

Copepods  
Feeding  
Non-algal diets  
Bacteria  
Ciliates

Copépodes  
Nutrition  
Détritus  
Bactéries  
Ciliés

# Factors controlling utilization of non-algal diets by particle-grazing copepods. A review

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## ABSTRACT

Marine copepods can potentially obtain food from any known stock of organic matter, in either dissolved or particulate form. Filtering mechanisms utilized by these crustaceans allow them to capture particles of various sizes, in the form of detritus and living prey. With the exception of phytoplankton, the role of detritus, bacteria, ciliates and flagellates in the diets of copepods is still poorly known, despite the relative importance of their standing stock. The evaluation and comparison of their contribution depend on the standardization of parameters for all categories of particles, in order to define: 1) their trophic value (i.e. C/N, protein and carbohydrate contents...); 2) their utilization (i.e. ingestion and assimilation rates); 3) their role in the transfer of organic matter to copepods (i.e. respiration, growth and production rates). Depending on the type of food and behaviour of the consumer, factors controlling the ingestion rate are not necessarily correlated with the trophic value of the food. Digestive enzyme activities also depend on the concentration and composition of the particles. However, we have yet to establish the relationships between those activities, and to determine what copepods need during their developmental phases. Generally, data on the chemical composition of natural diets and on the digestion strategy of copepods are few. The paucity of such information is critical because the available data are inadequate to evaluate existing theories and do not permit the matching of most of the recent models on nutrition with experimental findings obtained with copepods.

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## RÉSUMÉ

### Facteurs de contrôle et utilisation des régimes naturels par les copépodes marins filtreurs

Les copépodes marins pélagiques disposent d'un potentiel alimentaire varié appartenant aux divers stocks connus de matière organique, dissoute et particulaire. Les mécanismes de filtration, mis en jeu par ces crustacés, permettent la capture des particules de tailles diverses. Cet ensemble de particules comprend des détritiques et des proies vivantes, d'origine végétale et animale. À part le matériel d'origine phytoplanctonique, le rôle des détritiques, des bactéries, des ciliés et des flagellés dans le régime des copépodes est encore bien mal connu, malgré leur biomasse relative importante. Devant les lacunes et les contradictions rencontrées dans la littérature, liées essentiellement à l'hétérogénéité de ces régimes alimentaires, nous devons maintenant chercher à standardiser, pour toutes ces catégories de particules, un ensemble de paramètres définissant : 1) leur valeur nutritive (i.e. C/N; contenu en protéines-glucides...); 2) leur utilisation (i.e. taux d'ingestion et d'assimilation); 3) leur rôle dans le transfert de matière à l'échelon secondaire (i.e. taux de respiration, de croissance et de production). Une telle standardisation est indispensable pour évaluer et comparer l'importance relative de chaque catégorie de particules dans la nutrition des copépodes. Selon le type de nourriture et le comportement du consommateur, les facteurs contrôlant le taux d'ingestion ne sont pas nécessairement corrélés avec la valeur nutritive du régime. Chez les copépodes, l'activité des enzymes digestives dépend aussi de la composition chimique et de la concentration des substrats. Cependant, nous ne connaissons pas encore les

relations existant entre ces activités physiologiques et les besoins métaboliques des copépodes au cours de leurs phases de croissance. En général, les informations relatives à la composition chimique des régimes naturels et aux stratégies de capture et de digestion, sont trop peu nombreuses. Elles ne permettent pas encore d'évaluer l'adéquation ou l'inadéquation entre les modèles les plus récents concernant la nutrition et les résultats expérimentaux obtenus avec les copépodes.

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## INTRODUCTION

Considering the volume of the whole ocean, several reports suggest that detritus amounts to about  $2 \times 10^{13}$  kg, which is five times more than the phytoplankton biomass and ten times less than the amount of dissolved organic carbon; the biomass of bacterioplankton represents only  $10^{11}$  kg (Cauwet, 1978; 1981). Similar proportions have been reported elsewhere (Duursma, 1961; Conover, 1978; MacKinnon, 1981; Nienhuis, 1981). More than 70% of the particulate matter is inorganic (Wangersky, 1965).

The production, transformation and decomposition of organic matter vary according to the depth of the water column (Cauwet, 1981): 1) in the upper layer (< 500 m), most production of organic matter and recycling of detritus is due to the living organisms; 2) in deeper waters, as particles sink chemical processes of sorption and dissolution, as well as bacterial activity are responsible for transformation and decomposition. These transformations lead to pools of organic matter with abundance, size, composition and nutritive characteristics depend on where and when they were available for zooplankton.

In oceans and coastal waters, the food of particle-grazing copepods comprises both living and non-living particulate organic matter. This material can originate either directly from primary production, herbivore grazing followed by predation, or from detritus, with attendant bacteria, protozoa and particle-feeders. Understanding the quantitative dynamics of the flux of matter from the producers to other trophic levels remains a primary aim. The utilization by pelagic and coastal copepods of non-living particles as well as living-particles, including bacteria, microzooplankton, and phytoplankton, to meet their metabolic demands

has been the subject of a number of investigations (see reviews by Jørgensen, 1966; Darnell, 1967; Marshall, 1973; Conover, 1978; Sorokin, 1978). However, the non-algal fraction of organic particles is often considered as a supplementary food source for over-wintering and deep-sea copepods (Seki, Kennedy, 1969; Corner *et al.*, 1974; Harding, 1974), or when primary production is less than the food requirements of the populations (Heinle, Flemer, 1975; Sorokin, 1978). The non-living fraction has been generally assumed to be a poor food source which can not be readily metabolized (Jørgensen, 1962; Marshall, 1973; Heinle *et al.*, 1977).

Among all the possible pathways involved in the utilization of organic matter by copepods (Fig. 1), the one-link design in laboratory experiments is not necessarily realistic; rather, a combination of pathways seems to provide a more probable utilization of the food existing in nature (Pomeroy, 1974). The quality of the food, expressed in terms of respiration, assimilation, growth or reproduction, has been explored for only a few species of phytoplankton. The trophic value of most of the naturally occurring particles on which copepods feed is still unknown. The assessment of the value of a specific food, especially with reference to growth, fecundity and survivorship of pelagic crustaceans, is complicated if the separation of each category of food must be made. Most organisms do best in mixtures of different algal species, detritus and algae, or bacteria and algae (Nassogne, 1970; Paffenhöfer, 1970; Provasoli *et al.*, 1970; Heinle *et al.*, 1977). Apart from nutritional deficiencies, some algae, as well as bacteria, can be toxic or can produce toxic metabolites (Marshall, Orr, 1955; Urry, 1965; Conover, 1979; Porter, Orcutt, 1980).

