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# Old and New Perspectives on Zooplankton and Vertical Particle Flux

by

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## Abstract

Our understanding of the relationships between zooplankton and vertical flux of particles in the North Atlantic has matured over the last half century. Evolving from the simple concept of "grazing inhibits sedimentation", the relationship gained additional system-dependent quantitative as well as qualitative dimensions. The "zooplankton" and mediated processes such as production of feces are now recognized to be diverse and pivotal components influencing the distribution of oceanic carbon. New aspects, such as the magnitude of the downward flux of carbon via migrant zooplankton stocks or leaching of dissolved organic carbon from zooplankters and feces in the water column and in particle collectors, have recently received elucidation. This paper sketches the progression of some of the milestones and indicates the most recent developments in the "zooplankton - vertical flux" concept.

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## Introduction

Plankton research relevant to the magnitude of vertical particle flux as influenced by metazooplankton has a long and impressive history, which began with what we may now consider to be amongst the most fundamental concepts in biological oceanography and progressed to newest insights as facilitated by modern technology. With respect to metazooplankton, these investigations may be categorized into four chronological phases which emphasized: (1) pelagic recycling, (2) export production, (3) particle destruction and modification, and (4) zooplankton migration and DOC (dissolved organic carbon) distribution. I shall present a short (by no means exhaustive) historical overview of some of the milestones in this area of research as well as some of the most current findings, which appear to be closing some gaps in our understanding of energy flow in marine systems.

I note that I shall confine this paper to influences of metazooplankton of a size beginning in the upper mesoplankton category (Sieburth *et al.* 1978) and not consider the potentially important effects of small microheterotrophs such as ciliates. Further, as the intention of this paper is to draw attention to the progression in research as related to the magnitude of vertical particle flux, I shall not attend to the various influences of zooplankton on biochemical characteristics of particles. Rather the reader is referred to the articles cited herein, particularly those regarding the biological pump.

## Pelagic recycling

The recycling of phytoplanktonic biomass as mediated by grazing has an inhibiting effect upon vertical particle flux. The first investigations implicating the importance of zooplankton for the vertical flux of particles were conducted over half a century ago with observations that e.g. in the northern North Atlantic there existed an inverse relationship between the size of phytoplankton and metazooplankton stocks, and Braarud (1935) attributed this to grazing. This was no trivial observation but a major insight at its time.

Twenty years later Halldall (1953) and other investigators realized that the life cycles of key zooplankton species were pivotal in regulating these patterns, and these insights eventually led to present-day "match - mismatch" theories of phytoplankton accumulation vs. zooplankton grazing (e.g. Parsons *et al.* 1984). The actual implications for vertical particle flux were at best inferred back in the 1950s. It was not until the 1970s, when sediment traps were beginning to be used more extensively, that the close and inverse coupling of sedimentation of phytoplankton to grazing pressure could be conclusively shown (e.g. Smetacek 1980) and these relationships have been implemented in models in the last decade (e.g. Aksness and Wassmann 1993, Fasham 1995).

Notably, grazing was coupled with not only the excretion of dissolved inorganic components such as nitrogen (Conover and Corner 1968), which could be used to refuel phytoplanktonic primary production, but also with the production of fecal pellets (e.g. Paffenhöfer and Knowles 1979, Dam and Peterson 1988). This proved to be central to subsequent related research.

## Zooplanktonic particles as accelerators of vertical flux

Despite the key sedimentation-inhibiting feature of grazing, in many aspects zooplankton appeared to enhance sinking of particles. Many key components of sinking material were zooplanktonic in origin: this included carcasses, mucous aggregates and especially fecal pellets. Such observations spurred a series of experiments addressing the sinking rates of feces (Smayda 1969, Schrader 1971, Ferrante and Parker 1977, Honjo and Roman 1978, Bienfang 1980, Bruland and Silver 1981, Madin 1982), and the importance of feces as relatively large vehicles sinking at rates of some few to over 1000 m $d^{-1}$ (Deibel 1990 for a summary) was recognized. In particular, the process of interest for flux studies was incorporation of small particles into large packets. Ittekot and Degens (1984) stated, "In short, the sedimentation process in the aquatic environment is biologically controlled. It ensures that even clay-sized particles will reach the deep sea floor within a matter of days, which would have otherwise remained suspended for years.... The vehicles of transport are metabolic products of planktonic organisms like fecal pellets and mucopolysaccharides [mucous aggregates], which are produced in the surface layers of the ocean."

