ICES Statutory Meeting

C.M. 1993/L:13
Biological Oceanography Committee

PLANKTONIC PROTOZOA IN COPEPOD DIET: EXAMPLES FROM THE NORTH ATLANTIC AND THE NORTH PACIFIC

by

Dian J. Gifford
Graduate School of Oceanography
University of Rhode Island
Narragansett, Rhode Island 02882-1197
USA
Telephone: (401) 792-6690FAX: (401) 792-6240
E-mail: D.GIFFORD (Omnet); gifford@gsosun1.gso.uri.edu (Internet)

ABSTRACT

Planktonic Protozoa are ubiquitous and abundant in the euphotic zones of marine waters. They function as important trophic intermediaries in pelagic food webs by repackaging small bacterial and algal cells into food items which are accessible to larger consumers. Although it has long been observed that calanoid copeods which feed in the euphotic zone tend to be omnivorous, they are often treated as if they are exclusively herbivorous in both mathematical models and manipulative experiments.

The objective of this paper is to compare the diets of two copepod species which are characteristic of two large oceanic areas: *Calanus finmarchicus* dominates zooplankton biomass in the North Atlantic and *Neocalanus plumchrus* dominates zooplankton biomass in the North Pacific.

Experiments were performed at sea to measure ingestion of phytoplankton and Protozoa by copepods. Experiments with *Calanus finmarchicus* were done as part of the Marine Light-Mixed Layers (**ML-ML**) program in the North Atlantic. Experiments with *Neocalanus plumchrus* were done as part of the Subarctic Pacific Ecosystem Research (**SUPER**) program in the North Pacific. The experimental design consisted of classical on-deck bottle incubations in which the disappearance of prey was monitored. Experimental treatments consisted of the natural microplankton assemblage with copeods added; control treatments consisted of the natural microplankton assemblage alone.

A significant portion of the diet of both copepod species consisted of planktonic Protozoa. Both *Calanus finmarchicus* and *Neocalanus plumchrus* cleared Protozoa at rates significantly greater than the rates at which they cleared phytoplankton. Protozoa comprised up to 80% of *N. plumchrus* carbon ingestion during spring. In contrast, although clearance rates were high, protozoa comprised 20% of *C. finmarchicus* carbon ingestion in spring and 5% in late summer. The difference in diet is attributed to the different phytoplankton environments in the two oceans.

INTRODUCTION.

The objective of this paper is to compare diets of copepods which dominate the mesozooplankton biomass of two high latitude oceans, the North Atlantic and the oceanic subarctic Pacific. The copepods are *Neocalanus plumchrus* in the North Pacific and *Calanus finmarchicus* in the North Atlantic.

Protozoa in marine ecosystems. Nano- and micro- plankton are defined on the basis of size as organisms 2-20 μm and 20-200 μm respectively (sensu SIEBURTH, SMETACEK and LENZ, 1978). The nano- and micro- zooplankton constitute the animal components of the nano- and micro- plankton. Herein, the two categories are termed collectively "microzooplankton" for simplicity. These operational categories contain a diversity of taxa including ciliate, heterotrophic flagellate, heterotrophic dinoflagellate, and sarcodine Protozoa and metazoan nauplii. Microzooplankton are ubiquitous and abundant in the euphotic zones of marine waters (BEERS, 1978; CONOVER, 1982), but have not been studied extensively in oceanic waters until last decade.

Planktonic Protozoa perform a number of functions in marine ecosystems. They are major grazers of phytoplankton (e.g., GIFFORD, 1988 and studies cited therein) and bacteria (e.g., SHERR, RASSOULZADEGAN and SHERR, 1989). They are major recyclers of nutrients (e.g., CARON, 1991). By virtue of endosymbiotic relationships, a number also function as primary producers (e.g., STOECKER, 1991). And, they function as a trophic link between microbial loop organisms and higher order consumers (e.g., STOECKER and CAPUZZO, 1990; GIFFORD, 1991). This last function is the focus of this paper.

Protozoa in copepod diet. It is now recognized that planktonic Protozoa function as important trophic intermediaries in pelagic food webs by repackaging small bacterial and algal cells into food items which are accessible to larger consumers. Although it has long been observed that calanoid copepods which feed in the euphotic zone tend to be omnivorous (e.g., LEBOUR, 1922; DIGBY, 1954; ANRAKU and OMORI, 1963; PAFFENHOFER and KNOWLES, 1980), they are often treated as if they are exclusively herbivorous in both mathematical models and manipulative experiments. Qualitatively, direct observation of gut contents reveals that tintinnid ciliates, whose hard loricae are preserved after digestion, are ingested by many calanoid copepods (e.g.,LEBOUR, 1923; MARSHALL and ORR, 1955; MULLIN, 1966; ZEITSCHEL, 1967; HARDING, 1974), and tintinnid loricae have been observed in copepod fecal pellets (TURNER and ANDERSON, 1983). The usually more abundant aloricate ciliates do not possess hard parts which survive digestion and are not easily observed in guts or fecal material.

Laboratory studies using cultured prey have documented consumption of tintinnid Protozoa by a number of calanoid copepod species, and demonstrate the potential importance of these prey in the diets of their consumers (reviewed by STOECKER and CAPUZZO, 1990; GIFFORD, 1991). Recent studies employing natural prey assemblages

demonstrate that calanoid copepods consume a number of protozoan taxa under field, as well as laboratory, conditions at rates and in quantities which are physiologically important to the consumers. The evidence to date comes from several copepod genera and a diversity of marine environments. GIFFORD and DAGG (1988) found that *Acartia tonsa* females in a subtropical estuary obtained significant nutrition from protozoan prey, with Protozoa making a greater contribution to diet during summer when large phytoplankton cells were rare. BARTHEL (1988) observed that late stage copepodid and female *Calanus finmarchicus, C. glacialis* and *C. hyperboreus* in a diversity of environments in the Greenland Sea consumed ciliates and heterotrophic dinoflagellates proportionate to their abundances in situ. Because of their large size, ciliate Protozoa constituted a significant proportion of the copepods' carbon intake, even though they were not as numerically abundant as smaller phytoplankton cells.