The biochemical composition of most particulate foods captured by zooplankton has been largely ignored. This

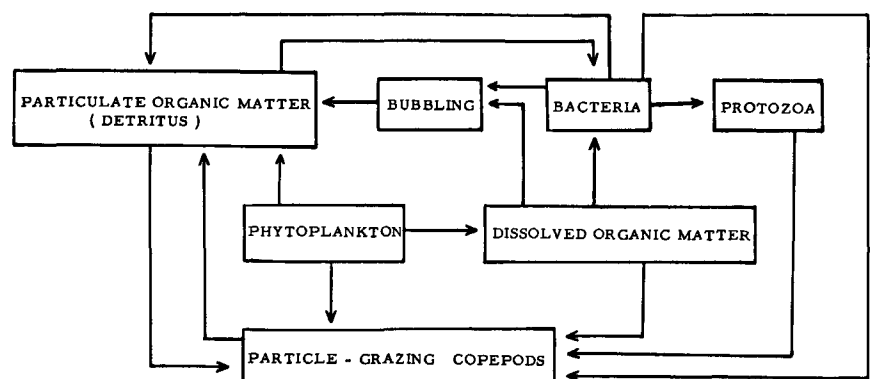


Figure 1  
Diagram of the various pathways involved in utilization of organic matter by copepods.

is unfortunate, in view of the fact that the digestive capability and growth/ingestion efficiency of various zooplankters are influenced by the quality of their algal food as defined by the proportions of certain major biochemicals (Provasoli, d'Agostino, 1969; Sick, 1976; Mayzaud, Poulet, 1978; Scott, 1980). How zooplankton make the decision to capture a fraction of their food from living resources and the remainder from the detritus food chain is unknown. This report reviews current observations and relevant concepts on the feeding of marine copepods in order to show that the utilization of algal and non-algal diets are perhaps, governed by the same rules.

#### PREFERENTIAL UTILIZATION OF PARTICULATE MATTER OVER DISSOLVED MATTER

It is generally agreed that most of the food of marine crustaceans is ingested in particulate form (Anderson, Stephens, 1969; Corner, 1978; Stewart, 1979; Stephens, 1980). Direct uptake of dissolved compounds by zooplankters is controversial. Experiments carried out with several species suggested that zooplankton, specially at the pre-feeding and various developmental stages, may adsorb dissolved matter (Table 1). Anderson and Stephens (1969) could not detect any significant uptake of amino acids and glucose by either *Artemia salina* nor *Tigriopus californicus*. They considered that all uptake was associated with microorganisms on the exoskeleton of the crustaceans. Even though the role of dissolved matter as a direct food source is equivocal, or may not be quantitatively important, various chemicals nevertheless act on the feeding processes through chemoreception, as demonstrated for marine organisms ranging from bacteria to fish (Adler, 1969; Mackie, Grant, 1974; Dempsey, 1978). A diversity of excretory molecules of plant and animal origin act as allelochemicals (Whittaker, Feeny, 1971). Depending on the nature of the molecules, stimulation of the specific chemoreceptors may trigger or inhibit sexual, feeding or social

behaviour. Experiments have demonstrated that dissolved organic matter could play a direct role in the location of prey (Bainbridge, 1953; Hamner, Hamner, 1977; Poulet, Marsot, 1980), in the feeding rate and selectivity of food (Poulet, Marsot, 1978; 1980), in the inhibition of feeding (Porter, 1977; Conover, 1979) and recently in aggregation (Poulet, Ouellet, 1982). The chemical nature of these active compounds is still unknown except for certain amino acids (Hamner, Hamner, 1977; Poulet, Marsot, 1980; Poulet, Ouellet, 1982). These molecules originating from a chemical source can be detected at very low concentrations ( $< 10^{-5}$  Moles; Mackie, Grand, 1974; Poulet, Ouellet, 1982), far below the ordinary background levels of dissolved organic carbon in the sea. Soft-bodied invertebrates are capable of absorbing dissolved matter at natural concentrations *via* wall-cell carrier—transport systems (Stewart, 1979). In contrast, marine crustaceans, such as copepods, apparently do not possess such abilities. While the enormous stock of dissolved carbon in sea-water may not have direct trophic significance for zooplankton, the detection of specific molecules, thus indirectly utilizing solutes, constitutes a major feeding adaptation among pelagic crustaceans, permitting the location, detection and selection of solid prey (Fuzessery, Childress, 1975; Hamner, Hamner, 1977; Poulet, Marsot, 1978; 1980).

A possible additional indirect source of dissolved organic matter depends on the initial formation of particles resulting from the dissolution of bubbles in the water column or their breakage at the sea surface (Baylor *et al.*, 1962; Sutcliffe *et al.*, 1963; Johnson, 1976; Johnson, Cook, 1980). Growth of *Artemia* was used as a preliminary test of whether such organic particles might constitute a satisfactory food for marine filter-feeders (Baylor, Sutcliffe, 1963), but these observations have never been confirmed; particles produced by bubbling should be reexamined as a possible food for marine zooplankton.

Table 1  
Direct uptake of dissolved organic matter by zooplankton.

Organism in experiment	Developmental stage	Type of molecule	Concentration	Uptake	% body weight	T°C	Authors
<i>Euchaeta japonica</i>	nauplii	Enriched medium CEM 1 (EDTA + trace metals)	mg	Increase survival		10	Lewis and Ramnarine (1969)
<i>Calanus finmarchicus</i>	not provided	Total hydrolyzate of algae ( $^{14}\text{C}$ polysaccharides)	1-10 mg.l $^{-1}$	0.71-4.26	0.2-1.2 0.9-1.3	7	Khaylov and Yerokhin (1971)
<i>Tigriopus brevicornis</i>				3-12 8.mg $^{-1}$ .day $^{-1}$			
<i>Euphausia krohnii</i>	Eggs; Nauplii	Labelled amino acids	10 $^{-3}$ -10 $\mu\text{g.l}^{-1}$	38-310 1-4 $\times 10^3$ pg*			Pavillon (1977)
<i>Cyclops oithonoides</i>	not provided	Labelled glucose	0.02-1 g.l $^{-1}$	10-100 cpm.mg $^{-1}$ $\times 10^3$		22	Gyllenberg and Lundqvist (1978)
<i>Daphnia magna</i>	adults	$^{16}\text{C}$ amino acids in mixtures	0.125 n mol of each	0-0.15 n mol. vial $^{-1}$ .h $^{-1}$			Gardner and Miller (1981)
<i>Neocalanus plumchrus</i>	adults	Labelled glucose	2.3 $\times 10^{-9}$ mol	via dermal glands and midgut			Chapman (1981)

\* : (Pavillon: personal communication).

To further assess the importance of converting dissolved carbon to particulate form, we need to evaluate the quantitative significance of bubbling processes relative to the production and composition of particles by other means in the sea. Johnson and Cook (1980) showed that the sizes of particles formed were a function of the initial bubble size and of the concentration of organic materials that were present. Living particles of small size can also be adsorbed on bubbles. Recently, Weber *et al.* (1983) have indicated the mechanism (i.e. interception) of scavenging of waterborne bacteria by rising bubbles.