In their conclusion Ittekot and Degens alluded to mucous aggregates, the origins of which were less well known in the early 19080s. Since then, aggregates such as those from oceanic pteropods (see Gilmer and Harbison 1986 for the feeding biology of some pteropod molluscs) have been shown to sink at rates of up to 1000 m $d^{-1}$ (Noji *et al.* submitted - a). Reported in the same paper, mucous aggregates were observed at the seafloor at depths of over 1000 m.

Carcasses of dead zooplankters also may contribute significantly to vertical particle flux. Documentation in the literature is not extensive, as the mode of input to trap material - active swimming of living vs. passive sinking of dead or dying organisms - is often not identifiable and may lead to misinterpretation of trap data (e.g. Harbison and Gilmer 1986). However, Bathmann *et al.* (1991) showed that even in depths well below the stratum of a population of *Limacina retroversa* pteropods, trap material was dominated by the input of shells from this species in late summer 1988 in the eastern Norwegian Sea.

## Destruction and modification of sinking particles

The concept of large rapidly sinking zooplanktonic particles "dropping like stones" to the sea floor seemed to be a good one for a brief period of time. However, it soon became evident that the concept did not agree with most field data on the vertical distribution of fecal pellets in the water column (Krause 1981, Bathmann *et al.* 1987) or their sedimentation rates in discrete depths (e.g. Smetacek 1980, Bathmann *et al.* 1987, Pilskaln and Honjo 1987). In almost all cases, the concentration or sinking rates of pellets nearer to the surface were larger than at depth. This led Smetacek (1980) to state, "The negative correlation between copepod numbers and the ratio of [fecal pellets : copepods] suggests coprophagy..." He further suggested that low rates of pellet sinking contribute to the pool of detritus via disaggregation of the suspended feces.

Coprophagy - the ingestion of feces - became a major theme of research in the 1980s and in grazing experiments several microscopical investigations (e.g. Ayukai 1987) apparently substantiated its existence. Yet it was soon shown that ingestion by zooplankton was not the only process accounting for the field data "anomalies". In the late 1980s in a series of experiments using $^{14}C$-labelled fecal pellets, Lampitt *et al.* (1990) demonstrated that in fact the bulk of fecal material after incubation with copepods was not consumed but fragmented to microscopically unidentifiable detritus - a process they termed coprorhexy. Sophisticated image-analytical techniques later verified the importance of this process for feces "destruction" and pointed out that an accompanying dispersion of the content of fecal fragments - coined coprochaly - led to a reduction in density (Noji *et al.* 1991). Both coprorhexy and coprochaly result in slower sinking velocities or longer retention time in the water column. Notably in 1988 the fragmentation of large sinking particles such as fecal pellets and marine snow was deduced to be a key midwater process necessary to explain depth-dependent patterns of bacterial metabolism (Cho and Azam 1988, Karl *et al.* 1988, Suess 1988), and it was suggested that midwater zooplankters were the key mediators of fragmentation.

## Vertical migration, zooplankton metabolism and distribution of DOC

Much of the research on vertical particle flux with reference to zooplankton was summarized in the late 1980s and 1990s in reviews (e.g. Fowler and Knauer 1986, Longhurst and Harrison 1989, Silver and Gowing 1991) on the biological carbon pump and the special role of zooplankton in structuring marine biological regimes (e.g. Noji 1991, Banse 1995). In these works it was noted that the vertical migration of plankton can also be a factor in vertical flux especially with regard to the excretion of DIN (dissolved inorganic nitrogen) (Longhurst and Harrison 1988). The fact that diel migrant plankton feeding near the surface but excreting at depth, e.g. below a stable pycnocline, could be significant and account for over one-fifth of nitrogen export was reported recently by Dam *et al.* (1995)[2]. The production of DOC by migrant zooplankton may influence carbon distribution in a similar fashion.

