

## Zooplankton grazing and growth: Scaling within the 2–2,000- $\mu\text{m}$ body size range

*Per Juel Hansen and Peter Koefoed Bjørnsen*<sup>1</sup>

Marine Biological Laboratory, Strandpromenaden 5, DK-3000 Helsingør, Denmark

*Benni Winding Hansen*

Roskilde University, Department of Life Sciences & Chemistry, P.O. Box 260, DK-4000 Roskilde, Denmark

### Abstract

In order to study the size dependency of grazing and growth rates in zooplankton, data were collected from laboratory studies in the literature, covering both limnic and marine organisms. Data were obtained from about 60 species of nano-, micro-, and mesozooplankton, representing flagellates, ciliates, rotifers, meroplankton larvae, copepods, and cladocerans. Estimates of maximum ingestion and clearance were extracted from functional responses (ingestion rates as a function of food density) established from laboratory experiments. Maximum specific rates were expressed as a function of predator body volume. Maximum specific clearance and ingestion rates decreased with predator volume within each group of zooplankton, with a common exponent (scaling factor) of  $-0.23$  ( $\text{SE} = \pm 0.12$ ) in accordance with previous findings. However, significant differences were found between groups. In particular, among the protists, ciliates display maximum ingestion, growth, and clearance rates that exceed those of dinoflagellates by a factor of 2–4. Among the metazooplankton, calanoid copepods have maximum clearance rates that exceed those of filter-feeding cladocerans and meroplankton larvae by a factor of 10. Because of these differences between the groups, the entire set of observations could not be fitted by an overall regression.

Quantification of zooplankton grazing and production has been subject to intensive research for decades. A variety of methods have been introduced, including radioactive tracers (Haney 1971; Roman and Rublee 1981; Servais et al. 1985), inert food particles (Fenchel 1980a,b,c; Jonsson 1986), metabolic inhibitors (Fuhrman and McManus 1984; Sanders and Porter 1986), disappearance rate of food particles (Frost 1972), growth kinetics in laboratory cultures (Fenchel 1982), preincubation size fractionation (Capriulo and Carpenter 1980), gut pigment content (Mackas and Bohrer 1976), dilution series (Landry and Hassett 1982), and egg production (Kiørboe et al. 1985a). These methods have produced valuable results for specific applications, but so far no simple and integrative reference method has emerged that can be incorporated into carbon flux studies as an equivalent to standard methods such as the  $^{14}\text{C}$  method for determination of pelagic primary production, the oxygen method for community respiration measurements, and the quantification of the vertical flux of particulate organic material by sediment traps. Most methods for determination of zooplankton grazing are not applicable to field measurements, and their accuracy may be affected by incubation effects, artificiality of tracer food particles, and other methodological problems (Peters and Downing 1984; Stoecker 1988; Carrick et al. 1992).

An alternative approach to direct field measurements of zooplankton grazing and growth rates has been the appli-

cation of rates obtained in the laboratory (e.g. Christoffersen et al. 1990; Weisse et al. 1990; Riemann et al. 1990). During the past two decades considerable data on ingestion, growth, and clearance rates for different zooplankton groups have been published. Reviews published so far have focused on specific taxonomic zooplankton groups (e.g. Fenchel 1980a,b,c; Peters and Downing 1984; Knoechel and Holtby 1986). The comparability of zooplankton grazing rates from the literature, whether from field or laboratory experiments, is limited by methodological differences and by the use of different, often not directly comparable units and model fits.

Our aim was to synthesize literature data of laboratory measurements of grazing and growth rates, including zooplankton from heterotrophic nanoflagellates to crustaceans for marine and freshwater species, in order to provide a basis for comparing new data with those obtained previously from different studies by using a variety of methods and units, to determine body size dependency of maximum ingestion rate, clearance rates, and half-saturation constant within and between different groups of zooplankton, and to evaluate the applicability of laboratory data to pelagic carbon flux studies.

### Materials and methods

**Data acquisition and processing**—This study does not offer a complete review of zooplankton grazing, but rather analyzes the bulk of the literature on laboratory studies of different zooplankton groups, including flagellates, ciliates, rotifers, meroplankton larvae, copepods, and cladocerans. Data collection and analysis required formulating basic assumptions concerning the dependence of clearance and ingestion rates on food quantity and quality and on temperature, and establishing criteria for data selection and data rejection as described below.

<sup>1</sup> Present address: National Environmental Research Institute, Frederiksborgvej 399, DK-4000 Roskilde, Denmark.

### Acknowledgments

We thank Tom Fenchel and Thomas Kiørboe for constructive criticism and discussion. The study was supported by the Danish Natural Science Foundation grant 11-0420-1 and 9502163-28808.

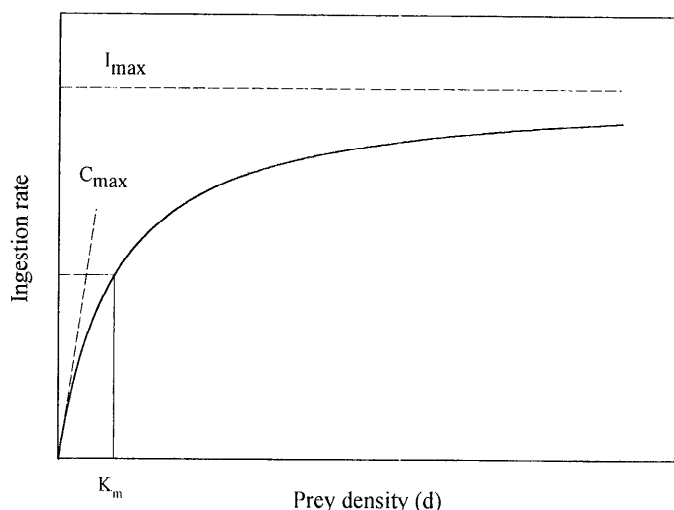


Fig. 1. The functional response in zooplankton. Michaelis-Menten kinetics illustrating the maximum ingestion ( $I_{\max}$ ), maximum clearance ( $C_{\max}$ ) and the half-saturation constant ( $K_m$ ).

**Food quantity**—The dependence of grazer activity on food quantity is well studied in laboratory experiments, which universally have shown that ingestion rate ( $I$ ) approaches a maximum rate ( $I_{\max}$ ) at high prey densities ( $d$ ) and is approximately proportional to  $d$  at low densities. Several different formulas for this functional response have been proposed, including a rectilinear model, an exponential model, and a Michaelis-Menten (Monod) equation. These different models typically fit data equally well (e.g. Mullin et

al. 1975). We have chosen the hyperbolic formula (Michaelis-Menten kinetics) because it is theoretically the best founded (Holling 1959; Fenchel 1988) and is widely used to describe dose-response relationships. We are aware, however, that a lower threshold food density below which grazing apparently ceases has been demonstrated in a few copepods (e.g. Frost 1975; Kjørboe et al. 1985b). Ingestion rates [ $I(d)$ ] can be expressed as

$$I(d) = \frac{I_{\max} d}{(K_m + d)}, \quad (1)$$

where  $K_m$  is the half-saturation food density, i.e.  $I(K_m) = I_{\max}/2$ .

Clearance [ $C(d)$ ] can be expressed as

$$C(d) = \frac{I(d)}{d} = \frac{C_{\max} K_m}{K_m + (d)}, \quad (2)$$

where  $C_{\max}$  is maximum clearance obtained at low prey density. By inserting  $d = K_m$  in Eq. 1 and 2, it follows that

$$K_m = \frac{I_{\max}}{C_{\max}}. \quad (3)$$

$I_{\max}$ ,  $C_{\max}$ , and  $K_m$  are illustrated in Fig. 1.

Estimates of maximum ingestion and clearance rates were extracted from functional responses (ingestion rates as a function of food density) established from laboratory experiments, and rates were divided by predator body volume to obtain specific rates. For those studies where data were not explicitly fitted to the hyperbolic model (Eq. 1), data points from the published graphs were digitized from enlarged photocopies of the original figures in the primary reference and

Table 1. Carbon: volume ratio for either live or fixed zooplankton.

	Fixative	C: vol (g C cm <sup>-3</sup> )	Reference
Flagellates	Aldehyde	0.22	Børsheim and Bratbak 1987
	Live	0.10	Børsheim and Bratbak 1987
Ciliates	Lugol	0.15	Debiase et al. 1990
	Lugol	0.09	Debiase et al. 1990
	Live	0.07	Fenchel and Finlay 1983
	Lugol	0.09	Heinbokel 1978
	Lugol	0.19	Putt and Stoecker 1989
	Formalin	0.14	Putt and Stoecker 1989
	Live	0.11	Verity and Langdon 1984
Rotifers	Live	0.10	Boraas 1983
	Live	0.12	Boraas 1983
	Live	0.11	B. Hansen et al. unpubl.
Meroplankton larvae	Model*	0.19	B. Hansen 1993
	Model*	0.12	B. Hansen unpubl.
	Live†	0.08	B. Hansen et al. unpubl.
Copepods	Live‡	0.13	Berggreen et al. 1988
Nauplii	Live‡	0.11	Berggreen et al. 1988
Copepodites	Live‡	0.16	Durbin and Durbin 1978
Mean ± SE		0.126±0.040	n = 18

\* Body volume estimated from water displaced with a plasticine model.

† Carbon value measured by infrared gas analysis; volume assumed rotational ellipsoid with ellipsoid cross section divided by 2.

‡ Carbon value from length/carbon regressions and body volume estimated from geometrical forms.

Table 2.  $Q_{10}$  values for maximum clearance ( $C_{\max}$ ), maximum ingestion ( $I_{\max}$ ), respiration ( $R$ ), and maximum growth rates ( $\mu_{\max}$ ) for zooplankton covering 8 orders of magnitude in body size. Data are from primarily laboratory studies or subsidiary experimental in situ studies,  $n = 42$ . Total mean  $\pm$  SD of  $Q_{10} = 2.80 \pm 0.29$ .

	Temp. (°C)	$Q_{10}$	Reference
$I_{\max}$			
Flagellates	12–22	2.8	Sherr et al. 1988
Ciliates	15–25	3.7	Rassoulzadegan 1982
	12–22	2.0	Sherr et al. 1988
	5–25	2.7	Verity 1985
Meroplankton larvae	11–18	3.2	Bayne 1965
	10–20	3.4	Crisp et al. 1985
	16–24	3.4	Ukeless and Swecney 1969
	17–25	2.4	Walne 1964
	6–18	3.0	Sprung 1984b
Copepods	4.5–16	2.4	Durbin and Durbin 1992
	5–15	3.9	Kjørboe et al. 1982
Mean $\pm$ SE		2.97 $\pm$ 0.16	
$C_{\max}$			
Ciliates	15–25	4.0	Rassoulzadegan 1982
	5–25	1.6	Verity 1985
Meroplankton larvae	10–20	3.4	Crisp et al. 1985
Rotifers	10–20	2.4	Gilbert and Bogdan 1984
Copepods	5–15	3.2	Deason 1980
Mean $\pm$ SE		2.94 $\pm$ 0.45	
$R$			
Ciliates	15–25	2.6	Verity 1985
Meroplankton larvae	12–18	3.1	Sprung 1984c
Copepods	10–20	3.0	Comitta 1964
	10–20	2.0	Comitta and Comitta 1964
	20–25	2.1	Gaudy and Boucher 1983
	10–15	3.1	Mullin and Brooks 1970
	8–15.5	1.8	Vidal 1980b
Mean $\pm$ SE		2.51 $\pm$ 0.61	
$\mu_{\max}$			
Flagellates	14–26	2.5	Caron et al. 1986
Ciliates	8–20	2.9 ( $n=3$ )	Fenchel 1968
	10–25	2.8 ( $n=10$ )	Finlay 1977
	15–20	3.0	Hamilton and Preslan 1969
	5–15	2.0	Verity 1985
	15–25	1.5	Verity 1985
Meroplankton larvae	12–18	1.9	Sprung 1984a
Copepods	10–15	3.0 ( $n=2$ )	Mullin and Brooks 1970
Mean $\pm$ SE		2.72 $\pm$ 0.26	

fitted by iterative nonlinear regression. If both ingestion rate and clearance rate were given,  $I_{\max}$  was estimated from the best fit of the measured ingestion rate to Eq. 1,  $C_{\max}$  from the best fit of clearance to Eq. 2, and  $K_m$  was calculated from Eq. 3. If only ingestion rate or clearance was given,  $I_{\max}$  or  $C_{\max}$  together with  $K_m$  were estimated from best fit to Eq. 1 or 2, and the third parameter ( $C_{\max}$  or  $I_{\max}$ , respectively) was calculated from Eq. 3.

Estimates of  $I_{\max}$  were converted into biovolume units. Values of  $I_{\max}$  and  $C_{\max}$  were normalized against predator body volume ( $P_{vol}$ ) and presented as  $h^{-1}$ . Estimates of  $K_m$  were converted into units of prey biovolume and given in parts per million. Zooplankton biomass was converted into biovolume assuming  $0.45 \text{ g C (g DW)}^{-1}$  and  $0.12 \text{ g C cm}^{-3}$

(Table 1). Body length was converted into dry weight by empirical length–weight regressions (McCauley 1984) or into biovolume by using geometrical formulae. Predator and prey sizes were expressed as body volume or as equivalent spherical diameter (ESD), defined as the diameter of a sphere with equal volume: body volume =  $\pi/6 \text{ ESD}^3$ . Data points in figures represent mean values for each species in order to avoid overrepresentation of some well-studied species.

**Food selectivity**—The range of potential food for a planktonic predator is limited by the structure of its feeding apparatus. Within these structural limits predators may select food particles on the basis of size, motility, surface characteristics, biochemical composition, and other factors (e.g.

