

REVIEW

On the diets of calanoid copepods

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ABSTRACT: A review of the literature (ca 1900 to 1992) on copepod feeding indicates that combinations of stochastic and deterministic processes result in behaviors, or feeding strategies, that optimize nutritional gain from the food environment, and further, that strategies change in response to environmental variability. Because the diet is the product of a feeding strategy, one may gain insight into the ways in which copepods respond to their food environments by measuring their diets. Investigations of the links between copepod feeding and production suggest that dietary diversity is often a key to the procurement of a nutritionally complete ration, and the optimization of secondary production within constraints dictated by the physical environment. The ability to eat different kinds of foods (omnivory) and the tendency to include a variety of foods in the daily ration may enhance the probability of obtaining a nutritionally complete ration in variable, nutritionally dilute, food environments. The notion that the relationship between feeding and production in copepods is driven by dietary diversity is derived in part from a recent recognition of the diversity of microplanktonic organisms that potentially or actually contribute to the diet. Further, the concept is consistent with current trophic dynamic models in which food webs are envisioned as complex interwoven systems rather than short, simple chains.

INTRODUCTION

This paper is concerned with the diets of small calanoid copepods, which historically have been considered predominantly herbivorous or omnivorous. The term 'diet' is defined here as the amount of each kind of food that an animal ingests over some period of time. This definition emphasizes the links between the quantitative aspects of feeding, viz. the ingestion rate, and the qualities of the particles ingested.

Attempts to measure the copepod diet and to understand its significance in terms of secondary production have been prominent themes in the literature for many decades (cf. Marshall & Orr 1955, Ryther 1969, Morey-Gaines 1980, Lasker 1988, Kleppel et al. 1991). It has become apparent that both the kinds and quantities of food in the diet affect copepod production (Durbin et al. 1983, Roman 1984) and, ultimately, production at higher trophic levels (Hardy 1924, Ryther 1969, Smith & Eppeley 1982). It has also become evident that, in addition to chance encounters with food particles, there is a cognitive component to feeding (Donaghay

& Small 1979, Alcaraz et al. 1980, Strickler 1982). Copepods can actively search for, capture and choose to ingest or reject potential food particles.

If feeding can be selective, then the role that copepods play in the ecosystem is, in part, a function of the strategies they use to obtain their diets. The feeding strategy represents the copepod's response to a food environment composed of many kinds of particles, which is acted upon by an array of fluid dynamic processes (Legendre & Demers 1984, Haury & Pieper 1988, Rothschild 1988, Rothschild & Osborne 1988). Understanding the relationship between feeding and production depends upon one's ability to measure that environment and to understand some of the mechanisms that underlie the copepod's response to it.

Recent reviews (e.g. Paffenhöfer 1988) have emphasized the relationship between copepod feeding, anatomical structure and behavior. This paper considers a somewhat different perspective, the relationship between the food environment, the diet and production. I will trace the evolution of current thinking on copepod feeding and, in doing so, will describe the changing

focus of feeding theory from carbon-based models to nutritional models which consider the consequences of the copepod's responses to both the quantitative and qualitative attributes of the food environment.

FEEDING STRATEGIES – ADAPTIVE RESPONSES TO ENVIRONMENTAL VARIABILITY

There are well over 1000 extant species of marine and estuarine calanoid copepods (Raymont 1983). The feeding activities of relatively few of these have been studied. Most of the existing measurements have been made in the dark, at experimentally specified temperatures and in homogeneously distributed, unialgal food environments with cultured copepods when possible (e.g. Mullin & Brooks 1967, Paffenhöfer 1970, 1971, Harris & Paffenhöfer 1976, Paffenhöfer & Harris 1976). Among the goals of these studies has been to determine, in a systematic way, the effect of varying physical environment, food composition and food concentration on feeding rates [see major summaries or edited volumes by Parsons et al. (1977), Kerfoot (1980) Raymont (1983)]. It has been observed that: (1) feeding activity is influenced predictably by temperature (Heinle 1969, Kiørboe et al. 1982, 1985); (2) within limits imposed by the physical environment, the ingestion rate varies rectilinearly with particle concentration, the initial slope of the relationship being affected by particle size or biomass (Mullin 1963, Parsons et al. 1967, Hargrave & Geen 1970, Frost 1972, 1977, Nival & Nival 1973, 1976, Mullin et al. 1975, Reeve & Walter 1977, Bartram 1980, Poulet & Marsot 1980, but also see Mayzaud & Poulet 1978, Huntley 1981); and (3) the rate at which water is processed to remove particles (i.e. the clearance or 'filtration' rate) is governed by the sensory-motor capabilities of the copepod species and by specific attributes (e.g. size distribution) of the particles in the food environment (Paffenhöfer 1971, 1988, Frost 1972). Paffenhöfer (1988) described the variety of density-dependent clearance patterns exhibited by calanoid copepods and showed how different responses arise from the anatomical and physiological adaptations of different species.