Despite the fact that an impressive amount of data and insight was collected regarding vertical flux, in the 1990s scientists continue to be plagued with imbalances in flux budgets. Consequently additional sinks for carbon have been sought (and found), one of the most important of which appears to be the accumulation of DOC in surface waters and export to depth after the main season of phytoplankton growth (e.g. Michaels *et al.* 1994, Carlson and Ducklow 1995; Table I)). The source of this DOC can be phytoplanktonic exudation as well as heterotrophic degradation of particulate organic carbon, much of which may be channelled through feces (e.g. Jumars *et al.* 1989). In fact Urban-Rich (submitted) concluded from her experiments on copepod fecal pellets that half of the carbon content of *Calanus* fecal pellets may be lost after production via leaching.

The vertical zooplankton-mediated distribution of DOC may be effected in two obvious ways: via swimming of the plankters and by sedimentation of DOC containing particles or aggregates. The vertical migration of plankters with reference to DOC was briefly mentioned above and shall be discussed further below, and the reader is accordingly referred to following paragraphs. The sinking of DOC-bearing particles is a topic, which has received very little attention until recently, despite the fact that scientists should have realized (perhaps some did) that the DOM (dissolved organic matter) content associated with sinking particles may be significant. This can be deduced from reports of reductions in POC in e.g. ageing fecal pellets (e.g. Turner 1979) as well as the release of DOC from detritus and aggregates (e.g. Kerner and Edelkraut 1995). Further, reports in the literature, although few, indicate that the DOC content of pellets and aggregates is as large or larger than the POC component (Herndl and Peduzzi 1988, Urban-Rich submitted). Few measurements of DOC have been made on trap material (Khripounoff and Crassous 1994, Körtzinger *et al.*

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[2] In the strictest sense, the vertical flux of DIN, DOC and respiratory carbon - the main topics of research in this section - is not vertical "particle" flux. However, no present-day paper addressing zooplankton and (particle) flux can ignore these features. The fact that they are less tangible may be a reason for their late recognition as being key aspects of vertical "element" flux.

1994). The primary reason for this was that contamination of trapped material with DOC leached from swimmers (U.S. GOFS 1989) was considered to be a prohibitive problem. Consequently, the normal procedure for processing trap samples was and still is limited to the measurement of particulate carbon on filters; a potentially important carbon source - pDOC (particle-associated DOC) - was ignored in models using sediment-trap data. Noji *et al.* (submitted - b) have demonstrated that this can lead to grave errors in estimates of carbon flux as quantified by sediment traps. From statistical treatment of data including not only "standard" particulate biomass parameters but also swimmer biomass and DOC, they have shown that for two annual deployments of sediment traps in the central Greenland Sea over half of the carbon associated with sinking particles was in dissolved form (Table I). This indicates that sediment-trap investigations may be grossly underestimating rates of carbon flux if the dissolved organic component is not considered.

In addition to the new investigations on the role of pDOC in vertical flux, vertical migration of zooplankton is now recognized to be a potentially important factor in flux studies. For JGOFS stations off Bermuda, Dam *et al.* (1995) reported, "If the [respiratory carbon] fluxes due to [vertical] migrators are considered in calculations of export production, the percentage of production exported.... would increase by an average of 25 % for carbon.... Diel-migrant zooplankton should be included in calculations of export...." This was a key insight for carbon-flux researchers.

Further, from unpublished data collected by H.-J. Hirche (Alfred-Wegener-Institute, Bremerhaven) it can be shown that a significant release of respiratory carbon by overwintering *Calanus* copepods in the Greenland Basin occurs. Very recently, these data were included in flux estimates of biogenic carbon by Noji *et al.* (1996), who in a report to MAST (Marine Science and Technology, Brussels) concluded that Hirche's estimates accounted for roughly 3 g C $m^{-2}$ $a^{-1}$, which was twice the annual passive flux of POC in sinking particles recorded at depths of about 200 m (Table I). Thus, in addition to diel-migrant flux, the ontogenetic or seasonal-migrant flux of respiratory carbon may also be a considerable factor in the downward transport of carbon. Certainly in marine systems such as the North Atlantic, in which seasonal migrations are integral to the life cycles of dominant zooplanktonic herbivores, this factor should not be ignored in carbon budgets.