Recent studies of freshwater Protozoa suggest that, in addition to being of suitable size, they are rich in dietary components required by suspension-feeding copepods. Most metazoans require specific essential polyunsaturated fatty acids (PUFAs), sterols and amino acids in their diets (reviewed by PHILLIPS, 1984; STOECKER and CAPUZZO, 1990). The limited data on the biochemical composition of marine protozoa suggest that they are rich in nitrogen-containing compounds; their C:N ratios are lower than the ratios characteristic of phytoplankton (reviewed by STOECKER and CAPUZZO, 1990; GIFFORD, 1991). Although the fatty acid biochemistry of marine ciliates has not been studied, two freshwater ciliates, *Paramecium* sp. and *Tetrahymena* sp., contain significant concentrations of lipids and PUFAs (NOZAWA and THOMPSON, 1979; HOLZ and CORNER, 1987; AARONSON and BAKER, 1961; KANESHIRO, BEISCHERL, MERKEL and RHOADS, 1979). Amino acids most likely to be deficient in metazoan prey include methionine, histadine, lysine and arginine. Protozoans appear to have these as free amino acids (FAAs) (KIDDER, 1967) and thus should provide a balanced source of FAAs for their consumers (FYHN, 1989).

Consumption of protozoan prey may affect copepod condition and production. *Acartia tonsa* females produced ~25% more eggs when tintinnid Protozoa or rotifers were included in the diet (STOECKER and EGLOFF 1987). Under conditions of prolonged cultivation the body size of *Pseudocalanus elongatus* increased significantly when the heterotrophic flagellate *Oxyrrhis marina* was included in the diet, in contrast to a diet consisting solely of phytoplankton (BRETELER, SCHOGT and GONZALEZ 1990). GATTEN, SARGENT, FORSBERG, O'HARA and CORNER (1980) related egg production by *Calanus finmarchicus* to the level of lipid in phytoplankton and its assimilation by the copepods. If Protozoa, in general, are lipid-rich, they are likely to contribute significantly to the metabolism of their consumers, particularly genera such as *Calanus* and *Neocalanus* which accumulate lipid reserves during much of their life cycle.

Ecological setting.

North Pacific. Experiments in the North Pacific were performed as one

component of the **SUPER** (**SU**barctic **P**acific **E**cosystem **R**esearch) program, an interdisciplinary effort supported by the U.S. National Science Foundation. The oceanic subarctic Pacific Ocean is characterized by relatively constant, low levels of chlorophyll a throughout the annual cycle, with concentrations rarely exceeding 0.5 $\mu g\ L^{-1}$. Despite a pulse of primary production in spring, phytoplankton does not accumulate as a bloom (McALLISTER, PARSONS and STRICKLAND, 1960; CLEMONS and MILLER, 1984; SAMBROTTO and LORENZEN, 1986). The phytoplankton community is dominated by small cells (BOOTH, LEWIN and NORRIS, 1982; TAYLOR and WATERS, 1982), with cells $< 5\ \mu m$ contributing approximately 2/3 of phytoplankton carbon (BOOTH, 1988; BOOTH, LEWIN and LORENZEN, 1988). Although major nutrient levels are reduced during summer, nitrate is never depleted and concentrations remain high throughout the year (ANDERSON, LAM, BOOTH and GLASS, 1977; WHEELER and KOKKINAKIS, 1990). The distinguishing physical features of the region are a low-salinity layer of surface water located above a permanent halocline at ~130 m, which strongly inhibits deep convective mixing.

The mesozooplankton community of the region is dominated by three endemic copepod species of the genus *Neocalanus*: *N. plumchrus* (Marukawa), *N. flemingeri* Miller and *N. cristatus* (Kroyer). Their life cycles in the area are such that females produce eggs using lipid reserves acquired during the previous growing season. The eggs are released at depth during winter or early spring. The eggs develop to nauplius stage VI or copepodid stage I as they ascend to the surface where they feed and develop further to copepodid stage V. Having accumulated lipid, copepodid stage Vs make an ontogenetic migration to deep water and remain there until they molt to adults, reproduce and die in late fall or winter (MILLER, FROST, BATCHELDER, CLEMONS and CONWAY, 1984; MILLER and CLEMONS, 1988). These large-bodied copepods are the largest standing stock of biomass in the system from late winter through spring (FULTON, 1978; 1983). During their growing season, copepodid stages of *N. plumchrus* is restricted almost entirely to the water column above the seasonal thermocline (MILLER and SUPER GROUP, 1984).

The classical explanation for the observed constant levels of chlorophyll in the oceanic subarctic Pacific posits that, because of the dominant copepods' unique life history pattern, phytoplankton growth and copepod grazing are in balance in the spring, with copepods cropping the phytoplankton as soon as it is produced (McALLISTER, PARSONS and STRICKLAND, 1960; HEINRICH, 1962; PARSONS and LEBRASSEUR, 1968; MILLER, FROST, BATCHELDER, CLEMONS and CONWAY, 1984). However, studies conducted during the first SUPER expeditions to the area in 1984 demonstrated that the copepod community, in toto, does not exert sufficient grazing pressure to balance phytoplankton growth (MILLER and SUPER GROUP, 1988; LANDRY and LEHNER-FOURNIER, 1988; DAGG, 1993) during spring and early summer when the large-bodied copepods are present in surface waters. Nor does this "major-grazer hypothesis" explain the persistence of balance after the copepods enter diapause and leave the euphotic zone.

The feeding appendages of *Neocalanus* spp. are structured so that the copepods are capable of capturing particles >2-3 μm, but they clear cells <5 μm with reduced efficiency (FROST, LANDRY and HASSETT, 1983). Hence, they are able to utilize some of the small cells which dominate the subarctic Pacific phytoplankton. However, in the dilute environment of the oceanic subarctic Pacific, *Neocalanus* spp. are unable to consume sufficient phytoplankton to meet even basic respiratory requirements (MILLER and SUPER GROUP, 1988; LANDRY and LEHNER-FOURNIER, 1988; DAGG, 1991). In contrast, in other high latitude environments where standing stocks of plant cells are higher, and phytoplankton cell sizes are larger, *Neocalanus* spp. consume phytoplankton at rates and in amounts sufficient to meet metabolic and reproductive needs (DAGG, VIDAL, WHITLEDGE, IVERSON and GOERING, 1982; DAGG and WYMAN, 1983).

