Comparison of Marine Copepod Outfluxes: Nature, Rate, Fate and Role in the Carbon and Nitrogen Cycles

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We compare the nature of copepod outfluxes of nonliving matter, the factors controlling their rate and their fate, and finally their role, particularly their relative importance in the carbon and nitrogen cycle. Copepods release dissolved matter through excretion and respiration and particulate matter through production of faecal pellets, carcasses, moults, and dead eggs. Excretion liberates several organic C, N, and P compounds and inorganic N and P compounds, with inorganic compounds constituting the larger part. The faecal pellets of copepods are covered by a peritrophic membrane and have a highly variable size and content. There is less information on the nature of other copepod particulate products. The weight-specific rates of posthatch mortality, respiration, excretion, and faecal pellet production have similar C or N levels and are higher than those of moulting and egg mortality. In general, most important factors controlling these rates are temperature, body mass, food concentration, food quality, and faunistic composition. Physical and biological factors govern the vertical fate of copepod products by affecting their sedimentation speed and concentration gradient. The physical factors are sinking speed, advection, stratification, turbulent diffusion, and molecular diffusion. They influence the sedimentation speed and degradation of the copepod products. The biological factors are production, biodegradation (by zooplankton, nekton, and microorganisms) and vertical migration of copepods (diel or seasonal). Physical degradation and biodegradation by zooplankton and nekton are faster than biodegradation by microorganisms.

The most important copepod outfluxes are excretion and faecal pellet production. Excretion offers inorganic nutrients that can be directly used by primary producers. Faecal pellets have a more important role in the vertical transport of elements than the other particulate products. Most investigation has focused on carbon burial in the form of copepod faecal pellets, measured by sediment traps, and on the role of ammonia excretion in nutrient recycling. Full evaluation of the role of copepod products in the transport and recycling of elements and compounds requires a quantification of all copepod products and their different fates, particularly detritiphagy, remineralization, and integration as marine snow.

1. INTRODUCTION

A pressing issue for the international community is understanding natural and anthropogenic forcing of the nutrient and carbon biogeochemical cycles. The rapidly increasing anthropogenic pressure and the "greenhouse effect" have turned eutrophication and global change into key issues in marine research. To cope with these phenomena, a good knowledge of the sources and sinks of both nutrient and carbon cycles is necessary, because they are

closely linked, as nutrient and light availability drive the biogenic components of the carbon cycle.

The oceans are likely to be a major sink for released anthropogenic carbon on a long-term basis (Wollast, 1991). Marine flora incorporate inorganic carbon into organic molecules, constituting 40% of the total organic carbon production of the earth, and 95% of this production is by phytoplankton (Duarte and Cebrian, 1996). The carbon entering the upper ocean can be transferred to deep waters via three pathways; a physical one (the solubility pump; i.e., the transport of inorganic and organic carbon by deep convection) and two biological ones (the carbonate pump and the biological CO_2 pump; i.e., active and passive vertical transport of biogenic particles; Sundquist, 1993).

The biological CO_2 pump largely relies on zooplankton. Despite the small size of zooplankton organisms (μm to mm size scale), their total biomass is estimated to be greater than that of other marine consumers such as zoobenthos and zoonekton (Conover, 1978). Herbivorous zooplankters consume more than 40% of the phytoplankton production (Duarte and Cebrian, 1996, and references therein) and release into the surrounding water a variety of liquid and solid materials that contribute to the dissolved matter (DM) and particulate matter (PM), respectively. DM and PM can accelerate the vertical transport of carbon and nutrients to deep water. An important process accelerating vertical fluxes of phytoplankton organic matter is the compaction and packing of this matter into faecal pellets by herbivorous zooplankton (e.g., Smayda, 1971; Turner, 2002). The intensity of this process varies according to the faecal pellet and zooplankton characteristics as well as environmental factors, so that carbon and nutrients will either be rapidly transported out of the eutrophic zone or be recycled in their production zone (Turner, 2002). These different fates of carbon and nutrients transported through zooplankton products highlight the "switching" role of zooplankton in the cycle of these elements.

The fact that zooplankton can drive the carbon and nutrient cycles by recycling or export of their products makes study of the fates of these products necessary. Furthermore, zooplankton outfluxes give information on the fates of pollutants, as zooplankters can transport elements and unassimilated organisms (even still living) through the sinking of their products (Fowler and Fisher, 1983). Pollutants can be concentrated in these products and transferred by ingestion to other organisms (Fowler, 1977).

Reviews already exist on zooplankton-dissolved products (Corner and Davies, 1971; Le Borgne, 1986) and on zooplankton faecal pellets (Turner and Ferrante, 1979; Fowler and Knauer, 1986; Fowler, 1991; Noji, 1991; Turner, 2002). The purpose of this review is not to repeat what has been discussed earlier. The information compiled is focused on copepods, dominant mesozooplankters in the world ocean, in terms of both abundance

(55%–95%, Longhurst, 1985) and biomass (up to 80%, Kiørboe, 1998). However, comparison with other groups is attempted, and for processes that are common for all zooplankton and for which available information refers to mixed zooplankton rather than copepods *per se*, the term "zooplankton" instead of "copepods" is used. The analysis of all PM and DM products is based on their nature, the factors controlling their rate and their fate, and finally their role, particularly in their relative importance in the carbon and nitrogen cycles. Note that this role depends on the variability of the zooplankton biomass for which the reader can refer to other reviews (e.g., Mauchline, 1998). An evaluation of this comparative information in terms of needs and cautions to be taken for future studies is also attempted. This can provide appropriate information on the strategy chosen for experimental work and can help in the modeling of ecosystems by identifying the relative importance of all processes implicated, by improving their parameterization, and by defining the forcing factors.

2. NATURE OF COPEPOD OUTFLUXES

Copepods (and other zooplankters) produce DM actively by excretion and respiration (DM passively released from PM is discussed later [Section 4.1]). Respiration produces only CO_2, whereas excretion implicates many products, as detailed below. Excretion is considered here to be the actively released liquid forms of remaining end products of metabolism (assimilated material). Indirect release of solutes, such as from phytoplankton, caused by sloppy feeding of copepods, are not a copepod outflux and therefore will not be discussed. Aspects of metabolic pathways and the anatomy related to excretion can be found in Regnault (1987), concerning crustaceans, and in Wright (1995).

2.1. Nature of excretion

2.1.1. Chemical forms of nitrogen excretion

Ammonia constitutes from 50% to 90% of the total nitrogen excreted by zooplankton (ammoniotelic animals) (Roger, 1978; Regnault, 1987; Le Borgne, 1986; Le Borgne and Rodier, 1997, and references therein). The form of ammonia excreted by zooplankton, whether unionized ammonia (NH_3) or ammonium ions (NH_4^+), is not certain (for crustaceans, see Regnault, 1987). In the following, no distinction is made between the two forms, and the chemical symbol NH_4^+ is used for simplicity. The other

nitrogen-containing substances excreted by zooplankton are organic: urea (e.g., Båmstedt, 1985; Miller, 1992; Conover and Gustavson, 1999) and amino acids (e.g., Gardner and Paffenhöfer, 1982; Regnault and Lagardère, 1983; Dam *et al.*, 1993). Uric acid excretion seems to be exceptional (Regnault, 1987, and references therein), and there is no evidence of excretion of soluble proteins (Corner and Newell, 1967). There is an important variability on the proportion of organic nitrogen in total nitrogen excretion, with authors finding high (Johannes and Webb, 1965; Le Borgne, 1973, 1977) or low proportion of organic nitrogen (Corner and Newell, 1967; Corner *et al.*, 1976; Dam *et al.*, 1993). This variability could be explained by the experimental conditions, such as abnormally high animal concentrations, the temperature, and the animal species (Le Borgne, 1986). Another reason is the transformation of excreted organic nitrogen to ammonia by bacterial activity, which could cause an overestimate (20%) of ammonia excretion (Mayzaud, 1973). In addition, nitrogen in the food content positively influences the percentage of ammonia to total nitrogen excreted (Miller, 1992). Finally, the excretion of some substances can occur occasionally, as has been described for amino acid nitrogen, which can be excreted in "spurt events" of 20–60 min (Gardner and Paffenhöfer, 1982).

2.1.2. Chemical forms of phosphorus excretion

In general, more than 50% of the total phosphorus excreted by copepods is in an inorganic form, as orthophosphate (PO_4) (Corner and Davies, 1971, and references therein; Roger, 1978, and references therein; Båmstedt, 1985). No information was found on the chemical composition of the excreted organic fractions. In *Calanus* spp., the variability of the ratio of inorganic to organic phosphorus excreted relates to the food level (Butler *et al.*, 1970). Temperature does not seem to influence this ratio (Le Borgne, 1982).

2.1.3. Chemical forms of carbon excretion

Excretion of dissolved organic carbon (DOC) by copepods includes the previously mentioned organic nitrogen compounds (i.e., urea and amino acids) and organic phosphorus excretion, as well as monosaccharides and polysaccharides (Strom *et al.*, 1997). The dissolved organic carbon excreted can be refractory as well as labile (Park *et al.*, 1997). Although experiments characterizing the carbohydrates released by copepod excretion have yet to be performed (Park *et al.*, 1997), it is well known that DOC is also liberated from copepod particulate products (Section 4.1.1.4) and has an important role in the DOC pool (Section 5.1.1.2 and Section 5.2.1.1).

2.2. Nature of copepod particulate matter outfluxes

2.2.1. Faecal pellets

2.2.1.1. Peritrophic membrane

Copepods produce membrane-covered faecal pellets (Gauld, 1957; Yoshikoshi and Ko, 1988). In general, a peritrophic membrane is also found in other crustaceans (shrimps, Caridea: Forster, 1953; and euphausiids: Moore, 1931), whereas it is lacking in ciliates, tintinnids (Stoecker, 1984) and gelatinous zooplankton (salps, pteropods, doliolids: Bruland and Silver, 1981).

The peritrophic membrane of copepods (Ferrante and Parker, 1977; Yoshikoshi and Ko, 1988) appears to constist of chitinous microfibrils and a ground substance containing acid mucopolysaccharides and proteins, but its chitinous nature has been doubted by Honjo and Roman (1978).

Several hypotheses exist concerning the role of this membrane. First, to protect the delicate midgut epithelium from damage by hard or sharp particles in the food (Yoshikoshi and Ko, 1988). Second, the peritrophic membrane of copepods would also be a means to compact the pellet content to help speedy removal of indigestible remains of food from the water where the animals are feeding (Gauld, 1957). Third, another function could be to prevent the food from passing through the gut too quickly, allowing the regulation of the intestinal transit and the assimilation rate (Reeve, 1963). Finally, the peritrophic membrane could function as a filter, allowing economic and effective use of secreted enzymes. In any case, whatever the functional significance of the peritrophic membrane, it is not necessarily the same among copepods that have different modes of life. This is shown by the thickness of the membrane: Free-living copepods, which can consume sharp-edged hard diatoms, have thick peritrophic membranes, whereas parasitic ones, which can consume mucus that is secreted by the gills of the marine bivalve host, have much thinner membranes (Yoshikoshi and Ko, 1988).

2.2.1.2. Shape, size, colour, content, and chemical composition

Most copepods have cylindrical pellets, as do euphausiids (Gauld, 1957; Fowler and Small, 1972; Martens, 1978; Cadée et al., 1992; Yoon et al., 2001). Different shapes have been identified for other zooplankters: rectangular (salps), coil and conical (pteropod and heteropod molluscs) (Bruland and Silver, 1981; Yoon et al., 2001), oval (amphipods and ostracods: review by Noji, 1991), spherical, or ovoid (Gowing and Silver, 1985).

