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Assumptions inherent in the use of a popular method for estimating *in situ* feeding rates of herbivorous copepods, the gut fluorescence method, were examined by comparing gut evacuation rates (GERs) of feeding and non-feeding *Calanus marshallae*. Copepods were fed four concentrations of the diatom, *Thalassiosira weissflogii*, labelled with 68-germanium, a radioactive analog of silicon. GERs of copepods transferred to either filtered seawater or to identical concentrations of unlabelled *T. weissflogii* were not significantly different, although the rates of each tended to decline with time following transfer from the labelled food. GERs calculated over the initial 90 min interval following transfer were on average 11.5 % lower than GERs calculated over the initial 20 min. GERs

measured at 500, 1000, 2000, and 4000 cells ml-1 were not significantly different, although rates tended to decrease for food concentrations less than 2000 cells ml-1.

GERs of the dominant herbivorous copepods near 33°N, 139°W were measured during four seasonal VERTEX cruises conducted between July 1987 and May 1988. GERs decreased with copepod body size and ranged from 0.50 to 7.43 % min^{-1}. The power function $GER = aL^b$ provided the best fit to these data, using total body length (L) as the independent variable. This equation explained between 54 and 73% of the variation observed on individual cruises and 44% of the variation for the pooled data from all cruises. The exponent (b) was the same for all cruises (-1.27), and appeared independent of temperature, species composition, and food concentration. By fitting GERs to a model ($GER = [a(e^{cT})(L^b)]$ that expressed GER as a function of copepod total length (L) and temperature (T), 64% of the seasonal variation in GERs could be explained.

Short term ingestion rates calculated by the gut fluorescence method for copepods collected during the four VERTEX cruises were compared with estimated metabolic requirements. For the vast majority of copepods, ingestion rates were not sufficient to meet metabolic demands. This conclusion was unchanged even after increasing gut pigment values by 33% to account for assumed losses of pigment occurring during gut passage. These results imply that most copepods must be feeding omnivorously. For many species, carnivorous food intake would have to exceed herbivorous consumption to meet metabolic requirements.

Seasonal Dynamics and Allometric Considerations of Feeding and Food Processing for Macrozooplankton in the Northeast Pacific Ocean

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Chapter I

General Introduction

With few exceptions, copepods are the dominant constituent of the plankton in estuarine and marine waters and may rank as the world's most abundant metazoans (Raymont, 1983). Because of their abundance, copepods play a key role in marine food webs and considerable effort has been devoted to studying their physiology and behavior. The research described in this thesis examines critical assumptions inherent in the application of a popular method for estimating *in situ* feeding rates of herbivorous copepods (the gut fluorescence method). After critical examination of this method, it was utilized to determine the gut evacuation rates (GERs) and feeding rates of several species and developmental stages of subtropical copepods collected near the VERTEX seasonal station in the NE central Pacific ocean. These data were used to examine the relationship between GERs and copepod body size, temperature, time of year, and gut fullness. Herbivorous feeding rates calculated by the gut fluorescence method were compared to respiration rates to assess the prevalence and importance of omnivorous feeding.

Quantification of the rate of food intake by copepods has been an active area of research for several decades, with early studies evaluating grazing rates by making counts, either manually or electronically, of the number of phytoplankton cells in grazed and control beakers (e.g., Harvey, 1937; Mullin, 1963; Frost, 1972; Richman *et al.*, 1977; Conover and Mayzaud, 1984). These studies identified several important factors that influence copepod feeding (e.g.,

temperature, body size, and the size and abundance of food particles). However, it became apparent early on that laboratory measurements of feeding rates were of questionable relevance to feeding rates actually occurring under natural conditions. Studies showed that copepod feeding behavior was complex and dependent on many factors that either could not be easily simulated in laboratory or were affected by confinement [e.g., experimental container size (Mullin, 1967), experiment duration (Roman and Rublee, 1980), food quality (Paffenhöfer and Van Sant, 1985; Cowles *et al.*, 1988), light levels (Head *et al.*, 1985; Mobley, 1987), prior feeding history (Donaghay and Small, 1979), and enzyme adaptation (Mayzaud and Poulet, 1978; Mayzaud *et al.*, 1984)] In addition, physiological activities and biochemical components of some copepod species were reported to be altered due to the stress associated with capture and confinement under laboratory conditions (Ikeda, 1977; Ikeda and Skjoldal, 1980). These findings emphasized the importance of developing *in situ* techniques to measure physiological rate processes (Haney, 1971; Mackas and Bohrer, 1976; Roman and Rublee, 1981).