There has, over the past 2 decades, been a continuous interest in field-validation of these laboratory observations by the use of *in situ* measurements (Mackas & Bohrer 1976, Boyd et al. 1980, Dagg & Grill 1980, Kiørboe et al. 1982, Dagg & Wyman 1983, Schnack & Elbrächter 1983, Turner 1984b, Kleppel 1988) and incubation experiments with natural particle samples (Poulet 1973, 1978, Poulet & Chanut 1975, Roman & Rublee 1981, Gifford & Dagg 1988, White & Roman 1991, 1992, Kleppel 1992). Although field

methodologies are imperfect and sometimes controversial (Harbison & McAlister 1980, Conover et al. 1986, Lopez et al. 1988, Penry & Frost 1990, 1991, Gieskes et al. 1991, Head & Harris 1992, but also see Kiørboe & Tiselius 1987, Dam & Peterson 1988, Durbin et al. 1990), they have helped us to better appreciate that the complex food environments to which copepods are exposed in nature are reflected in the diets (Kleppel & Pieper 1984, Turner 1984a, b, c, 1985, 1987, Hopkins 1985, Kleppel et al. 1988, 1991) and, therefore, the feeding strategies (Price 1988) of these animals.

The question of whether copepods feed selectively, by evaluating the suitability of individual particles as food, or non-selectively, by randomly searching the environment with feeding currents and ingesting every particle that is captured, has been debated since at least the first half of the century (Easterly 1916, Cannon 1928, Lowndes 1935, Harvey 1937). The latter model was favored until the mid-1970s (Anraku & Omori 1963, Wilson 1973). Filtration was thought to be the principle food-catching mechanism (Anraku & Omori 1963, Wilson 1973), though raptorial processes were also reported (Richman & Rogers 1969). Boyd (1976) proposed that the filtering apparatus, the second maxillae, generally behave as 'leaky sieves', retaining particles larger than the distance between setae on the endites (the intersetal distance) most efficiently.

Increasingly, however, observers (e.g. Poulet & Chanut 1975) reported that, contrary to filtration theory (such as the leaky sieve model), copepods can capture particles smaller than the intersetal distance. A lack of the necessary musculature, however, obviates the possibility that intersetal distances could be altered (Richman et al. 1977). Nonetheless, in 'quasi-natural' particle environments (where water samples are passed through a mesh to remove large organisms, then incubated in bottles), copepods located and grazed down peaks in the food size-frequency spectrum over a range of particle sizes (Poulet 1973, 1974, 1978, Poulet & Chanut 1975, Poulet & Marsot 1980). Koehl & Strickler (1981) and Paffenhöfer et al. (1982) demonstrated that in the low Reynolds number environments within which they exist, copepods are suspension feeders. The second maxillae are effectively paddles, which can push parcels of water containing particles toward the mouth, rather than filtering particles from the water.

Regardless of the mechanism, both size-selective and non-selective feeding have been documented. Cowles (1979) placed these apparently contradictory observations in perspective by proposing that feeding strategies vary with food environment. He demonstrated that, consistent with optimal foraging theory,

copepods from waters off Peru feed size-selectively when food is abundant and non-selectively when food is scarce. Price et al. (1983) and Price & Paffenhöfer (1986) clarified the situation further by demonstrating cinematographically that cell-size mediated differences in appendage movements lead to differences in particle capture mechanisms.

Coincident with research on the mechanics of capturing food has been an interest in the cognitive aspects of feeding (food detection, 'decisions' to ingest or reject). Sensory perception exists in both far (remote) and near (at the mouth) fields (Gerritsen & Strickler 1977, Alcaraz et al. 1980, Yen 1988). Strickler & Bal (1973), Strickler (1982) and Legier-Visser et al. (1986) have articulated models of prey detection from remote chemical and tactile stimuli. Chemoreceptors at the mouthparts, responsible for near-field discrimination of food, were described by Friedman & Strickler (1975) and Friedman (1980).

Considerable experimental data confirm the existence of sensory perception. Birge (1898) reported that freshwater copepods reject the dinoflagellate *Ceratium* sp. *Calanus finmarchicus* also rejects *Ceratium* sp. (Harvey 1937). Huntley et al. (1986) reported that several dinoflagellate species produce chemical substances that induce avoidance and morbidity in *Calanus pacificus*; other dinoflagellates are readily ingested (Mullin & Brooks 1967, Paffenhöfer 1971). Mullin (1963) demonstrated that *Calanus helgolandicus* ingests exponentially growing algae at higher rates than it does senescent algae. Similarly, Houde & Roman (1987) reported that *Acartia tonsa* would ingest more exponentially growing, than senescent, diatoms per unit time. This would result in higher maximum ingestion rates on senescent cells, but larger and nutritionally richer rations from log-phase cells. Paffenhöfer & Van Sant (1985) showed that the ingestion rate of *Eucalanus pileatus* varies such that live phytoplankton > dead phytoplankton > fecal pellets. Poulet & Marsot (1978) reported that copepods ingest microcapsules impregnated with extracts from phytoplankton at higher rates than capsules impregnated with seawater when both capsule types are present in the same container. Cowles et al. (1988) showed that *A. tonsa* distinguishes nutritional quality in mixtures of nutritionally rich and poor cells of the same diatom species. Kiørboe (1989) corroborated these observations, noting further that egg production was influenced by the qualitative aspects of feeding.

Experience with a food also influences particle capture and hence, apparent selective behaviors (Harvey 1937, Price & Paffenhöfer 1984, Donaghay 1988). Particle rejection, for instance, declines with experience.

