can traverse the TZ more rapidly). There is an increase in smaller particles at the thermocline and deeper down, larger particles tend to be more numerous.

- The material that is settling appears to be composed of TEP (transparent exopolymer particles) and a few component particles (this is from samples in upwelling regions). 40-50% of the organic carbon in sinking POC is TEP. BUT, below the TZ, very little of the organic carbon is in the form of TEP. This indicates that the composition is preferentially changing.

- Repeated aggregation and disaggregation of particles can convert them from labile to more refractory.

- Sediment traps have problems. In particular, it is frequently difficult (impossible) to actually identify what is in the trap.

- Very little is known about the micro-zooplankton communities and how they affect the particulate flux and the transformation between POC and DOC.

SW: Doesn't see a lot of TEP in samples, but this may be an artifact. Measurements are tricky. Bulk organic carbon content tends to remain fairly constant (percentage-wise), but this is only on 4 samples.

LS/SW: Interstitial waters within particles maybe part of the flux , but they would not be counted as particulate.

GAJ: What are the important mechanisms?

AA: What determines the interactions between the various fractions (dissolved, particulate etc.). The breaking up of particles by organisms? Repeated aggregation and disaggregation?

Will Berelson (Particles)

- Not all material is the same. Examine the ratio of biogenic Si to organic C in sediment traps and how this ratio changes with depth.

- There is a systematic change in slope between less siliceous and more siliceous systems. This may be due to changes in the settling speeds of particles with different compositions -- carbon-rich particles sink more slowly.

- Regions with higher C export have curves with higher curvature. The more a region exports, the more material "goes away" in the upper ocean. As export production increases, the fraction of exported carbon lost in the upper 1000 m also increases.

GAJ: Particle shape may also account for some of the changes in particle settling velocity. For example, diatoms with spines tend to settle slower.

RR: Can perhaps explain changes in Si:C ratio through community changes in the food web.

KS: Cannot ignore temporal changes: pulses might drive the structure of the community.

WB: Results on timescales more applicable to climate change.

RJ: Margins (where diatoms tend to be more numerous) can be more efficient at getting

material to the bottom.

AA: Diatoms and dissolution kinetics vary widely, and one must take care in comparing regions and times.

Mike Bacon (Particles)

- Sediment traps are useful, but have problems. Use radioisotope information (especially thorium) to estimate fluxes instead of sediment traps. Thorium deficits relative to secular equilibrium are explained by losses to particle flux. Note that, for depths greater than about 200 m one is pushing the data since there is a new equilibrium established and the changes in Th concentration are small relative to the background concentrations.

- Using particle composition relative to Th (for example to get carbon on particles > 53 μm) gives flux components, such as POC. It is assumed that the particles used to determine composition represent the average sinking particles (this is a crucial assumption). Using thorium is a way to convert concentration measurements into estimates of particle flux.

- Using this method for EqPac data, shows agreement with Martin curve

- At Bermuda, at a depth of 3200 m, collected flux accounts for approximately 70% of the overhead production; roughly 30% removed by lateral transport. But, there are large ($\pm$ 50%) seasonal swings in flux of 230Th. These are correlated with mass flux variations. The variations on a seasonal timescale result from aggregation/disaggregation or repackaging of material.

- These changes are too large to come from production in the euphotic zone and so must come from mid-water, most likely from re-packaging of particles.

DS: What is the difference between C/Th on different particle classes? For example, some of the high fluxes result from salp fecal pellets. Does a salp fecal pellet have a different C/Th than other types of particle?

NF: C/Th should be lower for fecal pellets generally than for diatom/phytoplankton aggregates.

AA: Can one use different isotopes to look at different particle size classes?

MB: Yes, use three Th isotopes for example.

Wilf Gardner (Particles)

- Compilation of 15 years of transmissometer data from WOCE, JGOFS, SAVE etc. Data include basin-wide transects. See http://www-ocean.tamu.edu/~pdgroup/index.html

- Beam cp data correlated with POC

- Use satellite data at 555 nm to correlate with POC leaving top 30 m.