Poulet and Marsot 1978; Jonsson 1986; Van Alstyne 1986). Maximum clearances for different predators are only comparable when measured on a prey of optimal size. We have recently reviewed the sparse literature on size selectivity by planktonic predators (Hansen et al. 1994) and found that the size ratio between predators and their optimal prey varies significantly among taxonomic groups. Accordingly, we excluded studies in which it could be documented that particles were of a suboptimal size (i.e. where the predator:prey size ratio predicts less than half of the clearance on the optimal prey; Hansen et al. 1994).

**Temperature dependence**—The dependence of biological process rates ( $r$ ) on temperature ( $t$ , °C) is usually expressed in terms of an exponential function:

$$\log(r_t) = \log(r_0) + \log Q_{10} \frac{(t - t_0)}{10}. \quad (4)$$

Literature values of  $Q_{10}$  for clearance, ingestion, respiration, and growth rates vary between 1.5 and 4.0 within the temperature range 5–25°C (Table 2). No consistent differences appear between parameters or taxonomic groups, and the overall average  $Q_{10}$  of 2.8 has therefore been applied in this study for conversion of ingestion rate and clearance and data adjusted to a standard temperature of 20°C. A consequence of using the same  $Q_{10}$  value for these two parameters is that the half-saturation prey density  $K_m$  ( $=I_{\max}/C_{\max}$ ) becomes temperature independent.

**Evaluation of datasets**—Data on maximum growth rates were collected from the literature to compare with maximum specific ingestion rates. Most estimates of maximum growth were from numerical response curves. Because data were lacking, we also used data from experiments where food was evidently abundant.

Maximum specific clearance rate of an organism is a function of the area within which particles can be captured, the speed with which the organism swims or moves its feeding appendages, and the swimming speed of the prey. Generally, data of this kind are sparsely available in the literature, and we were only able to estimate maximum specific clearance rates for organisms in which either flagella or cilia are involved in locomotion and capture of prey. Maximum clearance of an organism that uses flagella or cilia for locomotion can be estimated by multiplication of swimming speed and projected filter area of the predator, assuming that the swimming speed of the prey is negligible. Swimming speed data were collected from literature covering flagellates, ciliates, rotifers, and meroplankton larvae. Filter area was calculated as the projected area of the organism, assuming spherical shape. This rough approximation may lead to both overestimation (organisms are often elongated) and underestimation (filter area is larger than predicted because the diameter of filtering structure may be larger than the diameter of the cell or the effective hydrodynamic filter area may reach beyond the filtering structure; e.g. Fenchel 1982).

## Results

Maximum specific ingestion rates ( $I_{\max}$ ), maximum specific growth rates ( $\mu_{\max}$ ), maximum specific clearance rates

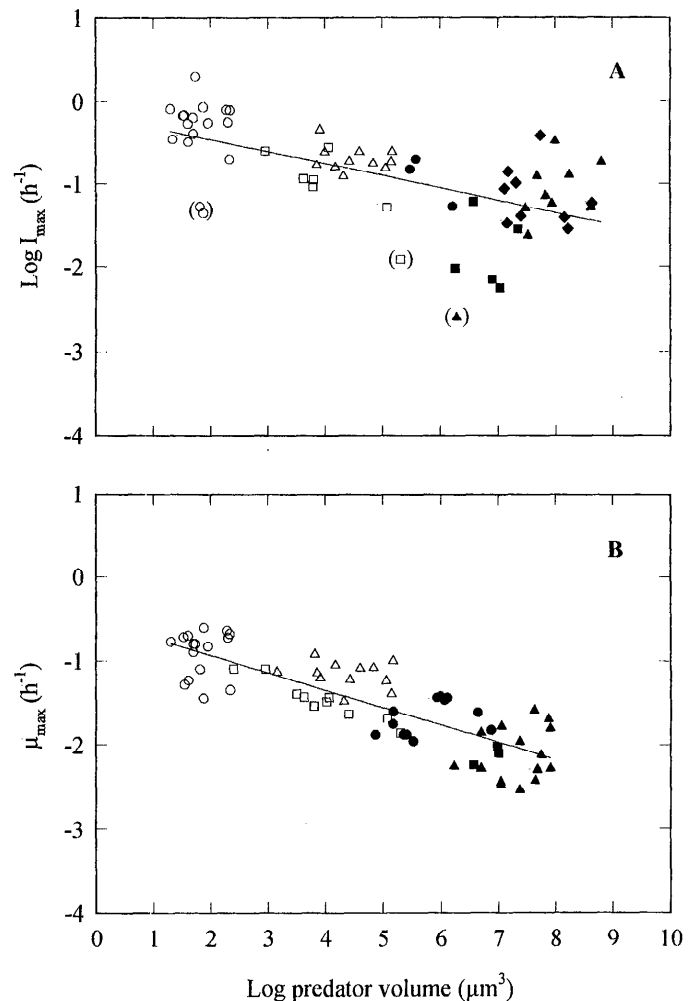


Fig. 2. Metabolic rates for different zooplankton taxa as a function of body volume. Maximum specific ingestion rates (A) and maximum specific growth rates (B). Dinoflagellates,  $\square$ ; other flagellates,  $\circ$ ; ciliates,  $\triangle$ ; rotifers,  $\bullet$ ; meroplankton larvae,  $\blacksquare$ ; copepods,  $\blacktriangle$ ; cladocerans,  $\blacklozenge$ . An overall regression line is indicated by a solid line. Symbols in parentheses were not included in the regression because growth yield ( $=\mu/I$ ) was  $\sim 100\%$  or even above. References to source of data are listed in Tables 3 and 4.

( $C_{\max}$ ), and  $K_m$  were related to predator volume ( $P_{\text{vol}}$ ) by log-log regressions within each of the following seven zooplankton groups: dinoflagellates, other flagellates, ciliates, rotifers, meroplankton larvae, cladocerans, and copepods (Figs. 2–4, Tables 3–5). Further statistical analysis was carried out by  $F$ -tests of a series of models by using the 14 independent log-log regressions as a base model. Observed values were compared to modeled values estimated from the regression equations, and squared deviations between observations and model estimates were calculated and summed up as SSD (sum of squared deviations). This procedure enabled us to change the model and follow the resulting change in SSD as well as the contribution to this change from different zooplankton species and groups.

The first step was to test whether a reduction to a common scaling factor for all regression lines was possible. The 14

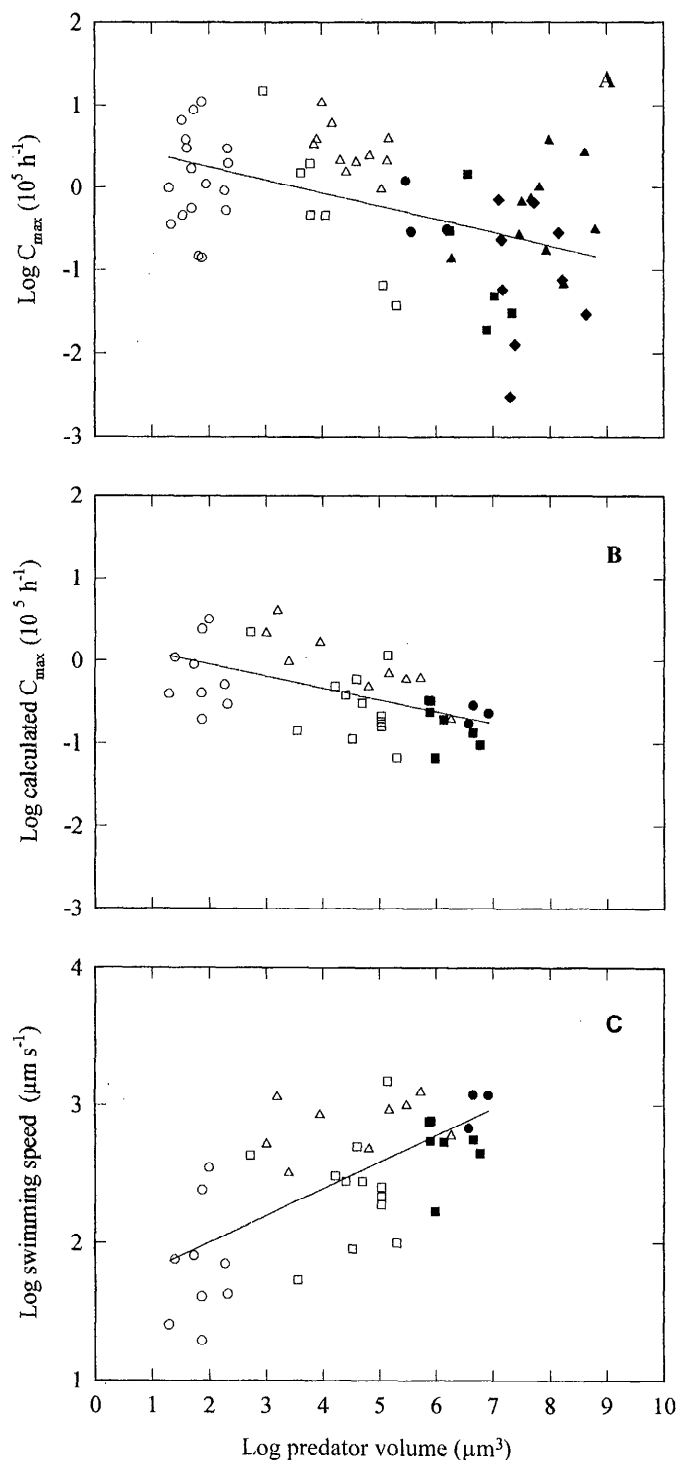


Fig. 3. Maximum specific clearance rates and swimming speed as a function of body volume for flagellated and ciliated zooplankton taxa. Symbols as in Fig. 2. Measured maximum specific clearance rates (A), maximum specific clearance estimated from swimming data and projected area of the organisms (B), and absolute swimming speed (C). Overall regression lines are indicated by a solid line. References to source of data are listed in Tables 3 and 8.

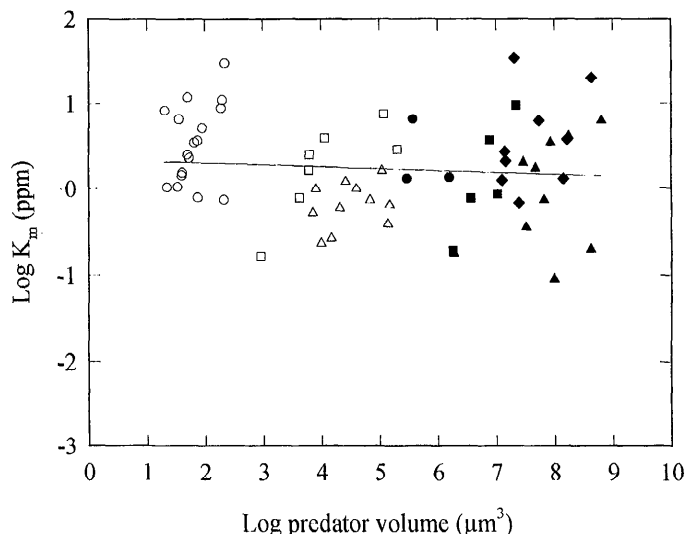


Fig. 4. Values of half-saturation constant,  $K_m$ , for grazing of different zooplankton taxa. Symbols as in Fig. 2. An overall regression line is indicated by a solid line. References to source of data are listed in Table 3.

independent regressions were used as a base model. When a common slope was forced upon the regression lines, SSD increased. A maximum likelihood estimate for a common scaling factor was found by iterative manipulation of the models with a variety of common slopes until the new SSD reached a minimum. The increase in SSD was then related to the reduction in the model dimension (from 28 to 15, i.e. one slope and 14 independent intercepts) by an  $F$ -test. A model with a common scaling factor was rejected at  $P < 0.05$ , and a similar result occurred when clearance and ingestion rates were treated separately. One data point (the cyclopoid copepod, *Oithona nana*) was the major contributor to the increase in SSD (Table 6). With this data point removed the model was accepted at  $P > 0.1$ . The maximum likelihood estimate for a common scaling exponent was  $-0.23$  (SE of  $\pm 0.12$ ).

The next step was to test whether all data could be described by common regression lines, for maximum specific clearance and maximum specific ingestion. Again, the forcing of a general regression for all data resulted in an increase of SSD, which was related to the reduction in model dimension (from 15 to 3; i.e. one slope and two intercepts) by an  $F$ -test. This model was rejected at  $P < 0.01$ . A similar result was found when the two lines (clearance and ingestion) were allowed different slopes. Several zooplankton groups contributed to the significant increase in SSD. Dinoflagellates and meroplankton larvae contributed most to the SSD increase in the estimates of maximum ingestion by having lower maximum specific ingestion rates compared to the other groups. Ciliates and copepods contributed most to the SSD increase in the estimates of maximum clearance rates by having higher rates compared to the other groups.

As a consequence of a common slope, the half-saturation constant  $K_m (=I_{\text{max}}/C_{\text{max}})$  is independent of body size within each group of zooplankton. The general mean value of  $K_m$  for all groups is  $\sim 2$  ppm (vol/vol), corresponding to a prey

Table 3. The functional response parameters for different zooplankton taxa. Data were not corrected for temperature differences.