THE DIET AND THE FOOD WEB: DEMISE OF THE DIATOM → COPEPOD LINK

Productive pelagic food chains have been characterized as having relatively few links between primary producers and top consumers and by energetic transfer efficiencies on the order of 15 to 20 % (Lindeman 1942, Ryther 1969). Characteristic of such food chains is a direct link between an important group of primary producers, usually the diatoms, and an abundant herbivorous crustacean, such as the copepods. The diatom→copepod link has been a key element in the classical pelagic food chain for at least 6 decades. There is strong evidence, however, that this concept is simplistic and misleading. That is not to suggest that copepods do not eat diatoms. Rather, I would argue that attempts to relate feeding and production by means of a single energetic link are contrary to the current understanding of how matter and energy move through ecosystems. There is ample evidence that copepod diets are frequently broad or diverse, composed of a variety of different kinds of foods.

The diatom→copepod link arose for several reasons. (1) Diatoms are relatively abundant in the net phytoplankton, especially in productive ecosystems. They were long ago identified as one of the principal foods in copepod diets (Fleming 1939). (2) Dinoflagellates, the other major class of net phytoplankton, grow more slowly than diatoms. They are often scarce in the phytoplankton, relative to diatoms, and some are avoided by copepods. Historically, they have not been considered important in copepod diets. (3) Until recently, the microbial food web was poorly understood, and small phytoplankton (i.e. 2 to 5 µm equivalent spherical diameter, ESD) being inefficiently captured by adult copepods, were thought to be nutritionally insignificant. (4) Most calanoid copepods seemed morphologically suited for herbivory (Anraku & Omori 1963). Because the importance of protozoans in the plankton was not appreciated until recently, most studies of carnivorous feeding by copepods focused on predation of copepod eggs and nauplii (Dagg 1977, Landry 1981, Conley & Turner 1985, Smith & Lane 1987). In other than a few species, such as *Centropages furcatus* (Paffenhöfer & Knowles 1980), carnivory was thought to be inconsequential to the diets of most calanoid copepods. (5) Although copepods can ingest detritus (Roman 1977, Downs & Lorenzen 1985), detritivory was considered a secondary source of nutrition (Paffenhöfer & Van Sant 1985), limited principally to copepods in estuaries (Heinle et al. 1977, Roman et al. 1983).

A new understanding of the relationships between copepods and the food environment has been emerging over the past 2 decades. At least 3 novel concepts

about trophic structure have affected the general perception of this relationship: (1) energy flows through complex food webs rather than along simple food chains; (2) small phytoplankton and microzooplankton are important in metazoan food webs; and (3) fluxes of materials and energy through ecosystems are governed, in part, by the relationships between food nutritional composition and the nutritional needs of the feeders, rather than simply by the carbon balance between them.

By accepting the notion that energetic pathways in pelagic ecosystems involve complex, highly interactive 'webs', rather than simplistic, linear chains, we are compelled to re-examine the diatom→copepod link. As stated above, the problem with this link is not whether copepods eat diatoms but rather the perception that copepod feeding strategies can be characterized by a single, simple interaction.

The overwhelming body of evidence now suggests that copepod diets are, indeed, diverse. Fig. 1, which