Methods used to estimate *in situ* feeding rates of copepods have generally employed techniques requiring incubation and/or gut analyses. Incubation techniques typically enclose a volume of water containing a natural plankton assemblage and incubate the assemblage at the depth of capture for a specified period of time. The advantage of this technique is that feeding rates can be determined under natural light conditions and at the predator/prey densities found

in the field. Several types of incubation chambers of varying complexity have been used. Gliwicz (1968) estimated freshwater zooplankton grazing rates by comparing the amounts of phytoplankton, bacteria, and detritus in control versus experimental chambers incubated *in situ* for specified periods of time. Experimental chambers contained natural populations of particulate matter and actively feeding zooplankton which were captured by opening and closing the chamber at depth. Control chambers collected material in a like manner; however, zooplankton were anaesthetized with physostigminum salicylicum. The decrease of phytoplankton and bacteria in the control chamber relative to the experimental chamber provided an estimate of *in situ* feeding rate.

The marine equivalent of the Gliwicz chamber is the so-called Haney chamber (Haney, 1971). This incubation method employs a Niskin-type bottle that closes at depth to trap zooplankton, and simultaneously releases either an isotope, labelled food, or an inhibitor into the grazing chamber. Accurate assessment of the results obtained with these chambers requires that controls adequate to account for all of the pools of the isotope be utilized, and that incubations be short to avoid changes in the specific activity of labelled material and isotope recycling (Roman and Rublee, 1981). Shortcomings of this method are that it cannot be used at night to label phytoplankton, and potential errors due to the recycling of isotopes from excretion and egestion and selective feeding on larger phytoplankton with a lower specific activity may result in an underestimation of zooplankton grazing rate (Roman and Rublee, 1981).

The gut fluorescence method was initially described by Mackas and Bohrer (1976). This method estimates *in situ* grazing rates by measuring a tracer of consumed food (S) and independently determining the time required for food to pass through the gut (T_g). As indicated by Mackas and Bohrer (1976), at the time of capture the amount of tracer (S) in a copepod's gut represents the integral of its ingestion rate over the gut passage time (T_g). Mathematically, this relationship can be expressed as:

$$S = (1-A)\int_{T_c}^{T_c-T_g} I\,dt \qquad (1\text{-}1)$$

where A is the fractional loss of the tracer in the gut, I is the instantaneous ingestion rate, and T_C is the time of capture. Integrating this equation gives the average ingestion rate:

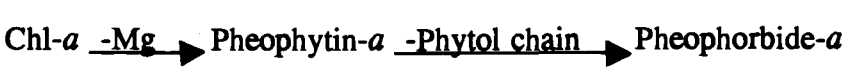
$$\bar{I} = S\left(\frac{1}{T_g}\right)(1-A) \qquad (1\text{-}2)$$

The tracer (S) used by the gut fluorescence method is the fluorescence of chlorophyll-derived pigments. These pigments are synthesized only by autotrophic organisms; however, both herbivorous and carnivorous feeding by copepods may contribute to pigments measured in the gut. Pigments consumed during carnivorous feeding are due to phytoplankton contained in the guts of prey items. The gut fluorescence method does not distinguish between primary (herbivory) and

secondary (carnivory) sources of pigment, although the method is usually considered to provide a measure only of herbivorous feeding.

The concentration of chlorophyll-derived pigment (i.e., chlorophyll + pheopigment) in copepod guts is typically determined using the standard fluorometric method for chlorophyll (Yentsch and Menzel, 1963; Holm-Hansen *et al.* 1965; Strickland and Parsons, 1972). The wide band filters commonly placed in fluorometers for this method are optimal for the detection of chlorophyll-*a*; however, fluorescence from chlorophylls *b* and *c* may also be detected. Trees *et al.* (1985) have shown that the amount of chlorophyll-*a* calculated by the fluorometric method can be over- or underestimated when significant quantities of chlorophyll-*c* or chlorophyll-*b* are present, respectively.