Predator species	Predator volume ( $\mu\text{m}^3$ )	Temp. ( $^{\circ}\text{C}$ )	$I_{\text{max}}$ ( $\text{h}^{-1}$ )	$C_{\text{max}}$ ( $10^3 \text{ h}^{-1}$ )	$K_m$	Reference
Nanoflagellates (except dinoflagellates)						
<i>Actinomonas mirabilis</i>	7.50E+01	2.00E+01	8.60E-01	1.10E+01	7.80E-01	Fenchel 1982
<i>Bodo designis</i>	5.40E+01	2.00E+01	1.99E+00	8.71E+00	2.28E+00	Eccleston-Parry and Leadbeater 1994
<i>Ciliophrys infusionum</i>	2.20E+02	2.00E+01	7.90E-01	1.98E+00	3.02E+01	Eccleston-Parry and Leadbeater 1994
<i>Codostiga gracilis</i>	3.50E+01	2.00E+01	6.90E-01	4.50E-01	6.50E+00	Eccleston-Parry and Leadbeater 1994
<i>Diaphanoeca grandis</i>	4.00E+01	1.50E+01	3.30E-01	2.30E+00	1.44E+00	Andersen 1988/1989
<i>Jakoba libera</i>	7.50E+01	2.00E+01	4.50E-02	1.40E-01	3.62E+00	Eccleston-Parry and Leadbeater 1994
<i>Monosiga</i> sp.	2.00E+01	2.00E+01	8.10E-01	9.80E-01	8.30E+00	Fenchel 1982
<i>Ochromonas</i> sp.	5.00E+01	2.00E+01	4.20E-01	1.70E+00	2.50E+00	Anderson et al. 1989
<i>Ochromonas</i> sp.	2.00E+02	2.00E+01	5.70E-01	5.20E-01	1.10E+01	Fenchel 1982
<i>Paraphysomonas imperforata</i>	2.12E+02	2.00E+01	2.00E-01	2.97E+00	7.40E-01	Eccleston-Parry and Leadbeater 1994
<i>Paraphysomonas vestita</i>	1.90E+02	2.00E+01	8.00E-01	9.10E-01	8.80E+00	Fenchel 1982
<i>Pleoromonas jaculans</i>	5.00E+01	2.00E+01	6.50E-01	5.50E-01	1.18E+01	Fenchel 1982
<i>Pseudobodo tremulans</i>	9.00E+01	2.00E+01	5.60E-01	1.10E+00	5.10E+00	Fenchel 1982
<i>Pseudobodo</i> sp.	3.35E+01	1.50E+01	4.10E-01	3.90E+00	1.05E+00	Rivier et al. 1985
<i>Pseudobodo</i> sp.	2.20E+01	1.80E+01	2.90E-01	2.80E-01	1.04E+00	Parslow et al. 1986
<i>Spumella</i> sp.	6.54E+01	2.50E+01	9.00E-02	2.50E-01	3.45E+00	Hollen and Boraas 1991
<i>Stephanoea diplocostata</i>	2.00E+01	1.80E+01	3.00E-01	1.60E+00	1.90E+00	Geider and Leadbeater 1988
<i>S. diplocostata</i>	8.30E+01	2.00E+01	3.00E-01	4.58E+00	1.54E+00	Eccleston-Parry and Leadbeater 1994
Dinoflagellates						
<i>Gymnodinium</i> sp.	9.00E+02	1.20E+01	1.12E-01	6.50E+00	1.65E-01	Strom 1991
<i>Gyrodinium spirale</i>	1.15E+04	1.50E+01	1.70E-01	2.70E-01	3.88E+00	Hansen 1992
<i>Oblea rotunda</i>	6.13E+03	2.00E+01	9.30E-02	1.94E+00	1.66E+00	Strom and Buskey 1993
<i>Oxyrrhis marina</i>	6.30E+03	2.00E+01	1.12E-01	4.50E-01	2.50E+00	Gaines unpubl.
<i>Protoperidinium crassipes</i>	2.04E+05	1.90E+01	1.10E-02	3.30E-02	2.86E+00	Jeong and Latz 1994
<i>Protoperidinium divergens</i>	1.19E+05	1.90E+01	4.76E-02	5.90E-02	7.46E+00	Jeong and Latz 1994
<i>Protoperidinium hirobis</i>	4.20E+03	2.00E+01	1.15E-01	1.50E+00	7.80E-01	Jacobson and Anderson 1993
Ciliates						
<i>Eutimninus pectinis</i>	1.50E+04	1.80E+01	1.30E-01	4.86E+00	2.64E-01	Heinbokel 1978
<i>Favella ehrenbergii</i>	2.10E+05	2.00E+01	1.30E-01	2.82E+00	2.35E-01	Buskey and Stoecker 1988
<i>Favella ehrenbergii</i>	9.56E+04	1.80E+01	2.15E-01	1.26E+00	6.20E-01	Hansen et al. 1991
<i>Helicostomella subulata</i>	2.10E+04	1.80E+01	1.00E-01	1.73E+00	5.90E-01	Heinbokel 1978
<i>Lohmaniella spiralis</i>	1.50E+05	1.20E+01	1.10E-01	1.73E+00	6.40E-01	Jonsson 1986
<i>Strobilidium cf. spiralis</i>	2.65E+04	2.00E+01	1.89E-01	1.54E+00	1.22E+00	Verity 1991
<i>Strombidium reticulatum</i>	4.00E+04	1.20E+01	1.10E-01	8.80E-01	1.00E+00	Jonsson 1986
<i>Strombidium sulcatum</i>	1.00E+04	2.20E+01	4.81E-01	7.34E+00	6.65E-01	Bernard and Rassoulzadegan 1990
<i>S. sulcatum</i>	1.00E+04	2.20E+01	3.91E-01	8.63E+00	4.53E-01	Bernard and Rassoulzadegan 1990
<i>S. sulcatum</i>	1.00E+04	2.20E+01	1.51E-01	3.70E+01	4.12E-02	Bernard and Rassoulzadegan 1990
<i>Tintinnopsis cf. acuminata</i>	8.10E+03	1.80E+01	3.80E-01	3.13E+00	9.90E-01	Heinbokel 1978
<i>Tintinnopsis acuminata</i>	7.10E+03	2.00E+01	1.70E-01	3.33E+00	5.20E-01	Verity 1985
<i>Tintinnopsis dadayi</i>	1.13E+05	2.00E+01	1.55E-01	9.50E-01	1.63E+00	Verity 1991
<i>Tintinnopsis vasculus</i>	6.90E+04	1.50E+01	1.07E-01	1.45E+00	7.30E-01	Verity 1985

Table 3. Continued.

Predator species	Predator volume ( $\mu\text{m}^3$ )	Temp. ( $^{\circ}\text{C}$ )	$I_{\text{max}}$ ( $\text{h}^{-1}$ )	$C_{\text{max}}$ ( $10^6 \text{ h}^{-1}$ )	$K_m$	Reference
<b>Rotifers</b>						
<i>Brachionus calyciflorus</i>	1.60E+06	2.00E+01	5.40E-02	3.00E-01	1.36E+00	Rothhaupt 1990b
<i>Brachionus plicatilis</i>	2.80E+05	2.10E+01	5.10E-01	3.20E-01	1.63E+01	Korstad et al. 1989
<i>B. plicatilis</i>	2.80E+05	2.10E+01	1.70E-01	1.39E-01	2.05E+01	Korstad et al. 1989
<i>B. plicatilis</i>	2.80E+05	2.00E+01	1.60E-01	5.00E-01	3.50E+00	Starkweather 1988
<i>B. plicatilis</i>	9.16E+05	1.80E+01	1.20E-01	2.95E-01	1.54E+00	Hansen et al. 1997
<i>Brachionus rubens</i>	3.00E+05	2.00E+01	1.50E-01	1.20E+00	1.32E+00	Rothhaupt 1990b
<b>Meroplankton larvae</b>						
<i>Mediomastus fragile</i>	3.70E+06	1.20E+01	2.70E-02	6.40E-01	7.70E-01	Hansen 1993
<i>Mytilus edulis</i>	5.10E+05	1.80E+01	4.00E-02			Jespersen and Olsen 1982
<i>M. edulis</i>	7.10E+06	1.80E+01	2.30E-02			Jespersen and Olsen 1982
<i>M. edulis</i>	5.10E+05	1.90E+01		3.24E-01		Riisgård et al. 1981
<i>M. edulis</i>	1.40E+06	1.90E+01		3.19E-01		Riisgård et al. 1981
<i>M. edulis</i>	2.10E+06	1.90E+01		3.18E-01		Riisgård et al. 1981
<i>M. edulis</i>	4.10E+06	1.90E+01		3.15E-01		Riisgård et al. 1981
<i>M. edulis</i>	9.40E+05	1.80E+01	5.60E-03	3.60E-01	1.58E-01	Sprung 1984b
<i>M. edulis</i>	1.90E+06	1.80E+01	3.70E-03	3.00E-01	1.24E-01	Sprung 1984b
<i>M. edulis</i>	3.90E+06	1.80E+01	8.00E-03	1.82E-01	4.40E-01	Sprung 1984b
<i>M. edulis</i>	9.90E+05	1.80E+01	4.40E-03	1.81E-01	1.90E-01	Sprung 1984b
<i>M. edulis</i>	1.90E+06	1.80E+01	3.10E-03	1.91E-01	1.40E-01	Sprung 1984b
<i>M. edulis</i>	3.90E+06	1.80E+01	6.60E-03	1.09E-01	2.20E-01	Sprung 1984b
<i>Nassarius obsoletus</i>	2.20E+07	2.00E+01	1.23E-02	3.40E-02	3.60E+00	Pechenik and Fischer 1979
<i>N. obsoletus</i>	2.20E+07	2.00E+01	4.20E-02	2.40E-02	1.78E+01	Pechenik and Fischer 1979
<i>N. obsoletus</i>	2.20E+07	2.00E+01	4.60E-02	3.40E-02	1.36E+01	Pechenik and Fischer 1979
<i>Ostrea edulis</i>	7.80E+06	2.10E+01	7.80E-03	2.10E-02	3.71E+00	Crisp et al. 1985
<i>Philine aperta</i>	4.48E+06	1.25E+01	4.30E-03	1.10E-02	8.70E-01	Hansen and Ockelmann 1991
<i>P. aperta</i>	6.27E+06	1.25E+01	1.51E-03	1.63E-02	9.30E-01	Hansen and Ockelmann 1991
<i>P. aperta</i>	1.19E+07	1.25E+01	1.20E-03	2.84E-02	4.20E-01	Hansen and Ockelmann 1991
<i>P. aperta</i>	1.51E+07	1.25E+01	3.90E-03	1.90E-02	2.11E+00	Hansen and Ockelmann 1991
<i>P. aperta</i>	2.80E+07	1.25E+01	3.60E-03	5.50E-02	6.50E-01	Hansen and Ockelmann 1991
<b>Copepods</b>						
<i>Acartia hudsonica</i>	8.65E+07	1.60E+01	3.87E-02	1.12E-01	3.45E+00	Durbin and Durbin 1992
<i>Acartia tonsa</i>	2.98E+07	1.80E+01	4.18E-02	2.08E-01	2.01E+00	Kjørboe et al. 1985a
<i>Aetideus divergens</i>	1.77E+08	1.20E+01	1.66E-01	4.90E-02	3.42E+00	Robertson and Frost 1977
<i>A. divergens</i>	1.77E+08	1.20E+01	6.32E-02	2.13E-02	2.92E+00	Robertson and Frost 1977
<i>A. divergens</i>	1.77E+08	1.20E+01	1.65E-02	2.38E-02	6.93E+00	Robertson and Frost 1977
<i>Calanus helgolandicus</i>	4.16E+08	1.00E+01	1.88E-02	9.40E-01	2.00E-01	Corner et al. 1972
<i>Calanus pacificus</i>	6.37E+08	1.25E+01	8.29E-02	1.12E-01	7.41E+00	Frost 1972
<i>C. pacificus</i>	6.37E+08	1.25E+01	7.72E-02	1.37E-01	5.65E+00	Frost 1972
<i>C. pacificus</i>	6.37E+08	1.25E+01	9.85E-02	1.71E-01	5.78E+00	Frost 1972
<i>Centropages hamatus</i>	4.80E+07	1.50E+01	7.40E-02	4.30E-01	1.73E+00	Kjørboe et al. 1982
<i>Diaptomus gracilis</i>	3.30E+07	5.00E+00	5.10E-03	1.40E-01	3.50E-01	Vanderploeg et al. 1984
<i>Eucalanus pileatus</i> C2	9.82E+07	2.00E+01	3.40E-01	3.70E+00	9.00E-02	Paffenhöfer and van Sant 1985
<i>Oithona nana</i>	1.90E+06	1.00E+01	9.00E-04	4.80E-02	1.80E-01	Lampitt and Gamble 1982
<i>Pseudocalanus</i> sp.	6.66E+07	1.25E+01	3.33E-02	4.60E-01	7.25E-01	Frost 1980

Table 3. Continued.