## UTILIZATION OF DETRITUS

Few records exist of detrital feeding by copepods. Experiments in which artificially-produced or natural detritus were used generally gave contradictory results. Five types of detritus have been considered: 1) artificial detritus; 2) plant and animal detritus of recognizable planktonic origin; 3) naturally occurring detritus from coastal or estuarine surface water; 4) structureless aggregates from deep water; and 5) detritus originating from coastal macrophytes. Depending on the category, detritus types 1 to 3 are readily ingested by copepods, whereas types 4 and 5 are not eaten at all. *Tigriopus* sp. was fed on dried-pulverized mulberry leaves (Egami, 1951), and cultures of *Temora* sp. survived well when provided with pulverized fish food (Gaudy, pers. comm.). Freshly dead and decomposed phytoplankton cells and fecal material are usually consumed by zooplankton (Paffenhöfer, Strickland, 1970; Pechen-Finenko, Pavlovskaya, 1975; Paffenhöfer, Knowles, 1979). Natural suspensions of particulate matter, 20 to 80% of which are composed of detritus, are not only ingested and assimilated but also could form a dominant fraction of the copepod's diet (Petipa *et al.*, 1970; Gerber, Marshall, 1974; Poulet, 1976; Roman, 1977; Chervin, 1978). Chopped detritus from growing wild rice (Heinle *et al.*, 1977) or from macrophytes (Roman, 1977), as well as organic flakes (Paffenhöfer, Strickland, 1970), were never ingested or were poorly assimilated by copepods.

These studies only list the positive and negative responses but have not examined the real factors controlling the utilization of detritus. Among these factors are the types and ages of the detritus diet. During aging, the detritus pool becomes available at different rates to consumers; detritus derived from phytoplankton decays more quickly and hence is utilized more readily than detritus originating from macrophytes (Tenore, 1977; Tenore, Hanson, 1980; Skopintsev, 1981).

Recent studies on the selective feeding of copepods have shown new concepts which can be extrapolated to the detritus food chain. Hence, selective utilization of detritus may depend on both physical state and chemical composition of the particles. Extremely small-sized detritus or flakes exceeding the range of maximum filtration efficiency of copepods may be poorly captured. Particles can be utilized by copepods between  $\sim 1$  to

200  $\mu\text{m}$  equivalent spherical diameter (Marshall, 1973; Frost, 1972; 1975; Conover, 1978; Poulet, 1978; Harris, 1982).

The concentration of food can also affect feeding behaviour. Frost (1972) demonstrated that the ingestion rate of *Calanus pacificus* feeding on phytoplankton cultures was constant and independent of food level when particulate carbon was greater than 200  $\mu\text{g.C.l}^{-1}$ . Below this level, the ingestion rate was directly proportional to the concentration of food, regardless of cell size. Similarly, a saturation-type curve was obtained when food concentration exceeding the upper natural level ( $> 800 \mu\text{g.C.l}^{-1}$ ) was offered to *Pseudocalanus minutus* over a period of time shorter than that needed for acclimation (Mayzaud, Poulet, 1978).

The amount of detritus offered to copepods in some experiments exceeded the concentration of seston normally found in nature. Nor was the size of the detritus utilized in those experiments really considered. For example, Heinle *et al.* (1977) provided copepods with 6 to 100  $\text{mg.l}^{-1}$  of artificial detritus, while Chervin (1978) worked with concentrations higher than 0.6  $\text{mg.l}^{-1}$ , and Petipa *et al.* (1974) used a detritus concentration 1000 times that found in the sea. Under such very high concentrations, copepods are likely to reach feeding saturation or even to cease feeding, so that the conclusion of these authors that detritus was a poor source of food are not totally valid and should be reconsidered. At concentration levels below the saturation level ( $< 500 \mu\text{g.C.l}^{-1}$ ), it appears that ingestion and assimilation rates are positively correlated with the amount of detritus available (Fig. 2A, Poulet, 1976; Fig. 2B, Chervin, 1978). Selection for detritus can be examined with the selectivity index (E) following Ivlev (1955). The index computed for *Pseudocalanus minutus* feeding on both living and non-living particles showed positive selection for detritus in 56% of the

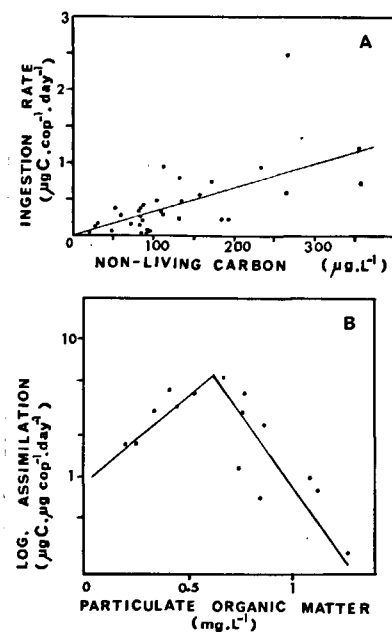


Figure 2 Relationships between abundance of particulate matter and A) ingestion rates of *Pseudocalanus minutus* (from Poulet, 1976); and B) assimilation rates by natural assemblages of coastal copepods (from Chervin, 1978).

experiments, alternating temporally with negative values, apparently without any seasonal pattern (Poulet, 1976). There was no clear, preferential uptake of a given category of particles. Similar observations were reported by Chervin (1978). Her values for (E) were all positive at concentrations below  $400 \mu\text{g.C.l.}^{-1}$  and all negative for higher concentrations.

Paffenhöfer and Strickland (1970) suggest that selectivity for detritus may be associated more with the physical state of the particles than with their chemical composition. Recent observations by Poulet and Marsot (1978; 1980), demonstrate to what extent copepods will eat detritus when presented with a choice between it and living particles. Tests using artificially manufactured microcapsules ( $\sim 8$  and  $\sim 50 \mu\text{m}$ ) offered to *Eurytemora*, *Acartia* and *Calanus*, showed that the ingestion rates of the three copepods depended on the type of microcapsules. Those releasing molecules were preferentially eaten, while those containing no stimulatory compounds were either avoided, broken down into smaller pieces and finally rejected, or ingested at a very low rate (Poulet, Marsot, 1978; 1980). When inert beads (8 and  $20 \mu\text{m}$ ) and phytoplankton (5 to  $10 \mu\text{m}$ ) were mixed in suspension, *Calanus* selectively ingested the living cells and readily avoided the beads (Donaghay, Small, 1979). As a first approximation, an analogy can be made between the capture of artificial beads and that of detritus by copepods. I assume that refractory detritus similar to those studied by Paffenhöfer and Strickland (1970), or described by Gordon (1970), are poorly ingested simply because they lack specific chemicals which could stimulate the copepod's chemoreceptors. Non-stimulatory compounds in water-insoluble particles may consist of humus, chitin or any other stable polymers.

Detritus composed of recognisable plant or animal materials may be chemically "active" particles which release molecules by diffusion, by autolysis of dead cells, by biodegradation by attached bacteria or from metabolites of the bacteria themselves (Newell *et al.*, 1981). Sanders (1972) found that the net release of soluble organic matter from detritus ( $29 \mu\text{g.l.}^{-1}.\text{day}^{-1}$ ) during decomposition in lake water may be 2-6 times that of phytoplankton ( $4-11 \mu\text{g.l.}^{-1}.\text{day}^{-1}$ ) in the photic zone. The chemical activity of the detritus, expressed as the amount and type of molecules released during degradation, should be incorporated in future studies related to feeding. They might, as an attractant or repellent, induce copepods to select or reject, on a chemosensory basis, non-living particles undergoing decomposition or colonization by microorganisms.