The size of zooplankton faecal pellets varies from a few micrometers for the "minipellets" of protozoans and small invertebrates (3–50 μm: Gowing and Silver, 1985) to several millimeters for pellets from large crustaceans (Fowler and Small, 1972) and gelatinous zooplankton (Bruland and Silver,

1981). The size of copepod faecal pellets increases with the ingestion rate (Dagg and Walser, 1986; Huskin *et al.*, 2000). The size of the animal also influences positively the size of pellet (Paffenhöfer and Knowles, 1979; Harris, 1994; Uye and Kaname, 1994); however, this relationship is considered to be weak (Feinberg and Dam, 1998). Food concentration can influence the pellet size, positively (up to a saturation point) (Gaudy, 1974; Ayukai and Nishizawa, 1986; Bathmann and Liebezeit, 1986; Dagg and Walser, 1986; Butler and Dam, 1994; Feinberg and Dam, 1998; Tsuda and Nemoto, 1990; Huskin *et al.*, 2000) or negatively, depending on the food type ingested (Feinberg and Dam, 1998). The quality of food also influences the size of faecal pellets, as shown by different laboratory diets (diatoms, flagellates, dinoflagellates, or ciliates) (Turner, 1977; Hansen *et al.*, 1996a; Feinberg and Dam, 1998) and in field studies (Frangoulis *et al.*, 2001).

The colour of faecal pellets will depend on the diet of the animal: olive-green to brown from diatoms (Feinberg and Dam, 1998; Urban-Rich *et al.*, 1998), bright green from photosynthetic flagellates, pink or orange from heterotrophic dinoflagellates, white from ciliates (Feinberg and Dam, 1998), and red from a carnivorous diet (Urban-Rich *et al.*, 1998).

Numerous studies that have examined the faecal pellet content show that it varies from a fluffy, amorphous material, where phytoplankton cells are only occasionally observed, to a sac filled exclusively with intact, and even viable, phytoplankton cells (Porter, 1973; Eppley and Lewis, 1981; Bathmann *et al.*, 1987; references in the review by Turner, 2002).

The chemical composition of faecal pellets is complex. Several pigments (Currie, 1962; Bathmann and Liebezeit, 1986; Head and Harris, 1992, 1996; Head and Horne, 1993; Head *et al.*, 1996; Stevens and Head, 1998) as well as lipids, amino acids, hydrocarbons, sugars, sterols, wax esters, pigments, trace elements, radionuclides, and alumino-silicate particles have been found in faecal pellets (reviews by Fowler and Knauer, 1986; Fowler, 1991; Turner, 2002). Herbivorous copepods can produce toxin-containing faecal pellets after ingesting toxic algae (Maneiro *et al.*, 2000; Wexels Riser *et al.*, 2003). Considering that the aim of this study is the role of the carbon and nutrients cycle, we discuss only the C, N, and P content of pellets.

The C, N, and P composition (Table 1) depends on food quantity and quality (Johannes and Satomi, 1966; Honjo and Roman, 1978; Anderson, 1994; Urban-Rich *et al.*, 1998), animal size (Small *et al.*, 1983), animal species, animal assimilation efficiency, and pellet compaction (e.g., González and Smetacek, 1994). Some studies make estimations of faecal C vertical flux using such literature values. Caution should be taken using literature values expressed as an amount of the element per pellet (e.g., nanograms C pellet^{-1}) or per pellet volume (e.g., nanograms C μm^{-3}), as a large range of variation (more than one order of magnitude) is found among these data (Table 1).

Table 1 Carbon, nitrogen and phosphorus content of fresh copepod faecal pellets. In studies with mixed copepod species, species described are the most dominant

Faecal pellet producer	Food conditions (area, if natural food conditions)	C % DW	C ng pel⁻¹	C pg μm⁻³	N % DW	N ng pel⁻¹	N pg μm⁻³	P % DW	C:N	C:P	N:P	Source
Single copepod species												
Acartia clausi	Coccolithophores culture	—	133–276	0.53–1.10*	—	13–28	0.05–0.11*	—	—	—	—	Honjo and Roman, 1978
Acartia clausi	Natural food (Woods Hole, Massachusetts)	—	96–187	0.38–0.75*	—	15–38	0.06–0.15*	—	—	—	—	Honjo and Roman, 1978
Acartia tonsa	*Thalassiosira weissflogii* culture	—	—	0.17–2.50	—	—	0.06–0.78	—	3.2–7.1	—	—	Butler and Dam, 1994
Acartia tonsa	*Thalassiosira weissflogii* culture	—	—	0.28	—	—	—	—	—	—	—	Hansen *et al.*, 1996a
Acartia tonsa	*Rhodomonas baltica* culture	—	—	0.39	—	—	—	—	—	—	—	Hansen *et al.*, 1996a
Acartia tonsa	*Thalassiosira* sp. and *Isochrysis galbana* culture	—	—	—	—	—	—	—	10–16	—	—	Checkley and Enzeroth, 1985
Calanus finmarchicus	Natural food (Barents Sea)	—	—	0.05	—	—	0.01	—	7.0	—	—	González and Smetacek, 1994
Calanus glacialis	Natural food (NE Greenland shelf)	—	377	0.05*	—	22	<0.01*	—	—	—	—	Daly, 1997
Calanus hyperboreus	Natural food (NE Greenland shelf)	—	1450	0.04*	—	125	<0.01*	—	28.5	—	—	Daly, 1997
Calanus pacificus	*Thalassiosira weissflogii* culture	—	—	—	—	—	—	—	7.5	—	—	Downs and Lorenzen, 1985
Eucalanus pileatus	*Rhizosolenia alata* culture	—	—	—	—	—	—	—	14.8	—	—	Paffenhöfer and Knowles, 1979

Metridia longa	Natural food (NE Greenland shelf)	—	1140	0.21*	—	70	0.01*	—	—	—	—	Daly, 1997
Pontella meadii	Natural food (Galveston Bay, Texas)	12.0	—	—	2.7	—	—	—	4.8	—	—	Turner, 1979
Temora stylifera	*Hymenomonas elongata* culture	—	154	0.43*	—	18	0.05*	—	8.3	—	—	Abou Debs, 1984
Temora spp.	*Thalassiosira* sp. and *Isochrysis galbana* culture	—	—	—	—	—	—	—	8–25	—	—	Checkley and Enzeroth, 1985
Mixed copepods												
Pseudocalanus spp., *Temora longicornis*	*Thalassiosira weissflogii* culture	25.0	—	—	3.0	—	—	—	7–9	—	—	Morales, 1987
Clausocalanus spp., *Euchaeta* spp., *Orthona* spp., *Oncaea mediterranea*	Natural food (East Pacific Ocean off California)	29.6	—	—	4.8	—	—	—	6.1	—	—	Small *et al.*, 1983
Calanus finmarchicus, Oithona similis, Pseudocalanus elongatus, Temora longicornis,	Natural food (Bjornafjorden)	—	—	0.06	—	—	—	—	—	—	—	González *et al.*, 1994
Calanus helgolandicus, Centropages typicus, Euchaeta marina, Euchirella rostrata	Natural food (NW Mediterranean Sea)	24.8–26.3	—	—	5.3	—	—	0.3	4.9–6.0	79.2	17.2	Marty *et al.*, 1994
Mesozooplankton Copepods	Natural food (western coast of Mexico)	12.0–27.0	—	—	—	—	—	—	—	—	—	Andrews *et al.*, 1984
Mesozooplankton Copepods	Natural food (Irish Sea)	—	56–145	—	—	9–19	—	—	6.2–10.4	—	—	Claustre *et al.*, 1992
Mesozooplankton Copepods	Natural food (off Bermuda)	—	—	0.01–0.25	—	—	—	—	—	—	—	Urban-Rich *et al.*, 1998

*Estimated mean values using average volume.

2.2.2. *Carcasses and moults*

Copepod carcasses are distinguished from live animals by their condition, ranging from slight damage or a few missing appendages to empty broken exoskeletons (Haury *et al.*, 1995). Copepod carcasses are also more transparent than copepods collected alive because of a loss of the dorsal muscle and internal tissue (Harding *et al.*, 1973; Genin *et al.*, 1995; Haury *et al.*, 1995). The exoskeleton is often split between the cephalic and thoracic segments (Wheeler, 1967; Harding *et al.*, 1973). Individuals broken or partially crushed by net towing can be recognized by the loss of some appendages (Haury *et al.*, 1995), whereas the remaining appendages are in good condition (i.e., there is no loss of segments from the swimming legs, and tissue is present in the first antennae) (Wheeler, 1967).

Although moults have similar appearance to carcasses because the exoskeleton is also split between the cephalon and thoracic segments, they can be distinguished from recently formed carcasses because they do not contain residual tissue at all and the exoskeleton is often complete at least for freshly produced moults. However, highly degraded moults may be difficult to distinguish from carcasses.

2.2.3. *Dead eggs*

Copepod eggs that do not hatch will be considered as "dead eggs." This includes unfertilized eggs (oocytes), sterile eggs, and dead eggs *sensu stricto*. Unfertilized eggs are easily distinguished from fertilized eggs, as only the latter have two or more visible nuclei (Ianora *et al.*, 1992; Poulet *et al.*, 1994).

The two types of resting (dormant) eggs, subitaneous (nondiapause) and quiescent, can lead to wrong estimates of egg mortality, as these eggs can hatch after long periods (from a few days up to 40 years: Marcus *et al.*, 1994; Marcus, 1996; Marcus and Boero, 1998), whereas the estimates of egg mortality are carried out over short periods. However, most resting eggs have typical spiny coverings and can be distinguished (Belmonte *et al.*, 1997).

The C content of copepod eggs varies between 15 and 6000 ng C egg^{-1} (Kiørboe *et al.*, 1985; review by Huntley and Lopez, 1992; Kiørboe and Sabatini, 1994, and references therein). Nitrogen content is 9 ng N egg^{-1} for *Acartia tonsa* eggs (Kiørboe *et al.*, 1985) and 5 ng N egg^{-1} for *Paracalanus parvus* eggs (Checkley, 1980). Egg carbon or nitrogen content is estimated as a proportion of egg volume (Checkley, 1980; Huntley and Lopez 1992; Hansen *et al.*, 1999).

3. FACTORS CONTROLLING THE RATE OF COPEPOD OUTFLUXES

The range of rates of copepod outfluxes of dissolved and particulate matter is shown in Table 2. The weight-specific posthatch mortality rate of Table 2 is based on direct estimates from two studies (Kiørboe and Nielsen, 1994;

Table 2 Order of magnitude of copepod weight-specific outflux rates

Process	Process rate		Source
	$gN\ gN_{cop}^{-1}\ d^{-1}$	$gC\ gC_{cop}\ d^{-1}$	
Excretion	0.13–0.23	0.09–0.12 (DOC)	Small *et al.*, 1983
	0.06–0.36	—	Verity, 1985
	—	0.04–0.08 (DOC)	Steinberg *et al.*, 2000
	0.01–0.48 (generally <0.20)	—	Review by Corner and Davies, 1971
	0.04–0.25	—	Checkley *et al.*, 1992, and references therein
Respiration	—	0.06–0.13	Small *et al.*, 1983
	—	0.04–0.18	Steinberg *et al.*, 2000
Faecal pellet production	0.01–0.02	0.02–0.08	Daly, 1997; Small *et al.*, 1983
	—	0.01–0.84 (generally <0.24)	Review by Corner *et al.*, 1986; Small and Ellis, 1992
Posthatch mortality	0.03–0.14[a]	0.03–0.21[a]	Kiørboe and Nielsen, 1994; Roman *et al.*, 2002
Egg mortality[b]	<0.01 to 1.20[b]	—	Checkley *et al.*, 1992, and references therein; Campbell *et al.*, 2001
	0.01 to 0.68[b] (average 0.20)	—	Review by Mauchline, 1998
	—	<0.01 to 0.87[b] (generally <0.07)	Park and Landry, 1993, and references therein; Campbell *et al.*, 2001
	—	average 0.37[b,c]	Peterson and Dam, 1996
Moulting	—	<0.01–0.02	Vidal, 1980

cop: copepod.

[a] Range could be larger and estimated by growth rates, see text for details.