Table I. Annual downward flux of biogenic carbon (g $m^{-2}$ $a^{-1}$) in the Greenland Sea (modified from Noji *et al.* 1996).

| | |
|---|---|
| *New Production* | 57 |
| *Particle-bound carbon measured by sediment traps at 200 m* | |
| POC | 1.5 |
| pDOC | 2.5 |
| Carbonate-C | <0.1 |
| Downward mixing of DOC | 24 - 48 |
| Respiratory carbon of migrant zooplankton | 3.5 |
| *Total* | 31.5 - 55.5 |

## Conclusion

The means by which zooplankters regulate vertical (particle) flux are many (Figure 1) and range from the most fundamental concepts of marine biology to new observations still liable to dissection by peers wielding the scientific scalpel. The accumulation of knowledge on this topic (as for others) can be attributed to three impetuses: historical insight, technological development, and (occasionally) objective reconsideration of accepted concepts. The last presents the biggest problem for scientists.

With regard to metazooplankton and reconsideration of concepts, it was gratifying to read the following from Verity and Smetacek (1996): ".... a major impediment to improved conceptual models is the historic focus on resource-driven or 'bottom-up' factors.... 'Top-down' trophic effects may be equally important in specifying the occurrence of particular taxa, the biomass within

adjacent trophic levels, and the morphology of dominant herbivores and carnivores."
.... as well as the magnitude and character of vertical particle flux (personal *addendum*).

**Milestones in the "Zooplankton - Vertical Flux" Concept**

Grazing Reduces Plankton Stocks
Grazing Reduces Vertical Particle Flux
Grazing is Proportional to Fecal Pellet Production
Fecal Pellets & Carcasses Sink!
Fecal Pellets Do Not Sink!!
Coprophagy
Coprorhexy, Coprochaly
Substrate for Microbes
DOM Production and Downward Mixing
Diel Migrant DIN
Diel-Migrant Respiration
Seasonal-Migrant Respiration
Particle-Associated DOC

Figure 1. Some of the milestones in research on the influences of mesozooplankton on vertical flux.

As has been the case for the last half century, our gaps in understanding the flow of carbon and other essential elements shall slowly be filled (and presumably on occasion emptied again) according to the technology, insight and open-mindedness especially of individuals in the scientific community. The particular case of "zooplankton and vertical flux" exemplifies this. As for now, intensifying research on the rates and processes associated with the production and distribution of DOC as well as respiratory carbon of migrant zooplankton would be much welcomed.

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## References

Aksnes, D. L., Wassmann, P. (1993). Modeling the significance of zooplankton grazing for export production. Limnol. Oceanogr. 38: 978-985

Ayukai, T. (1987). Rate of filtering of fecal pellets by *Acartia omorii* (copepoda; calanoida). J. Oceanogr. Soc. Japan. 42: 487-489

Banse, K. (1995). Zooplankton: pivotal role in the control of ocean production. Ices J. Mar. Sci. 52: 265-277

Bathmann, U. V., Noji, T. T., Bodungen, B. v. (1991). Sedimentation of pteropods in the Norwegian Sea in autumn. Deep-Sea Res. 38(10): 1341-1360

Bathmann, U. V., Noji, T. T., Voss , M., Peinert, R. (1987). Copepod fecal pellets: abundance, sedimentation and content at a permanent station in the Norwegian Sea in May/June 1986. Mar. Ecol. Prog. Ser. 38: 45-51

Bienfang, P. K. (1980). Herbivore diet affects fecal pellet settling. Can. J. Fish. Aq. Sci. 37: 1352-1357