## UTILIZATION OF FECES

Zooplankton fecal material is a constituent of detritus, the production and transport of which has been measured under various conditions (see review by Paffenhöfer, Knowles, 1979). However, the importance of this organic pool as a source of food for copepods is still poorly known. Paffenhöfer and Knowles (1979) demonstrated that *Eucalanus pileatus* and *Temora*

Table 2

Grazing rates ( $\text{ml.swept clear.copepod}^{-1}.\text{day}^{-1}$ ) on fecal pellets versus grazing rates on phytoplankton cells of *Rhizosolenia* by *Eucalanus pileatus* (from Paffenhöfer, Knowles, 1979).

Fecal pellets	Phytoplankton
150	195
195	160
250	210
270	470
300	410
370	360

*stylifera* grazed fecal pellets and cells of *Rhizosolenia* at similar rates (Table 2), but the nutritional value of feces for filter-feeders depends on several factors. Assuming a mean assimilation efficiency of 70% (Conover, 1966), the amount of plant food released as pellets is 30%. The ecological importance of pellets depends on the further utilization of organic matter from a previously incompletely assimilated food source (Paffenhöfer, Knowles, 1979). The volume of pellets of most zooplankters ranges from  $3 \times 10^3$  to  $10^8 \mu\text{m}^3$ , corresponding to a particle size range of about 18 to  $600 \mu\text{m}$  spherical diameter (Fowler, Small, 1972; Small *et al.*, 1979; Paffenhöfer, Knowles, 1979). Below  $300 \mu\text{m}$ , these particles are compatible with the filtering capacity of most copepods. The availability of pellets to pelagic particle-feeders depends also on their sinking rate and on the length of time a pellet remains a single particle. Sinking rates of laboratory-produced fecal pellets vary from 5 to  $400 \text{m.day}^{-1}$  (Honjo, Roman, 1978), in the same range as the calculated values from Stokes law (Schrader, 1971; Hofman *et al.*, 1981) but lower than those estimated for natural zooplankton pellets ( $30-2700 \text{m.day}^{-1}$ ; Small *et al.*, 1979; Bruland, Silver, 1981). Downward transport is reduced or, can be stopped, if size is small enough, or if there is a decrease in the density of the feces. Under such circumstances, fecal material might be trapped in the thermocline (Krause, 1981) and, thus, might contribute to the patchy distribution of a food resource at a given depth. In addition, there might be an increase in residence time of organic matter within the water column. Normally, most of the pellets produced in the euphotic zone are consumed or degraded in the upper section of the water column, with only 0.2% of the daily production reaching the sea floor (Hofman *et al.*, 1981).

Disintegration of feces results from biodegradation by attached heterotrophic microorganisms, as well as from the mechanical breakdown by grazing zooplankters. At  $20-30^\circ\text{C}$ , the temperature of surface waters in temperate regions in summer and in tropical regions, fecal pellets are completely degraded in 1 or 2 days (Honjo, Roman, 1978; Paffenhöfer, Knowles, 1979). According to Turner (1979), changes in carbon and nitrogen contents of the feces occurred very rapidly at  $22^\circ\text{C}$ , following the colonization and degradation of membranes by rod-shaped bacteria and ciliates. At  $5^\circ\text{C}$ , pellets were still intact in shape and composition after 14 days of incubation (Fig. 3). It appears, therefore, that the significance of feces as a food source for zooplankton depends also on the degree of colonization by bacteria. Turner's results (1979) show that fecal material will be

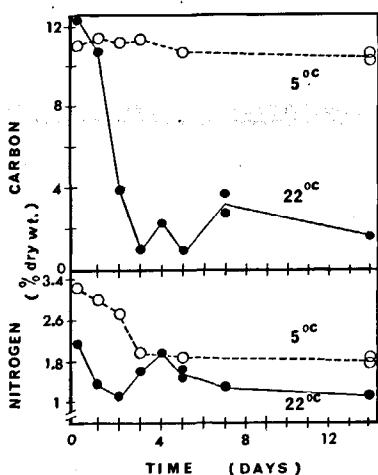


Figure 3  
Changes in the carbon and nitrogen contents of copepod fecal pellets during colonization by bacteria (from Turner, 1979).

a significant food source for zooplankton both before and during the first part of the biodegradation process; that is, when detritus is young (< 3 days; Fig. 3). The removal of organic matter by attached bacteria and the reduction in size of particles through disintegration tend to reduce their nutritional value and availability to consumers of higher trophic levels. Thus, some kind of competition for nutrients exists between bacteria and copepods within the detritus food chain. There is probably a critical period, varying with temperature (Fig. 3), or there may be a particular depth at which pellets plus attached microorganisms reach an optimum food value, after which the nutritional value decreases. At low temperatures (~ 5°C), the final disintegration will take longer.

Reduction of particle sizes may also occur during the feeding by particle-grazing zooplankton resulting from the handling, mastication and rejection of particles (Conover, 1966; Parsons *et al.*, 1967; Marshall, 1973; Poulet, 1973; 1974; O'Connors *et al.*, 1976; Frost, 1977; Poulet, Marsot, 1980). The resulting accumulation of fine particles (< 10 µm) at the left-hand side of the particle spectrum may correspond to as much as 30% of its initial standing stock (O'Connors *et al.*, 1976; Poulet, Marsot, 1980). Another important change is the increase in the surface/volume ratio of these new particles. It remains to be evaluated whether such a physical transformation favours colonization by bacteria which, in turn, contributes to the enrichment of detritus.

## UTILIZATION OF BACTERIA

When living particles become scarce or limited one of the alternatives for copepods is to shift their feeding to resources from the detritus food chain. Bacteria are probably the most important producers of organic matter from detritus, but although their biomass and production in the open sea are often large (Table 3),

Table 3

Approximation of living carbon production and biomass in the sea.  $t = 10^3$  kg (from Sorokin, 1978, and Nienhuis, 1981).

Source of carbon	Production $10^9$ .t.C.yr <sup>-1</sup>	Biomass $10^9$ .t.C
Bacteria	24	0.23
Phytoplankton	19	0.45
Zooplankton	4.24	1.72

Table 4

Reports of bacteria as known food ingested by copepods.