[b] Calculated from female weight-specific egg production rate (references in table) and egg hatching success (Ianora *et al.*, 1992; Jónasdóttir, 1994). Adult copepod females constitute generally less than 10% of the copepod population (Dauby, 1985); therefore, egg mortality rate constitutes, for the whole population, 10 times fewer body losses.

[c] For herbivorous species, assuming that all assimilated nitrogen is channeled into egg production in adult females.

Roman et al., 2002), and thus is too limited in range (and environments) to allow us to examine patterns. Growth rates could give a good indication of what weight-specific mortality rates look like in copepods across the globe. In these two studies, mean growth rate, averaged over 1 (Kiørboe and Nielsen, 1994) or 4 (Roman et al., 2002) years, is almost equal to mean weight-specific mortality rate (difference less than $0.005 \, d^{-1}$). This indicates that we could use the global syntheses of weight-specific growth rates for marine copepods (Hirst and Lampitt, 1998; Hirst and Bunker, 2003; Hirst et al., 2003) and conclude from these syntheses that average weight-specific mortality rate can be expected to be close to $0.14 \pm 0.21 \, d^{-1}$ (Hirst et al., 2003).

The ranges for posthatch mortality, respiration, excretion, and faecal pellet production have the same order of magnitude and are higher than those of moulting and egg mortality (Table 2). A comparison of simultaneous measures of rates of respiration, excretion, and faecal pellet production was made by Small et al. (1983). They concluded that on nitrogen-specific basis, faecal pellet production rate represents a body loss that is more than eight times less that of excretion, whereas on a carbon basis, faecal pellet production rate represents a body loss more than twice less than that lost in respiration.

However, the relative importance of these processes in the carbon and nutrient cycle will depend not only on their rate but also on their nature and fate as well as on copepod biomass variability.

3.1. Factors controlling the rate of copepod dissolved matter excretion

The three main factors influencing excretion of DM are temperature, individual body mass (size) (Ikeda, 1985), and the amount of food (Le Borgne, 1986). The factors discussed below are from literature on N and P excretion and not on DOC excretion (unless specified), for which less information exists. However, for DOC excretion, common controlling factors with N and P excretion can be expected as for all metabolic processes (e.g., temperature, body mass).

3.1.1. Factors controlling the excretion rate

3.1.1.1. Temperature
In all zooplankton, excretion is positively related to water temperature for N, P (Hargrave and Geen, 1968; Nival et al., 1974; Roger, 1978; Ikeda, 1985; Ikeda et al., 2001), and DOC (Steinberg et al., 2000). Most frequently, the relationship between excretion (as for other metabolic rates) and temperature in marine zooplankton is described by Q_{10} (Prosser, 1961). The values of

Q_{10} for copepod excretion in the marine environment range from 1.8 to 2.0 for ammonia and from 1.6 to 1.9 for phosphate excretion rates (Ikeda *et al.*, 2001).

3.1.1.2. Body mass (size)
There is a positive, nonlinear relationship between the excretion rate per individual and the body mass (Mayzaud, 1973; Nival *et al.*, 1974; Ikeda, 1985; Verity, 1985; Ikeda *et al.*, 2001).

3.1.1.3. Faunistic composition
Faunistic composition influences excretion; however, in some cases, this factor can be partly (or even totally) caused by body mass variations. There are differences in excretion rates between species (even of the same genus) (e.g., Gaudy *et al.*, 2000), stages, and sexes (e.g., Butler *et al.*, 1970).

3.1.1.4. Food concentration
Most studies have positively related excretion to food concentration (Butler *et al.*, 1970; Takahashi and Ikeda, 1975; Gardner and Paffenhöfer, 1982; Kiørboe *et al.*, 1985; Anderson, 1992; Urabe, 1993), although a negative relation (for nauplii and copepodite stage II) (Paffenhöfer and Gardner, 1984), or even no relationship (Hernandez-Leon and Torres, 1997), has also been described. Takahashi and Ikeda (1975) found excretion increasing with food concentration (as chl *a*), but only up to 15 μg chl *a* l^{-1}, and decreasing above this level.

3.1.1.5. Food quality
Copepod excretion rate has been linked positively to the food content in P (i.e., negatively to the ratio of C:P) (Gulati *et al.*, 1995) and N (i.e., negatively to the ratio of C:N) (Anderson, 1992). Phosphorus excretion is also negatively related to the food N:P ratio (Urabe, 1993).

3.1.1.6. Biomass or density
Biomass or density increase has been described as influencing the copepod excretion positively (Satomi and Pomeroy, 1965; Nival *et al.*, 1974) or negatively (when density exceeded 400 copepods l^{-1}) (Hargrave and Geen, 1968). For Satomi and Pomeroy (1965), an increase or decrease can be observed depending on species or the other factors affecting excretion.

3.1.1.7. Light
Artificial light, compared to darkness, has a positive effect on nitrogen (Mayzaud, 1971) and phosphorus excretion (Fernandez, 1977). However, below a certain threshold of light intensity, no excretion rate increase is observed (review by Le Borgne, 1986).

3.1.1.8. Salinity

Salinity affects excretion in some copepod species (Hargrave and Geen, 1968). However, Gaudy *et al.* (2000) showed that salinity has no effect on *Acartia clausi*, whereas for *Acartia tonsa*, there is an effect when increasing the salinity that can be positive or negative, depending on temperature.

3.2. Factors controlling the rate of copepod particulate matter outfluxes

3.2.1. Factors controlling the faecal pellet production rate

3.2.1.1. Body mass

Faecal pellet production rate has been described as being positively related to animal mass (Reeve, 1963; Paffenhöfer and Knowles, 1979). This is related to the positive relationship between the faecal pellet production rate and ingestion rate (Corner *et al.*, 1972; Gaudy, 1974; Gamble, 1978; Huskin *et al.*, 2000; Nejstgaard *et al.*, 2001), with the latter increasing with animal mass (Paffenhöfer and Knowles, 1978).

3.2.1.2. Copepod faunistic composition

There are differences in the rate of faecal pellet production among copepod species (Daly, 1997). The age of the animal has been found to affect faecal pellet production rate; *Centropages typicus* females decrease their faecal pellet production with age (Carlotti *et al.*, 1997). Female copepods generally produce more pellets than males (Marshall and Orr, 1972), but this may be a result of differences in mass. Faecal pellet production rate, expressed in terms of pellet number produced per individual, is higher in copepods (Gamble, 1978; Honjo and Roman, 1978; Ayukai and Hattori, 1992) than in salps (Madin, 1982) and euphausiids (Ayukai and Hattori, 1992). However, these groups show similar levels in terms of N or C produced per dry weight of individual (Small *et al.*, 1983).

3.2.1.3. Food concentration and quality

The food concentration was found to influence positively faecal pellet production rate, at least for copepodite V and adult copepods (as discussed below, the only study found on earlier stages indicated no influence of food concentration). A positive curvilinear relationship between food concentration (number of diatom cells) and faecal pellet production rate was reported for *Calanus helgolandicus* females and stage V copepods (Corner *et al.*, 1972), for *Calanus finmarchicus* females (Marshall and Orr, 1955), for *A. tonsa* females (Butler and Dam, 1994), and for *Paracalanus aculeatus* females (Paffenhöfer *et al.*, 1995). Paffenhöfer (1994) did not find such a relation for early copepodites (CII) of *Eucalanus pileatus*, although it was present in

adults. Food quality in terms of size, type, and age has been reported to influence faecal pellet production of *C. finmarchicus* females (Marshall and Orr, 1955). The faecal pellet production rate of *C. helgolandicus* when fed with dinoflagellates shows higher or lower rates than when fed with diatoms, depending on the dinoflagellate species (Huskin *et al.*, 2000; Kang and Poulet, 2000). However, much lower rates are reported when they are fed with coccolithophores (Huskin *et al.*, 2000) or heterotrophic flagellates (Feinberg and Dam, 1998). Feeding history can also influence faecal pellet production rate, as a higher rate was observed in *C. finmarchicus* females coming from a low food environment than those coming from a high food environment (Rey *et al.*, 1999).

3.2.1.4. Temperature and light

Marshall and Orr (1955) and Carlotti *et al.* (1997) observed an increase in the faecal pellet production rate with temperature for *Calanus finmarchicus* (between 5° and 15°C) and *Centropages typicus* (between 15° and 20°C).

Marshall and Orr (1955) also observed that faecal pellet production was higher in darkness. Because of the light factor, the diel variation of faecal pellet production rate observed in the North Sea may be explained by the influence of light as assumed by Martens and Krause (1990).

3.2.2. Factors controlling the posthatch mortality rate

Posthatch mortality of copepods (and other zooplankters) has numerous causes. These can be internal (developmental stage, senescence, genetic background), external (starvation, predation, parasitism), or a combination of external and internal factors (e.g., efficiency of enzymatic activity is a function of temperature) (reviews by Genin *et al.*, 1995; Ohman and Wood, 1995; Haury *et al.*, 1995, 2000; Gries and Güde, 1999). Posthatch mortality rates increase with temperature in both sac and broadcast-spawning copepods (Hirst and Kiøboe, 2002). Mortality in sac spawners is independent of body weight, whereas in broadcasters it decreases slightly with body weight. The proportion of total adult mortality caused by predation is independent of temperature, on average accounting for around two-thirds to three-quarters of the total (Hirst and Kiørboe, 2002).

3.2.3. Factors controlling the moulting rate

In copepods, the moulting rate increases with temperature, food concentration, and growth rate (Marshall and Orr, 1972; Vidal, 1980; Souissi *et al.*, 1997; Hirst and Bunker, 2003) and decreases with body mass (Souissi *et al.*, 1997; Twombly and Tish, 2000) and age (Lopez, 1991). High food

concentration *in situ* has a much lower effect on moulting rate than in laboratory observations at the same temperature (Campbell *et al.*, 2001). In the presence of light, compared to darkness, the moulting rate is higher (Marshall and Orr, 1972).

3.2.4. *Factors controlling egg mortality rate*

Egg predation by copepods themselves (egg cannibalism, Kang and Poulet, 2000; Kiørboe *et al.*, 1988; Peterson and Kimmerer, 1994), other invertebrates such as polychaetes (Marcus, 1984; Marcus and Schmidt-Gegenbach, 1986), and fish (Landry, 1978; Redden and Daborn, 1991; Conway *et al.*, 1994) is an important cause of egg mortality. Egg cannibalism represents between 10% and 30% of egg mortality (Kiørboe *et al.*, 1988), whereas predation by fish has been reported to be a major cause of egg mortality (Landry, 1978). Egg mortality in copepods depends also on the food type ingested (diatoms increase and flagellates decrease mortality) (Ban *et al.*, 1997; Ianora *et al.*, 1995), increases with age (Jónasdóttir, 1994), and abundance of adult females and juveniles (Ohman and Hirche, 2001), but is not correlated with chl *a* or breeding intensity (Ianora *et al.*, 1992; Laabir *et al.*, 1995). Egg mortality in broadcasters is much greater than in sac spawners, because of egg hatch failure, egg sinking, higher rates of predation, and higher advection losses (Hirst and Kiørboe, 2002). Some authors (Ianora *et al.*, 1992; Laabir *et al.*, 1995) found no correlation between temperature and egg mortality, whereas other authors found a positive relationship (hatching success decreasing) (Uye, 1988) or a negative one (hatching success increasing) (Nielsen *et al.*, 2002). Hirst and Kiørboe (2002), reviewing field measurements on egg mortality, concluded that egg mortality rates increase with temperature in both sac- and broadcast, spawning copepods. The importance of egg mortality as an outflux depends also on the total (dead and living) egg production rate that is affected by species, temperature, photoperiod, and food concentration and quality (Marshall and Orr, 1952; Kiørboe *et al.*, 1985; Bautista *et al.*, 1994; Jónasdóttir, 1994; Jónasdóttir *et al.*, 1995; Calbet and Alcaraz, 1996; Hopcroft and Roff, 1996; Ban *et al.*, 1997; Kleppel *et al.*, 1998; Campbell *et al.*, 2001).