Predator species	Predator volume ( $\mu\text{m}^3$ )	Temp. ( $^{\circ}\text{C}$ )	$I_{\text{max}}$ ( $\text{h}^{-1}$ )	$C_{\text{max}}$ ( $10^5 \text{ h}^{-1}$ )	$K_m$	Reference
<b>Cladocerans</b>						
<i>Bosmina longirostris</i>	2.53E+07	2.25E+01	3.50E-02	1.30E-02	5.10E-01	Schoenberg 1989
<i>B. longirostris</i>	2.43E+07	2.25E+01	8.30E-02	2.10E-02	8.90E-01	Schoenberg 1989
<i>Bosmina longispina</i>	1.42E+07	2.00E+01	3.37E-02	2.27E-01	2.69E+00	Johnsen and Børshelm 1988
<i>Ceriodaphnia reticulata</i>	1.24E+07	1.20E+01	7.80E-02	2.70E-01	2.85E+00	Philippova and Postnov 1988
<i>C. reticulata</i>	1.74E+07	2.25E+01	2.26E-01	3.50E-02	1.59E+00	Schoenberg 1989
<i>C. reticulata</i>	1.53E+07	2.25E+01	1.14E-01	1.50E-02	2.07E+00	Schoenberg 1989
<i>Chydorus</i> sp.	1.91E+07	2.25E+01	1.10E-01	7.00E-03	4.99E+01	Schoenberg 1989
<i>Chydorus</i> sp.	2.18E+07	2.25E+01	1.60E-01	2.10E-03	2.43E+01	Schoenberg 1989
<i>Daphnia magna</i>	1.01E+09	2.00E+01	4.90E-02	3.30E-02	1.19E+00	Porter et al. 1982
<i>D. magna</i>	2.09E+08	2.00E+01	7.84E-02	3.29E-01	2.38E+01	Philippova and Postnov 1988
<i>D. magna</i>	6.07E+08	2.00E+01	9.30E-02	1.17E-01	8.00E+00	Philippova and Postnov 1988
<i>D. magna</i>	4.83E+08	1.70E+01	2.46E-02	1.41E-02	1.74E+01	Kersting and van der Leeuf 1976
<i>D. magna</i>	1.05E+09	2.00E+01	5.64E-03	6.10E-02	9.67E-01	McMahon and Rigler 1965
<i>D. magna</i>	1.05E+09	2.00E+01	1.88E-02	4.25E-02	4.42E+00	McMahon and Rigler 1965
<i>D. magna</i>	1.05E+09	2.00E+01	1.54E-02	3.10E-02	4.96E+00	McMahon and Rigler 1965
<i>D. magna</i>	1.05E+09	2.00E+01	6.76E-02	5.85E-02	1.04E+01	McMahon and Rigler 1965
<i>D. magna</i>	1.80E+07	2.00E+01	2.59E-02	1.66E-01	1.56E+00	McMahon 1965
<i>D. magna</i>	2.20E+07	2.00E+01	2.16E-02	1.62E-01	1.33E+00	McMahon 1965
<i>D. magna</i>	2.70E+07	2.00E+01	3.23E-02	8.30E-02	3.88E+00	McMahon 1965
<i>D. magna</i>	2.80E+07	2.00E+01	3.49E-02	8.50E-02	4.11E+00	McMahon 1965
<i>D. magna</i>	3.00E+07	2.00E+01	2.23E-02	1.41E-01	1.58E+00	McMahon 1965
<i>D. magna</i>	3.10E+07	2.00E+01	3.23E-02	7.20E-02	4.47E+00	McMahon 1965
<i>D. magna</i>	3.30E+07	2.00E+01	3.94E-02	6.20E-02	6.37E+00	McMahon 1965
<i>Daphnia pulex</i>	1.90E+08	2.00E+01	3.70E-02	2.60E-01	1.41E+00	Lampert 1977
<i>D. pulex</i>	2.50E+07	2.00E+01	6.10E-02	3.90E-01	1.25E+00	Lampert 1977
<i>D. pulex</i>	6.40E+08	2.00E+01	2.80E-02	2.10E-01	1.31E+00	Lampert 1977
<i>Daphnia rosea</i>	9.20E+07	1.50E+01	2.30E-02	7.20E-02	3.20E+00	DeMott 1982
<i>D. rosea</i>	1.80E+06	1.50E+01	1.20E-01	2.44E+00	5.00E-01	DeMott 1982
<i>Daphnia schroederi</i>	1.00E+09	2.00E+01	5.20E-02	1.74E-02	3.00E+01	Hayward and Gallup 1976
<i>D. schroederi</i>	1.90E+08	2.00E+01	6.70E-02	4.90E-02	1.38E+01	Hayward and Gallup 1976
<i>Simocephalus vetulus</i>	2.79E+07	1.20E+01	1.90E-01	3.24E-01	6.00E+00	Philippova and Postnov 1988
<i>S. vetulus</i>	1.05E+08	1.20E+01	1.62E-01	2.50E-01	6.50E+00	Philippova and Postnov 1988



density of  $\sim 240 \mu\text{g C liter}^{-1}$  (Fig. 4). The maximum likelihood estimate of the scaling exponent determined on the basis of growth rates was not different from that obtained on the basis of ingestion rates (not shown), indicating that growth yields ( $=\mu/I$ ) among groups are not different and equal on average 0.33 (Table 7).

Among the protists, ciliates have maximum specific ingestion rates that on average exceed those of dinoflagellates of a similar size by a factor of  $\sim 2$  (Fig. 2A). This difference in metabolic rate is also seen in data on maximum specific growth rates, where the difference is a factor of  $\sim 3$  (Fig. 2B, Table 4). Similarly, ciliates have clearance rates that exceed those of the dinoflagellates by a factor of 4, resulting in an apparent lack of size dependency among the entire assemblage of protists (Fig. 3A). Consequently, ciliates have a  $K_m$  that is lower as compared to the flagellates. Maximum specific clearance calculated by multiplication of swimming speed and area of the filtering apparatus (*see materials and methods*) gave results that are in accordance with the actually measured clearance rates for the flagellates (Fig. 3, Table 8) but not for the ciliates. The calculated clearance rates for ciliates were generally underestimated by a factor of 2–3, indicating that the difference in swimming speed between ciliates and flagellates only partly accounted for the difference in observed clearance rates.

Among the metazooplankton, meroplankton larvae appear to have maximum specific ingestion rates that are almost an order of magnitude lower compared to the other groups. However, such a large difference is not seen in the data on maximum growth rates. Copepods (calanoids) on the other hand display maximum specific clearances that are considerably higher compared to cladocerans of a similar size. Consequently, the half-saturation constant of the cladocerans exceeds that of calanoid copepods by a factor of 8.

An analysis of intraspecific variation was only possible in a few species belonging to the metazooplankton. The variations in the functional response are best illustrated by the cladoceran *Daphnia magna* (*see Table 3*). Intraspecific variation in maximum clearance and ingestion rates is large, exceeding a factor of 10. In this case, the variation found within a single study is similar to the variation among different studies.

## Discussion

**Scaling**—Metabolic rates expressed in terms of growth rates or weight-specific respiration rates tend to decrease with body size, when organisms covering a large size span are compared (Zeuthen 1953; Hemmingsen 1960). Describing weight-specific respiration with the allometric equation,  $R = aW^b$ , Hemmingsen (1960) found a scaling exponent of  $-0.25$  in poikilotherm metazoa and protozoa. However, he found that poikilotherm metazoa have specific respiration rates that are  $\sim 8$  times higher than protozoa. Fenchel (1968, 1974) found that metazoa had specific growth rates that were only two times higher than those of protozoa of similar body size. Later, Fenchel and Finlay (1983) reviewed all published data on protozoan respiration. They found that the data on respiration rates show a large variation even within species,

related to the physiological state of the organisms during measurements. They concluded that physiological rates of protozoa and heterotherm metazoa were similar. Likewise, Fenchel (1986) compiled data on maximum clearance obtained on filter-feeding protozoa and some groups of metazoan filter-feeders. Covering a size span of  $\sim 10$  orders of magnitude, maximum specific clearance was found to decrease with an exponent of about  $-0.25$ .

In accordance with Fenchel and Finlay (1983), we found no consistent difference in maximum physiological rates between protozoa and metazoa. However, we found that some zooplankton groups deviate significantly from the overall log-log regression. Consequently, the scaling factor derived from an overall regression across functionally different groups will depend on the balance between the groups within the entire data set. For instance, an overrepresentation of copepods would reduce the overall scaling factor for  $C_{\text{max}}$  (cf. Fig. 3). This becomes particular critical if a limited size range of organisms with a high degree of functional diversity (e.g. crustaceans) is analyzed. Our approach was to derive a common scaling factor from regressions within functionally homogeneous assemblages of zooplankton. It is noteworthy that the scaling factor derived by this approach ( $-0.23$ ) is consistent with other estimates derived from a wide range of body sizes.

**Variation between groups of zooplankton**—If the growth rates of ciliates are extrapolated to the size of small heterotrophic flagellates (excluding dinoflagellates), the derived growth rate would be about three times higher than actual flagellate rates (Fenchel 1991). Recently, a number of growth rate values for larger flagellates (e.g. dinoflagellates) have been published and these maximum growth rates are about three times lower compared to planktonic ciliates of similar size (Hansen 1992; Sherr and Sherr 1994). Our data confirm this difference for growth as well as for ingestion rates (Fig. 2). The reason for the difference in metabolic rates between ciliates and flagellates remains unanswered.

An interesting observation from our data is the apparent lack of scaling in maximum clearance rates if all protists are treated as one group. This can only partly be explained by the high swimming speed found in the ciliates (Fig. 3), because clearance calculated on the basis of swimming speed underestimates the actual clearance of ciliates by a factor of 2 or 3. An underestimate of the effective filter area of ciliates probably explains this difference. Ciliate filtering structures (membranellae) generally reach beyond the cell width, and the effective hydrodynamic filter area may reach beyond the filtering structure (Fenchel 1982; Buskey and Stoecker 1988).

Peters and Downing (1984) compiled published ingestion rates of crustacean metazooplankton reported from both laboratory and field studies at food concentrations of between 0.2 and 50 ppm and found a strong size dependence (scaling exponent of between  $-0.26$  and  $-0.45$ ). In our study, which builds on another set of data, only a small decrease in metazooplankton maximum growth rates with volume was observed, although no size dependency was found in estimates of maximum specific ingestion or clearance rates. The lack of size dependence of maximum ingestion and clearance

Table 4. Maximum growth rates for different zooplankton taxa. Data were not corrected for temperature differences.

Predator species	Predator volume ( $\mu\text{m}^3$ )	Temp. ( $^{\circ}\text{C}$ )	$\mu_{\text{max}}$ ( $\text{h}^{-1}$ )	Reference
Nanoflagellates (except dinoflagellates)				
<i>Actinomonas mirabilis</i>	7.50E+01	20	0.250	Fenchel 1982
<i>Bodo designis</i>	5.40E+01	20	0.160	Eccleston-Parry and Leadbeater 1994
<i>Ciliophrys infusionum</i>	2.20E+02	20	0.045	Eccleston-Parry and Leadbeater 1994
<i>Codosiga gracilis</i>	3.50E+01	20	0.052	Eccleston-Parry and Leadbeater 1994
<i>Diaphanoeca grandis</i>	4.00E+01	15	0.120	Andersen 1988/1989
<i>Jakoba libera</i>	7.50E+01	20	0.036	Eccleston-Parry and Leadbeater 1994
<i>Monosiga</i> sp.	2.00E+01	20	0.170	Fenchel 1982
<i>Ochromonas</i> sp.	2.00E+02	20	0.190	Fenchel 1982
<i>Ochromonas</i> sp.	5.00E+01	20	0.127	Anderson et al. 1989
<i>Paraphysomonas imperforata</i>	2.12E+02	20	0.210	Eccleston-Parry and Leadbeater 1994
<i>Paraphysomonas vestita</i>	1.90E+02	20	0.230	Fenchel 1982
<i>Pleuromonas jaculans</i>	5.00E+01	20	0.160	Fenchel 1982
<i>Pseudobodo tremulans</i>	9.00E+01	20	0.150	Fenchel 1982
<i>Pseudobodo</i> sp.	3.35E+01	15	0.115	Rivier et al. 1985
<i>Spumella</i> sp.	6.54E+01	25	0.133	Hollen and Boraas 1991
<i>Stephanoeca diplocostata</i>	2.00E+01	18	0.079	Geider and Leadbeater 1988
<i>S. diplocostata</i>	8.30E+01	20	0.035	Eccleston-Parry and Leadbeater 1994
Dinoflagellates				
<i>Amphidinium crassum</i>	3.15E+03	15	0.024	Hansen 1992
<i>Gymnodinium</i> sp.	9.00E+02	12	0.035	Strom 1991
<i>Gyrodinium dominans</i>	1.04E+04	15	0.020	Hansen 1992
<i>Gyrodinium spirale</i>	1.15E+04	15	0.022	Hansen 1992
<i>Gyrodinium</i> sp.	2.50E+02	15	0.048	Hansen 1992
<i>Oblea rotunda</i>	6.13E+03	20	0.029	Strom and Buskey 1993
<i>Oxyrrhis marina</i>	6.30E+03	20	0.029	Gaines unpubl.
<i>Protoperidinium crassipes</i>	2.04E+05	19	0.013	Jeong and Latz 1994
<i>Protoperidinium divergens</i>	1.19E+05	19	0.019	Jeong and Latz 1994
<i>Protoperidinium hirobis</i>	4.20E+03	20	0.050	Jacobson and Anderson 1993
<i>Protoperidinium pellucidum</i>	2.53E+04	15	0.014	Hansen 1992
Ciliates				
<i>Eutimninus pectinis</i>	1.50E+04	18	0.073	Heinbokel 1978
<i>Favella ehrenbergii</i>	2.10E+05	20	0.029	Buskey and Stoecker 1988
<i>F. ehrenbergii</i>	9.56E+04	15	0.034	Hansen et al. 1991
<i>Helicostomella subulata</i>	2.10E+04	18	0.027	Heinbokel 1978
<i>Lohmaniella spiralis</i>	1.50E+05	12	0.044	Jonsson 1986
<i>Pseudobalanion planctonicum</i>	1.44E+03	18.5	0.063	Müller 1991
<i>Strobilidium</i> cf. <i>spiralis</i>	2.65E+04	20	0.060	Verity 1991
<i>Strombidium reticulata</i>	4.00E+04	12	0.036	Jonsson 1986
<i>Strombidium sulcatum</i>	6.50E+03	20	0.120	Fenchel and Jonsson 1988
<i>Tintinnopsis acuminata</i>	7.10E+03	20	0.072	Verity 1985
<i>Tintinnopsis</i> cf. <i>acuminata</i>	8.10E+03	18	0.051	Heinbokel 1978
<i>Tintinnopsis dadayi</i>	1.13E+05	20	0.058	Verity 1991
<i>Tintinnopsis vasculus</i>	6.90E+04	15	0.050	Verity 1985
Rotifers				
<i>Asplancha priodonta</i>	1.31E+06	19	0.0330	Stemberger and Gilbert 1985
<i>Brachionus calyciflorus</i>	1.61E+06	20	0.0320	Guisande and Mazuelos 1991
<i>B. calyciflorus</i>	1.60E+06	20	0.0420	Guisande and Mazuelos 1991
<i>B. calyciflorus</i>	1.15E+06	25	0.0540	Boraas 1983
<i>B. calyciflorus</i>	1.50E+06	20	0.0300	Rothhaupt 1990a
<i>B. calyciflorus</i>	7.50E+05	19	0.0340	Stemberger and Gilbert 1985
<i>B. calyciflorus</i>	6.90E+05	25	0.0530	Boraas and Bennett 1988
<i>Brachionus plicatilis</i>	5.90E+05	20	0.0730	Doohan 1973
<i>B. plicatilis</i>	8.00E+05	20	0.0310	Starkweather 1988
<i>B. plicatilis</i>	2.10E+06	18	0.0200	Hansen et al. 1997
<i>Euchlanis dilatata</i>	4.37E+06	22	0.0300	King 1966
<i>Keratella cochlearis</i>	7.50E+04	19	0.0120	Stemberger and Gilbert 1985
<i>Keratella crassa</i>	3.40E+05	19	0.0100	Stemberger and Gilbert 1985
<i>Keratella earlinea</i>	2.30E+05	19	0.0120	Stemberger and Gilbert 1985

Table 4. Continued.