- Transmissometer measures particles < 20 μm, can use other data (e.g., Ian Walsh's camera systems) to get larger particles

General Discussion -- Particles

GAJ: What are the roles of organisms, TEP, silica etc. in determining particle flux? Is there

a relation between seasonality/regionality in particle flux and the organisms? What about the role of repackaging, either biologically or through aggregation and disaggregation?

SW: A lot of what we collect is collected operationally. Are we seeing the real thing, or is what we are seeing partly an artifact of our measurements? What is it that we are describing?

DI: Where are things happening? At the surface or in the midwater or both?

KW: What is the role of the organisms? What happens in the surface mixed-layer (and the midwater) to affect what is falling out the bottom? What is the role of community structure in these different environments? How do the mid-water organisms respond to what is falling down?

WB: Are the organisms controlling the sinking velocities of particles and the kinetics of their transformation? What are the properties of particles that we should be concerned with? Size distribution, chemical composition, density, lability, morphology.

SW: We don't have biomarkers for the processes we are interested in. For example, we cannot tell using a biomarker whether a particle has been grazed upon or transformed by bacteria.

NF: Perhaps there are radioisotope markers?

RR: Mechanisms affecting particles in the TZ are essentially the same as those affecting particles in euphotic zone. We should perhaps concentrate on what is unique about the TZ that makes it distinct from the upper ocean.

RJ: A good idea to examine timescales appropriate for climate change. In addition, might also consider measuring export with respect to the deep mixed layer rather than shallower depths. If this is done, then the margins become more important

KB: How good are the mechanistic predictions of flux from the euphotic zone? How accurate are these predictions? Need to know this since this is what drives the deeper communities.

AA: Particularly important are seasonality and episodic events in primary production.

DS: There are troubles with sediment traps (but they're one of the few games in town). Neutrally buoyant traps collect different amounts than tethered traps.

RL: The mesopelagic is inherently difficult to study − maybe good to move away from the margins so as to simplify things.

RJ: If there is a need to link changes in flux to climate, then the margins are needed. The margins are actually simpler than one might think.

Bacteria

Craig Carlson (Prokarotes – Overview)

- Bacterial activity and diversity may be driven by the existence of hotspots (e.g., marine snow particles): if so, then the bacterial community will be quite complex. Also shows that bacteria are not passive, but can actively go after organic material

- Organic material can be transported into the mesopelagic by three basic mechanisms: transport on particles; mixing (transport of DOM across isopycnals); vertical migration.

- Observations are that POM decreases by about 75% by 500 m, and by about 90% by 1000 m. Originally thought that this was a result of transformation of the particulate material by attached bacteria. However, measurements of the respiration rate of attached bacteria produced estimates of low production rates for attached bacteria, especially compared with the total bacterial production. This would have indicated a low particle turnover rate.

- The particle decomposer paradox (Dave Karl): sinking particles are a poor environment for bacterial growth. For example, there is considerable abiotic shear associated with sinking particles; also grazing of bacteria by zooplankton.

- Cho & Azam (1988) showed that >95% of mesopelagic bacteria are free-living and that they form about 43% of the POC. What is more, they estimated that bacterial carbon demand could be accounted for by the decrease in particulate material − there are some estimates (Ducklow?) that bacterial demand for organic matter exceeds the local export rate. However, one still has to get the carbon from its particulate form to a dissolved form for the free-living bacteria. Some of this balance may be dealt with DOC being mixed down deeper into the ocean by convective deep mixing (Hansell and Carlson, 2001).

- Care has to be taken since bacterial production is not equivalent to bacterial carbon demand. This is because of the low (<20%) production efficiencies. One reason for this low efficiency is that bacteria keep themselves in a "ready state" to be able to take advantage of occasional food sources.