North Atlantic. Experiments in the North Atlantic were performed as a component of the Marine Light - Mixed Layers (**ML-ML**) program, a large multi-investigator program supported by the U.S. Office of Naval Research. The **ML-ML** study site is located in the high latitude North Atlantic at 59°N, 21°W, south of the Subarctic Front, an area characterized by extreme seasonal forcing of biology and physics. Convective cooling of the water column during winter produces a deep mixed layer of at least several hundred meters, which mixes new nutrients into the system (ROBINSON, et al. 1979). Irradiance and phytoplankton standing stocks are low, and phytoplankton growth is believed to be very low. With the onset of stratification in ~ April, standing stocks of chlorophyll increase (WILLIAMS and HOPKINS, 1974), and a prominent bloom typically occurs in May, with chllorophyll levels reaching 2-5 $\mu g\ L^{-1}$. Classically, the bloom has been described as dominated by diatoms (e.g., COLEBROOK, 1982). However, the bloom in 1991 was dominated by *Phaeocystis pouchettii*. *Calanus* spp. appear in the euphotic zone at this time, where they are believed to produce more than one generation (CONOVER, 1988). It appears that their grazing has little impact on the bloom and that most of the phytoplankton sink to the bottom (PARSONS and LALLI, 1988). Transition to the summer phytoplankton community, characterized by dinoflagellates and *Rhizoselenia* spp., occurs in June, when euphausiids, siphonophores and ctenophores also appear (e.g. COLEBROOK 1984; WILLIAMS and LINDLEY, 1982). Maximum water column stability occurs in August.

METHODS.

North Pacific experiments. Methods for the North Pacific experiments are described in detail in GIFFORD and DAGG (1991) and GIFFORD (1993a; 1993b). Experiments were done at Ocean Stations P (50°N, 145 °W) and R (53°N, 145 °W) in the subarctic Pacific Ocean during June, 1987. *N. plumchrus CV* and were collected by vertical hauls of a "bag sampler" (C.B. Miller, unpublished). Copepods were collected from a depth of 50 m through the mixed layer (mixed layer depth = 35-40 m). The net was equipped with a large volume, non-filtering cod end (REEVE, 1981) which collected copepods in good condition, with their plumose setae intact. Copepods were sorted

directly from the aquarium cod ends into 2-liter polycarbonate incubation bottles with plastic soup ladles.

North Atlantic experiments. Experiments were done in May and August 1991, following methods described by GIFFORD (1993a) and GIFFORD, FESSENDEN and GARRAHAN (submitted). The May experiments were done after the peak of the spring bloom. Copepods were collected at night by vertical hauls of a 335 μm mesh, 1-m diameter closing ring net. *Calanus finmarchicus* were sorted under a dissecting microscope using a wide bore pipette and transferred to 1-Liter polycarbonate incubation bottles containing seawater collected from the middle of the mixed layer.

All experiments. Seawater containing the microplankton assemblage was collected from the middle of the mixed layer in Go-flo bottles. Water was siphoned gently through wide bore silicon tubing into a 20-liter polycarbonate carbuoy, mixed gently with a teflon paddle, and siphoned through silicon tubing into polycarbonate bottles. The Go-flo bottles, incubation bottles and tubing were cleaned according to the protocol of FITZWATER, KNAUER and MARTIN (1982). Temperature and salinity were recorded from CTD traces obtained immediately before the Go-flo bottles were deployed.

The experimental design consisted of an experimental treatment in which the microplankton prey assemblage was incubated in bottles with copepods and a control treatment in which bottles contained only the prey assemblage. Microplankton samples were collected from each incubation bottle at the beginning and end of each experiment: one liter of seawater was preserved in 20% (v/v) acid Lugols solution (THRONDSEN, 1978) for later processing by inverted microscopy. Chlorophyll samples were collected from all treatments at the beginning and end of all *Calanus finmarchicus* experiments, for later analysis by fluorometry. After addition of the copepods to experimental treatments, all bottles were topped up with microplankton assemblage, sealed with Parafilm to exclude airspace, which destroys delicate aloricate ciliate prey, and capped. The bottles were rotated slowly along their vertical axes in an on-deck incubator whose temperature was maintained by flowing seawater. Ambient light was dimmed by covering the incubator with a translucent tarpaulin. Experimental duration was 24h. Copepods were acclimated to the experimental conditions for 1-2 hours before initial treatments were harvested. Copepods were collected throughout all cruises for ancillary measurements of dry weight. Initial experimental conditions are summarized in Table 1.

The details of microplankton sample processing are discussed by GIFFORD and DAGG (1991), GIFFORD (1993a), and GIFFORD, FESSENDEN and GARRAHAN (1993b), and are not repeated here except to note that the experimental design requires that absolute numerical abundances of the protozoan prey be measured and that the volumes of the prey items be estimated in order to calculate their carbon content. Success depends on separating the copepod feeding signal from counting variation. Because the coefficient of variation of the counting method is ~20%, optimally the copepods should clear ~40% of the volume in the incubation bottles (GIFFORD, 1993a). Statistically significant

changes in abundance are resolved in prey categories containing abundant cells, i.e., in which 100-200 cells are counted (VENRICK 1978). Per capita clearance rates of copepods on microzooplankton in the most abundant size categories were calculated from FROST's (1972) equations. Because only a few of the 50 to 70 prey categories present in each experiment contained sufficient numbers of individuals to permit calculation of clearance rates only categories containing > 100 cells were used to calculate clearance rates. A grand mean of clearance rates on these abundant prey categories was then calculated. Total ingestion was calculated by multiplying clearance rate by the initial standing stock of Protozoa (MARIN, HUNTLEY and FROST 1986). Descriptive statistics of feeding rates were calculated according to SOKAL and ROHLF (1981).

RESULTS.

North Pacific.