Copepod species	Authors
<i>Tisbe furcata</i>	Lwoff, 1927; Brown and Sibert, 1977; Vandenberghe and Bergmans, 1981
<i>Tigriopus japonicus</i>	Hanaoka, 1973; Ogawa, 1977;
<i>Acartia clausi</i>	Sorokin <i>et al.</i> , 1969
<i>Eucalanus attenuatus</i>	
<i>Paracalanus parvus</i>	Vandenberghe and Bergmans, 1981
<i>Tisbe holothuriae</i>	
<i>Tisbe battagliai</i>	
<i>Tisbe holothuriae</i>	Rieper, 1978
<i>Calanipeda aquadulcis</i>	Zhukova, 1963
<i>Rhincalanus cornutus</i>	Sorokin, 1978
<i>Pleuromamma abdominalis</i>	
<i>Euchaeta marina</i>	
<i>Eucalanus attenuatus</i>	
<i>Paracalanus parvus</i>	
<i>Acartia clausi</i>	
<i>Acartia danae</i>	Petipa <i>et al.</i> , 1975
<i>Clausocalanus mastigophorus</i>	
<i>Eucalanus attenuatus</i>	
<i>Paracalanus parvus</i>	
<i>Undinula darwini</i>	

their role in the transfer of energy to zooplankton is almost unknown. Bacteria probably represent a major pathway whereby fractions of organic matter not normally accessible to zooplankton re-enter the grazing food chain (Fig. 1). The ingestion of bacteria by copepods has been reported several times under laboratory conditions when high cell densities were used (Table 4). Among the major problems encountered by copepods are the very small size and the presumably low concentration of free-living bacteria. Marshall (1973) argued that in the free state bacteria could not form an important part of the diet, except when aggregated onto particles large enough to be retained by their feeding appendages, as shown earlier by Sorokin (1971; Fig. 4), and more recently with harpacticoid copepods by Reiper (1978; Table 5).

Figure 4

Consumption of various types of food by marine copepods: 1) free-living bacterioplankton; 2) flocs of bacterioplankton; 3) diatoms (from Sorokin, 1971).

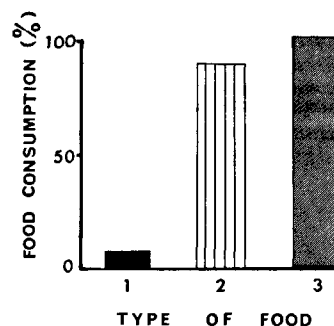


Table 5

Relationship between the ingestion rate of a harpacticoid copepod (*Tisbe holothuriae*) and the size of food offered as bacteria (Strain Schelei 20; from Reiper, 1978).

Type of food	Concentration of bacteria ( $\times 10^6$ .ml <sup>-1</sup> )	Ingestion rate (no.cop <sup>-1</sup> .h <sup>-1</sup> )
Free floating bacteria	2	852
(size: ~ 2-4 µm)	0.5	48
Flocs of bacteria	1.1	2366
(size: 125-250 µm)	2.1	152000

According to Sorokin (1978) natural bacteria concentrations in sea water usually range from 10 to 30  $\mu\text{g.C.l.}^{-1}$ , although higher values have been reported for coastal waters in tropical regions. These values are about 10 to 20 times less than total particulate organic carbon and are the same order of magnitude as living particulate matter, including all organisms less than 200  $\mu\text{m}$ , found in coastal waters (Sutcliffe, 1972; Poulet, 1976; Mayzaud, Taguchi, 1979). The relationship between size and concentration of algae as food has been discussed recently by Poulet and Marsot (1980), showing that copepods could obtain a similar quantity of food from any particle size class, providing that the decrease in the particle size was balanced by an increase of the number of particles (Fig. 5).

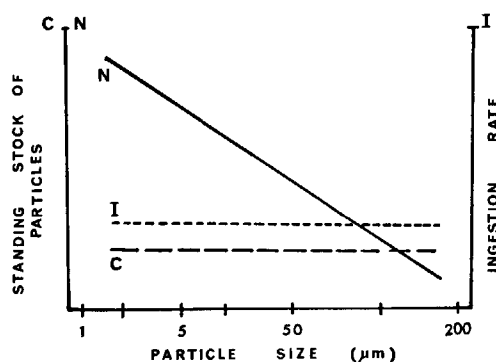


Figure 5  
Schematic relationship between the number and concentration of particles and the ingestion rate of copepods. I: ingestion rate; C: concentration; and N: number of particles.

This relationship can be expressed as follows: assuming that

$$C = V_i N_i, \text{ let}$$

$$I_i = f_i(C_i) = f_i(V_i, N_i) \text{ and}$$

$$I_j = F_j(C_j) = F_j(V_j, N_j) \text{ where}$$

I = ingestion rate, C = concentration, N = number of particles and where i and j are the size ranks of the particles in  $\mu\text{m}$  and V is the particle volume in  $\mu\text{m}^3$ . Then if

$$I_i = I_j \approx \text{constant, then } C_i = C_j \text{ and } V_i N_i = V_j N_j.$$

Knowing that  $V_i \neq V_j$  with  $i < j$ , the food uptake (I) would be constant in both size classes, when  $N_i > N_j$ , when

$$N_i = K N_j; \text{ with } K = V_j/V_i.$$

The value of K is variable and depends on the ratio of the volumes of the particles captured by copepods. With particles as small as bacteria ( $i < 4 \mu\text{m}$ ), this ratio may be very high (Table 6). The population densities of free-living ( $< 0.6 \mu\text{m}$ ) and attached bacteria in the continental shelf region correspond to 0.6 to  $2.4 \times 10^8$  and to 0.4 to  $20.1 \times 10^6 \text{ cells.l}^{-1}$ , respectively (Hodson *et al.*, 1981). Similar concentrations have been reported by Newell *et al.* (1981). Even though bacteria are very small, high densities ( $N_i$ ) in sea water may be compatible with the high values of K required for a constant ingestion rate, given that the number of phytoplankton cells ( $N_j$ ) is generally of the order of  $10^2$  to  $10^3 \text{ cells.l}^{-1}$ , except during blooms. This means that in nature,

Table 6

Values of K when the size ( $\mu\text{m}$ ) of the particulate food ranges from bacteria (i) to phytoplankton (j).

i	j	K
0.2	5	$1.6 \times 10^4$
0.5	5	$1 \times 10^3$
1	5	$1.2 \times 10^2$
0.2	10	$1.3 \times 10^5$
0.5	10	$8 \times 10^4$
1	10	$1 \times 10^3$

ingestion of free-living bacteria by filter-feeding copepods is probably not common unless densities are greater than  $10^8 \text{ cells.l}^{-1}$ .

The population density of bacteria can increase with the colonization of phytoplankton debris (Newell *et al.*, 1981). Newell *et al.* (1981) also demonstrated that detritus from *Chaetoceros tricornutum*, which has an initial size mode of 2  $\mu\text{m}$ , formed bacterio-organic aggregates with a size mode of 8-20  $\mu\text{m}$  in non-sterile media. A shift in the size mode did not occur after sterilization. These aggregates were very similar in size to those described in natural waters by Hobbie *et al.* (1972) and to the naturally occurring particles commonly grazed by both "small" (Poulet, 1974; 1978; Conover, 1978) and "large" copepods (Harris, 1982).

Ten years ago, the role of inert particles, the mechanism of bacterial attachment to detritus and the association of bacteria with aggregates was reviewed (Jannasch, Pritchard, 1972; Floodgate, 1972; Wiebe, Pomeroy, 1972). Among the three phases leading to the formation of bacterio-aggregates, the most interesting is the final one, where multiplication occurs and contributes to the formation of a micro-ecosystem (Floodgate, 1972). Several investigators found that 80% of the bacteria were floating free in the water column (Wangersky, 1977). Nienhuis (1981), in reviewing the literature, reported that unattached bacteria may be in a resting stage, whereas the attached bacteria were physiologically more active because of the greater availability of energy sources in the enriched microzones. Other data do not support this concept, but show that the two populations have about the same activity per unit cell volume (Hodson *et al.*, 1981).