- Dave Smith (1992) observed higher hydrolytic activity of enzymes on aggregates than in seawater − specifically of proteases and phosphotases. This leads to a conceptual model of the uncoupled solubilization of particles. Particles can fill-up with dissolved organics from this increased enzymatic activity and result in plumes of dissolved organics which in their turn can act as hotspots for free-living bacteria.

- Ploug & Grossart (1999) showed that an aggregate, through sinking, can facilitate the diffusion of O2 through the particle (oxygen can be 9 times higher in a sinking particle than compared with an aggregate on a solid surface). This allows higher bacterial respiration rates and consequently shorter POC turnover times.

- There are some pressure and temperature effects associated with bacteria. Turley et al. (2000) showed that although bacterial biomass and production decreased with depth, cell-specific growth rates increased with depth. It could be that faster falling aggregates do not degrade as fast because the bacterial communities attached to the particles cannot adapt fast enough.

- Not only does bacterial biomass decrease with depth, but also the bacterial community changes with depth. In the euphotic zone, bacteria dominate whereas below euphotic zone archaea dominate. We know very little about the archaea.

- Things we would like to know: better estimates of prokaryotic respiration and growth rates; how does variability in the microbial community structure affect particles and DOM, and vice versa; we need to understand the small scales in order to understand the larger scales.

KW: Are there bacterial aggregates? If so, can zooplankton munch on them?

CC: Some bacterial do produce exopolymers and can get quite clumpy.

RJ: We need to know more precisely how much carbon is moving through the system (we need better measurements of efficiencies).

CC: If production estimates are significantly off the mark, one can tell any story one likes.

NF: What happens to the bacteria? Particularly if they don't eat for a while.

CC: Autolysis, viral lysis, grazing. Phosopholipids in the cell wall will break apart quite quickly.

Richard Rivken (Bacteria – Unpublished Work, do NOT cite without permission)

- Approximately 15-20% of primary production is exported out of the euphotic zone. Most of this is remineralized back into CO_2 by community respiration in the mesopelagic. The amount of remineralization depends upon the size structure of the particles, their sinking velocity, chemical composition as well as on the structure of the mesopelagic food web and the interactions between the food web and the particles.

- Estimate globally what the bacterial respiration is. Although there's uncertainty in the numbers, TZ respiration by bacteria maybe more than can be accounted for by the flux of POC. The missing amount may come from export of DOC.

MF: Are we in a position to make such a claim with the uncertainty that is in the measured values that we have at the moment?

DS: What about zooplankton?

RR: Duarte claims that mesozoan respiration is only 5-10% of the total, a small amount.

Dennis Hansell (DOC)

- DOC accumulates in the surface waters in the tropics because of the stable stratification that is there. In the tropics, typical values are 50 µM at about 250 m.

- This DOC gets exported into the deep oceans − basically DOC export occurs when exportable DOC is present at the time of overturning.

- General decline in deep water DOC concentrations from the poles along the conveyer-belt: 40-50 µM in northern poles, 43 µM in the deep tropical Atlantic, 41 µM in the Southern Ocean and 34 µM in the northern Pacific. There are a couple of inexplicable glitches in the Indian Ocean and Pacific.

- DOC contributes about 30-40% of the AOU in waters of the upper main pycnocline, <10% in the deeper water.

- Annual global export of DOC estimated to be 0.7-3 Pg C y-1, which accounts for about 20% $\pm$ 10% of total export.

- Hardly any data on DON and DOP.

General Discussion (Bacteria)

How do bacteria attached to particles and free-living bacteria interact with each other?

Are the attached bacteria the ones doing the remineralization? What are the relative roles of remineralization and solubilization (breaking apart).

What is the role of hotspots − the concept is somewhat controversial.

What is the role of community structure?

What regulates bacterial numbers?

There is more there than just bacteria − archaea. What is the role of archaea and how do they respond to changes in DOC (both individually and in terms of the community)?

Quantification: direct measurements of respiration and growth efficiencies − for deep bacteria this will require new technologies.