Microplankton assemblage. The standing stock of chlorophyll a averaged 0.4 $\mu g\ L^{-1}$ during June, 1987. The phytoplankton assemblage was dominated by cells <5 μm (BOOTH, LEWIN and POSTEL, 1993). The protozoan assemblage collected from the middle of the mixed layer at Stations P and R was dominated numerically by aloricate ciliates, primarily oligotrichous forms. The predatory aloricate ciliate *Didinium* sp. was present in low abundances. Tintinnid ciliates comprised, on average, 2.25% of total ciliates, with greater abundances at station R later in June. Other heterotrophic taxa included thecate dinoflagellates >20 μm, primarily *Protoperidinium* spp., and athecate dinoflagellates >20 μm, primarily *Gyrodinium* spp. Radiolarians made a small contribution to microzooplankton numbers. Protozoan carbon biomass ranged from 1.25 to 5.27 $\mu gC\ L^{-1}$ (mean = 3.32 μgCL^{-1} ±1.28 s.d.). Radiolarians made a small contribution (mean = 1.29%) to protozoan biomass.

Copepod feeding rates. There was no copepod mortality in any of the experiments. *Neocalanus plumchrus* cleared Protozoa at rates ranging from 7.18 to 39.04 ml $copepod^{-1}\ h^{-1}$ (mean = 22.73 ± 11.33 s.d.). Phytoplankton cells >20 μm were cleared at the same rates as protozoan prey. 55% of the incubation volume was cleared on average in the experiments. The mean growth coefficient (k in FROST's (1972) equations) of the protozoan assemblage was not significantly different from zero (mean = -0.003 h^{-1} ± .01 s.d) for all experiments. The mean grazing coefficient (g in FROST's (1972) equations) was 0.02 h^{-1} ±0.01 s.d. *Neocalanus plumchrus* ingested 0.67 to 3.91 μg protozoan-C $copepod^{-1}\ d^{-1}$ (mean = 1.58 μgC ± 1.12 s.d.) (Table 2), accounting for ~77% of its nutrition (Figure 1).

North Atlantic.

Microplankton assemblage. In May, the standing stock of chlorophyll a averaged 0.90 $\mu g\ L^{-1}$, with 67-84% <20μm following the decline of the *Phaeocystis*

bloom. During August, the standing stock of chlorophyll a averaged 1.39 $\mu g\ L^{-1}$, with 67-83% < 20μm. *Nitzschia* spp. dominated the phytoplankton > 20 μm numerically in May, with centric diatoms and thecate dinoflagellates present at lower levels. In August, the microphytoplankton assemblage was more diverse, consisting of *Rhizoselenia* spp., and a number of thecate and athecate dinoflagellates. The microzooplankton was dominated by aloricate ciliates, primarily oligotrichous forms, during both May and August. Tintinnid ciliates comprised < 1% of total ciliates in both months. Heterotrophic dinoflagellates were present during both seasons, with the heterotrophic genus *Protoperidinium* abundant during May. Numerical abundances of Protozoa were approximately twice as high in August as in May.

Copepod feeding rates. There was no copepod mortality in the experiments. *Calanus finmarchicus* cleared Protozoa at mean rates of 7.76 ml copepod^{-1} h^{-1} ± 0.01 s.d. in May and 6.17 ml copepod^{-1} h^{-1} ± 1.20 s.d in August. Phytoplankton cells > 20 μm were cleared similar rates to protozoan prey. Chlorophyll was cleared at mean rates of 2.12 ml copepod^{-1} h^{-1} ± 0.00 s.d. in May and 1.77 ml copepod^{-1} h^{-1} ± 0.41 s.d. in August. The mean growth coefficient, k, of the protozoan assemblages was 0.01 d^{-1} in May and ~0 d^{-1} in August. The mean grazing coefficient, g, was 0.05 d^{-1} in May and 0.08 d^{-1} in August. Total ingestion was 1.08 μg C copepod^{-1} d^{-1} in May. Of this, 89% was derived from phytoplankton and 11% from Protozoa. Total ingestion was 2.7 μg C copepod^{-1} d^{-1} in August, with 96% derived from phytoplankton and 5% derived from Protozoa (Table 2; Figure 1).

DISCUSSION.

The experiments document consumption of Protozoa by *Neocalanus plumchrus* CV in the subarctic Pacific environment and by *Calanus finmarchicus* CIV and CV in the high latitude North Atlantic. Both copepod species cleared protozoan prey at rates considerably higher than those at which they clear bulk chlorophyll a.

The protozoan assemblages in the North Pacific and the North Atlantic were typical of those observed in other oceanic areas, with oligotrich ciliates dominating the microzooplankton numerically and in terms of biomass (e.g., BEERS and STEWART, 1971; BEERS, REID and STEWART, 1975; HALLDAL, 1953; TANIGUCHI, 1984).

On the basis of body weight and lipid content, *Neocalanus plumchrus* in the subarctic Pacific in 1987 required 5.1 $\mu g\ c\ d^{-1}$ to satisfy basic respiratory requirements. The calculated requirement for *N. plumchrus* is similar to DAGG's (1991) estimate of 6.2 $\mu g\ C\ d^{-1}$. In the experiments described above, *N. plumchrus* obtained at most 3.9 μgC d^{-1} from the planktonic Protozoa enumerated in the experiments, accounting for ~77% of basic respiratory requirements. Adding the 1-2 μgC d^{-1} that the copepods obtain from bulk phytoplankton (DAGG and WALSER, 1987), *N. plumchrus* nearly satisfies its daily respiratory needs. On the basis of body weight, *Calanus finmarchicus* in the North

Atlantic in 1991 required on the order of 1.4 μg C d^{-1} to satisfy basic respiratory requirements (IKEDA, 1970). In May, after the decline of the spring bloom, *C. finmarchicus* fell short of this amount, obtaining ~80% of its daily respiratory needs. In August, *C. finmarchicus* obtained ~200% of daily respiratory needs.