3.3. Relationships between the different outfluxes

Many of the processes presented above are interrelated, and this is partly explained by the fact that they depend on common external (e.g., temperature, food) or internal factors (e.g., species, body mass, sex). A good positive relationship was reported between respiration and excretion, in laboratory

experiments, using one predator species and a stable food type (Kiørboe *et al.*, 1985). Also, *in situ* short time experiments (month or season) have established the same relation during a period dominated by one predator species or by a homogeneous population dominated by one group (Satomi and Pomeroy, 1965; Le Borgne, 1973; Gaudy and Boucher, 1983). Statistically significant relationships between phosphorus and nitrogen excretion were also reported first in laboratory experiments, using one predator species and a stable food type, and second *in situ* during a short period (month or season) dominated by one predator species or by a homogeneous (essentially one group) population (Le Borgne, 1973; Roger, 1978, and references therein). Wen and Peters (1994) constructed an empirical model using data from published studies and found a strong nonlinear relationship between phosphorus and nitrogen excretion rates, with small biases resulting from taxonomic differences. However, their model used mostly data from non-feeding animals. The ratios of respiration to excretion and of phosphorus to nitrogen excretion (usually expressed as the atomic ratio O:N, O:P, and N:P) vary between species (Gaudy and Boucher, 1983, and references therein), between stages of development, and between type of food ingested (Conover and Corner, 1968; Le Borgne, 1986).

Egg production can be related to phosphorus excretion and faecal pellet production. During egg formation, more phosphorus is retained by females, resulting in a reduced excretion of this element (Gaudy and Boucher, 1983). At 20 °C, the total egg production during the lifespan of a *C. typicus* female is related to their corresponding total cumulated faecal pellet production (Carlotti *et al.*, 1997). Excretion of nitrogen and phosphorus can be related to moulting; excretion increases during moulting as, for example, phosphorus excretion in euphausiids (Ikeda and Mitchell, 1982) and ammonia excretion in decapod crustaceans (Regnault, 1987). Finally, the importance of growth, a key descriptor of copepod outflux rates, because of its relation to mortality, respiration, and moulting (Hirst and Bunker, 2003; Hirst *et al.*, 2003), should be pointed out.

4. VERTICAL FLUX

This section examines the factors controlling the vertical flux of copepod products (e.g., mg C m^{-2} d^{-1}). In experimental studies, the vertical flux (VF) (also called "sedimentation rate" in zooplankton studies) is expressed as the following depth-integrated flux:

$$\mathrm{VF} = \int_0^H \frac{\partial}{\partial_z}(sC)\mathrm{d}z = \int_0^H \frac{\partial}{\partial_z}\left(W_a C + W_s C - \tilde{\lambda}\frac{\partial C}{\partial_z}\right)d_z \qquad (1)$$

where s is the apparent velocity, C is the concentration of the zooplankton product, w_a is the vertical component of the water velocity vector, w_s is the gravitational settling velocity, $\tilde{\lambda}$ is the vertical turbulent diffusion coefficient, and H is the water column height. The unit vector along the vertical (z) points downward.

In plankton studies, the most commonly used term for the gravitational settling velocity is "sinking rate" and for the apparent velocity "sinking rate," "sinking speed," or "sedimentation speed" (physicists usually call it "deposition velocity" or "fall velocity"). Hereafter the terms "sinking speed" and "sedimentation speed" are used for the gravitational settling velocity, and the apparent velocity, respectively, to separate the units of velocity and avoid confusion between terms.

Sedimentation speed of dissolved matter is controlled only by water hydrodynamics (turbulent diffusion and advection). Hence, the following sections discuss the vertical flux of copepod particulate products. Various physical and biological factors affect the sedimentation speed and the concentration gradient of zooplankton particulate products in general. Passive vertical flux is distinguished from active vertical flux related to copepod migration.

4.1. Passive vertical flux

4.1.1. Physical factors influencing the passive vertical flux of particulate matter

4.1.1.1. Sinking speed
The sinking speed of a particle (w_s cm s^{-1}) depends on the shape and dimension or dimensions of the particle, the water molecular viscosity, and the difference between particle and water densities.

Depending on the particle shape, the sinking speed can be calculated from different equations. For example, for spherical particles the sinking speed can be calculated using the Stokes equation:

$$w_s = \frac{1}{18}\frac{1}{\mu}(\rho_s - \rho)gD^2 \tag{2}$$

where ρ_s is the particle density (g cm^{-3}), ρ is the water density (g cm^{-3}), g is the acceleration of gravity (cm s^{-2}), D is the sphere diameter (cm), and μ the water molecular viscosity (g cm^{-1} s^{-1}). For cylindrical and elliptical particles, Komar *et al.* (1981) modified the Stokes equation. For cylindrical particles (as copepod faecal pellets), the equation is:

$$w_s = 0.0790 \frac{1}{\mu}(\rho_s - \rho)gL^2\left(\frac{L}{D}\right)^{-1.664} \tag{3}$$

where L is the cylinder length (cm) and D is the cylinder diameter (cm).

The sinking speeds of copepod particulate products are compared with those of other zooplankton in Table 3.

(a) Faecal pellets. As shown above, the sinking speed of faecal pellets will depend on their shape, size, and density. Pellet width is the most influential parameter in the estimation of sinking speed compared to pellet length and density (Feinberg and Dam, 1998). The relationship to size of faecal pellets

Table 3 Comparison of the sinking speed of copepod particulate products with those of other zooplankton groups

Product	Group	Sinking Speed		Source
		m d^{-1}	cm s^{-1}	
Faecal pellet	Copepods	25–250	0.03–0.29	Smayda, 1971; Turner, 1977; Honjo and Roman, 1978; Small et al., 1979; Bienfang, 1980; Yoon et al., 2001
	Appendicularians	25–166	0.03–0.19	Gorsky et al., 1984
	Doliolids	41–405	0.05–0.47	Bruland and Silver, 1981; Deibel, 1990
	Euphausiids	15–860	0.03–1.00	Fowler and Small, 1972; Youngbluth et al., 1989; Cadée et al., 1992; Yoon et al., 2001
	Pteropods	65–1800	0.08–2.08	Bruland and Silver, 1981; Yoon et al., 2001
	Heteropods	120–650	0.14–0.75	Yoon et al., 2001
	Salps	40–2700	0.05–3.13	Bruland and Silver, 1981; Madin, 1982; Yoon et al., 2001
Carcasses	Copepods	35–720	0.04–0.83	Apstein, 1910; Gardiner, 1933; Seiwel and Seiwel, 1938
	Amphipods	875	1.01	Apstein, 1910
	Chaetognaths	435	0.50	Apstein, 1910
	Cladocerans	120–160	0.14–0.19	Apstein, 1910
	Euphausiids	1760–3170	2.04–3.67	Mauchline and Fisher, 1969; Fowler and Small, 1972
	Ostracods	400	0.46	Apstein, 1910
	Salps	165–250	0.19–0.29	Apstein, 1910
	Siphonophores	240	0.28	Apstein, 1910
Eggs	Copepods	30	0.03	Kiørboe et al., 1988
	Euphausiids	130–180	0.15–0.21	Mauchline and Fisher, 1969
Moults	Euphausiids	50–1020	0.06–1.18	Mauchline and Fisher, 1969; Nicol and Stolp, 1989, and references therein
Feeding nets	Larvaceans	120	0.14	Hansen et al., 1996b

has been shown by several workers (Smayda, 1969; Turner, 1977; Small *et al.*, 1979; Komar *et al.*, 1981; Alldredge *et al.*, 1987; Frangoulis *et al.*, 2001; Yoon *et al.*, 2001).

The pellet density depends strongly on the pellet size (inverse nonlinear relationship) and, to a lesser degree, on the type of material ingested (Table 4), whereas food concentration has only a small effect on pellet density (Feinberg and Dam, 1998). In the study of Feinberg and Dam (1998), pellet density was measured directly. However, most studies use indirect density estimations based on the pellet dimensions and their sinking speed, which are much easier to obtain than direct pellet density measures. Yoon *et al.* (2001) compared the density estimates using the equations of Komar *et al.* (1981), Stokes' law, and Newton's second law. They concluded that the relationship of Komar *et al.* gave the highest-density values followed closely by those of Newton's second law (difference $\sim 0.03 \, \text{g cm}^{-3}$), whereas Stokes' law underestimated the density (when used for nonspherical faecal pellets). They also concluded that the relationship of Komar *et al.* is appropriate for fresh faecal pellets from copepods feeding on natural food, but may not be representative of other faecal pellets (i.e., not fresh or from organisms feeding on cultured food).

The peritrophic membrane of copepods increases the sinking speed by providing a smooth covering that decreases frictional drag (Honjo and Roman, 1978). In addition, the peritrophic membrane probably contributes to compactness because the pellet volume increases when it is removed (Noji *et al.*, 1991).

(b) Other particulate products. The sinking speed of other particulate products will depend on the same factors described above (dimension, form, particle density, water density and viscosity). The dimension and density effects have been shown for euphausiid carcasses and moults (Mauchline and Fisher, 1969; Nicol and Stolp, 1989).

It is important to notice that the differential sinking speed of particles can cause aggregation, by collision of faster with slower sinking particles (McCave, 1984; Kiørboe, 1997) creating "marine snow" (i.e., flocculent amorphous aggregates >0.5 mm in diameter). The latter is a major source of particulate flux (Fowler and Knauer, 1986; Turner, 2002), and a large part of it consists of zooplankton products (e.g., faecal pellets, moults) (e.g., Silver *et al.*, 1978; Alldredge and Gotschalk, 1988; Bochdansky and Herndl, 1992; Alldredge, 1998).

4.1.1.2. Vertical advection

Upwelling events could counteract the sedimentation of particles (Alldredge *et al.*, 1987), as vertical upward velocities of water during upwelling vary generally from 2 to 84 m d^{-1} (<0.01 to 0.10 cm s^{-1}) (higher values can be found locally or temporally) (Wroblewski, 1977; Jacques and Tréguer, 1986;

Sarhan *et al.*, 2000) and thus are of the same range as the sinking speeds of some zooplankton products (Table 3). However, this does not always negatively affect their downward vertical flux, at least regarding faecal pellets, as faecal pellet production increases during upwelling conditions, enhancing the downward vertical flux (Knauer *et al.*, 1979).

4.1.1.3. Stratification and turbulent diffusion
Enhanced vertical stratification occurring at the thermocline can decrease the sedimentation speed of particles (González *et al.*, 1994). When such a strong stratification occurs, the water density and molecular viscosity increase rapidly with depth (i.e., the sinking speed of particles decreases, see Equations [2] and [3]), and the vertical turbulent diffusion coefficient decreases (see Equation [1]). As a result, particles can accumulate at the thermocline (Krause, 1981; Youngbluth *et al.*, 1989). Turbulence resulting from storms considerably enhances the transfer of particles through the thermocline (Krause, 1981).

Storms can prolong the residence time of particles in the mixed layer. Turbulent mixing prolongs the residence time of particles directly through the water movement transfer and indirectly through the physical degradation by breakdown, which, by reducing their size, decreases their sinking speed (for faecal pellets; Alldredge *et al.*, 1987). Finally turbulence can also enhance aggregation of particles (McCave, 1984) and formation of "marine snow" (Kiørboe, 1997).

4.1.1.4. Molecular diffusion and physical degradation by leaking
(a) Faecal pellets. Although all workers agree that broken faecal pellets have a higher leaking rate, the information concerning this leaking rate is contradictory. Jumars *et al.* (1989) suggested from model calculations that most solutes diffuse out of faecal pellets within several minutes. Møller *et al.* (2003) found that freshly expelled faecal pellets lost more than 20% of their carbon content within the first hour, but the release rate decreased afterward. Urban-Rich (1999) reported an 86% reduction in the faecal pellet DOC pool within 6 h. However, other authors suggested longer time scales. Alldredge and Cohen (1987) found that the peritrophic membrane of faecal pellets is an efficient diffusion barrier. Lampitt *et al.* (1990) showed that in 28 h, from less than 5% up to 15% of the pellet C is released as DOC from intact and broken pellets, respectively. Johannes and Satomi (1966) observed that intact faecal pellets, in the absence of bacteria, after 4 days lost 50% of their carbon content by leaking, especially when incubated in the dark. Strom *et al.* (1997) did not observe a DOC release from intact faecal pellets, whereas broken faecal pellets released DOC on time scales of hours or days, which was immediately taken up by bacteria.