KB: What are the pressure and temperature sensitivities of growth efficiency?

GJ: What is the role of bacterial size (mass & length)? How does bacterial degradation affect particle size/density and thus particle settling rates? If bacterial activity makes things more sticky (because of exudates) would this counter any particle break-up and possibly lead to larger particles? What is the role of bacterial processes in particle aggregation and disaggregation?

Zooplankton

Debbie Steinberg (Zooplankton Overview)

- We actually know quite a lot about marine snow communities.

- Zooplankton are able to transform particulate material. Zooplankton swimming and feeding can breakup large particles thereby increasing the concentrations of suspended material. They can also repackage material into fecal pellets which may have different settling velocities and propensity for remineralization. Zooplankton also excrete dissolved material, thereby transferring particulate material into a form that feeds the microbial loop.

- Zooplankton feed on marine snow and detritus. Detrital feeders include Oncaea, Scopalatum, polycheaete worms, amphipods. Number of zooplankton associated with marine snow increases with particle size (Kiørboe, 2000)).

- Surface zooplankton communities (especially community structure) affect the particle flux at depth. For example, salps produce large (a few mm by a few mm), rapidly settling fecal pellets which can often been seen intact in deep water traps (e.g., at the BATS site at 3200 m) especially during salp blooms (200-600 m-3).

- Feeding structures provide food and housing for zooplankton. Copepods are observed on feeding houses.

- Organisms feeding in the midwater exhibit adaptations for the environment. These include: Elongated midguts which allow for a longer time for food processing [RL:perhaps they act like a long reaction vessel with different enzymes acting in different regions of the gut]. Oncaea in particular has appendages that it can use for holding onto and scraping particles.

- Zooplankton gut analysis shows evidence of feeding on marine snow and other particles. This includes: the presence of "olive green debris" in the gut; the presence of mucous in the gut; the presence of cyanobacteria and small eukaryotes, too small for natural feeding and must have been consumed from detritus; the presence of algal cells (e.g., diatoms) in the guts of non-migrating, mesopelagic zooplankton.

- Swimmers do pose a definite problem for sediment traps and the interpretation of particle flux measurements. Traps at 1000 m can still have a swimmer problem, and it gets worse for shallower traps. Between 10-50% of the organisms may be swimmers, but these are usually removed by hand.

- Zooplankton assimilation efficiencies change with depth. May have assimilation efficiencies of approximately 70% in the surface waters, but for detrital feeders, this can be as low as 10-50%. Note, that when looking at the energy assimilation of organisms, one needs to take care to distinguish between ingestion and respiration.

- Estimates of the percentage of particle flux consumed or remineralized by zooplankton vary from a few percent (Lampitt, 1992; Steinberg, 1997) up to 100% (Banse, 1990; King et al. 1978).

- Vertical migration (i.e., active transport) can be important. At BATS, the biomass in the upper 200 m can double at night. The proportion of a species that migrates is variable − for some species, the whole population migrates.

- The mean gut passage times of strong vertical migrators is longer than that of weak or non-migrators (41-186 min for migrators, 15-30 min for non-migrators). However, with vertical swimming speeds of approximately 100 m h-1, this longer gut passage time will get material to below the euphotic zone, but not really deep. This also implies that migrators are migrating mostly with empty guts. At most, only one gut load gets to depth.

- Active POC flux averages between 1-7% of the passive flux, and can be as high as 14%. Transport of dissolved flux is higher, averaging 23% (14-42%).

- There are some, but few pressure effects. There is some change in respiration with pressure. Above about 800 m there is little effect. Visual predators do tend to show a greater pressure effect.

- Some things that we would like to know: we need improved sampling technology for the mesopelagic; we need biomass and species composition data; ideally, should sample particle flux, zooplankton, and bacteria together in one cruise; we know very little about the micro-zooplankton communities in the mesopelagic; what are the roles of thin layers and hotspots; what are the mesopelagic trophic pathways; we need to quantity zooplankton feeding rates on detritus; we need biomarkers for different repackaging mechanisms; what are the population, community and behavioral responses to changes in particle flux etc.; what are the effects/implications for climate change?