Predator species	Predator volume ( $\mu\text{m}^3$ )	Temp. ( $^{\circ}\text{C}$ )	$\mu_{\text{max}}$ ( $\text{h}^{-1}$ )	Reference
Rotifers (continued)				
<i>Philodina roseola</i>	7.47E+06	20	0.0150	Labadeva and Grerasimova 1985
<i>Polyarthra remata</i>	1.50E+05	19	0.0160	Stemberger and Gilbert 1985
<i>Synchaeta cecilia</i>	1.50E+05	20	0.0250	Egloff 1988
<i>Synchaeta oblonga</i>	2.60E+05	19	0.0120	Stemberger and Gilbert 1985
<i>Synchaeta pectinata</i>	8.60E+05	19	0.0330	Stemberger and Gilbert 1985
Meroplankton larvae				
<i>Mediomastus fragile</i>	3.70E+06	11	0.0023	Hansen 1993
<i>Mytilus edulis</i>	7.20E+06	18	0.0120	Sprung 1984a
<i>M. edulis</i>	1.40E+07	18	0.0100	Sprung 1984a
<i>M. edulis</i>	3.35E+07	18	0.0074	Sprung 1984a
<i>M. edulis</i>	6.57E+07	18	0.0060	Sprung 1984a
<i>M. edulis</i>	5.10E+05	18	0.0100	Jespersen and Olsen 1982
<i>M. edulis</i>	7.10E+06	18	0.0040	Jespersen and Olsen 1982
<i>Philine aperta</i>	1.00E+07	12.5	0.0037	Hansen and Ockelmann 1991
Copepods				
<i>Acartia tonsa</i>	4.20E+07	17	0.0190	Berggreen et al. 1988
<i>Centropages typicus</i>	7.50E+07	17	0.0150	Fryd et al. 1991
<i>Oithona colcarva</i>	1.10E+07	20	0.0034	Lonsdale 1981a,b
<i>Oithona davisae</i>	1.70E+06	20.5	0.0059	Uchima 1985
<i>Oithona plumifera</i>	1.10E+07	20	0.0037	Paffenhöfer 1993
<i>Oithona similis</i>	5.00E+06	15	0.0083	Sabatini and Kiørboe 1994
<i>O. similis</i>	5.00E+06	15	0.0042	Sabatini and Kiørboe 1994
<i>O. similis</i>	5.00E+06	10	0.0015	Eaton 1971
<i>Oncaea mediterranea</i>	2.37E+07	20	0.0108	Paffenhöfer 1993
<i>O. mediterranea</i>	2.37E+07	20	0.0029	Paffenhöfer 1993
<i>Pseudocalanus elongatus</i>	8.05E+07	12.5	0.0024	Paffenhöfer and Harris 1976
<i>P. elongatus</i>	5.55E+07	15	0.0045	Frost 1985
<i>P. elongatus</i>	8.05E+07	15	0.0094	Klein-Breteler et al. 1982
<i>Pseudocalanus moultoni</i>	4.76E+07	12	0.0023	Jonasdottir 1989
<i>Pseudocalanus newmani</i>	4.39E+07	12	0.0017	Jonasdottir 1989
<i>Pseudocalanus</i> sp.	1.13E+07	15.5	0.0104	Vidal 1980a

Table 5. Linear regression analysis for the relationship between size and half-saturation constant ( $K_m$ ), maximum clearance ( $C_{\text{max}}$ ), ingestion ( $I_{\text{max}}$ ), and growth rates ( $\mu_{\text{max}}$ ) for different zooplankton groups. Standard error (SE) is given in brackets. Significant relationships are marked (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ).

Zooplankton group	$C_{\text{max}}$	$I_{\text{max}}$	$K_m$	$\mu_{\text{max}}$
All groups	Log $a$ : $0.73 \pm 0.66$ $b$ : $-0.18 \pm 0.04^{**}$ $R^2=0.30$ , $n=58$	Log $a$ : $-0.04 \pm 0.38$ $b$ : $-0.16 \pm 0.02^{**}$ $R^2=0.51$ , $n=58$	Log $a$ : $0.35 \pm 0.58$ $b$ : $-0.03 \pm 0.03$ $R^2=0.01$ , $n=58$	Log $a$ : $-0.52 \pm 0.29$ $b$ : $-0.21 \pm 0.02^{**}$ $R^2=0.69$ , $n=69$
Metazooplankton	Log $a$ : $-0.45 \pm 0.77$ $b$ : $-0.03 \pm 0.18$ $R^2=0.001$ , $n=26$	Log $a$ : $-1.78 \pm 0.47$ $b$ : $0.08 \pm 0.11$ $R^2=0.021$ , $n=26$	Log $a$ : $0.13 \pm 0.65$ $b$ : $0.012 \pm 0.15$ $R^2=0.003$ , $n=26$	Log $a$ : $-1.64 \pm 0.26$ $b$ : $-0.02 \pm 0.07$ $R^2=0.005$ , $n=18$
Protozooplankton	Log $a$ : $0.32 \pm 0.52$ $b$ : $-0.02 \pm 0.07$ $R^2=0.003$ , $n=32$	Log $a$ : $0.10 \pm 0.24$ $b$ : $-0.20 \pm 0.031^{**}$ $R^2=0.57$ , $n=32$	Log $a$ : $0.73 \pm 0.51$ $b$ : $-0.16 \pm 0.07^*$ $R^2=0.17$ , $n=32$	Log $a$ : $-0.66 \pm 0.26$ $b$ : $-0.15 \pm 0.03$ $R^2=0.37$ , $n=39$
Dinoflagellates	Log $a$ : $4.18 \pm 0.27$ $b$ : $-1.08 \pm 0.17^{**}$ $R^2=0.91$ , $n=6$	Log $a$ : $0.15 \pm 0.23$ $b$ : $-0.27 \pm 0.15$ $R^2=0.45$ , $n=6$	Log $a$ : $-2.79 \pm 0.27$ $b$ : $0.77 \pm 0.17^*$ $R^2=0.83$ , $n=6$	Log $a$ : $-0.47 \pm 0.08$ $b$ : $-0.26 \pm 0.03^{**}$ $R^2=0.90$ , $n=11$
All flagellates	Log $a$ : $0.68 \pm 0.54$ $b$ : $-0.22 \pm 0.11$ $R^2=0.16$ , $n=21$	Log $a$ : $0.30 \pm 0.23$ $b$ : $-0.30 \pm 0.05^{**}$ $R^2=0.65$ , $n=21$	Log $a$ : $0.46 \pm 0.55$ $b$ : $-0.01 \pm 0.12$ $R^2=0.001$ , $n=21$	Log $a$ : $-0.45 \pm 0.23$ $b$ : $-0.26 \pm 0.04^{**}$ $R^2=0.64$ , $n=27$

Table 6. SSD (sums of squared deviations between observations and models) for three different models of log-log regressions of maximum specific ingestion and clearance rates to predator volume. The *F*-ratios and *P*-levels given for model 2 tested against model 1 and model 3 were tested against model 2. Model 1, independent regressions; model 2, same slope; model 3, common regression.

	Max. specific ingestion			Max. specific clearance		
	1	2	3	1	2	3
Dinoflagellates	0.21	0.21	0.62	0.29	2.07	2.33
Other flagellates	0.72	0.77	0.79	3.23	3.38	3.63
Ciliates	0.23	0.27	0.29	0.60	0.62	3.81
Rotifers	0.02	0.10	0.12	0.17	0.19	0.21
Meroplankton larvae	0.79	0.82	3.29	1.20	2.07	3.49
Cladocerans	1.00	1.01	1.15	5.01	5.20	7.25
Copepods*	0.80	1.29	1.84	2.52	2.63	4.07
( <i>Oithona nana</i> )	(0.12)	(1.52)		(0.04)	(0.83)	
All	3.76	4.49	8.10	13.11	16.17	24.79
<i>F</i> -ratio		1.58	4.62		0.96	7.46
<i>P</i>		>0.1	≤0.005		>0.1	≤0.005

\* Except *O. nana*.

rates in the present study is likely due to our coverage of a much smaller data set both in terms of the number of data points and body size range covered and our inclusions of a broader range of taxonomic groups.

Significant differences within taxonomic groups (e.g. copepods) may relate to different niches occupied by different subgroupings (families, genera, species). For example, Kiør-

boe and Sabatini (1995) found that broadcast spawners (calanoid copepods) grow faster than egg carriers (cyclopoid copepods) by 30–50% and have weight-specific fecundities that are 2.5 times those of the former. Even with these groupings, they found that specific growth and developmental rates did not vary with body mass in copepods, whereas weight-specific fecundity decreased with female body mass

Table 7. Average growth yield at maximum growth rates for different zooplankton taxa. v = volume; dw = dry weight; C = carbon; N = nitrogen; ca = calories.

	Yield	No. of species	Reference
Heterotrophic dinoflagellates	0.29 (v)	1	Gaines unpubl.
	0.18 (v)	1	Hansen 1992
	0.40 (v)	1	Jeong and Latz 1994
	0.10 (v)	1	Jacobson and Anderson 1993
	0.31 (v)	1	Strom 1991
Other flagellates	0.15 (v)	1	Strom and Buskey 1993
	0.36 (v)	1	Andersen 1988/1989
	0.33 (v)	2	Fenchel 1982
	0.34 (v)	2	Geider and Leadbeater 1988
	0.28 (v)	1	Rivier et al. 1985
Ciliates	0.40 (v)	2	Jonsson 1986
	0.39 (v)	1	Sheldon et al. 1986
	0.42 (C)	2	Verity 1985
Rotifers	0.36 (C)	2	Verity 1991
	0.30 (dw)	2	Boraas 1983
	0.45 (C)	1	Droop and Scott 1978
	0.29 (v)	1	Hansen et al. 1997
	0.43 (dw)	1	Schlüter et al. 1987
Meroplankton larvae	0.35 (ca)	1	Scott 1980
	0.29 (v)	2	Helm 1977
	0.39 (C)	1	Jespersen and Olsen 1982
	0.23 (dw)	1	Sprung 1983
	0.33 (dw)	1	Sprung 1984d
Copepods	0.33 (C)	1	Berggreen et al. 1988
	0.36 (N)	1	Corner et al. 1965
	0.34 (N)	1	Corner et al. 1967
Mean ± SE	0.33 ± 0.032	n = 33	

Table 8. Swimming speed and calculated maximum specific clearance for different zooplankton taxa. Data are not temperature corrected.

Zooplankton species	Vol. ( $\mu\text{m}^3$ )	Swimming speed ( $\mu\text{m s}^{-1}$ )	Specific clearance ( $10^5 \text{ h}^{-1}$ )	Reference
Nanoflagellates (except dinoflagellates)				
<i>Actinomonas mirabilis</i>	7.50E+01	240	2.40	Fenchel 1982
<i>Bodo designis</i>	5.40E+01	80	0.89	Eccleston-Parry and Leadbeater 1994
<i>Diaphanoeca grandis</i>	7.40E+01	40	0.40	Andersen 1988/1989
<i>Jakoba libera</i>	7.50E+01	19	0.19	Eccleston-Parry and Leadbeater 1994
<i>Monosiga</i> sp.	2.00E+01	25	0.39	Fenchel 1982
<i>Ochromonas minima</i> sp.	2.50E+01	75	1.09	Throndsen 1973
<i>Paraphysomonas imperforata</i>	2.12E+02	42	0.29	Eccleston-Parry and Leadbeater 1994
<i>Paraphysomonas vestita</i>	1.90E+02	70	0.51	Fenchel 1982
<i>Pyramimonas</i> cf. <i>disomata</i>	1.00E+02	350	3.17	Throndsen 1973
Dinoflagellates				
<i>Dinophysis acuta</i>	4.00E+04	500	0.59	Levandowsky and Kaneta 1987
<i>Gonyaulax polyedra</i>	2.57E+04	278	0.38	Levandowsky and Kaneta 1987
<i>Gymnodinium sanguineum</i>	1.67E+04	306	0.49	Levandowsky and Kaneta 1987
<i>Katodinium rotundatum</i>	5.30E+02	430	2.21	Levandowsky and Kaneta 1987
<i>Prorocentrum micans</i>	3.40E+04	90	0.11	Levandowsky and Kaneta 1987
<i>Protoperidinium pentagonum</i>	1.10E+05	252	0.21	Levandowsky and Kaneta 1987
<i>Protoperidinium subinerve</i>	5.00E+04	278	0.30	Levandowsky and Kaneta 1987
<i>Protoperidinium ovatum</i>	1.10E+05	188	0.16	Levandowsky and Kaneta 1987
<i>Protoperidinium cladicans</i>	1.10E+05	215	0.18	Levandowsky and Kaneta 1987
<i>Protoperidinium crassipes</i>	2.04E+05	100	0.07	Levandowsky and Kaneta 1987
<i>Protoperidinium</i> cf. <i>quinquecorne</i>	1.40E+05	1,500	1.16	Levandowsky and Kaneta 1987
<i>Scripsiella trochoidea</i>	3.60E+03	53	0.14	Levandowsky and Kaneta 1987
Ciliates				
<i>Blepharisma</i> sp.	1.83E+06	600	0.19	Sleigh and Blake 1977
<i>Didinium nasutum</i>	5.43E+05	1,250	0.61	Sleigh and Blake 1977
<i>Favella ehrenbergi</i>	1.50E+05	920	0.69	Buskey and Stoecker 1988
<i>Paramecium caudata</i>	3.03E+05	1,000	0.59	Sleigh and Blake 1977
<i>Pseudocohnilembus pussilus</i>	2.50E+03	320	0.97	Fenchel 1990
<i>Strombidium sulcatum</i>	9.00E+03	850	1.67	Fenchel and Jonsson 1988
<i>Tetrahymena</i> sp.	6.50E+04	480	0.48	Sleigh and Blake 1977
<i>Uronema marinum</i>	1.00E+03	520	2.15	Fenchel 1990
<i>Uronema</i> sp.	1.60E+03	1,150	4.06	Sleigh and Blake 1977
Meroplankton larvae				
<i>Cerastoderma edule</i>	8.30E+06	1,190	0.23	Jonsson et al. 1989
<i>Mediomastus fragile</i>	3.70E+06	682	0.17	B. Hansen unpubl.
<i>Philine aperta</i>	4.48E+06	1,200	0.28	Hansen and Ockelmann 1991
Rotifers				
<i>Asplancha girodi</i>	4.50E+06	564	0.13	Stemberger and Gilbert 1987
<i>Asplancha priodonta</i>	1.35E+06	540	0.19	Stemberger and Gilbert 1987
<i>Asplancha silvestrii</i>	5.98E+06	448	0.10	Stemberger and Gilbert 1987
<i>Brachionus calyciflorus</i>	9.71E+05	169	0.07	Stemberger and Gilbert 1987
<i>Brachionus plicatilis</i>	7.50E+05	760	0.33	Stemberger and Gilbert 1987
<i>B. plicatilis</i>	7.75E+05	550	0.24	B. Hansen unpubl.
<i>Synchaeta pectinata</i>	8.20E+05	770	0.33	Stemberger and Gilbert 1987