Table 4 Copepod faecal pellet sinking speed and density (fresh faecal pellets)

Faecal pellet producer	FP sinking speed (m d^{-1})	FP density (g cm^{-3})	Food conditions (area, if natural food conditions)	T°C	S	Source
Single copepod species						
Acartia clausi	74–210	—	Flagellates culture	15	33.1	Smayda, 1971
A. tonsa	80–150	—	Coccolith. culture	15	—	Honjo and Roman, 1978
A. tonsa	—	1.15	Diatoms culture	—	—	Butler and Dam, 1994
A. tonsa	33	1.13	Diatom 1 culture	—	—	Feinberg and Dam, 1998
A. tonsa	32 (high) 27 (low)	1.11	Diatom 2 culture	—	—	Idem
A. tonsa	20 (high) 28 (low)	1.10 (high) 1.11 (low)	Flagellate 1 culture	—	—	Idem
A. tonsa	20 (high) 24 (low)	1.15	Flagellate 2 culture	—	—	Idem
A. tonsa	27 (high) 23 (low)	1.14	Heter. Dinofl. culture	—	—	Idem
A. tonsa	17 (high) 21 (low)	1.20	Heter. flagel. 1 culture	—	—	Idem
A. tonsa	30 (high) 68 (low)	1.12 (high) 1.17 (low)	Heter. flagel. 2 culture	—	—	Idem
A. tonsa	45	1.13 (high) 1.12 (low)	Ciliates culture	—	—	Idem
Anomalocera pattersoni	25–220	1.15	Natural food (off Monaco)	14	—	Small *et al.*, 1979; Komar *et al.*, 1981
Calanus finmarchicus	—	1.19	Natural food (flagellates[a], off Newfoundland)	—	—	Urban *et al.*, 1993
C. finmarchicus	—	1.11	Natural food (diatoms[a], off Newfoundland)	—	—	Urban *et al.*, 1993
C. finmarchicus	180–220	—	Coccolith. culture	15	—	Honjo and Roman, 1978
Calanus sp.	70–171	1.17	Diatoms culture	15	29.2	Bienfang, 1980

Calanus sp.	51–152	1.11	Flagellates culture	15	29.2	Bienfang, 1980
Pontella meadii	18–153	—	Diatoms culture	22	34.5	Turner, 1977
P. meadii	15–125	—	Flagellates culture	22	34.5	Turner, 1977
Mixed copepods						
Temora longicornis, Pseudocalanus elongatus, Acartia clausi, Centropages hamatus	37–251	1.31–1.45	Natural (SBNS)	25	31.2	Frangoulis *et al.*, 2001
Clausocalanus arcuicornis, A. clausi, C. typicus, Coryceaus typicus	15–150	1.28	Natural (off Monaco)	14	—	Small *et al.*, 1979; Komar *et al.*, 1981
Copepods (>500 μm)	26–159	1.25	Natural (NE Atlantic)	18	—	Yoon *et al.*, 2001

In studies with mixed copepod species, the species described are the most dominant. Coccolith.: Coccolithophores, FP: faecal pellet, Diatom 1: *Thalassiosira weissflogii*, Diatom 2: *Chaetoceros neogracile*, Flagellate 1: *Rhodomonas lens*, Flagellate 2: *Tetraselmis* sp., Heter. Dinofl.: Heterotrophic dinoflagellate, Heter. flagel., Heterotrophic flagellate, Heterotrophic flagellate 1: *Cafeteria* sp., Heterotrophic flagellate 2: *Oikomonas* sp., Low: low food concentration, High: high food concentration (distinction between high and low food concentration is made only when it was significant at $P < 0.05$), SBNS: Southern Bight of the North Sea,

[a]Dominant phytoplankton group.

Several explanations exist for the discrepancies between the studies cited above. First, some studies were not experimentally designed to allow estimation of leakage during the period immediately following release, as in Møller *et al.* (2003). Second, food concentration differences could also explain the divergence of those studies. Head and Harris (1996) observed no leak of DOC, DON, pigments, or biogenic silica after 4 days from faecal pellets originating from high food conditions, whereas under low food conditions, for the same period, leaking occurred. Møller *et al.* (2003) suggested that the high leakage rate they found could be associated to the high food concentrations of diatoms in their experiment. Other possible explanations are the nonlinearity of the leaking process and incubation differences (i.e., temperature differences and the use of a stationary or a spinning incubator allowing simulation of the free-falling of particles). Lee and Fisher (1994) examined the leaking of carbon from faecal pellets and reported that temperature increase and the use of a spinning wheel increases the leaking rate. Moreover, leaking rate is high during the first days and decreases progressively.

On nutrients release, Head and Harris (1996) observed 20%–30% of the total nitrogen leaking out of copepod faecal pellets in 2 days. However, this was observed only for pellets produced under low food concentration, whereas no leaking was observed even after 4 days for pellets produced under high food concentration (Head and Harris, 1996).

(b) Carcasses. Degradation of copepod carcasses generally starts with a rapid leaking of soluble internal organic compounds during the first 24 h of decomposition (Seiwel and Seiwel, 1938; Harding *et al.*, 1973; Lee and Fisher, 1992, 1994). With a stationary incubator, the leaking rate of carcasses was faster than that of faecal pellets at both low (2 °C) and high temperatures (18 °C). However, with a spinning incubator, at high temperatures the leaking rate of carcasses and faecal pellets were similar (Lee and Fisher, 1994).

4.1.2. Biological factors affecting the passive vertical flux of particulate matter

The biological factors that influence the passive vertical flux of copepod (and other zooplankton) products are production and biodegradation. The factors influencing the production rate of copepod products were examined earlier (Section 3). Biodegradation depends on zooplankton itself, nekton, and microorganisms (hereafter biodegradation is considered to include consumption of zooplankton products).

4.1.2.1. Zooplankton and nekton mediated biodegradation

(a) Coprorhexy and coprochaly. Copepods affect the degradation of their own pellets by coprorhexy and coprochaly. Coprorhexy is the fragmentation of faecal pellets without ingestion, whereas coprochaly is the destruction of

the peritrophic membrane (Lampitt *et al.*, 1990; Noji *et al.*, 1991). These processes occur within hours, and thus they are faster than biodegradation by microorganisms, which takes days or weeks (Section 4.1.2.2). Their combined effect could reduce faecal pellet sinking speed from 25% to 50% (Noji *et al.*, 1991). In addition, they increase the leaking of dissolved elements (Lampitt *et al.*, 1990), as well as the substrate for microorganisms (larger surface area to volume ratio and greater porosity of less dense particles) (Noji *et al.*, 1991).

(b) Coprophagy. Coprophagy is the ingestion of faecal material. Copepods have been reported to practice coprophagy on their own faecal pellets (Lampitt *et al.*, 1990). Coprophagy is explained by the nutritive value of faecal pellets, as marine organisms can obtain a substantial fraction of the organic material required for maintenance metabolism by ingesting faecal pellets (Frankenberg and Smith, 1967; Paffenhöfer and Knowles, 1979; González and Smetacek, 1994).

The coprophagy rate will depend on the type of pellets and the type of animal (Frankenberg and Smith, 1967). First, faecal pellet type in terms of size, sinking speed, and carbon–nitrogen content influences this rate. For the same amount of faecal matter produced, several small pellets have more chances of being ingested (than one big faecal pellet), and their slower sinking speed increases this probability (Paffenhöfer and Knowles, 1979). The coprophagy rate was found to be positively related to the carbon and nitrogen content of faecal pellets (Frankenberg and Smith, 1967). Second, depending on the type of animal, high or low coprophagy rate (or even absence of coprophagy) can be found in copepods (Noji *et al.*, 1991), as in other marine animals (Frankenberg and Smith, 1967).

As in the case of coprorhexy and coprochaly, coprophagy will finally reduce the vertical flux of faecal pellets. These losses can be important at times, as copepods, particularly the genus *Oithona*, may constitute a "coprophagous filter" that significantly reduces the vertical flux of faecal pellets (González and Smetacek, 1994; González *et al.*, 1994). *Oncaea* seems to play a similar scavenging role: It has been observed to feed on sinking larvacean houses (Alldredge, 1972; Alldredge and Silver, 1988) and is probably also capable of intercepting sinking marine snow and faeces (Skjoldal and Wassmann, 1986). The biomass ratio between such essentially pellet-reworking copepods (e.g., *Oithona*) and essentially pellet-producing copepods (calanoids) may be used to predict relative pellet retention or vertical flux of calanoid faecal pellets (Svensen and Nejstgaard, 2003).

(c) Detritiphagy on other particulate products. Carcasses are known as a possible (although insufficient) food source for copepods (Yamaguchi *et al.*, 2002), euphausiids, fishes, or gelatinous zooplankton (Haury *et al.*, 2000), but they are considered less nutritious than living copepods (Genin *et al.*, 1995). Genin *et al.* (1995) considered that because the external

appearance of carcasses is almost identical to that of living individuals, the ability of predators to distinguish between them should be low. This assumption could be also expanded to dead eggs because predation on eggs exists (Section 3.2.4). However, for moults this assumption could not be true because they could be easily distinguished from live copepods by their transparency.

4.1.2.2. Biodegradation by microorganisms and remineralization

(a) Faecal pellets. Turner (2002) extensively reviewed biodegradation of faecal pellets by microorganisms and concluded that this is mainly brought about by bacteria and protists that show a microbial colonizing succession on faecal pellets, initiated essentially by internal bacteria probably originating from ingestion, and depends on the diets under which the faecal pellets are produced.

There is some dispute about the time needed for the degradation of faecal pellets. Some laboratory studies showed that the surface membrane of faecal pellets, produced by animals on cultured diets, is degraded after 3–11 days at high temperatures (20°–25 °C), whereas at lower temperatures (5 °C), membranes remain intact for 20–35 days (Honjo and Roman, 1978; Turner, 1979). The same range for membrane degradation time (4–10 days) was found by Alldredge *et al.* (1987) for faecal pellets from natural diets at 15 °C, whereas for total degradation of the pellets, 8–12 days were necessary. In contrast, other experiments with faecal pellets produced from natural diets (Small and Fowler, 1973), as well as culture studies (Jacobsen and Azam, 1984), have shown pellets to remain intact for several weeks at temperatures as high as 18 °C.

Active remineralization of large sinking particles is, in general, low, as these particles are poor habitats for bacterial growth (Karl *et al.*, 1988). Copepod faecal pellets are an exception, as they contain bacteria when they are produced and are also rapidly colonized by bacteria from the water column (see above). Therefore, active remineralization in faecal pellets must be more important than in other biogenic particles. Johannes and Satomi (1966) found that the C, N, and P content of faecal pellets decreases faster with bacterial activity. In addition; Jacobsen and Azam (1984) found that faecal pellet carbon remineralization by bacteria to CO_2 amounts to 0.5% of the pellet carbon per day. When microzooplankton is added, this remineralization rate doubles.

(b) Carcasses. Degradation of copepod carcasses by microorganisms begins on the exoskeleton and progresses into the organism through the mouth (Harding *et al.*, 1973; Poulicek *et al.*, 1992, and references therein). Degradation increases with temperature, but it is unlikely that the copepod

intestinal flora contributes significantly to degradation (Harding *et al.*, 1973). Carcasses are rapidly covered by bacteria already existing on the living organism, followed by a colonization by external bacteria (Poulicek *et al.*, 1992, and references therein).