Due to fecal and excretory losses, respiratory demands are considerably less than the amount of ingestion required for growth. For *N. plumchrus* in the North Pacific and *Calanus finmarchicus* in the North Atlantic in May to grow and reproduce, additional ingestion must occur. This may be obtained from a number of sources. It is likely that the carbon content of the Protozoa is higher than calculated for two reasons. First, the microscopic measurements of protozoan dimensions are conservative: irregular structures which are difficult to measure, such as ciliate oral membranelles and tails, are not included in organismal geometry. Second, the carbon biomass calculated from PUTT and STOECKER's (1989) empirical relationship is conservative. 20% (v/v) acid Lugols solution was chosen as a fixative because it preserves virtually all planktonic ciliates and athecate dinoflagellates, organisms for which preservation can be problematic (GIFFORD, 1985; 1992). However, the preserved cells shrink dramatically by a large, but inconsistent, factor, losing as much as 50% of their volume (GIFFORD, 1993a). Protozoan carbon biomass is not corrected in this factor, and is likely to be considerably higher than calculated. Additional nutritional sources must also be considered. Heterotrophic flagellates <20 μm are an obvious additional nutritional source, not examined directly in the experiments. These organisms were abundant in the mixed layer of the subarctic Pacific during June, 1987 (BOOTH, LEWIN and POSTEL, 1993). From BOOTH, LEWIN and POSTEL's (1993) data for the abundance of heterotrophic flagellates at a depth of 20 m in the water column, and assuming that heterotrophic flagellates are cleared from the water at the same rate as ciliates and large phytoplankton cells, it is clear that heterotrophic flagellates <20 μm contribute potentially as much as ciliates and larger heterotrophic flagellates to the diet of *N. plumchrus*. Although heterotrophic flagellates were not enumerated in the North Atlantic experimens, a similar argument may be made for their role as prey items for *C. finmarchicus*. Copepod nauplii are another possible nutritional resource. They were present at levels of 10 to 80 L^{-1} in the microplankton assemblages of both oceans (Gifford, unpublished data), abundances too low to permit calculation of ingestion in the experiments. Even if ingestion of these large particles occurs as rare events, it will contribute significantly to consumer nutrition. Further, experiments performed in bottles do not resolve episodic events such as copepods feeding on patches of prey. Such rare, large meals may well be an important nutritional resource in nature. Considering these additional nutritional resources, *Neocalanus plumchrus* and *Calanus finmarchicus* appear to be able to meet their metabolic and reproductive requirements in their respective environments.

In the context of ecosystem function, it is of interest to consider the potential impact of consumer feeding activities on prey populations. *N. plumchrus* clears Protozoa at a mean rate of 0.55 L copepod^{-1} d^{-1}. The observed number of "*N. plumchhrus*-equivalents" i.e., total copepod abundance expressed in the currency of *N. plumchrus*

CVs (MILLER and SUPER GROUP, 1988), in the mixed layer in June 1987 was 0.28 copopods L^{-1} (data of D. Mackas). These copeods were able to clear 0.15 d^{-1} L, or ~15% of the water column. In order to sustain their populations, the protozoans would have to replace themselves at a rate of ~0.15 d^{-1}. This rate is in general agreement with the net ciliate growth rate of 0.10 d^{-1} observed in the mesocosm experiments conducted during June, 1987 (LANDRY, GIFFORD, KIRCHMAN, WHEELER and MONGER, 1993) It is also consistent with FROST's (1993) revised model of the subarctic Pacific ecosystem. Thus it appears that the grazing rates of *Neocalanus* spp. on Protozoa observed in this study are of appropriate magnitude to maintain the balance of the protozoan prey populations in the subarctic Pacific during late spring. Control of protozoan populations during other seasons is discussed by FROST (1993). A similar calculation for *Calanus finmarchicus* produces a similar result: *Calanus* abundance in the upper water column was 0.85 L^{-1} and 0.50 L^{-1} in May and August respectively (BATCHELDER, VanKEUREN, VALLAINCOURT and SWIFT, submitted). Making the simplifying assumption that all *Calanus* life history stages clear water at similar mean rates, for per capita clearance rates of 0.19 and 0.15 L copepod^{-1} d^{-1} in May and August, the *Calanus* assemblage was able to clear 16% and 8%, respectively, of the euphotic zone. To sustain their populations, the protozoan community would have to replace itself at rates of 0.08 to 0.16 d^{-1}. These rates are similar to those observed in the North Pacific.

In summary, *Neocalanus plumchrus* appears to be an indiscriminate omnivore in the subarctic Pacific environment, as suggested by FROST (1987), consuming micro-sized ($>20\mu m$) phytoplankton and Protozoa with equal efficiency, obtaining on the order of 80% of its nutrition from Protozoa. *Calanus finmarchicus* is equally indiscriminate in the high latitude North Atlantic environment. However, because phytoplankton stocks are higher and large phytoplankton cells are more abundant in the North Atlantic than in the North Pacific, *C. finmarchicus* obtains a greater fraction of its daily ration from chlorophyll.

Acknowledegments - Many thanks to the captains and crews of RV *T.G. Thompson* and RV *Endeavor* for facilitating the sea-going work in the North Pacific and the North Atlantic. I thank colleagues in the SUPER and ML-ML programs for generously sharing data, time, and ideas. Special thanks to C.B. Miller, B.W. Frost, B.C. Booth, H.P. Batchelder, J. Marra and M.J. Perry, and to E.J. Lessard for providing data on the carbon content of heterotrophic dinoflagellates prior to publication. J.E. Rabalais assisted with sample processing and data analysis in the North Pacific. P.R. Garrahan, E. Martin and L. Fessenden contributed to efforts in the North Atlantic. The National Science Foundation (OCE8613892) supported field work in the North Pacific. The U.S. Office of Naval Research (N00014-J-1437) supported fieldwork in the North Atlantic as well as manuscript production and the authors' travel to the 1993 ICES meeting.

LITERATURE CITED.

AARONSON, S. and H. BAKER, 1961. Lipid and sterol content of some protozoa. J. Protozool. 8: 274-277.

ANDERSON, G.C. LAM, B.C. BOOTH and J.M. GLASS, 1977. A description and factors affecting the process of production in the Gulf of Alaska. pp. 477-798 in: *Environmental Assessment of the Alaskan Continental Shelf, Vol. 7, Receptors-Fish, Littoral Benthos.* Boulder, Colorado, U.S. Department of Commerce and U.S. Department of Interior.