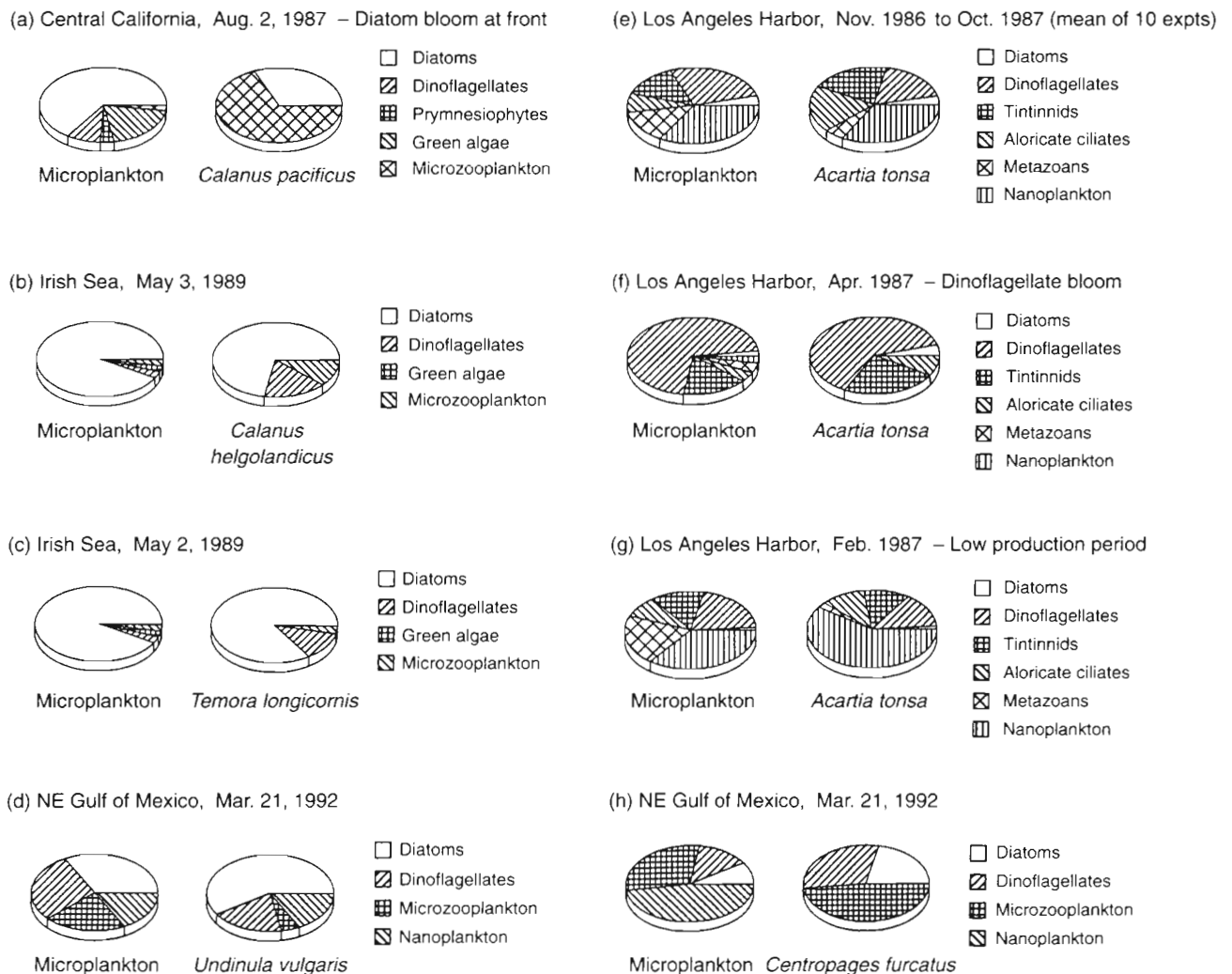


Fig. 1. Microplankton (= phytoplankton + microzooplankton) distributions in the food environment and in the diets of copepods from a variety of coastal ecosystems. Microplankton composition and diet of (a) *Calanus pacificus* off Central California, USA, and of (b) *C. helgolandicus* and (c) *Temora longicornis* in the Irish Sea were estimated by pigment analysis techniques described by Kleppel et al. (1988). In these analyses, fucoxanthin, peridinin, 19'-hexanoyl-oxyfucoxanthin, lutein and astaxanthin were used as biomarkers for diatoms, dinoflagellates, prymnesiophytes, green algae and microzooplankton respectively. Units of measurement are ng pigment l⁻¹ for microplankton and ng pigment copepod⁻¹ for copepods. Estimates of microplankton composition and diets of (d) *Undinula vulgaris* and (h) *Centropages furcatus* in the NE Gulf of Mexico, and of (e, f & g) *Acartia tonsa* in Los Angeles Harbor, were generated from bottle experiments with natural particles that were analyzed by microscopy (see Kleppel 1992). The units of the estimated microplankton concentrations are µg C l⁻¹. Copepod diets are expressed as µg C copepod⁻¹ d⁻¹. Data for (b & c) from Kleppel et al. (1991); data for (e, f & g) from Kleppel (1992). All other data were previously unpublished.

summarizes some of the available data on the composition of the copepod diet, illustrates that: (1) dietary diversity is the rule rather than the exception, i.e. copepod diets reflect the variety of phytoplankton and microzooplankton taxa present in the environment (e.g. Turner 1984b); and (2) the distributions of food groups in the environment and in the diet are often (but not always) different.

There is little doubt that copepods can be cognizant of the food environment and are exceptionally well adapted to respond behaviorally to variability within that environment. These responses represent feeding strategies which, it will be assumed, have evolved to optimize the nutritional gain realized from the food environment. In the following sections, some aspects of copepod diet composition are discussed and the hypothesis that dietary diversity increases the probability of obtaining a nutritionally complete ration is considered.

COMPOSITION OF THE COPEPOD DIET

It is well known that diatoms figure prominently in copepod diets, especially in productive (e.g. upwelling) ecosystems (Smith 1982, Schnack & Elbrächter 1981) and during blooms (Turner 1984c, 1985). The role of dinoflagellates in the copepod diet is more difficult to specify and seems to depend upon the copepod species in question (Morey-Gaines 1980), as well as on the species and physiological status of the dinoflagellate (Table 1). In attempting to understand the role of dinoflagellates (or any group of organisms) in the diet it is necessary to recognize that the dietary importance of dinoflagellate biomass, and the impact of copepod feeding on dinoflagellate biomass in the water column, are not necessarily the same thing. For example, copepod grazing accounts for <5 % of the dinoflagellate carbon in Chesapeake Bay (USA) during blooms (Sellner & Olson 1985), but dinoflagellates may contribute a large (though variable, e.g. <0.2 to >60 %, average = 33 % in Los Angeles Harbor, California, USA) portion of the carbon in the diets of common estuarine species (Kleppel 1992).

Although the C:N ratios of diatoms tend to be lower than those of dinoflagellates (T. Whitledge pers.

Table 1. Some dinoflagellate species that are ingested or rejected by copepods

Copepod	Dinoflagellate	Source
Ingested		
<i>Calanus pacificus</i>	<i>Gonyaulax catenella</i>	Huntley et al. (1986)
	<i>Gonyaulax acatenella</i>	
	<i>Gonyaulax polyedra</i>	
	<i>Gonyaulax sphaeroidea</i>	
	<i>Gyrodinium resplendens</i>	
	<i>Gyrodinium dorsum</i>	
	<i>Peridinium foliaceum</i>	
	<i>Gymnodinium splendens</i>	
<i>Paracalanus parvus</i>	<i>Gonyaulax tamarensis</i>	Dagg (1977)
	<i>Protoceratium reticulatum</i>	Huntley et al. (1986)
<i>Acartia tonsa</i>	<i>Gonyaulax tamarensis</i>	Dagg (1977)
	<i>Ceratium furca</i>	Morey-Gaines (1980)
	<i>Ceratium dens</i>	
	<i>Gonyaulax polyedra</i>	Kleppel (1992)
	<i>Prorocentrum micans</i>	
<i>Centropages typicus</i>	<i>Prorocentrum micans</i>	Smith & Lane (1985)
<i>Eucalanus pileatus</i>	<i>Prorocentrum micans</i>	Cowles & Strickler (1983)
Rejected		
<i>Calanus finmarchicus</i>	<i>Ceratium</i> sp.	Harvey (1937)
<i>Calanus pacificus</i>	<i>Scrippsiella trochoidea</i>	Huntley et al. (1986)
	<i>Gonyaulax tamarensis</i>	
	<i>Prorocentrum reticulatum</i>	
	<i>Ptychodiscus brevis</i>	
	<i>Gymnodinium flavum</i>	