The degradation rate for copepod carcasses was reported to be 11 days at 4 °C and 3 days at 22 °C (Harding *et al.*, 1973). Poulicek *et al.* (1992) found biodegradation rate values at 14 °C within this range, with most of the content of the carcasses (lipids and proteins) being degraded within 3 days, whereas for the chitinous structures, 8 days were necessary. Comparable degradation rates were found in *Anomalocera pattersoni* by Reinfelder and Fisher (1993). The biodegradation rate of carcasses is thus probably faster than that of faecal pellets (see above).

Concerning remineralization, a rapid release of phosphate within 24 h following the death of copepods has been reported (Seiwel and Seiwel, 1938). From one-third to one-fourth of the total phosphate is released during the first 12 h, and the total phosphate is released in 6 days (Cooper, 1935).

(c) Moults and eggs. No information was found for the time necessary for complete degradation of moults. However, we can assume that approximately 8 days are necessary, as for the chitinous structures of carcasses (Poulicek *et al.*, 1992).

Unfertilized eggs usually disintegrate fairly rapidly (<72 h) after being spawned (Jónasdóttir, 1994; Poulet *et al.*, 1994).

4.2. Vertical migration and active vertical flux

The flux of copepod products can be modified by "active" vertical flux because of the diel and seasonal migration of copepods. The larger copepods can undertake diel vertical migrations up to several hundreds of metres (review by Bougis, 1974). They are generally at the surface during the night and in deeper waters during the day. The percentage of the total mesozooplankton biomass (copepod dominated) constituted by diel vertical migrators is generally 10%–40% (Longhurst *et al.*, 1990, and references therein; Zhang and Dam, 1997).

Seasonal migrators overwinter at depths from 200 to 1000 m and perhaps deeper, resurfacing in spring to feed on the seasonal algal bloom. The surviving population is a small remnant of the population of the previous autumn (~25%) (Longhurst and Williams, 1992, and references therein). The contribution of this process to the total vertical flux is discussed in the following section, separately for each copepod product.

5. ROLE OF COPEPOD OUTFLUXES

5.1. Role of copepod dissolved matter outfluxes

5.1.1. Role of excretion

5.1.1.1. Role of excretion in the nutrient cycle

Excretion by marine organisms is important in nutrient cycles, as it produces readily assimilable inorganic and organic nutrients for primary producers, but zooplankton excretion is particularly important because its rate is higher than those of other marine invertebrates (for nitrogen, Corner and Davies, 1971).

Both inorganic and organic copepod excretion play a role in the nutrient cycle. All zooplankton organisms produce mainly inorganic forms of nutrients (Section 2.1) that are taken up by phytoplankton faster than organic forms (Corner and Davies, 1971). Inorganic nitrogen excretion is of primary importance, because ammonia is the preferred nitrogen form for many primary producers (Dugdale and Goering, 1967; Conway, 1977; Harrison *et al.*, 1996; Lomas *et al.*, 1996). The organic nutrients excreted by copepods can be used by bacteria and, in some cases, by phytoplankton, as, for example, urea (McCarthy, 1971), amino acids (Stephens and North, 1971), and organic phosphorus compounds (Corner and Davies, 1971).

The potential contribution of inorganic zooplankton excretion to nutrient requirements of phytoplankton is highly variable and lies between 2% and 300% (Båmstedt, 1985; review by Corner and Davies, 1971; review by Alcaraz, 1988; Alcaraz *et al.*, 1998; Le Borgne, 1986). This large variability can be explained by three factors.

First, the amount of nutrients excreted is a function of the zooplankton size-fraction. Microplankton and bacterioplankton usually show higher excretion rates of ammonia than do mesozooplankton and macrozooplankton (Smith, 1978a; Glibert, 1982; Hernandez-Leon and Torres, 1997). However, macrozooplankton and mesozooplankton can contribute significantly to the total regeneration of nitrogen (Roman *et al.*, 1988; Glibert *et al.*, 1992; Miller *et al.*, 1995, 1997), whereas specifically mesozooplankton excretion generally provides a more significant proportion of the total ammonia regenerated (Bidigare, 1983; Dam *et al.*, 1993; Miller and Glibert, 1998).

Second, there is the spatial variability of the excretion contribution to phytoplankton demand. In some areas, excretion supplies all the requirements in inorganic nitrogen (Verity, 1985) and phosphorus (Martin, 1968; Eppley *et al.*, 1973), whereas in other areas zooplankton regenerates only 2% of the daily ammonia requirements of phytoplankton (Biggs, 1982). Even in the same area, large variations can be found, as in the Catalan Sea

(western Mediterranean Sea), where the mesozooplankton contribution to the nitrogen requirement of phytoplankton varies from 5% to 285% (Alcaraz *et al.*, 1994). In general, the importance of zooplankton excretion in the regeneration of nutrients is high (>40%) in less productive areas, such as the open ocean, and low (<40%) in highly productive waters, such as those in areas of upwelling and in estuaries (Harrison, 1980; Le Borgne, 1986; Wollast, 1998).

Third, there is a temporal variation of the excretory contribution to phytoplankton needs, both seasonal and annual. Seasonal variation has been shown in Narragansett Bay (Rhode Island), with high values in autumn (182% for N and 200% for P) and low values in spring (3% for N and 17% for P) (Martin, 1968). Furthermore, year-to-year variation has also been evident (Harris, 1959). These temporal variations could be explained by the production of the system: When the system is more productive, as during the spring bloom in temperate areas or when upwelling occurs, the contribution is usually lower, and *vice versa* (review by Le Borgne, 1986).

Excretion of nitrogen during the diel migration of copepods can constitute at times an active flux (Hays *et al.*, 1997) similar to or even higher than the passive PON flux (Longhurst and Harrison, 1988, and references therein). However, when several regions are compared, the active flux of excretory nitrogen has generally a median value of 5% of the PON passive vertical flux (ranging from 1% to 140%) (Longhurst and Harrison, 1988, and references therein).

5.1.1.2. *Role of excretion in the carbon cycle*

Because of the close relationship between the carbon and nutrient cycles, copepod nutrient excretion plays an indirect role in the carbon cycle, but it has also a direct effect on the constitution of the DOC pool (see also Section 5.2.1.1). This pool is one of the largest organic carbon reservoirs on earth (Strom *et al.*, 1997). Evaluation of DOC sources is a major concern when studying the global carbon cycle because DOC makes up greater than 95% of the total organic matter in the ocean itself (Nagata and Kirchman, 1992). However, downward transport of dissolved excretion products out of the euphotic layer is generally considered negligible (McCave, 1975) and is ignored in the carbon/nutrient cycle (Wollast, 1998).

5.1.2. *Role of respiration*

For the same reasons as excretion, respiration is generally not taken into account in the downward export of carbon (Wollast, 1998; Wollast and Chou, 2001). Downward export of carbon by respiration does exist, coming

from copepods migrating vertically. In some areas, the amount of respiratory carbon transported out from the euphotic zone by migrant copepods can be of the same order of magnitude as that of gravitational particle sinking (Longhurst *et al.*, 1990; Zhang and Dam, 1997). However, on a global scale, carbon export by the respiration of migrant copepods represents ~1% of the global sinking flux of particles at 200 m depth (Longhurst and Williams, 1992), so respiration will not be further discussed.

5.2. Role of copepod particulate matter outfluxes

5.2.1. Role of faecal pellets

Copepod faecal pellets can transport an important amount of organic and inorganic matter over long distances. Many of them have high sinking speeds and a peritrophic membrane that retains elements to a greater degree than other products that originate from copepods (moults and carcasses), other zooplankton, and other pelagic organisms, including phytoplankton and fish (Fowler and Knauer, 1986).

Vertical transport might also occur when copepods eat at the surface at night and then produce faecal pellets after migrating down to deeper layers in the daytime (Morales *et al.*, 1993; Atkinson *et al.*, 1996; Bianchi *et al.*, 1999), but the quantity involved appears to be negligible (Atkinson *et al.*, 1996). The role of transport of matter by faecal pellets is further analysed in the following sections.

5.2.1.1. Role of faecal pellets in the carbon cycle
(a) Downward transport of particulate organic carbon (POC). Turner (2002) has brought together a growing body of literature that agrees that the contribution of mesozooplankton faecal pellets to the export of material and sequestration of carbon is generally minor or variable. Turner (2002) indicates that usually these pellets contribute between a few and some 30% of the vertical POC flux, although in some areas or periods they contribute a larger part (>80%) of the POC flux. The emerging view is that it is mainly macrozooplankton faecal pellets, phytoplankton, and marine snow that are involved in the sedimentary carbon flux; their relative contributions are highly variable and depend on multiple interacting factors (review by Turner, 2002) such as the physical and biological factors affecting the vertical flux of zooplankton products discussed above.

(b) Contribution to the DOC pool. The degradation of faecal pellets is a way in which DOC is added to the water column. In conditions of high faecal pellet production and degradation, leaking from faecal pellets may be

a significant contributor to the DOC pool and to bacterial growth, as an important amount of DOC would be liberated in the water column. DOC released by faecal pellets together with excretion and sloppy feeding could be a pathway of DOC to bacteria as important as that of DOC excretion directly from intact phytoplankton (Strom *et al.*, 1997; Urban-Rich, 1999; Møller and Nielsen, 2001; Møller *et al.*, 2003). This DOC is considered to be a high-quality substrate pool for bacteria (Hygum *et al.*, 1997; Urban-Rich, 1999).

(c) Dissolution of $CaCO_3$. The dissolution of $CaCO_3$ consumes CO_2 and is only thermodynamically possible at great depths (below 1500 m; i.e., lyso-cline) (Broecker and Peng, 1982). However, biologically mediated dissol-ution of $CaCO_3$ was observed at depths above the lysocline, among which was dissolution within copepod faecal pellets and guts (Milliman *et al.*, 1999). Biologically mediated dissolution processes can absorb as much anthropogenic CO_2 as 0.05 Gt C year^{-1} (Sabine and Mackenzie, 1991).

5.2.1.2. *Role of faecal pellets in the nutrient cycle*
Few studies exist on the vertical transport of nutrients by faecal pellets (compared to those on the transport of carbon). As discussed previously, faecal pellets have been shown to be mostly recycled at the surface; therefore, they generally contribute to regenerated production. Faecal pellets are reported to contribute little to nitrogen export to the benthos (Knauer *et al.*, 1979; Daly, 1997). Knauer *et al.* (1979) estimated that faecal pellets constituted up to 5% and 20% of the total particulate organic nitrogen (PON) and particulate organic phosphorus (POP) vertical flux, respectively. However, during upwelling conditions, the same authors estimated that these contributions increased up to 25% and 60% of the total PON and POP vertical flux, respectively.

5.2.1.3. *Role of faecal pellets in the nutrition of marine organisms*
Faecal pellets are known to contribute to the nutrition of many pelagic and benthic organisms (Frankenberg and Smith, 1967; Honjo and Roman, 1978; Paffenhöfer and Knowles, 1979; Youngbluth *et al.*, 1989; Mochioka and Iwamizu, 1996). They can transport organic matter of high nutritive value toward deeper layers (Fowler and Fisher, 1983). In this way, they can offer a substantial fraction to the maintenance metabolism (Frankenberg and Smith, 1967) of the pelagos and benthos by means of coprophagy and ingestion of "marine snow" (Frankenberg and Smith, 1967; Honjo and Roman, 1978; Paffenhöfer and Knowles, 1979; Turner, 1979; Bathmann and Liebezeit, 1986; Youngbluth *et al.*, 1989). Their consumption and nutritive value depend on the pellet size, shape, sinking speed, carbon, and nitrogen contents (Paffenhöfer and Knowles, 1979). Second, the active transport of faecal pellets and other particulate products by migrant copepods is important in the

nutrition of marine organisms, as it offers particulate products with a higher nutritional value than those falling from surface waters.