Once ingested, bacteria are probably assimilated by copepods. Sorokin (1978) found that bacteria were better assimilated (53 to 80%) than phytoplankton (41 to 66%) by both *Eucalanus attenuatus* and *Paracalanus parvus*. Following the classical concept of filter-feeding by copepods (Marshall, 1973; Nival, Nival, 1976; Boyd, 1976; Frost, 1977) and if filtration occurs by a sieving mechanism, it would be impossible for copepods to ingest single bacteria. It was assumed then that retention efficiency was nil for particles smaller than the aperture size of the filtering apparatus ( $> 5 \mu\text{m}$ ). However, recent observations based on a better understanding of fluid dynamics suggest that particles close to bacterial size might still be ingested (Rubenstein, Koehl, 1977; Poulet, Marsot, 1980; Alcaraz *et al.*, 1980; Koehl, Strickler, 1981).

The range of bacterial population densities ( $10^6$  to  $10^{10} \text{ cells.l}^{-1}$ ) reported by Sorokin (1978); Hobson *et*

*al.* (1981) and Newell *et al.* (1981) for various areas of the world ocean and coastal regions correspond to biomass ranging from 3 to 60  $\mu\text{g.C.l}^{-1}$ , using the conversion factor of  $0.25\text{--}0.5 \times 10^8$   $\mu\text{mol}$  of carbon per bacterium (Stanier *et al.*, 1970). The critical carbon concentration, at which *Calanus pacificus* reaches its maximum ingestion rate ( $I_{\text{max}}$ ) is about 200  $\mu\text{g.C.l}^{-1}$  when phytoplankton cells 10  $\mu\text{m}$  are provided (Frost, 1972). For smaller copepods such as *Pseudocalanus minutus* feeding on naturally occurring particles  $\leq 200$   $\mu\text{m}$ , the critical concentration is around 600  $\mu\text{g.C.l}^{-1}$  according to Mayzaud and Poulet (1978), Conover (1978) and Conover and Huntley (1980). Moreover, the growth efficiency of some copepod species is higher at food concentrations below 50  $\mu\text{g.C.l}^{-1}$  (Harris, Paffenhöfer, 1976; Checkley, 1980). Food concentrations required to satisfy copepod diet and growth are roughly equivalent to the average biomass of bacteria reported in seawater. However, the efficient utilization (ingestion and assimilation) of bacteria even at very high concentrations has not yet been demonstrated.

#### UTILIZATION OF CILIATES AND FLAGELLATES

It is worth noting that, during decomposition, 1 g dry-weight of detritus derived from the turtle grass *Thalassia testudinum*, contains about  $3 \times 10^9$  bacteria,  $5 \times 10^7$  flagellates and  $5 \times 10^4$  ciliates (Fenchel, 1970). Zhukova (1963) reported that  $5 \times 10^9$  cells of microorganisms could be harboured by each gram of detritus. Recent observations (Sherr *et al.*, 1982) also showed that biomass of protozoa reached  $3.8 \times 10^6$  cells  $\text{ml}^{-1}$  after 4 days of decomposition of dead *Peridinium* at 19–21°C. The potential value of detritus-dependent microorganisms as food for pelagic copepods has not been clearly evaluated. Few studies have quantified the trophic relationship between protozoa and copepods, although it has been shown that protozoa can be an important link between organic detritus and copepods (Porter, 1973; Heinle *et al.*, 1977; Berk *et al.*, 1977). As the main consumers of bacteria (Fenchel, 1982a; b), flagellates are natural links between the detritus-bacteria standing stock and higher zooplankton. The link is simple when copepods prey directly on them (Heinle *et al.*, 1977; Berk *et al.*, 1977; Klein Breteler, 1980). The relationship is more complex when pelagic copepods prey on nauplii of harpacticoids which consume detritus, bacteria or flagellates (Porter, 1973; Rieper, 1978; Tacks, Polk, 1982). Studies such as those of Beers and Stewart (1969) and Berk *et al.* (1977) suggest that ciliates are a principal component of the microzooplankton in seawater (10 to 90% of the biomass) and that copepods both graze and grow on them (Heinle *et al.*, 1977; Berk *et al.*, 1977).

#### NUTRITIVE STATUS OF THE POOLS OF SUSPENDED PARTICULATE ORGANIC MATTER

Fifteen years ago, Darnell (1967) stated that a rigorous demonstration of the nutritive role of organic matter should include the following four criteria:

- 1) availability of organic matter;
- 2) ability of the organisms to capture and handle the food material;
- 3) actual utilization of the organic matter in relation to the physical field conditions;
- 4) nutritive value of the consumed material.

These criteria apply to any type of suspended organic matter available to particle-grazing copepods. Problems relevant to each criterion are far from being understood. Those known best are criteria 1 and 2, which have been described in the earlier sections of this report; they have been also reviewed elsewhere (Conover, 1978; Conover, Huntley, 1980).

In the euphotic zone, we know that the various pools of organic matter can potentially satisfy the feeding, growth and reproduction requirements of copepods, but we still guess at the mechanisms. The critical carbon concentration allowing maximum ingestion rate ( $I_{\text{max}}$ ) was measured, and it ranged from 50 to 400  $\mu\text{g.C.l}^{-1}$ , depending on the size of the particles and on the species of copepod (Frost, 1972; Harris, Paffenhöfer, 1976; Mayzaud, Poulet, 1978; Checkley, 1980). The corresponding range for concentration of nitrogen is 10 to 50  $\mu\text{g.N.l}^{-1}$ , assuming a C/N ratio  $< 12$  for most edible particles (Eppley *et al.*, 1977). In oligotrophic waters, the food quantity may be ten times less and becomes a limiting factor (Riley, 1970). It has been observed that with a flattened particle spectrum (Sheldon *et al.*, 1972) and small total concentration, the selectivity of copepods decreases (Poulet, 1973; 1974). How do copepods really behave under such conditions? Do they extend their particle capture over the entire size spectrum (Poulet, 1973; 1974; 1978)?

Is there really a lower threshold concentration, defined as ( $P_o$ ) (Parsons *et al.*, 1967; Mullin *et al.*, 1975) at which ingestion rate is nil? There is probably no a single value of  $P_o$  identical for two size classes of particles. Following Frost (1975) and Conover (1979), it can be argued that  $P_o$  is dependent on cell size and is probably also species-dependent. With *Pseudocalanus minutus*, for example, the  $P_o$  values of a given particle of the spectrum ( $< 200$   $\mu\text{m}$ ) reported by Conover (1979) ranged from 0.01 ppm (for particles  $\sim 100$   $\mu\text{m}$ ) to 0.05 ppm (for particles  $\sim 2$   $\mu\text{m}$ ). This is roughly equivalent to a carbon concentration between 0.2  $\mu\text{g.C.l}^{-1}$  to 1.2  $\mu\text{g.C.l}^{-1}$ , assuming a conversion factor of 0.024 for the carbon to volume ratio (Poulet, 1976; 1977), but the scales of food concentrations we can observe are not necessarily those to which copepods actually respond.