with an scaling exponent of  $-0.26$  in both egg-carrying and broadcast spawners.

**Intraspecific variation**—We used only laboratory data with a complete functional response curve for each species. Also, average values of  $C_{\max}$ ,  $I_{\max}$ , and  $K_m$  were calculated, where several measurements have been performed, covering different sizes and developmental stages of a species. In spite of this, estimates of maximum clearance and ingestion rates still dis-

played considerable variation within zooplankton groups. The variations in maximum growth rates were generally much lower than those found for maximum specific clearance and ingestion rates. The variation found in both maximum specific ingestion and clearance rates was the same within and among different studies of the freshwater cladoceran *D. magna* and equals an order of magnitude. Considerable variation in feeding measurements may be due to organism differences as well as methodological and experimental limitations.

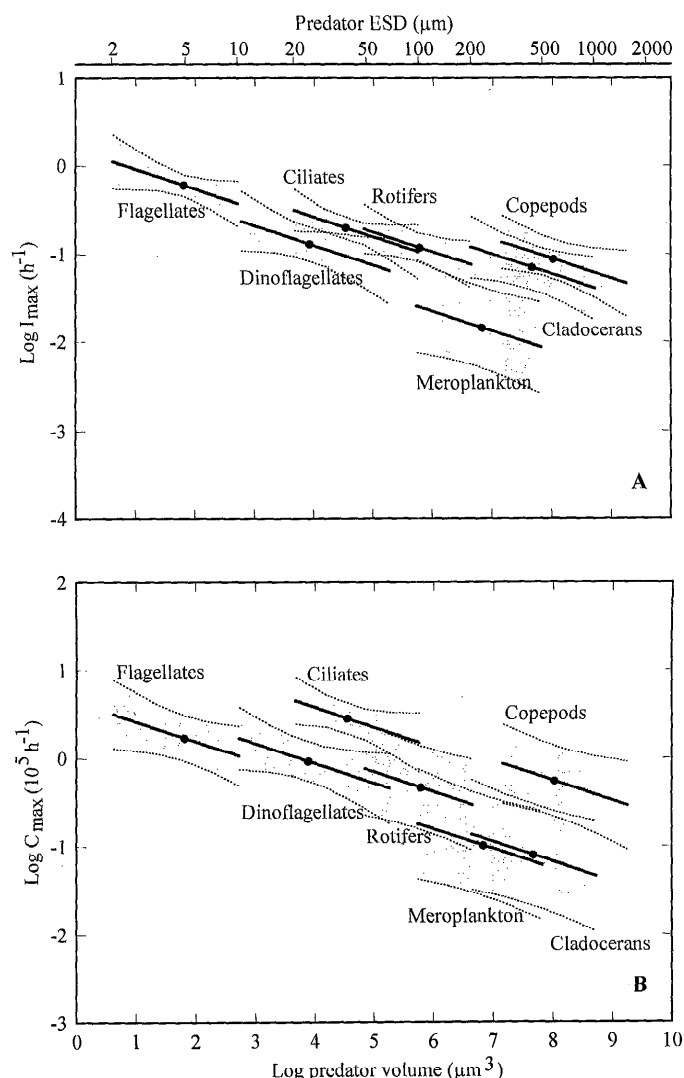


Fig. 5. Predicted maximum ingestion (A) and clearance rates (B) for the different groups of zooplankton estimated using the model of a common slope of  $-0.225$ . For each group of predators (e.g. cladocerans) estimates of maximum clearance and ingestion are shown with 95% confidence levels (mean  $\pm$  2 SE). Estimates of rates can be calculated from data in Table 9. Note that confidence limits relate to the maximum likelihood estimates and not to single observations.

The estimates of maximum clearance and ingestion rates rely on the calculation of carbon content and volume of both prey and predator. The variation in the prey carbon: volume ratio have been reported to increase by a factor of  $\sim 10$  going from bacteria to larger diatoms containing a large water vacuole (e.g. Strathmann 1967; Bjørnsen 1986; Verity et al. 1992). However, improved methods for the measurement of bacterial cell volumes have suggested the high carbon: volume ratios previously reported were too high (Fagerbagge et al. 1996). Among different algae with a similar cell volume, the carbon: cell volume ratio may differ by a factor of 4 (Strathmann 1967).

Table 9. Log-mean values of bodysize, maximum specific ingestion, and clearance rates. Estimates of rates can be calculated using the common scaling exponent of  $-0.23$ :  $\log(\text{rate}) = \log a - 0.23P_{\text{vol}}$ , where  $P_{\text{vol}}$  is the body volume of the predator,  $I_{\text{max}}$  is the maximum specific ingestion rate ( $\text{h}^{-1}$ ), and  $C_{\text{max}}$  is the maximum specific clearance rate ( $10^5 \text{ h}^{-1}$ ).

	Log $P_{\text{vol}}$	Log $I_{\text{max}}$	Log $C_{\text{max}}$
Dinoflagellates	3.88	$-0.889$	$-0.041$
Other flagellates	1.81	$-0.222$	0.233
Ciliates	4.50	$-0.693$	0.456
Rotifers	5.75	$-0.929$	$-0.330$
Meroplankton larvae	6.82	$-1.84$	0.987
Copepods (calanoid)	8.01	$-1.06$	$-0.267$
Cladocerans	7.65	$-1.15$	$-1.10$

**Prediction of zooplankton grazing rates**—This study facilitates comparison of grazing rates obtained in the field and in the laboratory. A basis for comparison with new measurements of grazing rates is provided in Fig. 5, and Table 9, which summarize the data analyzed in this study. For each group of predators (e.g. cladocerans), estimates of maximum clearance and ingestion are shown with 95% C.L.

Estimates of maximum grazing and growth rates obtained in the laboratory have been shown to correspond to maximum rates measured in field experiments for a number of zooplankton groups (e.g. Kiørboe et al. 1985b; Peterson et al. 1991; Nielsen and Kiørboe 1994). Thus, in the absence of direct measurements, estimates of grazing rates obtained through laboratory studies can be applied for use in pelagic carbon flow models (e.g. Christoffersen et al. 1990; Riemann et al. 1990; Maloney and Field 1991). However, laboratory data on maximum clearance and ingestion rates may overestimate the grazing potential of zooplankton compared to field situations (e.g. Cyr and Pace 1992). Therefore, comparison of grazing rates measured under different conditions should consider several possible concerns. Size selectivity should be taken into account. Zooplankton cannot be considered simply as a functionally uniform group of grazers that feeds on prey of  $\sim 1:10$  of their own body size as previously suggested (e.g. Azam et al. 1983), but must be divided into functional groups (Hansen et al. 1994). Prey density must be taken into account. The half-saturation constant  $K_m$  is on average  $240 \mu\text{g C liter}^{-1}$ , a biomass that is often encountered in meso- to eutrophic waters (Wetzel 1983). Thus, a grazing estimate calculated from either maximum ingestion or clearance rates would overestimate the grazing impact. The actual food may be of poor quality for the zooplankton either due to lack of essential nutrients or production of toxins (e.g. Lampert 1981; Huntley et al. 1986; Hansen 1989). Although food is plentiful and of the right size and quality, the predicted ingestion and clearance rates (Fig. 5, Table 5) have 2–3-fold confidence limits.

We think that future studies on zooplankton grazing will decrease the confidence ranges around the estimates, and we hope that this perspective will stimulate researchers to perform and present their studies on zooplankton grazing with a view to facilitating comparison.

## Conclusion

Taking the above-mentioned precautions into consideration, it is possible to predict the grazing activity on the basis of taxonomy, body size, temperature, and prey size and concentration. Equations are given for the estimation of maximum ingestion and clearance rates, allowing comparison with future laboratory and field-determined rates as well as providing rough estimates for their use in models on the flux of carbon flow in pelagic environments.

## References

- ANDERSEN, P. 1988/1989. Functional biology of the choanoflagellate *Diaphanoeca grandis* Ellis. *Mar. Microb. Food Webs* **3**: 35–50.
- ANDERSON, A., S. FALK, G. SAMUELSON, AND Å. HAGSTRÖM. 1989. Nutritional characteristics of a mixotrophic nanoflagellate, *Ochromonas* sp. *Microb. Ecol.* **17**: 251–262.
- AZAM, F., AND OTHERS. 1983. The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.* **10**: 257–263.
- BAYNE, B. L. 1965. Growth and the delay of metamorphosis of the larvae of *Mytilus edulis* L. *Ophelia* **2**: 1–47.
- BERGGREEN, U., B. HANSEN, AND T. KIØRBOE. 1988. Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: Implications for determination of copepod production. *Mar. Biol.* **99**: 341–352.
- BERNARD, C., AND F. RASSOULZADEGAN. 1990. Bacteria or microflagellates as a major food source for marine ciliates: Possible implications for the microzooplankton. *Mar. Ecol. Prog. Ser.* **64**: 147–155.
- BJØRNSSEN, P. K. 1986. Automatic determination of bacterioplankton biomass by image analysis. *Appl. Environ. Microbiol.* **51**: 1199–1204.
- BORAAS, M. E. 1983. Population dynamics of food-limited rotifers in two-stage chemostat culture. *Limnol. Oceanogr.* **28**: 546–563.
- , AND W. N. BENNETT. 1988. Steady-state rotifer growth in a two-stage computer-controlled turbidostat. *J. Plankton Res.* **10**: 1023–1038.
- BUSKEY, E. J., AND D. K. STOECKER. 1988. Locomotory patterns of the planktonic ciliate *Favella* sp.: Adaptations for remaining within food patches. *Bull. Mar. Sci.* **43**: 783–796.
- BØRSHEIM, K. Y., AND G. BRATBAK. 1987. Cell volume to cell carbon conversion factors for a bacterivorous *Monas* sp. enriched from seawater. *Mar. Ecol. Prog. Ser.* **36**: 171–175.
- CAPRIULO, G. M., AND E. J. CARPENTER. 1980. Grazing by 35 to 202  $\mu$ m microzooplankton in Long Island Sound. *Mar. Biol.* **56**: 319–326.
- CARON, D. A., J. C. GOLDMAN, AND M. R. DENNET. 1986. Effect of temperature on growth, respiration, and nutrient regeneration by an omnivorous microflagellate. *Appl. Environ. Microbiol.* **52**: 1340–1347.
- CARRICK, J. H., G. L. FAHNENSTIEL, AND W. D. TAYLOR. 1992. Growth and production of planktonic protozoa in Lake Michigan: In situ versus in vitro comparisons and importance food web dynamics. *Limnol. Oceanogr.* **37**: 1221–1235.
- CHRISTOFFERSEN, K., B. RIEMANN, L. R. KLYSNER, AND H. M. SØRENSEN. 1990. Quantitative importance of the microbial food web and plankton community structure in a eutrophic lake during a bloom of cyanobacteria. *Microb. Ecol.* **20**: 253–273.
- COMITTA, G. W. 1964. 6. Zooplankton. The energy budget of *Diaptomus sisiloides*, Liljeborg. *Int. Ver. Theor. Angew. Limnol. Verh.* **15**: 646–653.
- , AND J. J. COMITTA. 1964. Oxygen uptake in *Mixodiaptomus laciniatus* Lill. *Mem. Ist. Ital. Idrobiol.* **17**: 151–166.
- CORNER, E. D. S., C. B. COWEY, AND S. M. MARSHALL. 1965. On the nutrition and metabolism of zooplankton. *J. Mar. Biol. Assoc. U.K.* **45**: 429–442.
- , ———, AND ———. 1967. On the nutrition and metabolism of zooplankton. *J. Mar. Biol. Assoc. U.K.* **47**: 259–270.
- , R. N. HEAD, AND C. C. KILVINGTON. 1972. On the nutrition and metabolism of zooplankton 8. The grazing of *Biddulphia* cells by *Calanus helgolandicus*. *J. Mar. Biol. Assoc. U.K.* **52**: 847–861.
- CRISP, D. J., A. B. YULE, AND K. N. WHITE. 1985. Feeding by oyster larvae: The functional response, energy budget and a comparison with mussel larvae. *J. Mar. Biol. Assoc. U.K.* **65**: 759–783.
- CYR, H., AND M. L. PACE. 1992. Grazing by zooplankton and its relationship to community structure. *Can. J. Fish. Aquat. Sci.* **49**: 1455–1465.
- DEASON, E. E. 1980. Grazing of *Acartia hudsonica* (A. clausi) on *Skeletonema costatum* in Narragansett Bay (USA): Influence of food concentration and temperature. *Mar. Biol.* **60**: 101–113.
- DEBIASE, A. E., R. W. SANDERS, AND K. G. PORTER. 1990. Relative nutritional value of ciliate protozoa and algae as food for *Daphnia*. *Microb. Ecol.* **19**: 199–210.
- DEMOTT, W. R. 1982. Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina*. *Limnol. Oceanogr.* **27**: 518–527.
- DOOHAN, M. 1973. An energy budget for adult *Brachionus plicatilis* Muller (Rotatoria). *Oecologia* **13**: 351–362.
- DROOP, M. R., AND M. J. SCOTT. 1978. Steady-state energetics of a planktonic herbivore. *J. Mar. Biol. Assoc. U.K.* **58**: 749–772.
- DURBIN, E. G., AND A. G. DURBIN. 1978. Length and weight relationships of *Acartia clausi* from Narragansett Bay, R.I. *Limnol. Oceanogr.* **23**: 958–969.
- , AND ———. 1992. Effects of temperature and food abundance on grazing and short-term weight change in the marine copepod *Acartia hudsonica*. *Limnol. Oceanogr.* **37**: 361–378.
- EATON, J. M. 1971. Studies on the feeding and reproductive biology of the marine cyclopoid copepod *Oithona similis* Claus. Ph.D. thesis, Dalhousie Univ. 101 p.
- ECCLESTON-PARRY, J. D., AND B. S. C. LEADBEATER. 1994. A comparison of the growth kinetics of six marine heterotrophic nanoflagellates fed with one bacterial species. *Mar. Ecol. Prog. Ser.* **105**: 167–177.
- EGLOFF, D. A. 1988. Food and growth relations of the marine microplankter, *Synchaeta cecilia* (Rotifera). *Hydrobiologia* **157**: 129–141.
- FAGERBAGGE, K. M., M. HELDAL, AND S. NORLAND. 1996. Content of carbon, nitrogen, oxygen, sulfur and phosphorous in native, aquatic and cultured bacteria. *Aquat. Microb. Ecol.* **10**: 15–27.
- FENCHIEL, T. 1968. The ecology of marine microbenthos. 3. The reproductive potential of ciliates. *Ophelia* **5**: 123–136.
- . 1974. Intrinsic rate of natural increase: The relationship with body size. *Oecologia* **14**: 317–326.
- . 1980a. Suspension feeding in ciliated protozoa: Functional response and particle size selection. *Microb. Ecol.* **6**: 1–11.
- . 1980b. Suspension feeding in ciliated protozoa: Feeding rates and their ecological significance. *Microb. Ecol.* **6**: 13–25.
- . 1980c. Relation between particle size selection and clearance in suspension-feeding ciliates. *Limnol. Oceanogr.* **25**: 733–738.
- . 1982. Ecology of heterotrophic microflagellates. 2. Bioenergetics and growth. *Mar. Ecol. Prog. Ser.* **8**: 225–231.
- . 1986. Protozoan filter feeding. *Prog. Protistol.* **1**: 65–113.
- . 1988. Marine plankton food chains. *Annu. Rev. Ecol. Syst.* **19**: 19–38.