Braarud, T. (1935). The "Øst" expedition to the Denmark Strait 1929. II. The phytoplankton and its conditions of growth. Hvalrådets Skrifter 10

Bruland, K. W., Silver, M. W. (1981). Sinking rates of fecal pellets from gelatinous zooplankton (salps, pteropods, doliolids). Mar. Biol. 63: 295-300

Carlson, C. A., Ducklow, H. W. (1995). Dissolved organic carbon in the upper ocean of the central equatorial pacific ocean, 1992: daily and finescale vertical variations. Deep-Sea Res. II 42: 639-656

Cho, B. C., Azam, F. (1988). Major role of bacteria in biogeochemical fluxes in the ocean's interior. Nature 332: 441-443

Conover, R. J., Corner, E. D. S. (1966). Assimilation of organic matter by zooplankton. Limnol. Oceanogr. 11: 338-345

Dam, H. G., Peterson, W. T. (1988). The effect of temperature on the gut clearance rate constant of planktonic copepods. J. Exp. Mar. Biol. Ecol. 123: 1-14

Dam, H. G., Roman, M. R., Youngbluth, M. J. (1995). Downward export of respiratory carbon and dissolved inorganic nitrogen by diel-migrant mesozooplankton at the JGOFS Bermuda time-series station. Deep-Sea Res. I. 42: 1187-1197

Deibel, D. (1990). Still-water sinking velocity of fecal material from the pelagic tunicate *Dolioletta gegenbauri*. Mar. Ecol. Prog. Ser. 62: 55-60

Fasham, M. J. R. (1995). Variations in the seasonal cycle of biological production in subarctic oceans: a model sensitivity analysis. Deep-Sea Res. 42: 1111-1149

Ferrante, J. G., Parker , J. I. (1977). Transport of diatom frustules by copepod fecal pellets to the sediments of Lake Michigan. Limnol. Oceanogr. 22(1): 92-98

Fowler, S.W., Knauer, G. A. (1986). Role of large particles in the transport of elements and organic compounds through the oceanic water column. Prog. Oceanogr 16: 147-194

Gilmer, R. W., Harbison, G. R. (1986). Morphology and field behavior of pteropod molluscs: feeding methods in the families Cavoliniidae, Limacinidae and Peraclididae (Gastropoda: Thecosomata). Mar. Biol. 91: 47-57

Halldall, P. (1953). Phytoplankton investigations from weathership M in the Norwegian Sea. Hvalradets Skrifter. 38: 1-91

Harbison, G. R., Gilmer, R. W. (1986). Effects of animal behavior on sediment trap collections: implications for the calculations of aragonite fluxes. Deep-Sea Res. 33(8): 1077-1024

Herndl, G. J., Peduzzi, P. (1988). The ecology of amorphous aggregations (marine snow)in the northern Adriatic Sea: I. General considerations. Mar. Ecol. 9(1): 79-90

Honjo, S., Roman, M. R. (1978). Marine copepod fecal pellets: production, preservation and sedimentation. J. mar. Res. 36: 45-57

Ittekkot, V., Degens, E. T. (1984). Tracking of marine dissolved and particulate organic carbon - environmental implications. Neth. Inst. Sea Res. 10: 179-194

Jumars, P. A., Penry, D. L., Baross, J. A., Perry, M. J., Frost, B. W. (1989). Closing the microbial loop: dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. Deep-Sea Res. 36(4): 483-495

Karl, D. M., Knauer, G. A., Martin, J. H. (1988). Downward flux of particulate organic matter in the ocean: a particle decomposition paradox. Nature 332: 438-441

Kerner, M., Edelkraut, F. (1995). Decomposition of organic matter in aggregated seston from the elbe estuary: redox dependency and production of low molecular weight DOC compounds. Mar. Ecol. Prog. Ser. 123: 281-293

Khripounoff, A., Crassous, P. (1994). Particulate material degradation in sediment traps at 2000 m depth on the Meriadzeck Terrace (Bay of Biscay). Deep-Sea Res. I 41: 821-829