An alternative for copepods would be to utilize patchy accumulations of particles. This raises the problem of the ability of consumers to locate food material and to remain in its vicinity. Such mechanisms are governed by refined behavioural processes we have yet to discover. It is hard to determine how such mechanisms operate in the sea at scales from a few metres or centimetres (microscale level) to a few kilometres (mesoscale level), considering that location and attraction are known to occur on the scale of a few centimetres under undisturbed laboratory conditions (Bainbridge, 1953; Hamner, Hamner, 1977; Poulet, Ouellet, 1982).



Judging from recent data, particle-grazing copepods are well adapted to obtain and to handle all types of food originating from detrital or microplanktonic pools. Their ability to capture food does not depend entirely on the size (Poulet, Chanut, 1975; Poulet, Marsot, 1978), nor on the shape (Gifford *et al.*, 1981) nor on the abundance of the particles (Poulet, 1973; Richman *et al.*, 1980). It depends primarily on the copepod filtering mechanism (Rubenstein, Koehl, 1977; Poulet, Marsot, 1980). The feeding mechanisms which seem compatible with the capture of particles of various size observed among copepods are: 1) for large-sized particles, raptorial feeding (Conover, 1966; Poulet, Marsot, 1980); and 2) for small-sized particles (< 10  $\mu\text{m}$ ), impaction or ciliary-mucus feeding (Poulet, Marsot, 1980).

Type 1 has often been described in the literature and has been observed in recent films (Alcaraz *et al.*, 1980; Koehl, Strickler, 1981). Type 2 still remains speculative. Observations based on high-speed movies (Alcaraz *et al.*, 1980; Koehl, Strickler, 1981) have confirmed predictions concerning filter-feeding in laminar flows, i.e. at low Reynolds number (Purcell, 1977; Rubenstein, Koehl, 1977; Koehl, Strickler, 1981; Cowles, Strickler, 1983; Price *et al.*, 1983). These observations have further shown that the second maxillae of copepods do not behave like an ordinary sieve. Therefore, if all sizes of particles are driven to the mouth area without prior sorting by the setules of the feeding appendages, then copepods might ingest all types of particles originating from both the grazing and detritus food chains.

Concerning the third of Darnell's criteria, we still have very little information for marine copepods. Attempting to evaluate grazing in terms of particle size, temperature and grazer size, Conover and Huntley (1980), found empirically a relation for grazing which varies exponentially with increasing ambient temperature. Earlier observations by Lance (1964) and Fernandez (1977) also showed that temperature, salinity and light intensity have some effect on nutrition. Vidal (1980) has demonstrated the types of relationships existing between food, temperature and copepod growth rates.

For the last of the criteria listed by Darnell (1967) we can only guess how copepods might respond to differences in ambient food quality. The effect of food on growth and reproduction have been often related to the type and concentration of phytoplankton (Nassogne, 1970; Marshall, 1973; Paffenhöfer, Harris, 1976; Conover, 1978, among others). How biological functions are affected by the chemical composition of particles (Checkley, 1980) is not well known under natural food conditions.

Paloheimo and Dickie (1966) found that the growth efficiency of fish ( $K_1$ ) was linearly related to the ration as follows:

$$\log K_1 = \log (\Delta W/R \Delta t) = c - a - bR;$$

where  $\Delta W/\Delta t$  is the growth rate in time  $\Delta t$ ,  $R$  represents the ration and  $a$  and  $b$  are constants. Growth efficiency is also expressed as

$$K_1 = \frac{\Delta W}{R \Delta t}$$

Temperature and food concentration are known to affect ration and growth; thus,  $K_1$  will be also affected by ambient conditions. As mentioned by Reeve (1963) for *Artemia salina* and by Kerr (1971) for young salmon,  $K_1$  is not always linear; it can increase parallel to the ration up to a maximum value, after which it will become negative in response to changes occurring with time in the suitability of food sources. Because of the complex relationships existing between the growth efficiency of copepod and the ambient conditions, specifically food (Vidal, 1980),  $K_1$  combines all these variations and is therefore one of the best predictors of the nutritive value of the food utilized by copepods. The  $K_1$ -concept has been applied to various marine zooplankters (Conover, Lalli, 1974; Harris, Paffenhöfer, 1976; Scott, 1980; Checkley, 1980). The first applications of the concept for copepods (Mullin, Brooks, 1970; Corner *et al.*, 1976; Harris, Paffenhöfer, 1976) show a consistent pattern except for *Pseudocalanus elongatus*, whose  $K_1$  did not correlate either with food level or with ration. Values of  $K_1$  decreased with increasing ration, indicating that an upper critical food level existed above which the ration was higher than that necessary to obtain an optimum  $K_1$  ( $\sim 0.5$ ). Data obtained with *Paracalanus parvus* supports this concept (Checkley, 1980). Surprisingly, the critical values for food were less than  $50 \mu\text{gC.l}^{-1}$  (Harris, Paffenhöfer, 1976; Checkley, 1980). Moreover, Checkley (1980) showed that  $K_1$  based on egg production was also related to the carbon/nitrogen ratio of the available food (Fig. 6). These data allow speculations on how chemical components of the diet might control growth efficiency. They also suggest that nitrogen (hence protein) is a limiting nutrient; the C/N ratio may thus be a good estimator of the food value of particles.

The C/N ratio of naturally occurring particles, including most of the living and non-living material available to copepods, varies from 2 to 35 (Mann, 1972; Le Masson *et al.*, 1977; Eppley *et al.*, 1977). Colonization of detritus by bacteria contributes to its protein enrichment and thus to the lowering of the detritus C/N ratio (Mann, 1972; Turner, 1979). Most healthy phytoplankton cells have a C/N ratio in the range of 5 to 15 (Moal *et al.*, 1977; Checkley, 1980). Russel-Hunter (1970) mentioned that animals have nutritional requirements for protein which correspond to C/N ratios lower than 17. Substituting this value into Checkley's equation (1980),  $K_1 = 1.64 \times (C/N)^{-1}$ , gives a growth efficiency of 0.09 for copepods. If this model applies to copepods then,  $K_1$  values computed for the C/N ratios measured in the

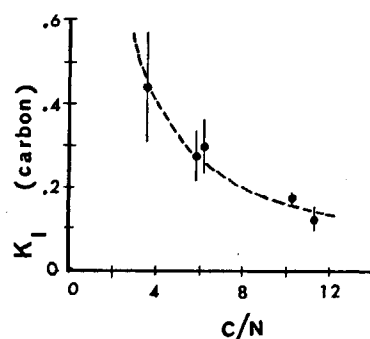


Figure 6  
Variations of the growth efficiency of copepod according to the values of the C/N ratio measured in the diet (from Checkley, 1980).

sea should fluctuate between 0.04 to 0.8. In fact, Tenore (1977) has shown for a deposit-feeding polychaete that fluctuations in nitrogen indeed reflect the variable nutritive value of suspended particles.

