Retention versus export food chains: processes controlling sinking loss from marine pelagic systems

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Key words: export and retention food chains, vertical flux, top-down regulation, zooplankton, global carbon flux

Abstract

The role of export and retention food chains for pelagic-benthic coupling is considered by evaluating different food chain scenarios and processes such as aggregation, grazing and zooplankton-mediated fluxes. The consequences of grazing of primary production by different zooplankton for the vertical export of particulate organic matter from the euphotic zone are discussed. Reference is made to existing data and algorithms regarding primary production and vertical export of carbon from the euphotic zone, both on annual and daily time scales. Examples regarding the role of nutrient addition, removal of pelagic carnivores and zooplankton grazing for vertical flux are presented. It is speculated how variable grazing impact of micro- and mesozooplankton, as well as herbivorous, omnivorous and carnivorous feeding strategies of mesozooplankton could compete with aggregation during phytoplankton blooms and influence export fluxes. It is concluded that the transport of particulate organic matter to depth not only depends on bottom-up regulation as determined by physical forcing, but also on the structure and function of the prevailing planktonic food web. Scenarios are presented which indicate that top-down regulation plays a pivotal role for the regulation of vertical flux. This conclusion may have crucial consequences for future biogeochemical programmes investigating pelagic-benthic coupling in the ocean. The endeavours of many research programmes are dominated by lines of thought where straightforward biogeochemistry and bottom-up regulation is the focus. Phyto- and zooplankton as well as process-oriented research activities have to be the focal point of future research if the current comprehension of export from and retention in the upper layers is going to make distinct progress.

Introduction

Retention and export food chains as well as sinking losses from marine pelagic systems have been ill-defined subjects in oceanography for more than 30 years. After the introduction of the food chain and food web concept in the late 1940’s, it took two decades before trophic relationships in plankton and benthos became the focus of mainstream research. The concept of new versus regenerated production was introduced by Dugdale & Goering (1967), but it had little influence on biological oceanography until the milestone publication of Eppley & Peterson (1979) (Figure 1). Their scheme suggests that the regulation of vertical flux is basically limited by new production, influenced by planktonic organisms and how these regulate the cycling of nutrient and organic matter (Platt et al., 1988). Retention food chains, which recycle organic matter and nutrients, minimise sinking losses while export food chains, which prevail during new production episodes, maximise them.

Mesozooplankton production, grazing and population dynamics have been intensively studied during the entire period of modern oceanography. For example, in the North Sea model by Steele (1974) all phytoplankton is grazed by mesozooplankton, and export to the benthos is comprised only by faecal pellets. This can be explained by the emphasis which has been given to the grazing food chain, essential for the exploitation of marine pelagic resources (Legendre, 1990), and the concern for the development and future of important fisheries world-wide (Iverson, 1991). The relationship between primary production, recycling, and the classical and microbial food web entered more recently
Figure 1. New and regenerated production are based on (a) the supply of the limiting (allochthonous) nutrients from the aphotic zone, by advection, run-off or from the atmosphere (straight arrows) and (b) the recycled (autochthonous) nutrients in the euphotic zone (circular arrows), respectively. New and regenerated production comprise total primary production. Export production is the amount of sinking organic carbon at the bottom of the euphotic zone and reflects new production.

into general consideration (Azam et al., 1983). Azam and coworkers introduced the concept of the microbial loop, by which energy recycled by the microbial community is made available for higher trophic levels of the classical food web through a protozooplankton shunt. Since then, (a) the regeneration of biomass and nutrients by the microbial community, (b) the channelling of microbial biomass and energy into the classical grazing food chain and (c) the role of dissolved organic carbon (Thingstad, 1995) has been a focus of marine research (Figure 2).

The connection between plankton and benthos by means of vertical flux measurements in the ocean was not investigated thoroughly before the 70’s (e.g. Smetacek et al., 1984; Graf, 1992). Surprisingly, plankton and benthos were more or less separate entities in the minds of most biological oceanographers until the late 1970’s. Vertical flux measurements using sediment traps became a major focus in oceanography in the 1980’s (Bloesch, 1996). The current understanding of the regulation of vertical flux is dominated by scientific approaches which perceive vertical flux to be regulated by bottom-up control (Figure 3). The vertical structure of the water column and the dynamics of nutrients, primary production and suspended biomass above the sediment traps are often compared to the resulting vertical flux (e.g. Smetacek et al., 1984; Wassmann, 1991; Bodungen et al., 1995). Indeed, the physical environment determines nutrient availability and hence the particles potentially available for sedimentation (e.g. Wassmann et al., 1991; Kiørboe, 1996). The question arises, however, if the focus on bottom-up control is sufficient to interpret and understand loss of suspended biomass, the vertical flux patterns, and the chemical and biological composition of sinking matter. For a review of top-down control focusing on the role of organism life cycles, predation and the structure of marine pelagic ecosystems, see Verity & Smetacek (1996).

The appearance of automatic sediment traps and long-term moorings in the deep ocean gave rise to substantial data sets of vertical flux with global coverage (e.g. Honjo, 1990; Iteket et al., 1996). A majority of recent vertical flux investigations such as the Global Ocean Flux Study (GOFS) have been dominated by biogeochemical, bottom-up interpretations. The dominance of biogeochemical approaches and the paucity of simultaneous investigations of the export and retention food chains above the sediment traps have provided information about the magnitude and patterns of biogenic fluxes, but little knowledge about the biological composition of the exported material, let alone the regulating mechanisms of export and retention food chains above the sediment traps, or the regulation of vertical flux.

It is now recognised that the link between biogenic particle production at the surface ocean and export to deeper waters is close (Deuser et al., 1981, Asper et al., 1992). It varies seasonally in dependence on physical and biological processes in the upper water column (Peinert et al., 1989; Kiørboe, 1996). The general succession of pelagic autotrophic communities, from diatom-domination following initial stratification to flagellate-domination under nutrient recycling conditions, has implications on organic matter export from the mixed layer. This is due to the role of diatoms in forming fast-sinking aggregates (e.g. Passow et al., 1994) as well as the evolution of the pelagic heterotrophic community and its role in particle export and recycling (e.g. Smetacek et al., 1984; Frost, 1991). The value of long-term recordings of particle flux using sediment traps, and the ability to conduct a wide range of specific analyses on the samples obtained, has greatly enhanced our understanding of the functioning of the oceanic system with respect to material transport between surface waters and abyssal depths. Today we know that vertical export of organic matter is a most important process which regulates (a) the residence time of phytoplankton, organic matter and nutrients in the upper ocean and (b) determines the amount, quality and temporal variation of organic matter supply to the deep ocean and sediments.