comm.), volume-specific concentrations of cellular nutrients were found to be 3 to 3.5 times higher, on average, in axenically cultured dinoflagellates than in diatoms of the same size, grown under identical conditions (Hitchcock 1982). Thus, over a range of particle sizes characteristic of those readily taken by copepods, dinoflagellates are estimated to provide 2 to 6 times more protein, 2.5 to 3.5 times more carbohydrate, and 1.1 to 3.0 times more lipid than diatoms of equivalent volume, under these idealized conditions (Fig. 2). Of course, in nature the nutritional environment is more complex, but it is useful to recognize that basic differences in nutritional value exist between taxonomic groups.

The relationships between the copepod diet and the microbial food web have only recently been elaborated. Protozoans are abundant in the sea and may consume a large portion of the daily primary production (Pomeroy 1974, Capriulo & Carpenter 1980, Banse 1982, Sherr et al. 1986, Stoecker & Capuzzo 1990, Gifford 1991, Lessard 1991). Certain protozoans are nutritious to copepods and are readily ingested

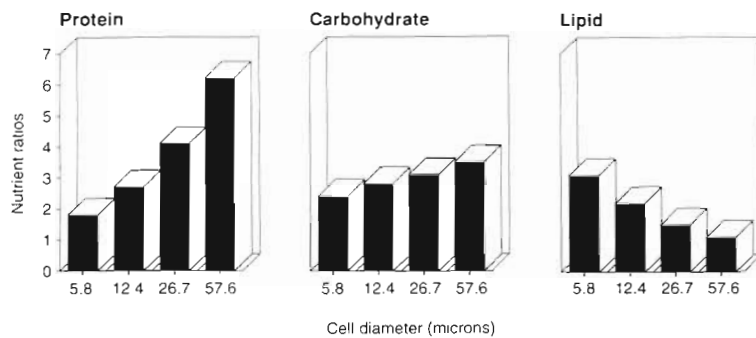


Fig. 2. Dinoflagellate:diatom cellular nutrient ratios calculated over a range of cell sizes that is exploited by calanoid copepods. Ratios are based on idealized estimates derived from relationships between cell volume and protein, carbohydrate and lipid content in axenic algal cultures (Hitchcock 1982). These ratios demonstrate that (1) fundamental differences in chemical composition exist in the phytoplankton which are reflected in taxonomic composition, and (2) nutritional relationships in the phytoplankton vary over the cell size spectrum

(Stoecker & Egloff 1987, Stoecker & Capuzzo 1990). Protozoans that ingest nano- and picoplankton may, in turn, be preyed upon by mesozooplankton, transferring previously unavailable energy into the metazoan food web (Sherr et al. 1986) (Table 2).

DIETARY DIVERSITY – ECOLOGICAL SIGNIFICANCE

Assuming that the copepod diet can be characterized as diverse – consisting of diatoms, dinoflagellates, microzooplankton and other kinds of particles – one must then ask, 'What adaptive advantage does a diverse diet have over a narrow one?' Two advantages are immediately apparent. First, the ability to eat a

variety of foods allows an animal to modify its diet with variability in the food environment, an asset in nutritionally dilute environments (Paffenhöfer 1984). Second, a diverse diet may increase the probability that the copepod will obtain a nutritionally complete ration.

Switching between herbivory and carnivory is an example of how copepods can respond to substantial changes in food composition. Switching behavior has been demonstrated in the laboratory (Landry 1981, Stoecker & Sanders 1985), and, more recently, corroborating evidence has been obtained from field studies (Gifford & Dagg 1988, Kleppel et al. 1988). Field data must be interpreted cautiously given the risk of bias introduced by hydrodynamic variability. However, significant

changes in the proportions of plant and animal biomass in the diet (rather than shifts from one extreme to the other) have been documented over relatively short periods of time. Typical frequencies of variability in the diet are on the order of hours to days, often in apparent response to changes in the food environment (Fig. 3). The effect of dietary switching on secondary production has not been quantified, though logically, the ability to obtain at least some minimal level of nutrition from a variety of food sources, would seem advantageous.