- Bacteria are also attached to copepods and parasites − each is an active migrator in the community.

AA: How much of the particulate material is remineralized from within, and how much from without (by zooplankton feeding for example)?

DS: Hard to separate out the two.

MB: Is flux/filter feeding a workable classification? Should it be more complex/more simple?

RN: What is the influence of O_2? For example O_2 minimum zones. (see KW talk)

??: The mortality rate of vertical migrators is essentially unknown (but see work by Hans Dam). Vertical migrators are really running a gauntlet.

Karl Banse (Zooplankton)

- There is actually more information out there, especially from the Russians (e.g., M.E. Vinogradov).

- At about 1000 m there is a change in the slope of the biomass concentration (mg m-3) with depth. Perhaps this indicates a change in supply and demand?

- Myctophids vertically migrate, and they are not greatly studied in the US.

Karen Wishner (Zooplankton)

- What is the significance of layers? Changes in biomass occur in layers of low O2. The depth of the oxycline can vary by as much as 100 m over time in any particular region. However, the deep biomass doesn't change, even though the surface conditions do change depending on magnitude of biomass and flux.

- There are other interfaces apart from those of low oxygen. Specifically, shear zones are important. Organisms are very sensitive to small gradients.

- Species become adapted to the system. For example, lifestages can be adapted to be either in the zone or in the interface.

- There is a diversity of trophic pathways (Gowing). Herbivory, carnivory, detritivory can occur all in one species! In addition, the flux can feed one component of the system which in its turn can be food for another component of the system. So changes in flux can have implications all round, not just fro those that directly feed on it.

- Changes in particle flux may stimulate population changes such as reproduction.

AA: There is very little known about gut pH [NF: typically 7-8 in copepods]

Nick Fisher

- What happens to something when it dies? How fast does it fall apart? There is a rapid loss of material initially, then it slows down. The rate of release from fecal pellets is slower than that from a corpse.

- Retention half-times for carbon for a corpse (algal cell): 1-2 days at 18°C, 5 days at 2°C. For a fecal pellet, the corresponding half-times are 15 days at 18°C and effectively infinite at 2°C.

- We can explain the relative rates of material loss of elements from phytoplankton cells by noting where the elements are located in the cell. If they are inside the cell, loss rates are similar to those for organic carbon. If the elements are on the cell wall, they tend to stay there.

- Assimilation of elements by zooplankton depend on where that element is on the cell. If inside the cell, then the element gets assimilated whereas what's on the cell

wall tends not to get ingested. Therefore, material that is inside the cell ends up getting recycled more, and could have a longer residence time in surface waters.

- Poisons in sediment traps can be bad news in that they produce a rapid leaching of carbon from material, converting POC into DOC (this might be particularly crucial for swimmers caught in the trap). Up to 30-40% of the material can be leached within a few hours.

Richard Lampitt (Zooplankton)

- Playing Devil's Advocate, how sure can we be that zooplankton actually do vertically migrate? Might it be that the signal we are seeing is an artifact of net-avoidance? If not, how much of the signal is due to vertical migration and how much from net avoidance?

- Vertically integrated daytime and nighttime biomasses disagree: daytime biomass < nighttime biomass most of the time.

- Organisms tend to get larger with increased depth, and in oligotrophic waters, the shift occurs higher up in the water column. Why?

- Zooplankton can grab hold of particles to feed.

- The Holocam − Laser Holographic Camera System. 9 ns exposure of 50 l of water. Image resolution as fine as 30-40 μm. Each holographic plate contains 10 TB of data. Can be used for examining 3-dimensional spatial relationships of organisms and particles in situ. Working on selling through WalMart K-Mart and other reputable purveyors of fine quality scientific equipment.