- . 1990. Adaptive significance of polymorphic life cycles in protozoa: Responses to starvation and refedding in two species of marine ciliates. *J. Exp. Mar. Biol. Ecol.* **136**: 159–177.
- . 1991. Flagellate design and function, p. 7–19. In D. J. Patterson and J. Larsen [eds.], *The biology of free-living heterotrophic flagellates*. Clarendon.
- , AND B. J. FINLAY. 1983. Respiration rates in heterotrophic, free-living protozoa. *Microb. Ecol.* **9**: 99–122.
- , AND P. R. JONSSON. 1988. The functional biology of *Strombidium sulcatum*, a marine oligotrich ciliate (Ciliophora, Oligotrichina). *Mar. Ecol. Prog. Ser.* **48**: 1–15.
- FINLAY, B. J. 1977. The dependence of reproductive rate on cell size and temperature in freshwater ciliated protozoa. *Oecologia* **30**: 75–81.
- FROST, B. W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.* **17**: 805–815.
- . 1975. A threshold feeding behavior in *Calanus pacificus*. *Limnol. Oceanogr.* **20**: 263–266.
- . 1980. The inadequacy of body size as an indicator of niches in the zooplankton. *Am. Soc. Limnol. Oceanogr. Spec. Symp.* **3**: 742–753.
- . 1985. Food limitation of the planktonic marine copepods *Calanus pacificus* and *Pseudocalanus* sp. in a temperate fjord. *Ergeb. Limnol.* **21**: 1–13.
- FRYD, M., O. H. HASLUND, AND O. WOHLGEMUTH. 1991. Development, growth and egg production of the two copepod species *Centropages hamatus* and *Centropages typicus* in the laboratory. *J. Plankton Res.* **13**: 683–689.
- FUHRMAN, J. A., AND G. B. MCMANUS. 1984. Do bacteria-sized marine eucaryotes consume significant bacterial production. *Nature* **310**: 1257–1260.
- GAUDY, R., AND J. BOUCHER. 1983. Relationship between respiration, excretion (ammonia and inorganic phosphorous) and activity of amylase and trypsin in different species of pelagic copepods from an Indian Ocean equatorial area. *Mar. Biol.* **75**: 37–45.
- GEIDER, R. J., AND B. S. C. LEADBEATER. 1988. Kinetics and energetics of growth of the marine choanoflagellate *Stephanoea diplocostata*. *Mar. Ecol. Prog. Ser.* **47**: 169–177.
- GILBERT, J. J., AND K. G. BOGDAN. 1984. Rotifer grazing: In situ studies of selectivity and rates, p. 97–133. In *Trophic dynamics of aquatic ecosystems*. AAAS Symp. 85. Westview.
- GUISANDE, C., AND N. MAZUELOS. 1991. Reproductive pattern of *Brachionus calyciflorus* Pallas at different food concentrations. *J. Plankton Res.* **13**: 279–286.
- HAMILTON, R. D., AND J. E. PRESLAN. 1969. Cultural characteristics of a marine hymenostome ciliate, *Uronema* sp. *J. Exp. Mar. Biol. Ecol.* **4**: 90–99.
- HANEY, J. F. 1971. An in situ method for the measurement of zooplankton grazing rates. *Limnol. Oceanogr.* **16**: 970–976.
- HANSEN, B. 1993. Aspects of feeding, growth and stage development by trochophora larvae of the boreal polychaete *Mediomastus fragile* (Rasmussen) (Capitellidae). *J. Exp. Mar. Biol. Ecol.* **166**: 273–288.
- , P. K. BJØRNSSEN, AND P. J. HANSEN. 1994. Prey size selection in planktonic zooplankton. *Limnol. Oceanogr.* **39**: 395–403.
- , P. J. HANSEN, AND T. G. NIELSEN. 1991. Effects of large nongrazable particles on clearance and swimming behaviour of zooplankton. *J. Exp. Mar. Biol. Ecol.* **152**: 257–269.
- , AND K. W. OCKELMANN. 1991. Feeding behaviour in larvae of the opisthobranch *Philine aperta*. I. Growth and functional response at different developmental stages. *Mar. Biol.* **111**: 255–261.
- , T. WERNBERG-MØLLER, AND L. WITTRUP. 1997. Particle grazing efficiency and specific growth efficiency of the rotifer *Brachionus plicatilis* (Müller). *J. Exp. Mar. Biol. Ecol.* **215**: 217–233.
- HANSEN, P. J. 1989. The red tide dinoflagellate *Alexandrium tamarense*: Effects on behaviour and growth of a tintinnid ciliate. *Mar. Ecol. Prog. Ser.* **53**: 105–116.
- . 1992. Particle size selection, feeding rates and growth dynamics of marine heterotrophic dinoflagellates, with special emphasis on *Gyrodinium spirale*. *Mar. Biol.* **114**: 327–334.
- HAYWARD, R. S., AND D. N. GALLUP. 1976. Feeding, filtering and assimilation in *Daphnia schoedleri* Sars as affected by environmental conditions. *Arch. Hydrobiol.* **77**: 139–163.
- HEINBOCKEL, J. F. 1978. Studies on the functional role of tintinnids in the Southern California Bight. I. Grazing and growth rates in laboratory cultures. *Mar. Biol.* **47**: 177–189.
- HELM, M. M. 1977. Mixed algal feeding of *Ostrea edulis* larvae with *Isochrysis galbana* and *Tetraselmis suecica*. *J. Mar. Biol. Assoc. U.K.* **57**: 1019–1029.
- HEMMINGSSEN, A. M. 1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Rep. Steno Mem. Hosp. Nord. Insulin Lab.* **8**: 1–110.
- HOLLEN, D. A., AND M. E. BORAAS. 1991. The feeding behaviour of *Spumella* sp. as a function of particle size: Implications for bacterial size in pelagic systems. *Hydrobiologia* **220**: 73–88.
- HOLLING, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* **91**: 385–398.
- HUNTLEY, M., P. SYKES, S. ROHAN, AND V. MARIN. 1986. Chemically-mediated rejection of dinoflagellate prey by the copepods *Calanus pacificus* and *Paracalanus parvus*: Mechanism, occurrence and significance. *Mar. Ecol. Prog. Ser.* **28**: 105–120.
- JACOBSON, D. M., AND D. M. ANDERSON. 1993. Growth and grazing rates of *Protoperdinium hirobis* Abé, a thecate heterotrophic dinoflagellate. *J. Plankton Res.* **15**: 723–736.
- JEONG, H. J., AND M. I. LATZ. 1994. Growth and grazing rates of heterotrophic dinoflagellates *Protoperdinium* spp. on red tide dinoflagellates. *Mar. Ecol. Prog. Ser.* **106**: 173–185.
- JESPERSEN, H., AND K. OLSEN. 1982. Bioenergetics in veliger larvae of *Mytilus edulis* L. *Ophelia* **21**: 101–113.
- JONASDOTTIR, S. H. 1989. Effects of food concentration on egg production rates of two species of *Pseudocalanus*: Laboratory observations. *J. Exp. Mar. Biol. Ecol.* **130**: 33–43.
- JOHNSON, G. H., AND K. Y. BØRSHEIM. 1988. Functional response and food selection of the water flea, *Bosmina longispina*. *J. Plankton Res.* **10**: 319–325.
- JONSSON, P. R. 1986. Particle size selection, feeding rates and growth dynamics of marine planktonic oligotrichous ciliates (Ciliophora: Oligotrichina). *Mar. Ecol. Prog. Ser.* **33**: 265–277.
- , C. ANDRÉ, AND M. LINDEGARTH. 1989. Swimming behaviour of marine bivalve larvae in a flume boundary-layer flow: Evidence for near-bottom confinement. *Mar. Ecol. Prog. Ser.* **79**: 67–76.
- KERSTING, K., AND W. VAN DER LEEUF. 1976. The use of the coulter counter for measuring the feeding rates of *Daphnia magna*. *Hydrobiologia* **49**: 233–237.
- KING, C. E. 1966. Food, age, and the dynamics of a laboratory population of rotifers. *Ecology* **48**: 111–128.
- KJØRBOE, T., F. MOHLENBERG, AND K. HAMBURGER. 1985a. Bioenergetics of the planktonic copepod *Acartia tonsa*: Relation between feeding, egg production and respiration, and composition of specific dynamic action. *Mar. Ecol. Prog. Ser.* **26**: 85–97.
- , ———, AND H. NICOLAISEN. 1982. Ingestion rate and gut clearance in the planktonic copepod *Centropages hamatus* (Liljeberg) in relation to food concentration and temperature. *Ophelia* **21**: 181–194.
- , ———, AND H. U. RIISSGÅRD. 1985b. In situ feeding rates