ANDERSON, O.R., 1983. *Radiolaria.* N.Y., Springer-Verlag. 355 p.

ANRAKU, M. and M. OMORI, 1963. Preliminary survey of the relationship between the feeding habit and structure of the mouthparts of marine copepods. Limnol. Oceanogr. 8: 116-126.

BARTHEL, K.-G., 1988. Feeding of three *Calanus* species on different assemblages of phytoplankton in the Greenland Sea. Meeresforsch. 32: 92-106.

BATCHELDER, H.P., J.R. Van KEUREN, R. VAILLANCOURT and E. SWIFT. Spatial and temporal distributions of acoustically estimated zooplankton biomass near the ML-ML station (59°30'N; 21°00'W) in the North Atlantic in May 1991. J. Geophus. Res. Submitted.

BEERS, J.R. and G.L. STEWART, 1971. Microzooplankton in the plankton communities of the upper waters of the eastern tropical Pacific. Deep-Sea Res. 18: 861-883.

BEERS, J.R., F.M.H. REID and G.L. STEWART, 1975. Microplankton of the north Pacific central gyre. Population structure and abundance, June 1973. Int. Revue ges. Hydrobiol. 60: 607-638.

BEERS, J.R., 1978. About microzooplankton. pp. 288-290 in: A. Sournia (ed.) *Phytoplankton Manual*, UNESCO, Paris.

BOOTH, B.C., J. LEWIN and R.E. NORRIS, 1982. Nanoplankton species predominant in the subarctic Pacific in May and June 1978. Deep-Sea Res. 29: 185-200.

BOOTH, B.C., 1988. Size classes and major taxonomic groups of phytoplankton at two locations in the subarctic Pacific Ocean in May and August 1984. Mar. Biol. 97: 275-286.

BOOTH, B.C., J. LEWIN and C.J. LORENZEN, 1988. Spring and summer growth rates of subarctic Pacific phytoplankton assemblages determined from carbon uptake and cell volumes estimated using epifluorescence microscopy. Mar. Biol. 98: 287-298.

BOOTH, B.C., J. LEWIN and J.R. POSTEL. Abundance and variability of autotrophs and microheterotrophs in the subarctic Pacific: Project SUPER. Progress in Oceanography, 32: in press.

BRETELER, W.C.M.K., N. SCHOGHT and S.R. GONZALEZ, 1990. On the role of food quality in grazing and development of life stages, and genetic change of body size during cultivation of pelagic copepods. J. Exp. Mar. Biol. Ecol. 135: 177-189.

CARON, D.A. 1991. Evolving role of protozoa in aquatic nutrient cycles. In: *Protozoa and Their Role in Marine Processes*, P.C. Reid, C.M. Turley and P.H. Burkill, editors. Springer Verlag, Berlin, pp. 387-403.

CLEMONS, M. and C.B. MILLER, 1984. Blooms of large diatoms in the oceanic, subarctic Pacific. Deep-Sea Res. 31: 85-95.

COLEBROOK, J.M., 1979. Continuous plankton records: seasonal cycles of phytoplankton and copepods in the North Atlantic Ocean and the North Sea. Mar. Biol. 53: 23-32.

COLEBROOK, J.M., 1984. Continuous plankton records: relationship between species of phytoplankton and zooplankton in the seasonal cycle. Mar. Biol. 51: 313-323.

CONOVER, R.J., 1982. Interrelations between microzooplankton and other plankton organisms. Ann. Inst. Oceanogr., Paris. 59(s): 31-46.

CONOVER, R.J., 1988. Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. Hydrobiologia 167/168: 127-142.

DAGG, M.J., J. VIDAL, T.E. WHITLEDGE, R.L. IVERSON and J.J. GOERING, 1982. The feeding, respiration and excretion of zooplankton in the Bering Sea during a spring bloom. Deep-Sea Res. 29: 45-63.

DAGG, M.J. and K.D. WYMAN, 1983. Natural ingestion rates of the copepods *Neocalanus*