Debby Ianson

- How to model different feeding behaviors? Flux feeding can be parameterized using a detection area and a relative velocity between the predator and prey. Such a formulation impacts the larger end of the particle size spectrum preferentially. Clearance feeding can be parameterized using a clearance rate.

- Zeroeth-order model: includes a food choice (cannibalism) for predators, yields a minimum local flux condition to support the system, adding a vertically migrating component of the zooplankton yields diel variation in the particle flux.

- There is not sufficient coverage of taxonomic or functional groups in available data.

- Can make net-avoidance corrections − these change the parameter fits from the models, but not the profile shape.

- Some limitations include catch efficiency. Also, there are missing size classes, for example between 330 μm and 4800 μm.

Models

Reiner Schlitzer

- Global distribution of dissolved nutrients tells us that biogeochemistry is occurring and these result in major signals. We can use this data to obtain some constraints

on the processes causing these distributions.

- Use a coarse resolution physical-biogeochemical global model. Below each grid of the model at the surface, there is a column and particles fall down this column. Changes in particle flux are modeled by a simple power-law PF=azb with particles being produced in the top two layers of the model.

- The aim of the technique/model is to determine the physics and the parameters a and b given the global distribution of nutrients. A Redfield ratio is assumed for organic matter and the model uses an inverse technique, iterating the solution. The technique changes the physics and the parameters a and b in order to minimize the difference between the modeled nutrient fields and the measured nutrient fields. One pitfall of this technique is that it cannot exclude the possibility of other minima existing. However, the same solution is obtained starting with a range of initial guesses, so there is some robustness to the model.

- The model does a good job of reproducing the CFC distributions − these are not used in the technique and so indicate that the physics, although coarse, is good.

- The global POC export (through 130 m) estimated from the model is 9.6 Gt C y-1 ($\pm$ 1).

- Can use algorithms to get flux from satellite primary production data and compare with the model. The model wants to have more export in the Southern Ocean and less in the North Atlantic than is seen in the satellite images. Could be that the satellite is missing the subsurface chlorophyll maximum and this is upsetting things.

- The model agrees better with the benthic oxygen fluxes than with satellite measurements (c.f. Jahnke).

- Globally, the value of b=0.973 which is larger than the Martin value, closer to the Suess value. There is considerable global variation in the modeled value of b, but curiously, in the VERTEX region, Martin's value is recovered.

- The model is a steady-state model and the biological interactions are included as essentially rate constants (i.e., there is no biological interpretation of the results).

Ray Najjar

- Examine the respiration rate in the shallow (upper 250 m) part of the euphotic zone: the decline in O2 with depth gives an estimation of the respiration rate.

- Community compensation depth (separating zones of net photosynthesis from net respiration) is about 80 m at BATS.

- Globally, there is outgassing of O2 in the spring and summer and ingassing during the fall and winter. Annual mean flux shows ingassing in tropics and high latitudes, outgassing in mid latitudes.

- Consistency between patterns of production and remineralization.

- Redfield ratios between 100-250 m give good agreement for O_2:C, higher than standard for C:N. Could be due to differences in compensation depths for nitrate and oxygen (nitrate is deeper). Integrating between 120-250 m gives better, but still higher C:N. Suggests biological origin for summer drawdown of DIC.

Rick Jahnke

- The biological community in the surface waters stimulates production, only secondarily alters flux.

- Changing the export horizon changes the estimates of primary production.

- Margins are important: coastal systems are generally more efficient

Lars Stemmann

- Do we know enough about rates and processes to predict particle size distributions in the mid-water? Can we predict vertical flux knowing the particle size spectra and the mechanisms?

- Data from DYFAMED JGOFS site. Model includes settling, coagulation, bacteria, zooplankton feeding (flux and filter). Model forced at 100 m with observed size spectrum, attempt to predict spectrum between 100 and 1000 m.

- Particle size data obtained used Underwater Video Profiler.

- Model has size-dependent functions for settling speed, coagulation, bacteria, zooplankton flux feeding and zooplankton filter feeding. Predict the size distribution at depth over time.