The particles that copepods eat vary in nutritional composition (Parsons et al. 1977, Hitchcock 1982, Stoecker & Capuzzo 1990) and feeding strategies which enable the copepod to sample a variety of foods may permit nutrients lacking in one source to be

Table 2. Evidence of carnivory among small calanoid copepods

Species	Relative importance in diet	Details	Source
<i>Centropages hamatus</i>	33 % of diet	Copepod nauplii	Conley & Turner (1985)
<i>C. typicus</i>	100 % of body C d ⁻¹	Fish larvae	Turner et al. (1985)
<i>C. typicus</i>	0–78 % of lab diet	Eggs of own species, with and without other food	Smith & Lane (1987)
<i>Acartia hudsonica</i>	73 % of lab diet	<i>Euterpina pectinatus</i> + <i>Gonyaulax tamarensis</i>	Turner & Anderson (1983)
<i>A. tonsa</i>	Up to ca 80 % of lab diets	Various microzooplankton/ algal mixtures	Stoecker & Sanders (1985), Stoecker & Egloff (1987)
<i>A. tonsa</i>	3–41 % of daily ration	Natural microplankton	Gifford & Dagg (1988)
<i>A. tonsa</i>	0–70 %	Natural microplankton	Kleppel (1992)
<i>Calanus pacificus</i>	22–94 %	Natural microplankton	Kleppel et al. (1988)
<i>C. pacificus</i>	Up to ca 100 % of lab diet	Copepod nauplii	Landry (1981)
<i>C. helgolandicus</i>	33 %	Natural microplankton	Kleppel et al. (1991)
<i>Temora longicornis</i>	54 %	Natural microplankton	Kleppel et al. (1991)
<i>Clausocalanus</i> spp.	55–97 %	Natural microplankton	Kleppel et al. (1988)

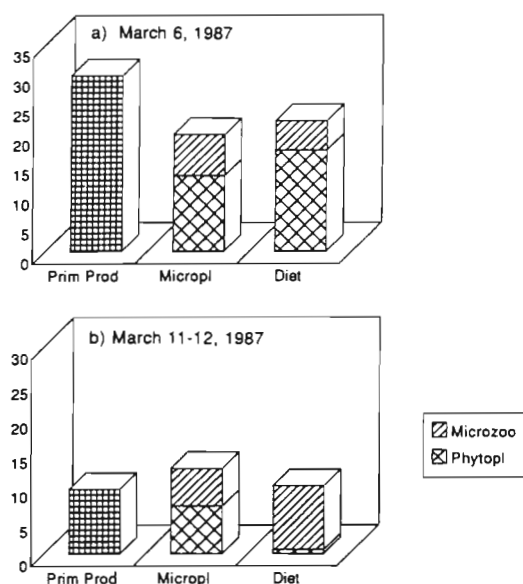


Fig. 3. *Calanus pacificus*. Example of relatively rapid shifts in observed diet coincident with variation in the food environment. Study was conducted off Santa Catalina Island, California, USA. Samples were collected in close spatial proximity of one another 5 d apart (March 6, 01:30 h, 33° 30' N, 118° 26' W; March 11–12, ca 00:00 h, 33° 30' N, 118° 23' W). (a) On March 6, primary production ($\text{mg C m}^{-2} \text{ h}^{-1}$) was relatively high, the microplankton was dominated by phytoplankton (biomass expressed as mg C m^{-2} , divided by 100 for scaling purposes), and the copepod fed primarily on phytoplankton (diet expressed as gut fullness, as ng C copepod^{-1} , multiplied by 10). (b) On March 11–12, primary production had declined to one-third its previous level, the phytoplankton biomass in the microplankton was half of its previous level (though the microzooplankton biomass was unchanged) and the diet of *C. pacificus* was dominated by microzooplankton. (After Kleppel et al. 1988)

obtained from others. For example, *Acartia tonsa* survived longer and grew at higher rates when its diet consisted of a mixture of the diatom *Thalassiosira weissflogii* and detritus than when each food was provided alone (Roman 1984). Although *T. weissflogii* provided a majority of the nutrients required by the copepod, the detritus provided C_{18} saturated and unsaturated fatty acids, and several amino acids (e.g. asparagine-glutamine, serine, taurine, tyrosine) that were scarce or lacking in the diatom. The significance of these findings is best appreciated in light of evidence that copepods seem incapable of storing amino acids (Goulden & Place in press). When dietary amino acid concentrations are inadequate for protein catabolism, deamination occurs and the ration is lost through ammonium excretion.

In another study, regression analyses were performed to determine the relationships between the egg production rate of *Acartia tonsa* and the daily ingestion rate of the copepod on various kinds of phyto- and

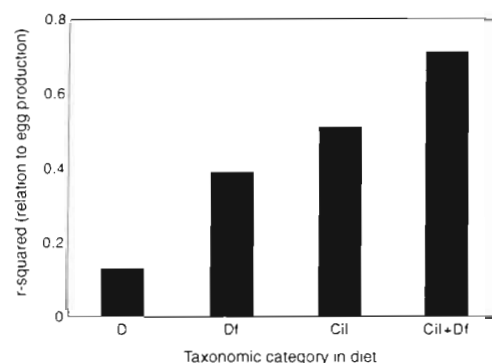


Fig. 4. *Acartia tonsa*. Proportion of variance explained by the relationship between egg production and various components of the diet of *A. tonsa* off southern California, USA, during 10 experiments between November 1986 and October 1987. The various biomass (as carbon) components of the diet are regressed against egg production, the bars in the figure representing the r^2 for the regression. Taxonomic categories are: D, diatoms; Df, dinoflagellates; Cil, ciliates (tintinnids + aloricate forms); Cil+Df, sum of ciliate + dinoflagellate biomass. (After Kleppel et al. 1991)

microzooplankton in quasi-natural food environments (Kleppel et al. 1991). The correlation of egg production to dietary microplankton biomass increased as diatoms < dinoflagellates < ciliates < dinoflagellates + ciliates (Fig. 4). [The addition of diatom biomass to the last regression did not improve the correlation ($r^2 = 0.60$)]. Apparently, the combination of dinoflagellates and ciliates in the diet contributed more than each food individually to egg production (Kleppel et al. 1991). Diatom biomass, which was not systematically associated with egg production, may serve other metabolic functions (see below).