5.2.1.4. Role of faecal pellets in the transport of toxins, pollutants, and pelagic sediments

Because faecal pellets are a means of transport of organic matter, they also transport the associated toxins, pollutants, and pelagic sediments. Toxic phytoplankton (Wexels Riser *et al.*, 2003) and numerous pollutants (see the review of Turner, 2002, for an extensive list) are transported by faecal pellets. These pollutants can be transferred by coprophagy to the benthic (Osterberg *et al.*, 1963; Elder and Fowler, 1977) or pelagic ecosystem (Krause, 1981), and thus be bioaccumulated in higher trophic levels. Sediment may be transported in copepod pellets in the plume of the Mississippi River (Turner, 1984, 1987) and in the highly turbid ecosystem of the Southern Bight of the North Sea (Frangoulis *et al.*, 2001).

5.2.2. Role of posthatch mortality

Dead organisms have a similar role to that of faecal pellets in the transport of matter in the carbon and nutrient cycles, in the nutrition of marine organisms (Wheeler, 1967), and in the transport of pollutants (Elder and Fowler, 1977; Fowler, 1977). However, they are less important than faecal pellets in the downward (passive) transport of matter because most carcasses originating from the upper layer of the water column decompose faster than faecal pellets (Smith, 1985; Fowler and Knauer, 1986; Lee and Fisher, 1994). However, the percentage of dead to total copepods increases with depth (Siokou-Frangou *et al.*, 1997), becoming higher than that of living copepods (Wheeler, 1967; Siokou-Frangou *et al.*, 1997; Yamaguchi *et al.*, 2002). Dead copepods have been found at great depths (4000 m), but they seem to result mostly from the local mortality of migrating organisms (Wheeler, 1967), thus constituting an active downward flux. Locally, this flux can have a significant effect on the downward transport of matter. On the diel scale, it can constitute up to 40% of the gravitational particle sinking (Zhang and Dam, 1997), and on the seasonal scale, it can be similar to the total passive flux of carbon (Hirche, 1997).

5.2.3. Role of moulting

Moults play a similar role to that of carcasses and faecal pellets, such as transport of matter in the carbon and nutrient cycles, nutrition of marine organisms (Wheeler, 1967), and transport of pollutants (Elder and Fowler,

1977; Fowler, 1977). However, moulting results in less body matter losses than faecal pellet production and posthatch mortality (Table 2). The downward transport of matter is also smaller than that of faecal pellets, despite the fact that they can have similar sinking speeds (Table 3). In fact, moults, like carcasses, retain fewer elements than faecal pellets because they degrade faster. This explains why they are rarely found in sediment traps, particularly in deep ones (review by Fowler and Knauer, 1986). Estimations of active flux of moults are lacking (Steinberg *et al.*, 2000).

5.2.4. Role of egg mortality

"Dead" eggs have a similar role to that of other particulate products in the nutrition of marine organisms (Section 3.2.4) and the transport of matter as pollutants (Elder and Fowler, 1977; Fowler, 1977), carbon, and nutrients. As a direct downward exporter of matter, eggs are less important than the other copepod particulate products because their sinking speed is less, their degradation is faster than that of other particulate products (Section 4.1.1.1. and Section 4.1.2.2.c), and predation decreases their passive vertical flux. However, egg predation may indirectly lead to outflux from surface waters through pellet production by predators, although a large proportion of eggs are viable after passage through the predator gut. High survival of copepod eggs has been reported for eggs passing through the guts of polychaetes (Marcus, 1984; Marcus and Schmidt-Gegenbach, 1986), hydromedusae (Daan 1989), and fish (Redden and Daborn, 1991; Conway *et al.*, 1994; Flinkman *et al.*, 1994).

6. DISCUSSION

Copepods release dissolved matter through excretion and respiration, and particulate matter through faecal pellet production, posthatch mortality, moulting, and egg mortality. Respiration produces only CO_2, whereas excretion includes inorganic compounds (ammonia, orthophosphate) together with several organic compounds of nitrogen and phosphorus (e.g., Gardner and Paffenhöfer, 1982; Båmstedt, 1985; Le Borgne, 1986; Regnault, 1987; Dam *et al.*, 1993). Inorganic excretion constitutes the larger part of the total excretion (e.g., Corner and Davies, 1971; Båmstedt, 1985; Le Borgne, 1986; Regnault, 1987; Le Borgne and Rodier, 1997); however, there is an important variability in the proportion of inorganic matter in the total excretion as a result of several factors, including temperature, species, and food (e.g., Mayzaud, 1973; Le Borgne, 1986; Miller, 1992). However, copepods release particulate matter through faecal pellet production, posthatch mortality,

moulting, and egg mortality. Copepod faecal pellets are covered by a peri-trophic membrane (Gauld, 1957; Yoshikoshi and Ko, 1988). This is also true for other many planktonic crustaceans (e.g., shrimps, euphausiids: Forster, 1953; Moore, 1931), but not for ciliates, tintinnids (Stoecker, 1984), or gel-atinous zooplankton (Bruland and Silver, 1981). There are several possible functions of the peritrophic membrane (e.g., protection of the midgut epi-thelium) that will depend on the animal mode of life (Gauld, 1957; Reeve, 1963; Yoshikoshi and Ko, 1988). Most copepods have cylindrical-shaped pellets (Gauld, 1957; Fowler and Small, 1972; Martens, 1978; Cadée *et al.*, 1992; Yoon *et al.*, 2001). Their size depends on the ingestion rate (e.g., Huskin *et al.*, 2000), animal size (e.g., Uye and Kaname, 1994), food type (e.g., Feinberg and Dam, 1998), and food concentration (e.g., Dagg and Walser, 1986; Tsuda and Nemoto, 1990; Butler and Dam, 1994; Feinberg and Dam, 1998; Huskin *et al.*, 2000). The colour of faecal pellets will depend on the diet of the animal (Feinberg and Dam, 1998; Urban-Rich *et al.*, 1998). Their content varies from an amorphous material to intact and even viable phytoplankton cells (e.g., review by Turner, 2002). The chemical compos-ition of faecal pellets is complex (pigments, lipids, amino acids, hydrocar-bons, sugars, trace elements, radionuclides, etc.) (e.g., review by Turner, 2002). The faecal C, N, and P composition (Table 1) will depend on the food quantity and quality (e.g., Urban-Rich *et al.*, 1998), animal size (Small *et al.*, 1983), animal species, animal assimilation efficiency, and pellet compaction (e.g., González and Smetacek, 1994). In estimations of faecal C, the vertical flux when using literature values, those expressed as an amount of the element per dry weight should be preferred to those expressed per pellet or per pellet volume (Table 1).

Copepod carcasses are distinguished from live animals by their condition, ranging from slight damage or a few missing appendages to empty broken exoskeletons (Haury *et al.*, 1995). Although moults have similar appearance, they can be distinguished from recently formed carcasses, as they do not contain any residual tissue and the exoskeleton is often complete, at least for freshly produced moults. Dead eggs include nonfertilized eggs, sterile eggs, and dead eggs *sensu stricto*. The two types of resting (dormant) eggs, sub-itaneous (nondiapause) and quiescent, can lead to wrong estimates of egg mortality, as these eggs can hatch after long periods (Marcus, 1996, 1998; Marcus and Boero 1998). The carbon or nitrogen content of eggs can be estimated using the egg volume (Checkley, 1980; Huntley and Lopez 1992; Hansen *et al.*, 1999). The review of the nature of these outfluxes showed that faecal pellets and excretion have been widely studied compared to the other outfluxes. However even for the "well-studied" outfluxes there are still unknowns, such as the chemical composition of the excreted phosphorus organic fractions.

The schematic diagram (Figure 1) summarizes the review of the factors affecting the rate and the vertical fate of copepod outfluxes (these factors are common for all products from zooplankton). For excretion rate, faecal pellet production rate, and moulting rate, the most important controlling factors of the rate are generally temperature (e.g., Marshall and Orr, 1955; Souissi *et al.*, 1997; Ikeda *et al.*, 2001), body mass (e.g., Paffenhöfer and Knowles, 1979; Souissi *et al.*, 1997; Ikeda *et al.*, 2001), food concentration (e.g., Marshall and Orr, 1955; Takahashi and Ikeda, 1975; Kiørboe *et al.*, 1985; Paffenhöfer *et al.*, 1995; Campbell *et al.*, 2001), food quality (e.g., Urabe, 1993; Gulati *et al.*, 1995; Kang and Poulet, 2000), and copepod faunistic composition (e.g., Daly, 1997; Gaudy *et al.*, 2000). Egg mortality rate depends on predation (e.g., Marcus and Schmidt-Gegenbach, 1986; Conway *et al.*, 1994; Kang and Poulet, 2000), the food type ingested (Ianora *et al.*, 1995; Ban *et al.*, 1997), animal age (Jónasdóttir, 1994), and temperature (Hirst and Kiørboe, 2002). For the posthatch mortality rate, factors are internal (developmental stage, senescence, genetic background) or external (temperature, starvation, predation, parasitism) (e.g., Ohman and Wood,
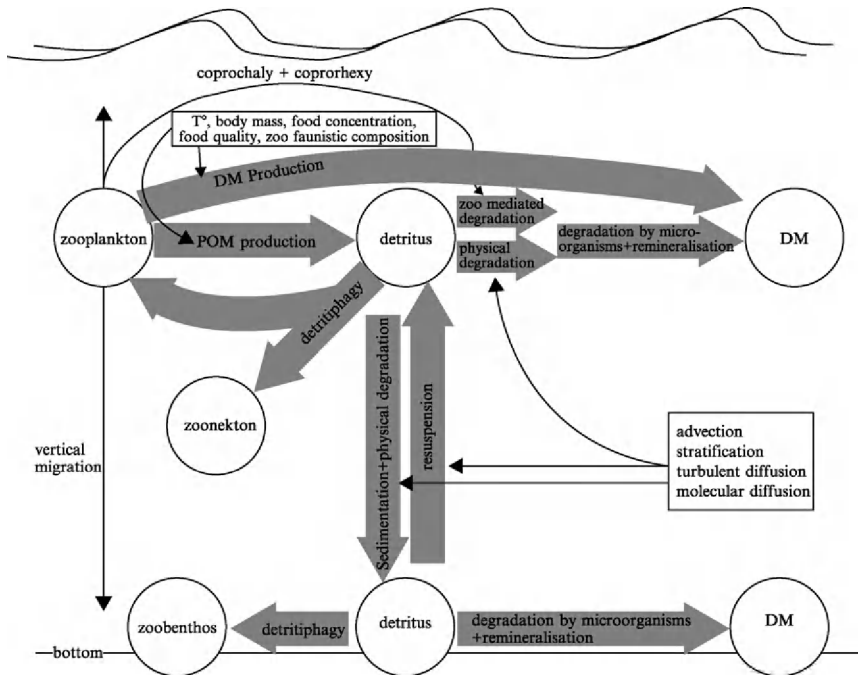

Figure 1 Diagram of the vertical fates of copepod (and other zooplankton) products and the factors controlling them. DM: dissolved matter, T°: temperature, zoo: zooplankton.

1995; Hirst and Kiørboe, 2002). Although several of the above relationships are clear (e.g., positive relationship between body mass and excretion), some are not well established (negative, positive or no relationship are found), and others are poorly studied (e.g., few studies concerning the influence of food type on excretion rate).