plumchrus and *Neocalanus cristatus* calculated from gut contents. Mar. Ecol. Progr. Ser. 13: 37-46.
DAGG, M.J. and W.E. WALSER, 1987. Ingestion, gut passage, and egestion by the copepod *Neocalanus plumchrus* in the laboratory and in the subarctic Pacific Ocean. Limnol. Oceanogr. 32: 178-188.
DAGG, M.J., 1991. *Neocalanus plumchrus* (Marukawa): life in the nutritionally dilute subarctic Pacific Ocean and the phytoplankton-rich Bering Sea. Proceedings of the Fourth International Conference on Copepoda. Bull. Plankton Soc. Japan, Special volume: 217-225.
DAGG, M.J. Sinking particles as a possible source of nutrition for the calanoid copepod *Neocalanus cristatus* in the subarctic Pacific Ocean. Deep-Sea Res. In press.
DAGG, M.J., 1993. Grazing on phytoplankton by the copepod community of the subarctic Pacific Ocean. Progress in Oceanography, 32: in press.
DIGBY, P.S.B., 1954. Biology of the marine planktonic copepods of Scoresby Sound, East Greenland. J. Anim. Ecol. 23: 298-338.
FITZWATER, S.E., G.A. KNAUER and J.H. MARTIN, 1982. Metal contamination and its effect on primary production. Limnol. Oceanogr. 27: 544-551.
FROST, B.W., 1972. Effects of size and concentration of food on the feedong behavior of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. 17: 805-815.
FROST, B.W., M.R. LANDRY and R.P. HASSETT, 1983. Feeding behavior of large calanoid copepods *Neocalanus cristatus* and *N. plumchrus* from the subarctic Pacific Ocean. Deep-Ses Res. 30: 1-13.
FROST, B.W., 1987. Grazing control of phytoplankton stock in the subarctic north Pacific Ocean: a model assessing the role of mesozooplankton, particularly the large calanoid copeods *Neocalanus* spp. Mar. Ecol. Progr. Ser. 39: 49-68.
FROST, B.W., 1993. A modelling study of processes regulating plankton standing stock and production in the open subarctic Pacific Ocean. Progress in Oceanography, 32: in press.
FYHN, M.J., 1989. First feeding of marine fish larvae: are free amino acids the source of energy? Aquaculture 80: 111-120.
GAINES, G. and F.J.R. TAYLOR, 1984. Extracellular digestion in marine dinoflagellates. J. Plankton Res. 6: 1057-1061.
GAINES, G. and M. ELBRACHTER, 1985. Heterotrophic nutrition. pp. 224-267 in: F.J.R. Taylor (ed.). *The Biology of Dinoflagellates*. Blackwell Scientific Publications, Oxford.
GATTEN, R.R., J.R. SARGENT, T.E.V. FORSBERG, S.C.M. O'HARA and E.D.S. CORNER, 1980. On the nutrition and metabolism of zooplankton. XIV. Utilization of lipid by *Calanus helgolandicus* during maturation and reproduction. J. Mar. Biol. Assoc., U.K. 60: 391-399.
GIFFORD, D.J., 1985. Laboratory culture of marine planktonic oligotrichs (Ciliata; Oligotrichida). Mar. Ecol. Progr. Ser. 23: 257-267.
GIFFORD, D., 1988. Impact of grazing by microzooplankton in the Northwest Arm of Halifax Harbour, Nova Scotia. Mar. Ecol. Progr. Ser. 23: 257-267.
GIFFORD, D.J. and M.J. DAGG, 1988. Feeding of the estuarine copepod *Acartia tonsa* Dana: carnivory vs. herbivory in natural microplankton assemblages. Bull. Mar. Sci. 43: 458-468.
GIFFORD, D.J., 1991. The protozoan-metazoan link in pelagic ecosystems. J. Protozool. 38: 81-86.
GIFFORD, D.J. and M.J. DAGG, 1991. The microzooplankton-mesozooplankton link: consumption of protozoa by the calanoid copepods *Acartia tonsa* Dana and *Neocalanus plumchrus* Marukawa. Marine Microbial Food Webs, 5: 161-177.
GIFFORD, D.J., 1993a. Consumption of planktonic marine protozoa by suspension feeding copepods. In: P.F. Kemp, et al. (eds.). *Current Methods in Aquatic Microbiology*. Lewis Publications, N.Y. In press.
GIFFORD, D.J., 1993b. Protozoa in the diets of *Neocalanus* spp. in the oceanic subarctic Pacific Ocean. Progress in Oceanography, 32: in press.
GIFFORD, D.J., L.M. FESSENDEN and P.R. GARRAHAN. Grazing by micro- and mesoozooplankton in the subarctic Atlantic Ocean: spring versus summer dynamics. J. Geophys. Res., submitted.
HALLDAL, P. 1953. Phytoplankton investigations from weathership M in the Norwegian Sea, 1948-49. Hvalaadets Skrifter 38: 1-91.
HARDING, G.C.H., 1974. The food of deep-sea copepods. J.Mar. Biol. Assoc. U.K. 54: 141-155.

HEINRICH, A.K., 1962. The life histories of plankton animals and seasonal cycles of plankton communities in the oceans. J. Conseil. Int. Explor. Mer 27: 15-24.
HOLZ, G.G. and R.L. CORNER, 1987. The composition, metabolism, and roles of lipids in Tetrahymena, pp. 99-122. In A.M. Elliott [ed.], The Biology of Tetrahymena. Dowden, Hutchinson and Ross, Inc., Stroudsburg, PA.
IKEDA, T., 1970. Relationship between respiration rate and body size in marine animals as a function of the temperature of habitat. Bull. Fac. Fish. Hokkaido Univ., 21: 91-112.
KANESHIRO, E.S., L.S. BEISCHEL, S.J. MERKEL and D.E. RHOADS, 1979. The fatty acid composition of *Paramecium aurelia* cells and cilia: changes with culture age. J. Protozool. 26: 147-158.
KIDDER, G.W., 1967. Nitrogen: Distribution, nutrition, and metabolism. pp. 93-161. In Florkin, M. and B.T. Scheer, Chemical Zoology, Vol. I. Protozoa, Academic Press, NY.
LANDRY, M.R. and J. LEHNER-FOURNIER, 1988. Grazing rates and behavior of *Neocalanus plumchrus*: implications for phytoplankton control in the subarctic Pacific. Hydrobiologia 167/168: 9-19.
LANDRY, M.R., D.J. GIFFORD, D.L. KIRCHMAN, P.A. WHEELER and B.C. MONGER, 1993. Direct and indirect effects of grazing by *Neocalanus plumchrus* on the dynamics of plankton communities in the subarctic Pacific, 32: In press.
LeBOUR, M., 1922. The food of plankton organisms. J. Mar. Biol. Assoc. U.K. 12: 644-677.
LeBOUR, M., 1923. Food of plankton organisms II. J. Mar. Biol. Assoc. U.K. 13: 70-92.
MARIN, V., M.E. HUNTLEY and B.W. FROST, 1986. Measuring feeding rates of pelagic herbivores: analysis of experimental design and methods. Mar. Biol. 93: 49-58.
MARSHALL, S.M. and A.P. ORR, 1955. The biology of a marine copepod. Springer-Verlag, Berlin.
MARSHALL, S.M., 1969. Protozoa Order: Tintinnida. No. 117-127. In: *Fiches d'Identification de Zooplancton*. J. Fraser and V. Kr. Hensen (eds.). Cons. Perm. Int. Explor. Mer, Charlottenlund.
McALLISTER, C.D., T.R. PARSONS and J.D.H. STRICKLAND, 1960. Primary productivity and fertility at Station "P" in the northeast Pacific Ocean. J. Cons. Int. explor. Mer. 25: 240-259.
MILLER, C.B., B.W. FROST, H.P. BATCHELDER, M.J. CLEMONS and R.E. CONWAY, 1984. Life histories of large, grazing copepods in a subarctic ocean gyre: *Neocalanus plumchrus, Neocalanus cristatus*, and *Eucalanus bungii* in the northeast Pacific. Progr. Oceanogr. 13: 201-243.
MILLER, C.B. and SUPER GROUP, 1988. Lower trophic level production dynamics in the oceanic subarctic Pacific Ocean. Bull. Ocean Res. Inst. Tokyo 26: 1-16.
MULLIN, M.M., 1966. Selective feeding by calanoid copepods from the Indian Ocean. pp. 545-554 In: H. Barnes (ed.) Some contemporary studies in marine science. George Allen & Unwin, Ltd., London.
NOZAWA, Y. and G.A. THOMPSON, Jr., 1979. Lipids and membrane organization in *Tetrahymena*, pp. 275-338. In Lavandowsky and S.H. Hunter (eds). Biochemistry and Physiology of Protozoa (2nd edition), Vol. 2, Academic Press, NY.
PARSONS, T.R. and R.J. LEBRASSEUR, 1968. A discussion of some critical indices of primary and secondary production for large scale ocean surveys. California marine Research Committee, CalCOFI Report 12: 54-63.
PARSONS, T.R. and C.M. LALLI, 1988. Comparative oceanic ecology of the plankton communities of the surarctic Atlantic and Pacific Oceans. Oceanogr. Mar. Biol. Ann. Rev. 26: 317-359.
PAFFENHOFER, G.-A. and S.C. KNOWLES, 1980. Omniverousness in marine copepods. J. Plankton Res. 2: 355-365.
PHILLIPS, N.W., 1984. Role of different microbes and substrates as potential suppliers of specific, essential nutrients to marine detritivores. Bull. Mar. Sci. 35:283-298.
PUTT, M. and D.K. STOECKER, 1989. An experimentally determined carbon:volume ratio for marine "oligotrichous" ciliates from estuarine and coastal waters. Limnol. Oceanogr. 34: 1097-1103.
REEVE, M.R., 1981. Large cod-end reservoirs as an aid to the live collection of delicate zooplankton. Limnol. Oceanogr. 26: 577-580.
ROBINSON, M.K., R.A. BAUER, and E.H. SCHROEDER, 1979. Atlas of North Atlantic monthly mean temperature and mean salinities of the surface layer. U.S. Naval Oceanographic Office Ref. Publ. 18,