Similarly, Støttrup & Jensen (1990) observed that *Acartia tonsa* ingests the small green alga *Dunaliella tertiolecta* in phytoplankton mixtures but ingestion is reduced and egg production declines when it is offered as a unialgal diet. The authors demonstrated that, while rich in total lipids, *D. tertiolecta* lacks polyunsaturated fatty acids larger than C_{18} , unlike other, small, algal species, which do support egg production.

FEEDING STRATEGIES AND THE NUTRITIONAL ENVIRONMENT

Controlled experiments have been conducted in the laboratory to ascertain the extent to which copepod feeding behaviors are consistent with the predictions of optimal foraging theory (DeMott 1989). The results of such studies frequently corroborate the theory (Cowles et al. 1988, DeMott 1989). In nature, however, the taxonomic and biochemical complexity of the food

Table 3. Summary of data on the chemical (protein, lipid, carbohydrate) compositions of copepods. nd: no data

Category	Chemical composition as % of dry wt			Source
	Protein	Lipid	Carbohydrate	
Gulf of Mexico copepods	29.6–67.7	2.9–56.3	nd	Morris & Hopkins (1983)
<i>Pleuromamma abdominalis</i>	50.3–57.9	8.3–6.8	nd	Morris & Hopkins (1983)
Mixed copepods	59.0	7.0	20.0	Brandt (1898), cited in Rayment (1983)
<i>Calanus finmarchicus</i>	30.0–77.0	10.5–47.0	nd	Orr (1934)
<i>C. helgolandicus</i>	75.2	11.0	nd	Nakai (1955), cited in Rayment (1983)
<i>C. helgolandicus</i>	43.0	46.0	9.0	Vinogradova (1964), cited in Rayment (1983)
<i>C. helgolandicus</i>	nd	28.0	nd	Lee et al. (1972)
<i>Acartia clausi</i>	79.3	2.7	nd	Nakai (1955), cited in Rayment (1983)
<i>A. tonsa</i>	27.7	19.5	25.4	Houde & Roman (1987)
Mean of all data	46.2	20.0	18.1	
Standard deviation	24.9	17.7	6.8	
% Coefficient of variation	53.9	88.5	37.6	

environment make it difficult to apply such models (Kleppel 1992). In part, the difference between the laboratory and the natural environment is that in the laboratory one can create clear distinctions within the food environment (e.g. nutritious vs non-nutritious food). In nature, such distinctions are not as clearcut; a food item may contain some nutrients but not others. It may be most effective, therefore, to describe natural food environments on the basis of their nutritional characteristics, and to describe the feeding activities of copepods as responses to nutrient distributions.

The emphasis of studies on copepod nutrition has been on individual nutrients, most notably, various forms of nitrogen (i.e. particulate organic N, amino acids, protein). Interest in nitrogen stems, in part, from its perceived importance to phytoplankton growth in the sea. Checkley (1980) was one of the first to suggest that nitrogen (as protein) ultimately limits copepod production in many areas. This hypothesis has, in fact, been supported in several coastal and nearshore ecosystems (Checkley 1980, Ambler 1985, Checkley et al. 1992). In *Acartia tonsa*, the functional ingestion response varies directly as protein content in the food environment (Houde & Roman 1987). *A. tonsa* takes up protein from its food more rapidly than other nutrients (Roman 1991) and both the ingestion and egg production rates of *A. tonsa* may be influenced by particulate organic nitrogen concentrations (Kjørboe 1989).

Nutrients, however, function interactively as well as individually. Certain lipids, for example, facilitate protein metabolism (Gallagher et al. 1979, Roman 1984), and the nutritional requirements of animals change with season, age, and physiological response to environmental variability. Therefore, the feeding strategy must simultaneously address 2 related functions: optimizing the acquisition of scarce but important nutrients, and satisfying the immediate nutritional and

physiological needs of the animal. For example, during all stages of growth, and especially in early life history, carbon, as protein, is taken up at a high rate by *Acartia tonsa*. However, adult females put carbon into lipid at higher rates than do immature copepodites (Roman 1991).

An examination of the chemical (nutritional) compositions of copepods (Table 3) shows that while chemical composition is, in general, quite variable, the lipid pool is by far the most variable (CV = 89%, as opposed to 54% for protein and 36% for carbohydrates). Structural and metabolic proteins are essential for all animals and their concentrations vary as the animal grows. Lipids, on the other hand, are used to store energy, and the specific energy storage needs of copepods can vary enormously through life. Lipid biochemistry subdivides the Copepoda on the basis of ontogeny (i.e. certain lipids are taken up rapidly for egg production; Roman 1991), activity (lipid storage may determine diapause success; Ohman 1987), recent feeding history (Hakanson 1984) and biogeography (offshore species generally store lipids, nearshore species tend not to; Dagg 1977, Miller et al. 1977).