Physical and biological factors govern the vertical fate of all zooplankton products (Figure 1). First, physical factors, such as sinking speed, advection, stratification, turbulent diffusion, and molecular diffusion, influence the sedimentation speed and degradation of the zooplankton products. The sinking speed of a particle depends on the shape and dimensions of the particle, the water molecular viscosity, and the difference between particle and water densities (e.g., Komar *et al.*, 1981). Upwelling events can counteract the sedimentation of particles (Alldredge *et al.*, 1987). Stratification can decrease the sedimentation speed of particles (e.g., Krause, 1981; González *et al.*, 1994), and turbulent mixing can prolong the residence time of particles in the mixed layer (Alldredge *et al.*, 1987). Leaking by molecular diffusion releases carbon and nutrients from pellets and carcasses and depends on temperature and turbulence and also in the case of faecal pellets food concentration (e.g., Lampitt *et al.*, 1990; Lee and Fisher, 1994; Head and Harris, 1996; Møller *et al.*, 2003). Second, the biological factors that govern the vertical fate of copepod products are production and biodegradation by zooplankton, nekton, and microorganisms. Biodegradation by zooplankton and nekton is done by detritiphagy (including coprophagy) (e.g., Frankenberg and Smith, 1967; González *et al.*, 1994; Haury *et al.*, 2000; Yamaguchi *et al.*, 2002) and, in the case of copepods, also by coprorhexy and coprochaly (Lampitt *et al.*, 1990; Noji *et al.*, 1991). Biodegradation occurs through the activities of bacteria and protists (e.g., review by Turner, 2002). Physical degradation and biodegradation by zooplankton and nekton are faster than biodegradation by microorganisms. The order of the biodegradation rate of copepod products by microorganisms depends strongly on temperature and in decreasing order of importance, is eggs (<3 days) (Jónasdóttir, 1994; Poulet *et al.*, 1994), moults (<8 days) (Poulicek *et al.*, 1992), carcasses (3–11 days) (Harding *et al.*, 1973; Poulicek *et al.*, 1992), and faecal pellets (3–50 days) (e.g., Small and Fowler, 1973; Alldredge *et al.*, 1987). Finally, diel (e.g., Longhurst *et al.*, 1990) and seasonal (Longhurst and Williams, 1992) vertical migration of copepods constitutes an active process that will also influence the vertical flux of copepod products.

The most important copepod outfluxes are excretion and faecal pellet production. Excretion offers inorganic nutrients that can be directly used by primary producers (Dugdale and Goering, 1967; Conway, 1977; Harrison *et al.*, 1996; Lomas *et al.*, 1996) and organic nutrients that can be used by bacteria and, in some cases, by phytoplankton (Corner and Davies, 1971; McCarthy, 1971; Stephens and North, 1971). The potential contribution of

copepod excretion to the nutrient requirements of phytoplankton is highly variable spatially and temporally (Corner and Davies, 1971; Båmstedt, 1985; Le Borgne, 1986; Alcaraz, 1988; Alcaraz et al., 1998). The active flux of excretory nitrogen during the diel migration of mesozooplankton generally makes little contribution compared to the PON passive vertical flux (Longhurst and Harrison, 1988, and references therein). The contribution of copepod DOC excretion to the DOC pool is not well known. This contribution needs more investigation to determine the quantity and composition of the excreted DOC, especially during a bloom situation, when copepods could be a major source of DOC to the water column.

Copepod particulate products are important in the transport of matter in the carbon (e.g., Strom et al., 1997; review by Turner 2002) and nutrient (Knauer et al., 1979; Daly, 1997) cycles, in the nutrition of marine organisms (e.g., Frankenberg and Smith, 1967; Paffenhöfer and Knowles, 1979; Mochioka and Iwamizu, 1996) and in the transport of toxins (Wexels Riser et al., 2003) and pollutants (e.g., Fowler, 1977; review by Turner 2002). On the basis of the literature presented, we believe their relative importance, in decreasing order, to be faecal pellets, carcasses, moults, and eggs. This relative importance can be demonstrated by comparing the biodegradation rates (see above) and sinking speeds (Table 3) of zooplankton particulate products. To summarize this in order of importance, Fowler and Small (1972), referring to euphausiids, stated that "faecal pellets sink at rates faster than those of eggs and about the same as those of moults. On the other hand, carcasses of the organisms that produce the faecal pellets sink two to four times faster than the fastest pellets. Dead euphausiids disintegrate into smaller pieces in a matter of days, whereas faecal pellets of these animals can remain intact for months. The rapid decomposition of carcasses slows the sinking rate of dead zooplankton."

In future studies, a wider research strategy is necessary, as discussed in the next five points. First, other zooplankton groups should be studied, because locally or temporally they can dominate total abundance and biomass of mesozooplankton and macrozooplankton (Alldredge, 1984; Longhurst, 1985) and constitute an important outflux. For example, in some areas and during some seasons, appendicularians, pteropods, and salps occur in high concentrations, and their feeding nets (together with the attached detritus) represent a significant sink of organic matter (Morris et al., 1988; Bathmann et al., 1991; Hansen et al., 1996b; review by Kiørboe, 1998) that can be as high as that of copepod faecal pellets (Vargas et al., 2002). The high particle content provides an important contribution to the nutrition of zooplankton (Alldredge, 1976; Steinberg et al., 1994, 1997; Steinberg, 1995) and anguilloid larvae (Mochioka and Iwamizu, 1996).

Second, it should be emphasized that measurements of nutrient regeneration using separate zooplankton fractions (such as micro-, meso-, and

macrozooplankton) should be treated with caution because in a natural food web, the trophic interactions between the fractions can result in a significantly different nutrient regeneration. Mesozooplankton, through grazing, excretion and "sloppy feeding," can affect nutrient regeneration from both phytoplankton (the primary consumers of nitrogen) and the protozoa (the primary regenerators of nitrogen). The net effect of mesozooplankton on the regeneration of nitrogen will be negative or positive depending on the trophic interactions between the microbial food web and microzooplankton and between microzooplankton and mesozooplankton (Glibert et al., 1992; Miller et al., 1995, 1997; review by Glibert, 1998).

Third, the match (time-lag) between the seasonal evolution of phytoplankton and zooplankton biomass can influence the export of matter in an ecosystem. For example, a high match (short time-lag) maintains phytoplankton biomass low, limiting the aggregation of large cells and, thus, their vertical export. This results in rapid recycling of phytoplankton in the water column and low sinking losses. This phenomenon, together with the retention of mesozooplankton particulate products in the water column, corresponds to a retention food chain, as opposed to an export food chain (review by Wassmann, 1998). Another consequence of a high match is that when this match occurs, microzooplankton is probably less grazed on by mesozooplankton, allowing a better recycling of nitrogen by microzooplankton. During this period, the system would be dominated by an herbivorous and retention web (the herbivorous web, including microbial components, as discussed in the review by Legendre and Rassoulzadegan, 1995). Therefore, to establish such indirect effects of zooplankton, vertical flux studies should examine the carbon-nutrient outflux from zooplankton, the vertical flux of phytoplankton and zooplankton products, the match between the seasonal evolution of phytoplankton and zooplankton biomass, the primary production, and the zooplankton trophic interactions and grazing pressure.

A fourth aspect appears when the potential contribution of nitrogen outfluxes of copepods and the nitrogen uptake of phytoplankton are compared (Table 5). This comparison shows that although several studies examined the potential contribution of copepod ammonia excretion to the nitrogen uptake of phytoplankton, few examined simultaneously the nitrogen supply from ammonia excretion and particulate nitrogen production. Table 5 shows that we found only one study (Small et al., 1983), limited to the nitrogen production from faecal pellets. This lack of interest in the particulate nitrogen production from copepods is the result of two assumptions: (1) the contribution of particulate nitrogen to the total nitrogen produced is much lower than that of ammonia excretion, and (2) excretion is an direct contribution to the ammonia pool, whereas previous degradation and remineralization are needed for particulate products. However, the first assumption may not always be true. Because the sum of all copepod PN production has a rate

Table 5 Mesozooplankton (dominated by copepods) nitrogen production (from ammonia excretion or faecal pellet production), phytoplankton nitrogen uptake and their ratio

Study area	Depth (m)	N supplied by mesozooplankton (μg N m^{-3} h^{-1})		N uptake by phytoplankton (μg N m^{-3} h^{-1})	Mesozooplankton N supply[a]/phyto N (%)	Source
		Ammonia excretion	FPP			
Sargasso Sea	0–200	—	—	140–1700 (NH$_4$)	10 (NH$_4$)	Dugdale and Goering, 1967
North Pacific Ocean	—	3–5		6–10 (NH$_4$)	45–50 (NH$_4$)	Eppley et al., 1973
Off Peru (coastal upwelling)	0–100	4–20	—	20–290 (NH$_4$)	1–30 (NH$_4$)	Smith, 1978a
Newport River estuary	1	4–400	—	40–4200 (NH$_4$)	8 (NH$_4$)	Smith, 1978b
Ross Sea	0–200	1–2	—	65–100 (NH$_4$)	2 (NH$_4$)	Biggs, 1982
East-central Pacific Ocean	0–100	12	1	63 (total N)	20 (total N)	Small et al., 1983
Off Morocco (upwelling)	0–40	46	—	124 (NH$_4$)	37 (NH$_4$)	Head et al., 1996
Mediterranean (Catalan) Sea						
coastal	0–100	20–33	—	11–20 (total N)	100–285 (total N)	
frontal	0–100	5–111	—	16–58 (total N)	9–189 (total N)	Alcaraz et al., 1988, 1994
offshore	0–100	1–13	—	3–39 (total N)	5–160 (total N)	

Values are range (two values) or mean (one value). FPP: faecal pellet production.

[a]Faecal pellet nitrogen production or ammonia excretion nitrogen production, or their sum when data from both were available.

close to the nitrogen excretion rate (Table 2), the particulate nitrogen may constitute an amount equal or greater than that originating from nitrogen excretion. In some periods or areas, the nitrogen from all PM together could be mostly remineralized in the water column and would be then be as important as excretion in the potential contribution to the uptake of primary producers. Therefore, future studies should examine simultaneously the contribution of excretion and particulate products to the nitrogen offered in the water column.

Finally, concerning carbon export, the emerging view is that it is mainly macrozooplankton faecal pellets, phytoplankton, and marine snow that are involved in the sedimentary carbon flux; their relative contributions are highly variable and depend on multiple interacting factors (review by Turner, 2002). However, there are still open questions about the pellets that stay in the water column: the "missing faeces." Among these missing faeces, a large part may be microzooplankton faecal pellets that are tiny and thus sink very slowly (Small *et al.*, 1987; Ayukai and Hattori, 1992). The quantity of missing faeces is poorly known because most studies investigating faecal pellet flux have not examined faecal pellet production, and this limits discussion (Dam *et al.*, 1993). Among the few studies on faecal pellet flux that include faecal pellet production values, some authors use direct measurements (Small *et al.*, 1983, 1989; Ayukai and Hattori, 1992; Wexels Riser *et al.*, 2001, 2002), but others are based on indirect estimations (Bathmann and Liebezeit, 1986; Voss, 1991; Roman and Gauzens, 1997; Roman *et al.*, 2000, 2002). Little is also known concerning the fate of the missing faeces, such as the relative roles of coprophagy (González and Smetacek, 1994), remineralization, and integration into marine snow. Future research should include the quantity and fate of the missing faeces and other zooplankton particulate products that remain in the water column.

In conclusion, it should be noted that for a long time, most scientific work on carbon burial caused by copepods was limited to faecal pellets, and as measured by sediment traps. The evaluation of the role of copepod particulate products on the transport and recycling of elements and compounds not only requires pellet flux measurements but also should attempt to quantify the production and fate of all products. Little is known of the relative effects of detritiphagy, remineralization, or integration into the marine snow, especially for copepod particulate products other than faecal pellets. Concerning nutrient recycling by copepods, many workers have examined only ammonia excretion. As discussed previously, in some periods or areas, the nitrogen from PM could be mostly remineralized in the water column and would then be as important as excretion. Furthermore, many workers have come to conclusions only in terms of percentages, without comparing the actual values obtained with those in literature, or only with literature of the same study area, thus often leading to speculative or limited discussion. For example, a

low contribution of faecal pellet carbon to the total carbon vertical flux could be relative to other sources of particulate matter. In shallow waters, other sources of particulate matter may be more important than in the open sea, thus reducing the relative faecal pellet contribution, whereas the absolute value of faecal pellet vertical flux can be higher than in the open sea. Therefore, to obtain a more constructive discussion, comparison of actual values obtained should be done with literature from other areas than the one studied to determine the importance of a process on a global scale. Also, although shallow coastal areas are sites of high production and carbon fluxes, few sediment trap studies have been carried out.

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