1339 pp.
SAMBROTTO, R.N. and C.J. LORENZEN, 1986. Phytoplankton and primary productivity . p. 249-282 in: *The Gulf of Alaska: Physical Environment and Biological Resources*. D.W. Hood and S.T. Zimmerman (eds.). Washington, D.C., U.S. Government Printing Office.
SHERR, E.B., F. RAZSSOULZADEGAN and B.F. SHERR, 1989. Bacterivory by pelagic choreotrichous ciliates in coastal waters of the northwest Mediterranean Sea. Mar. Ecol. Progr. Ser. 55: 235-240.
SIEBURTH, J. McN., V. SMETACEK and J. LENZ, 1978. Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. Limnol. Oceanogr. 23: 1256-1263.
SOKAL, R.R. and F.J. RHOLF, 1981. *Biometry, the principals and practice of statistics in biological research, 2nd edition*. San Francisco, W.H. Freeman and Sons.
STOECKER, D.K. and D.A. EGLOFF, 1987. Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers. J. exp. Mar. Biol. Ecol. 110: 53-68.
STOECKER, D.K. and J. M. CAPUZZO, 1990. Predation on Protozoa: its importance to zooplankton. J. Plankton Res. 12: 891-908.
STOECKER, D.K., 1991. Mixotrophy in marine planktonic ciliates: physiological and ecological aspects of plastid-retention by oligotrichs. In: *Protozoa and Their Role in Marine Processes*, P.C. Reid, C.M. Turley and P.H. Burkill, editors. Springer Verlag, Berlin, pp. 161-179.
TANIGUCHI, A., 1984. Microzooplankton biomass in the arctic and subarctic Pacific Ocean in summer. Mem. Nat. Inst. Polar Res. Special Issue No. 32: 63-76; 4 plates.
THRONDSEN, J., 1978. Preservation and storage. *Phytoplankton Manual*, UNESCO, Paris, p. 69-74.
TURNER, J.T. and D.M. ANDERSON, 1983. Zooplankton grazing during dinoflagellate blooms in a Cape Cod embayment, with observations on predation on tintinnids by copepods. P.S.Z.N.I. Mar. Ecol. 4: 359-374.
WILLIAMS, R. and C.C. HOPKINS, 1974. Sampling at Ocean Weather Station INDIA (59°W, 19°N) in 1974. Ann. Biol. 31: 57-60.
WILLIAMS, R. and J.A. LINDLEY, 1980. Plankton of the Fladden Ground during FLEX 76. III. Vertical distribution, population dynamics, and production of *Calanus finmarchicus* (Crustacea: Copepoda). Mar. Biol. 60: 47-56.
VENRICK, E.L. 1978. How many cells to count? *Phytoplankton Manual*. UNESCO, Paris, p. 167-180.
WHEELER, P.A. and S. A. KOKKINAKIS, 1990. Ammonium recycling limits nitrate use in the oceanic subarctic Pacific. Limnol. Oceanogr. 35: 1267-1278.
ZEITSCHEL, B. 1967. Die Bedeutung der Tintinnen als Glied der Nahrungskete. Helgol. Wiss. Meeresunters. 15: 589-601.

Table 1. Initial experimental conditions.

	N. plumchrus North Pacific June, 1987	*C. finmarchicus* North Atlantic May, 1991	*C. finmarchicus* North Atlantic August, 1991
Mixed layer temperature	7.0 °C	8.4 °C	12.8 °C
Chlorophyll	0.4 μgL^{-1}	0.90 μgL^{-1}	1.39 μgL^{-1}
Protozoa	1345-5039 L^{-1}	2058-2269 L^{-1}	5023-5405 L^{-1}
Copepod life history stage	CV	CV	CV
Incubation volume	2.0 L	1.0 L	1.0 L
Number coppods $bottle^{-1}$	2	10	15
Incubation duration	24 h	24 h	24 h

Table 2. Mean feeding rates on Protozoa.

	North Pacific June, 1987	North Atlantic May, 1991	North Atlantic August, 1991
Clearance rate (ml $copepod^{-1}$ h^{-1})	22.7	7.8	6.2
Ingestion rate (μgC $copepod^{-1}$ d^{-1})	3.7-12.8	0.9	2.6

Figure 1. Components of copepod diet.