- Modeled prediction of zooplankton and bacterial patterns and fluxes consistent with data. Flux feeding was found to be the most important processes affecting particles. Zooplankton can affect particles by reducing the mean size of the aggregates and hence the mean settling speed.

Adrian Burd

- Simple food-web model of the midwater − particle flux, a particle feeder and a predator and bacteria. How do changes in flux affect biological populations and vice versa.

- Regular, periodic changes in surface particle flux transformed into aperiodic changes at depth. Increased bacterial degradation decreases aperiodic fluctuations. Animal motion (vertically) dampens oscillations in animal populations.

- Adding quadratic mortality term changes system dynamics.

Final Day Conclusions

BACTERIA
What are the biggest uncertainties?
- Are particles being respired rather than solubilized?

- How does bacterial degradation affect particle properties?

- Do archaea respond to changes in their environment in a similar way to bacteria?

- What are the differences in regional distributions of bacteria?

- How do the bacteria fit into the twilight zone food webs? What role to viruses play in controlling the bacterial population?

What is crucial to know?
- What is the lability of DOC?

What would you like from the other groups?
- Simultaneous measurements of bacteria, zooplankton and particles.

What technologies would you like to see?
- Simultaneous measurements of bacteria, zooplankton and particles.

- Microbiological techniques to understand how bugs respond to their environment (*e.g.,* genomics, proteomics).

- Techniques to study microbial physiology, possibly in situ.

MODELS
What are the biggest uncertainties?
- Do we have valid, tractable formulations of what is going on?

- What is the physics of the twilight zone?

- How does the oxygen content of the oceans affect particle flux? How are these related and how do they relate to other environmental factors such as temperature?

- There are scale problems − unlike primary production where we can see from satellites what the spatial and temporal scales are, we have very little information on the corresponding scales in the twilight zone.

What is crucial?
- Do the various formulations (*e.g.,* of how flux changes with depth) actually matter for things like climate change?

- Should pursue different types of models (mechanistic, inverse, prognostic).

What would you like from other groups?
- What are the ways that complex processes can be put into models?

- Do model results make sense? Need the input of folks from other areas.

- Dependable estimates of export production.

What technologies would you like to see?
- Inverse models − perfect physics!

- A controlled-volume measurement campaign for inverse models.

- Coupling of inverse and forward models.

PARTICLES
What are the biggest uncertainties?
- What determines particle settling velocity and how big is it?

- How do we measure flux? What can we measure and how accurately can we measure it?

- What are the relative contributions to the export flux of DOC and POC regionally and temporally. What controls them?

- What are the various pathways that carbon can take from particles into other forms?

What is crucial?
- Comparison of inverse approach results and direct measurements.

- Can we relate particle properties to particle flux and the other way around?

What would you like to see from other groups?
- What is the production rate of particles in the twilight zone? Are the particles created there different in any way from those falling from the surface waters?

- How are particles re-packaged in the twilight zone?

What technologies would you like to see?
- Ways of measuring particle flux and particle properties.

- Particle imaging technologies − holocams everywhere! The introduction of the personal holocam.

ZOOPLANKTON
What are the biggest uncertainties?
- What is the biogeography of the twilight zone?

- What is the population dynamics and population response of organisms in the twilight zone?

- Microzooplankon!!!

- Small-scale particle zooplankton interactions.

- How do surface communities affect the flux entering the twilight zone?

- The role of interfaces and zones.

- Passive vs. active transport of material.

What is crucial?
- Food web structure − *e.g.,* who controls bacteria?

- How is carbon transport partitioned?

- The mechanisms and rates of detrital feeding.

What would you like from other groups?
- Biomarkers.

What technologies would you like to see?
- The ability to do physiological measurements (respiration, feeding responses etc.) in situ.

- Gels in sediment traps.

- 3D spatial relationships between organisms and particles (patchiness) − the holo-cam.

- New techniques for measurement of detrital feeding.

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