The fluorometric method distinguishes between chlorophyll and its degradation products, typically referred to as pheopigments. The two pathways thought to describe chlorophyll degradation in macrozooplankton guts are shown below (Shuman and Lorenzen, 1975):



Loss of the magnesium atom occurs following exposure to acidic conditions in the gut, while the phytol chain can be cleaved by the enzyme chlorophyllase, as well

as by light and acidic conditions (Schanderl *et al.*, 1962; Moreth and Yentsch, 1970; Jeffrey and Hallegraeff, 1987). As indicated above, the pheopigment, pheophorbide, appears to be the major form of degraded chlorophyll found in copepod fecal pellets, although small quantities of pheophytin may also be present (Lorenzen, 1967; Shuman and Lorenzen, 1975; Welschmeyer and Lorenzen, 1985). Pheophorbide-*a* and pheophytin-*a* fluoresce the same amount per molecule (Lorenzen and Downs, 1986) and cannot be distinguished using the standard fluorometric method. Therefore, gut pigment concentration is usually expressed as chlorophyll-*a* weight equivalents, and includes the sum of both chlorophyll and pheopigments (pheophorbide + pheophytin).

The fractional loss of pigment (A) is usually assumed to be zero when calculating ingestion rates using equation (1-2). This practice was based primarily on results obtained by Shuman and Lorenzen (1975). These authors reported that for every mole of chlorophyll-*a* ingested by grazers, a mole of pheophorbide-*a* appeared in egested fecal material. This stoichiometric conversion appeared to indicate that there was no loss of chlorophyll during the digestive process. Helling and Baars (1985) and Conover *et al.* (1986) have pointed out that the standard fluorometric equation (Strickland and Parsons, 1972) used by Shuman and Lorenzen to calculate the weight of pheopigments in fecal material actually expresses the quantity of pheopigments as the molar equivalent weight of chlorophyll-*a*. Thus, Shuman and Lorenzen's data actually show that 33% of ingested pigment was not accounted for. Subsequent to this finding, several studies

have examined the issue of pigment loss (Conover *et al.*, 1986; Kiorboe and Tiselius; Dagg and Walser, 1987; Dam and Peterson, 1988; Head, 1988; Lopez *et al.*, 1988; Pasternak and Drits, 1988; Peterson *et al.* 1990a; Penry and Frost, 1991). Reported percentages of unaccounted pigment have been shown to be extremely variable, ranging from 0 to 95 %. At present, the mechanisms which account for pigment loss (e.g., assimilation of pigment or degradation to non-fluorescing molecules) have not been resolved and there is disagreement regarding what fractional loss value, if any, should be used when calculating ingestion rates by the gut fluorescence method. This issue is discussed in Chapter 3 of this thesis.

Calculation of the time (T_g) required for food to pass through the copepod gut is not straightforward, as ingested material is thoroughly mixed in the anterior regions of the midgut prior to being packed into a fecal pellet, lined with a peritrophic membrane, and egested (Ong and Lake, 1969; Nott *et al.*, 1985). The mixing of food in the gut implies that there is no discrete time of gut passage. Rather, the time required for a given parcel of consumed food particles to be egested will be described by a probabilistic function, with the probability of a particular food particle remaining in the gut decreasing with increasing time. Most studies employing the gut fluorescence technique have sought to calculate the rate of food loss from the gut (i.e., GER), rather than the gut passage time.

The gut evacuation rate (GER) is typically determined by placing captured animals with full guts in filtered seawater, and at regular intervals removing a portion of the copepods and determining gut pigment concentration.

Several studies have shown that the decline of gut pigment following transfer of copepods to filtered seawater may be approximated by an exponential equation (Dagg and Grill, 1980; Dagg and Wyman, 1983; Kiørboe *et al.*, 1982; Dam and Peterson, 1988; Peterson *et al.*, 1990a):

$$S_t = S_0 e^{-Rt} \qquad (1\text{-}3)$$

where S_0 is the initial concentration of gut pigment, S_t is the amount remaining at time t, and R is the instantaneous gut evacuation rate. The reciprocal of R provides an estimate for the value of the gut retention time of food (T') in equation (1-2) (Mackas and Burns, 1986).