- of planktonic copepods: A comparison of four methods. *J. Exp. Mar. Biol. Ecol.* **88**: 67–81.
- , AND M. SABATINI. 1994. Reproductive and life cycle strategies in egg-carrying cyclopoid and free-spawning calanoid copepods. *J. Plankton Res.* **16**: 1353–1366.
- , AND M. SABATINI. 1995. Scaling of fecundity, growth and development in marine planktonic copepods. *Mar. Ecol. Prog. Ser.* **120**: 285–298.
- KLEIN-BRETELIER, V. C. M., H. G. FRANSZ, AND S. R. GONZALES. 1982. Growth and development of four calanoid copepod species under experimental and natural conditions. *Neth. J. Sea Res.* **16**: 195–207.
- KNOECHEL, R., AND B. L. HOLTBY. 1986. Construction and validation of a body-length-based model for the prediction of cladoceran community filtering rates. *Limnol. Oceanogr.* **31**: 1–16.
- KORSTAD, J., O. VADSTEIN, AND Y. OLSEN. 1989. Feeding kinetics of *Brachionus plicatilis* and *Isochrysis galbana*. *Hydrobiologia* **186**: 51–57.
- LABEDJEVA, L. J., AND T. N. GERASIMOVA. 1985. Peculiarities of *Philine roseola* (Ehrbg.) (Rotatoria, Bdelloidea)—growth and reproduction under various temperature conditions. *Int. Rev. Gesamten Hydrobiol.* **70**: 509–525.
- LAMPERT, W. 1977. Studies on the carbon balance of *Daphnia pulex* De Geer as related to environmental conditions. 2. The dependence of carbon assimilation on animal size, temperature, food concentration and diet species. *Arch. Hydrobiol. Suppl.* **48**: 310–335.
- . 1981. Inhibition and toxic effects of bluegreen algae on *Daphnia*. *Int. Rev. Gesamten Hydrobiol.* **66**: 285–298.
- LAMPITT, R. S., AND J. GAMBLE. 1982. Diet and respiration of the small planktonic marine copepod *Oithona nana*. *Mar. Biol.* **66**: 185–190.
- LANDRY, M. R., AND R. P. HASSETT. 1982. Estimating the grazing impact of marine micro-zooplankton. *Mar. Biol.* **67**: 283–288.
- LEVANDOWSKY, M., AND P. KANETA. 1987. Behaviour in dinoflagellates, p. 360–398. In F. J. R. Taylor [ed.], *The biology of dinoflagellates*. Bot. Monogr. 21. Blackwell.
- LONSDALE, D. J. 1981a. Influence of age-specific mortality on life history of two estuarine copepods. *Mar. Ecol. Prog. Ser.* **5**: 333–340.
- . 1981b. Regulatory role of physical factors and predation for two Chesapeake Bay copepod species. *Mar. Ecol. Prog. Ser.* **5**: 341–351.
- MCCAULEY, E. 1984. The estimation of the abundance and biomass of zooplankton in samples, p. 228–265. In J. A. Downing and F. H. Rigler [eds.], *A manual on methods for the assessment of secondary productivity in fresh waters*, 2nd ed. IBP Handbook 17. Blackwell.
- MACKAS, D. L., AND R. BOHRER. 1976. Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. *J. Exp. mar. Biol. Ecol.* **25**: 77–85.
- MCMAHON, J. W. 1965. Some physical factors influencing the feeding behaviour of *Daphnia magna* Straus. *Can. J. Zool.* **43**: 603–611.
- , AND F. H. RIGLER. 1965. Feeding rate of *Daphnia magna* Strauss in different foods labeled with radioactive phosphorus. *Limnol. Oceanogr.* **10**: 105–114.
- MALONEY, C. L., AND J. G. FIELD. 1991. The size-based dynamics of planktonic food webs. 1. A simulation model of carbon and nitrogen flows. *J. Plankton Res.* **13**: 1003–1038.
- MÜLLER, H. 1991. *Pseudobalanion planctonicum* (Ciliophora, Prostomatida): Ecological significance of a algivorous nanociliate in a deep meso-eutrophic lake. *J. Plankton Res.* **13**: 247–262.
- MULLIN, M. M., AND E. R. BROOKS. 1970. The effect of concentration of food on body weight, cumulative ingestion, and rate of growth of the marine copepod *Calanus helgolandicus*. *Limnol. Oceanogr.* **15**: 748–755.
- , E. F. STEWART, AND F. J. FUGLISTER. 1975. Ingestion by the planktonic grazers as a function of concentration of food. *Limnol. Oceanogr.* **20**: 259–262.
- NIELSEN, T. G., AND T. KJØRBOE. 1994. Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 2. Ciliates. *Limnol. Oceanogr.* **39**: 508–519.
- PAFFENHÖFER, G.-A. 1993. On the ecology of marine cyclopoid copepods (Crustacea, Copepoda, Cyclopoida). *J. Plankton Res.* **15**: 37–55.
- , AND R. P. HARRIS. 1976. Feeding, growth and reproduction of the marine planktonic copepod *Pseudocalanus elongatus* Boeck. *J. Mar. Biol. Assoc. U.K.* **56**: 327–344.
- , AND K. B. VAN SANT. 1985. The feeding response of a marine planktonic copepod to quantity and quality of particles. *Mar. Ecol. Prog. Ser.* **27**: 55–65.
- PARSLOW, J. S., G. J. DOUCETTE, F. J. R. TAYLOR, AND P. J. HARRISON. 1986. Feeding by the zooflagellate *Pseudobodo* sp. on the picoplanktonic prasinomonad *Micromonas pusilla*. *Mar. Ecol. Prog. Ser.* **20**: 237–246.
- PECHENIK, J. A., AND N. FISCHER. 1979. Feeding, assimilation, and growth of a mud snail larvae, *Nassarius obsoletus* (Say), on three different algal diets. *J. Exp. Mar. Biol. Ecol.* **38**: 57–80.
- PETERS, R. H., AND J. A. DOWNING. 1984. Empirical analysis of zooplankton filtering and feeding rates. *Limnol. Oceanogr.* **29**: 763–784.
- PETERSEN, W. T., P. TISELIUS, AND T. KJØRBOE. 1991. Copepod egg production, moulting and growth rates, and secondary production, in the Skagerrak in August 1988. *J. Plankton Res.* **13**: 131–154.
- PHILIPPOVA, T. G., AND A. L. POSTNOV. 1988. The effect of food quantity on feeding and metabolic expenditure in cladocera. *Int. Rev. Gesamten Hydrobiol.* **73**: 601–615.
- PORTER, K. G., J. GERRITSEN, AND J. D. ORCUTT, JR. 1982. The effect of food concentration on swimming patterns, feeding behavior, ingestion, assimilation, and respiration by *Daphnia*. *Limnol. Oceanogr.* **27**: 935–949.
- POULET, S. A., AND P. MARSOT. 1978. Chemosensory grazing by marine calanoid copepods (Arthropoda: Crustacea). *Science* **200**: 1403–1405.
- 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.
- RASSOULZADEGAN, F. 1982. Dependence of grazing rate, gross growth efficiency and food size range on temperature in a pelagic oligotrichous ciliate *Lohmanniella spiralis* Leeg., fed on naturally occurring particulate matter. *Ann. Inst. Oceanogr.* **58**: 177–184.
- RIEMANN, B., AND OTHERS. 1990. Carbon budgets of the microbial food web in estuarine enclosures. *Mar. Ecol. Prog. Ser.* **65**: 159–170.
- RIISGÅRD, H. U., A. RANDIØV, AND K. HAMBURGER. 1981. Oxygen consumption and clearance as a function of size in *Mytilus edulis* L. veliger larvae. *Ophelia* **20**: 179–183.
- RIVIER, A., D. C. BROWNEE, R. W. SHELDON, AND F. RASSOULZADEGAN. 1985. Growth of microzooplankton: A comparative study of bacterivorous zooflagellates and ciliates. *Mar. Microb. Food Webs* **1**: 51–60.
- ROBERTSON, S. B., AND B. W. FROST. 1977. Feeding by an omnivorous planktonic copepod *Aetideus divergens* Bradford. *J. Exp. Mar. Biol. Ecol.* **29**: 231–244.
- ROMAN, M. R., AND P. A. RUBLEE. 1981. A method to determine

- in situ* zooplankton grazing rates on natural particle assemblages. *Mar. Biol.* **65**: 303–309.
- ROTHHAUPT, K. O. 1990a. Population growth rates of two closely related rotifer species: Effects of food quantity, particle size, and nutritional quality. *Freshwater Biol.* **23**: 561–570.
- . 1990b. Changes of the functional responses of the rotifers *Brachionus rubens* and *Brachionus calyciflorus*. *Limnol. Oceanogr.* **35**: 24–32.
- SABATINI, M., AND T. KJØRBOE. 1994. Egg production, growth and development of the cyclopoid copepod *Oithona similis*. *J. Plankton Res.* **16**: 1329–1351.
- SANDERS, R. W., AND K. G. PORTER. 1986. Use of metabolic inhibitors to estimate protozooplankton grazing and bacterial production in a monomictic eutrophic lake with an anaerobic hypolimnion. *Appl. Environ. Microbiol.* **52**: 101–107.
- SCHLÜTER, M., C. J. SOEDER, AND J. GROENEWEG. 1987. Growth and food conversion of *Brachionus rubens* in continuous culture. *J. Plankton Res.* **9**: 761–783.
- SCHOENBERG, S. A. 1989. Effect of algal concentration, bacterial size and water chemistry on the ingestion of natural bacteria by cladocerans. *J. Plankton Res.* **11**: 1273–1295.
- SCOTT, J. M. 1980. Effect of growth rate on the food alga on the growth/ingestion efficiency of a marine herbivore. *J. Mar. Biol. Assoc. U.K.* **60**: 681–702.
- SERVAIS, P., G. BILLEN, AND J. V. REGO. 1985. Rate of bacterial mortality in aquatic environments. *Appl. Environ. Microbiol.* **49**: 1448–1454.
- SHELDON, R. W., P. NIVAL, AND F. RASSOULZADEGAN. 1986. An experimental investigation of a flagellate–ciliate–copepod food chain with some observations relevant to the linear biomass hypothesis. *Limnol. Oceanogr.* **31**: 184–188.
- SHERR, B. F., E. B. SHERR, AND F. RASSOULZADEGAN. 1988. Rates of digestion of bacteria by marine phagotrophic protozoa: Temperature dependence. *Appl. Environ. Microbiol.* **54**: 1091–1095.
- SHERR, E. B., AND E. B. SHERR. 1994. Bacterivory and herbivory: Key roles of phagotrophic protists in pelagic food webs. *Microb. Ecol.* **28**: 223–235.
- SLEIGH, M. A., AND J. R. BLAKE. 1977. Methods of ciliary propulsion and their size limitations, pp. 243–256. *In* T. J. Pedley [ed.], *Scale effects in animal locomotion*. Academic.
- SPRUNG, M. 1983. Reproduction of the mussel *Mytilus edulis* at Helgoland (North Sea). *Helgol. Meeresunters.* **36**: 243–255.
- . 1984a,b,c,d. Physiological energetics of mussel larvae (*Mytilus edulis*). 1. Shell growth and biomass. 2 Food uptake. 3. Respiration. 4. Efficiencies. *Mar. Ecol. Prog. Ser.* **17**: 283–293, 295–305; **18**: 171–178, 179–186.
- STARKWEATHER, P. L. 1988. Reproductive and functional response of the rotifer *Brachionus plicatilis* to changing food density. *Verh. Int. Verein. Limnol.* **23**: 2001–2005.
- STEMBERGER, R. S., AND J. J. GILBERT. 1985. Body size, food concentration, and population growth in planktonic rotifers. *Ecology* **66**: 1151–1159.
- , AND ———. 1987. Rotifer threshold food concentration and the size-efficiency hypothesis. *Ecology* **68**: 181–187.
- STOECKER, D. K. 1988. Are marine planktonic ciliates suspension-feeders. *J. Protozool.* **35**: 252–255.
- STRATHMANN, R. R. 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. *Limnol. Oceanogr.* **12**: 411–418.
- STROM, S. L. 1991. Growth and grazing rates of the herbivorous dinoflagellate *Gymnodinium* sp. from the open subarctic Pacific Ocean. *Mar. Ecol. Prog. Ser.* **78**: 103–113.
- , AND E. J. BUSKEY. 1993. Feeding, growth, and behavior of the thecate heterotrophic dinoflagellate *Oblea rotunda*. *Limnol. Oceanogr.* **38**: 965–977.
- THRONDSSEN, J. 1973. Mobility in some marine nanoplankton flagellates. *Norw. J. Zool.* **21**: 193–200.
- UCHIMA, M. 1985. Copulation in the marine copepod *Oithona davisae* Ferrari & Orsi. 2. Relationship between copulation and egg-laying. *Bull. Plankton Soc. Jpn.* **33**: 31–36.
- UKELESS, R., AND B. M. SWEENEY. 1969. Influence of dinoflagellate trichocysts and other factors on the feeding of *Crassostrea virginica* larvae on *Monochrysis lutherii*. *Limnol. Oceanogr.* **14**: 403–410.
- VAN ALSTYNE, K. L. 1986. Effects of phytoplankton taste and smell on the feeding behaviour of the copepod *Centropages hamatus*. *Mar. Ecol. Prog. Ser.* **34**: 187–190.
- VANDERPLOEG, H. A., D. SCAVIA, AND J. R. LIEBIG. 1984. Feeding rate of *Diaptomus similis* and its relation to selectivity and effective food concentration in algal mixtures and in Lake Michigan. *J. Plankton Res.* **6**: 919–941.
- VERITY, P. G. 1985. Grazing, respiration, excretion, and growth rates of tintinnids. *Limnol. Oceanogr.* **30**: 1268–1282.
- . 1991. Measurements and simulation of prey uptake by marine planktonic ciliates fed plastidic and aplastidic nanoplankton. *Limnol. Oceanogr.* **36**: 729–750.
- , AND C. LANGDON. 1984. Relationships between lorica volume, carbon, nitrogen, and ATP content of tintinnids in Narragansett Bay. *J. Plankton Res.* **6**: 859–868.
- , AND OTHERS. 1992. Relationship between cell volume and carbon and nitrogen content of marine photosynthetic nanoplankton. *Limnol. Oceanogr.* **37**: 1434–1446.
- VIDAL, J. 1980a,b. Physioecology of zooplankton. 1. Effects of phytoplankton concentration, temperature and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. 3. Effects of phytoplankton concentration, temperature, and body size on the metabolic rate of *Calanus pacificus*. *Mar. Biol.* **56**: 111–134, 195–202.
- WALNE, P. R. 1964. The culture of marine bivalve larvae, p. 197–210. *In* K. M. Vilbur and C. M. Yonge [eds.], *Physiology of mollusca*. Academic.
- WEISSE, T., AND OTHERS. 1990. Response of the microbial loop to the phytoplankton spring bloom in a prealpine lake. *Limnol. Oceanogr.* **35**: 781–799.
- WETZEL, R. G. 1983. *Limnology*, 2nd ed. Saunders.
- ZEUTHEN, E. 1953. Oxygen uptake as related to body size in organisms. *Q. Rev. Biol.* **28**: 1–12.

Received: 28 September 1995

Accepted: 24 February 1997