The proper way of describing the nutritional environment depends upon the question being addressed and on the forms in which nutrients are utilized by the animals. For example, different lipids perform vastly different functions and, as Støttrup & Jensen (1990) showed, some phytoplankton, while rich sources of total lipids, may lack the specific lipids critical to certain functions (e.g. egg production). Another example, shown in Fig. 5a to c, also illustrates this point, and emphasizes the relationship between the nutritional characteristics of the food environment and the nutritional requirements of the copepod. Fig. 5a, b shows that, while the amino acid distributions of the dinoflagellate *Amphidinium carteri* and the diatom *Thalassiosira*

weissflogii are similar, only the diatom contains the metabolic amino acid, ornithine (used in the Krebs and urea cycles). Ornithine is also present in the copepod *Calanus pacificus* (Fig. 5c). Thus, this copepod, feeding on *A. carteri* alone, would be unable to obtain for ornithine [note the implications in the context of the observations of Goulden & Place (in press), cited above]. Obviously, measuring total protein concentrations in the food environment would be inadequate to explain differences in the metabolism of *C. pacificus* caused by differences in amino acid composition of the algae. Thus, subtle differences in the nutritional structures of food environments can have significant ecological implications.

CONCLUSION

The purpose of feeding is to obtain the energy and materials needed to function, survive and ultimately reproduce. Although feeding strategies are limited by the sensory-motor capabilities of the species, they have been evolved to optimize nutritional gain for the individual, and thereby to enhance the fitness of the population.

To this end copepod diets tend to be diverse, reflecting the complexity of the pelagic food web. While classical trophic dynamic models emphasized simplicity, to minimize the leakage of energy from the chain, more recent ideas depict a series of alternative pathways along which matter and energy can travel to higher trophic levels. Consistent with this paradigm, diversity in copepod diets provides alternative pathways for obtaining required nutrients and increases the probability of obtaining a nutritionally complete ration. Production and nutrition are related, and nutritionally complete diets would seem to enhance the probability of success for the individual, and ultimately the population, within the environment.

The notions that the ecological goal of foraging behavior is to obtain a nutritionally complete ration, and that dietary diversity tends to optimize the probability of realizing that goal are not, in themselves, new concepts. Complete nutrition is a key element in aquaculture, and is intuitive in much of biology and ecology. Yet the point of this paper differs in fundamental ways from the tenets of aquaculture, and ecologists have only recently begun to acquire the tools to investigate the details of nutrition in marine ecosystems. While in aquaculture one seeks to understand nutrition in order to maximize the output, this paper has focused on understanding how animals respond to diversity and variability (attributes lacking or minimized in aquaculture) in the food environment. In doing so, one hopes to gain some basic appreciation and predictive sense of

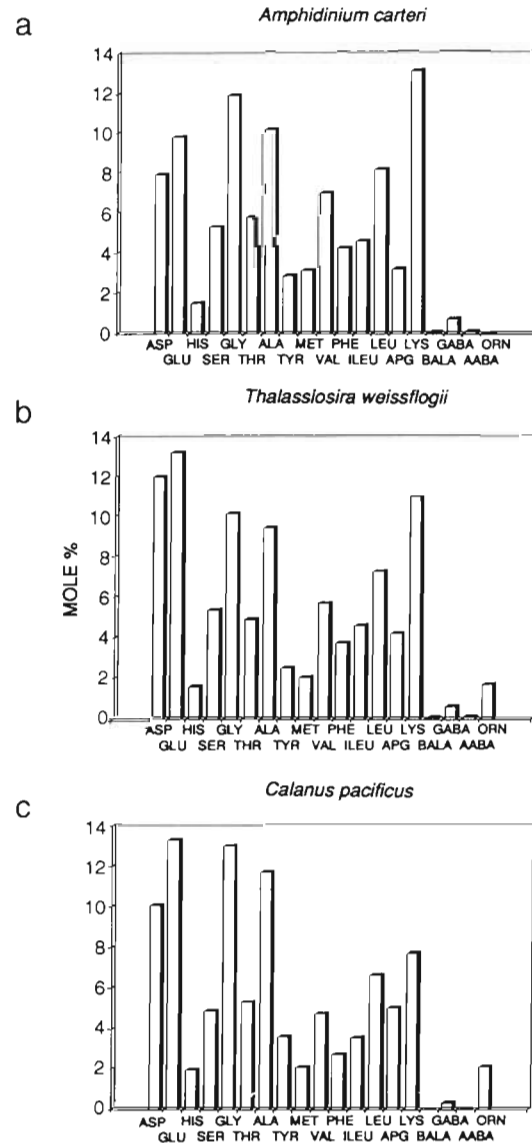


Fig. 5. Amino acid distributions in (a) *Amphidinium carteri* (Dinophyceae), (b) *Thalassiosira weissflogii* (Bacillariophyceae) and (c) *Calanus pacificus* (Copepoda: Crustacea). Histograms plotted with data from Cowie & Hedges (1992)

the partitioning of resources in marine ecosystems. Although the abilities to measure amino acids and lipid classes are not yet routine in most laboratories, the availability of the necessary technology is on the rise. Efforts to understand and model copepod feeding by combining concepts of nutritional biochemistry and optimal foraging theory have been largely successful, though limited (by the lack of technology) to relatively simple, laboratory experiments. As the technology becomes available, more realistic, complex and revealing experiments will be feasible.

The concepts discussed in this paper, dietary diversity and nutritional optimization, are readily illustrated

with copepods. However, these concepts are derived from a more general set of ideas about trophic dynamic processes, namely that matter and energy travel along diverse rather than simple paths. It is quite reasonable that diversity may be characteristic of animal diets, and not unique to a single group of crustaceans. Copepods may simply be good examples of a more general phenomenon in nature.

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