What do we know about other biochemical components of particles? Studies carried out so far have analysed spatio-temporal variations of the particulate organic carbon (POC; see reviews by Riley, 1970; Cauwet, 1981; Mackinnon, 1981; Nienhuis, 1981). What does POC mean to copepods? Scott (1980) found that the growth efficiency  $K_1$  of a marine particle-grazing rotifer *Brachionus plicatilis* was governed by the quality of its algal food as defined by the relative proportion of its biochemical components (proteins, carbohydrates, lipids). Work on the chemical composition of several phytoplankton species suggested that a ratio of 4.3.1 for proteins, carbohydrates and lipids may be suitable for the nutrition and growth of zooplankton (Parsons *et al.*, 1961) and of juvenile bivalves (Walne, 1970). However, for rotifers the optimum growth efficiency coincided with ratio 1.1.1. (Scott, 1980). Substrates of digestive enzymes are proteins, carbohydrates and lipids, which may be linearly related with enzyme activity in copepods (Mayzaud, Poulet, 1978). We found that the apparent affinity (1/km) and the rate of digestive capability ( $\tan \alpha = V_m/K_m$ ) for each enzyme varied with time according to the chemical composition and concentration of particles. Assuming that copepods are capable of adapting their digestion to variable ambient food (Mayzaud, Conover, 1976; Mayzaud, Poulet, 1978), the level of each chemical substrate should be examined in trophodynamic studies. Ratios found by Parsons *et al.* (1961), Walne (1970) and Scott (1980) are relevant to cells of phytoplankton only. Does seston have a ratio similar to phytoplankton? The poor nutritive values for non-algal particles often reported in the literature might be due simply to unbalanced levels of proteins, carbohydrates and lipids. We know the range of  $K_1$  for the C/N ratio for *Paracalanus* in culture (Fig. 6), but similar information is lacking for the major chemical components (proteins, carbohydrates, lipids) of suspended particles utilized by copepods under natural conditions. In a small marine basin it was shown that the ratios computed for these three components in suspended matter (< 200  $\mu\text{m}$ ) did not vary much with time nor with level of primary production (Mayzaud, Taguchi, 1979). At high primary production ( $\sim 1 \text{ g.C.m}^{-2}.\text{d}^{-1}$ ) the mean ratio was 6.2.1., while at low primary production ( $< 0.4 \text{ g.C.m}^{-2}.\text{d}^{-1}$ ) it was 7.2.1. In the lower St. Lawrence estuary a similar investigation was conducted during summer of 1975 (Poulet, Marty and Cossa, unpublished data). Figure 7 summarizes the variations of the C/N ratios (A) and of the protein-carbohydrate-lipid ratios (B) for two groups of particle spectra ( $F_1$  and  $F_2$ ) measured below and above the 15  $\mu\text{m}$  size limit. Following the conclusions advanced by Russel-Hunter (1970), Checkley (1980) and Scott (1980), our results suggest the following interpretations: 1) the A and B ratios are heterogeneous for naturally occurring particles, contrasting with those measured for phytoplankton cells; 2) the ratios vary from one type of spectrum to another and even between two size classes

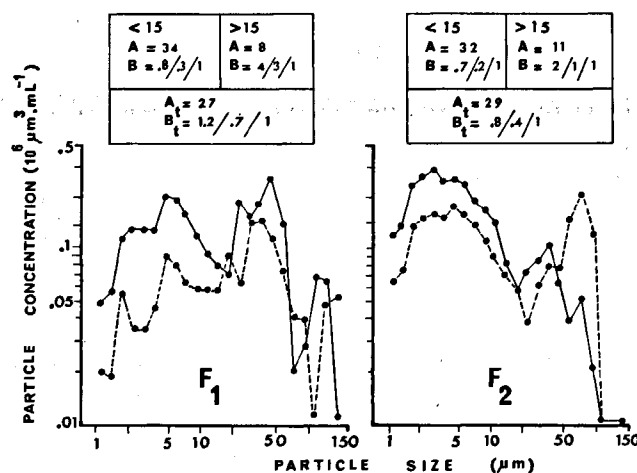


Figure 7

Relationships between the size and chemical composition of naturally occurring particles. Values are expressed in terms of C/N ratio (A); and protein-carbohydrate-lipid ratio (B); for particles smaller and larger than 15  $\mu\text{m}$  (< > 15); and total particles (1 to 150  $\mu\text{m}$ ) measured in two groups of particle spectra ( $F_1$  and  $F_2$ ). Number of measurements  $N \leq 37$ . Solid and dashed lines: limits of a group of spectra having similar shapes (from Poulet, Marty, Cossa, unpublished data).

in the same spectrum; 3) low C/N values (< 17) and "balanced" protein-carbohydrate-lipids ratios (1.1.1. to 4.3.1.) occur for particles larger than 15  $\mu\text{m}$  (Fig. 7, A, B > 15). Does this mean that the nutritive value of such particles would also yield the high  $K_1$  values for copepods feeding on them, as suggested by Checkley (1980) and Scott (1980)?

At the present time, our only certainty is that copepods preferentially graze on particles responsible for the biovolumes observed in particle spectra (Poulet, 1973; 1974; 1978; Conover, 1978; Richman *et al.*, 1980; Harris, 1982). The next logical step is to demonstrate how copepods adjust their selective feeding to various categories of particles so that ingestion of food yield a satisfactory growth/reproduction efficiency for survival in the ecosystem.

## CONCLUSIONS

The most obvious feature of this review is the paucity of information on several properties of the natural diets and on the contribution of non-algal, but living food sources, such as ciliates and flagellates in the transfer of organic matter in the marine food web. It has been shown that both non-algal and algal diets are consumed by copepods. The mechanisms and benefits of such opportunistic behaviour are not always clear. According to the optimal foraging theory (Schoener, 1971; Pike *et al.*, 1977) the components of a copepod's dietary regime should maximize energy intake per unit time. Following a recent model (Taghon, 1981), an optimal ingestion rate exists for any given quality of food; this rate should increase as food quality, in terms of calories, increases, to permit the consumer to maximize its net rate of gain. It is clear that several factors are capable of influencing ingestion rate, e.g. size, shape, abundance, palatability and composition of particles. Depending on the category of food and on the behaviour of the consumer, each

factor listed above may or may not act towards yielding a more nearly optimum rate of energy gain. As shown by Nicotri (1980), the attractiveness of a food for a given consumer may be related to the nutritive value of the food, whereas other consumers may respond to food morphology and availability; hence, factors controlling ingestion rates are not necessarily correlated with the trophic value of the food; i.e., the net energy transferred into respiration, growth and reproduction. Given the wide range of particle categories captured by copepods, factors controlling uptake, such as ingestion and rejection rates, and utilization, i.e. assimilation rates, should be standardized in terms of a few relevant physical and chemical parameters (i.e. size; C/N ratio, proteins, carbohydrates...), so as to permit comparisons between the roles of any particle (living and non-living) grazed by pelagic copepods. However, we can only speculate on the trophic value of each food stock until

more is known about its chemical composition and about the strategy for capture and digestion employed by copepods (Mayzaud, Poulet, 1978; Rubenstein, Koehl, 1977; Poulet, Marsot, 1980). Apart from its intrinsic interest as an aspect of copepod biology, the identification of the dietary properties of the food and feeding strategies of copepods is of importance in the understanding of the dynamic of the marine food web.

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