Since its introduction by Mackas and Bohrer (1976), the gut evacuation method has been used with increasing frequency to estimate *in situ* grazing rates of herbivorous zooplankton. The primary reasons for the popularity of this method are that 1) it can be easily accomplished in the field, 2) adequate fluorescent signals can be obtained from relatively small samples, and 3) the method requires a smaller investment of time and equipment than other *in situ* incubation techniques. The rapid acceptance of this technique was also hastened by studies that found good agreement between ingestion rates determined by the gut fluorescence technique and by other established methods (Kiørboe *et al.* 1985).

In recent years, the assumptions and practices associated with the gut fluorescence method have been critically examined. Concerns have been expressed regarding the determination and constancy of the GER (Dagg and Grill, 1980;

Baars and Oosterhuis 1984; Baars and Helling, 1985; Wang and Conover, 1986; Dagg and Walser, 1987) and the stability of the chlorophyll tracer (Conover *et al.*, 1986; Kiorboe and Tiselius; Dagg and Walser, 1987; Head, 1988; Lopez *et al.*, 1988; Pasternak and Drits, 1988).

The GER is usually measured by transferring copepods with full guts to filtered seawater and following the decline of gut fluorescence with time. This practice assumes that the rate at which food passes through the gut is the same for feeding and non-feeding copepods. Several investigators have suggested that the gut passage time of food may increase once copepods are transferred to an environment devoid of food (Dagg and Grill, 1980; Baars and Oosterhuis, 1984; Madin and Cetta, 1984; Murtaugh, 1984; Kiørboe *et al.* 1985, Kiørboe and Tiselius, 1987; Penry and Frost, 1990; Peterson *et al.*, 1990a). If correct, this would indicate that gut evacuation rates, and therefore ingestion rates, of feeding copepods are underestimated with the gut fluorescence method. The research described in Chapter Two of this thesis examines the validity of estimating GERs of feeding copepods by placing them in filtered seawater, the dependency of gut evacuation rate on food concentration, and establishes protocols by which this method can be used in the field.

Several studies that have used the gut fluorescence method to estimate *in situ* feeding rates of copepods have considered GERs to be a relatively conservative characteristic of copepod feeding behavior. GERs measured at one site, for a particular copepod, have been applied to animals collected at different times and

locations (Dagg and Grill, 1980; Bautista, 1988; Tsuda *et al.*, 1989), to other developmental stages (Baars and Fransz, 1984), and to other species (Nicolajsen *et al.* 1983; Baars and Fransz, 1984; Kiørboe *et al.*, 1985; Dagg *et al.* 1989; Tsuda *et al.*, 1989; Arinardi *et al.*, 1990). Other studies have measured GERs of field collected copepods by exposing the animals to elevated phytoplankton concentrations prior to GER measurement (e.g., Dagg and Grill, 1980; Batchelder, 1986). This practice increases the gut pigment content of the animals, which simplifies measurement of GER; however, it implicitly assumes that GERs are independent of food type or concentration.

In order for gut fluorescence method to be used effectively, it is essential to understand the dependence of GER on physical and biologic parameters. At the very least, it is necessary to determine the time scales over which significant changes in GER rate occur so that the frequency with which these rates must be measured can be determined. Several studies have demonstrated that GERs increase with temperature (Kiørboe *et al.*, 1982; Dagg and Wyman, 1983; Christoffersen and Jespersen, 1986; Dam and Peterson, 1988; Peterson *et al.*, 1990b), and other authors have found, or suggested, that GERs vary with ambient food concentration (Dagg and Walser, 1987; Tsuda and Nemoto, 1987), the level of gut fullness (Baars and Oosterhuis, 1984; Wang and Conover, 1986; Ellis and Small, 1989; Penry and Frost, 1990), food type or quality (Nicolajsen *et al.*, 1983; Baars and Helling, 1985; Head and Harris, 1987; Clarke *et al.*, 1988), and time of day (Arashkevich, 1977; Baars and Oosterhuis, 1984; Head, 1986). The research

described in Chapter Three of this thesis examines the dependency of GER on several of these parameters. GERs of abundant developmental stages of 17 species of copepods in the NE central Pacific Ocean were collected at different times of day, at stations separated by a few 10's to approximately 100 km. The data allowed an assessment of the temporal and spatial variability of GERs, and an assessment of intra- and inter-specific differences in GER.