Körtzinger, A., Schulz-Bull, D. E., Petrick, G., Duinker, J. C. (1994). Evidence for dissolution of fatty acids in sediment traps: impact on flux estimates. J. Geophys. Res. 99: 3407-3415

Krause, M. (1981). Vertical distribution of fecal pellets during FLEX'76. Helg. Meeresunters. 34: 313-327

Lampitt, R. S., Noji, T. T., Bodungen, B. v. (1990). What happens to zooplankton faecal pellets? Implications for material flux. Mar. Biol. 104: 15-23

Longhurst, A. R., Harrison, W. G. (1988). Vertical nitrogen flux from the oceanic photic zone by diel migrant zooplankton and nekton. Deep-Sea Res. 35: 881-889

Longhurst, A. R., Harrison, W. G. (1989). The biological pump: profiles of plankton production and consumption in the upper ocean. Prog. Oceanog. 22: 47-123

Madin, L. P. (1982). Production, composition and sedimentation of salp fecal pellets in oceanic waters. Mar. Biol. 67: 39-45

Michaels, A. F., Bates, N. R., Buesseler, K. O., Carlson, C. A., Knap, A. H. (1994). Carbon-cycle imbalances in the Sargasso Sea. Nature 372: 537-540

Noji, T. T. (1991). The influence of macrozooplankton on vertical particulate flux. Sarsia 76: 1-9

Noji, T. T., Bathmann, U. V., Bodungen, B. v., Voss, M., Antia, A., Krumbholz, M., Klein, B., Noji, C. I.-M., Peeken, I., Rey, F. (submitted-a). Clearance of picoplankton-sized particles and formaton of rapidly sinking aggregates by the euthecosomatous pteropod, *Limacina retroversa*. J. Plankton Res.

Noji, T. T., Rey, F., Miller, L. A., Børsheim, K. Y., Hirche, H.-J., Urban-Rich, J. (1996). Plankton dynamics and sedimentation. In: ESOP 1 (European Subpolar Ocean Programme 1) final report to MAST/DG XII. Brussels

Noji, T. T., Rey, F., Nortvedt, R., Børsheim, K.Y. (submitted-b). Dissolved organic carbon and underestimates of carbon flux by sediment traps. Nature.

Paffenhöfer, G.-A., Knowles, S. C. (1979). Ecological implications of fecal pellet size, production and consumption by copepods. J. mar. Res. 37: 35-49

Parsons, T. R., Takahashi, M., Hargrave, B. (1984). Biological oceanographic processes. Pergamon Press, Oxford, U.K., 330pp.

Pilskaln, C. H., Honjo, S. (1987). The fecal pellet fraction of biogeochemical particle fluxes to the deep sea. Global Biogeochem. Cycles 1: 31-48

Schrader, H.-J. (1971). Fecal pellets: role in sedimentation of pelagic diatoms. Science 174: 55-57

Sieburth, J. McN., Smetacek, V., Lenz, J. (1978). Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. Limnol. Oceanogr. 23: 1256-1263

Silver, M. W., Gowing, M. M. (1991). The "particle" flux: origins and biological components. Prog. Oceanog. 26: 75-113

Smayda, T. J. (1969). Some measurements of the sinking rate of fecal pellets. Limnol. Oceanogr. 14: 621-625

Smetacek, V. (1980). Zooplankton standing stock, copepod faecal pellets and particulate detritus in Kiel Bight. Estuar. Coast. Mar. Sci. 11: 477-490

Suess, E. (1988). Effects of microbe activity. Nature 333: 17-18

Turner, J. T. (1979). Microbial attachment to copepod fecal pellets and its possible ecological significance. Trans. Am. Microscop. Soc. 98: 131-135

Urban-Rich (submitted). DOC production and carbon cycling within fecal pellets the Greenland Sea. Limnol. Oceanogr.

U.S. GOFS (1989). Sediment trap technology and sampling. U.S. GOFS Planning Report 10.

Verity, P., Smetacek, V. (1996). Organism life cycles, predation, and the structure of marine pelagic ecosystems. Mar. Ecol. Prog. Ser. 1301-3: 277-293