One of the limitations of the gut fluorescence method is that it only provides an estimate of herbivorous feeding. Several studies have shown, or implied, that carnivory can provide an important fraction of the diet, even for copepods typically classified as herbivores (Hayward, 1980; Paffenhöffer and Knowles, 1980; Kleppel *et al.* 1988; Arinardi, 1990; Peterson *et al.*, 1990b). As part of the research described in Chapter Three, ingestion rates measured by the gut fluorescence method were compared with estimates of metabolic requirements to assess the importance of herbivorous feeding to dominant copepod species near the VERTEX seasonal station.

The final issue examined in this thesis was the relationship between GER and copepod body size. This issue has both theoretical and operational importance. Body size is an important determinant of many physiological and ecological rates (Peters, 1983). Allometric equations have been developed to describe the weight dependence of several physiological processes of copepods, including respiration (e.g., Ikeda, 1978; Uye and Yashiro, 1988), nitrogen and phosphate excretion (e.g., Ikeda and Mitchell, 1982; Vidal and Whitledge, 1982),

ingestion (e.g., Mullin and Brooks, 1976; Huntley and Boyd, 1984), and assimilation (e.g., Huntley, 1988). These equations allow a prediction of a particular rate to be made from measurements of copepod body size. Development of an allometric equation for GERs would be particularly useful because 1) rates are difficult to determine for small species because of the short times required to evacuate their gut contents, and 2) measurement of GERs for all species and developmental stages present in a given collection requires considerable investments of time and resources. Being able to predict GERs from copepod body size would greatly simplify determination of *in situ* ingestion rates, as such rates would require, in addition to body size, only measurement of gut pigment levels.

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Chapter II

Comparison of Gut Evacuation Rates of Feeding and Non-feeding *Calanus marshallae*.

Abstract

Gut evacuation rates were compared for feeding and non-feeding *Calanus marshallae* collected near Yaquina Bay, Oregon (44°37'N, 124°04'W) from June 1986 through May 1987. Evacuation rates were measured at four concentrations of *Thalassiosira weissflogii* from the decline of gut pigment fluorescence following transfer of copepods to filtered seawater and from the loss of cells labelled with 68-germanium, a radioactive analog of silicon. There was no significant difference between gut evacuation rates of feeding and non-feeding copepods over both short-term (20 min) and long-term (90 min) evacuation times. Furthermore, there was no difference between rates obtained using either ^{68}Ge or pigment as tracers of gut food passage. These results are discussed in the light of possible "dilution" of tracer in the guts of feeding copepods due to mixing with unlabelled food. Gut evacuation rates measured at food concentrations ranging from 500 to 4000 cells ml^{-1} were not significantly different, regardless of the technique employed.

Introduction

The gut fluorescence method has been utilized with increasing frequency in recent years to estimate *in situ* grazing rates of herbivorous zooplankton (e.g. Mackas and Bohrer, 1976; Boyd *et al.*, 1980; Dagg and Grill, 1980; Dagg and Wyman, 1983; Nicolajsen *et al.*, 1983; Baars and Oosterhuis, 1984; Kleppel *et al.*, 1985; Simard *et al.*, 1985). The method requires two quantities: the gut pigment concentration of recently captured copepods, which is determined fluorometrically, and an estimate of the copepod's gut evacuation rate (GER). Multiplication of these two values gives an estimate of short-term *in situ* egestion rates, which are presumed to be equivalent to ingestion rates at steady state if degradation of chlorophyll derivatives to non-fluorescing products during gut passage has been accounted for (Helling and Baars, 1985; Conover *et al.*, 1986; Dagg and Walser, 1987; Kiørboe and Tiselius, 1987).

GER is usually measured by transferring copepods with full guts to filtered seawater and following the subsequent decline in gut fluorescence with time. This procedure, however, must assume that the GER of non-feeding copepods is the same as that of copepods which are actively feeding. Several investigators have suggested that the food passage time may increase for zooplankton transferred to filtered seawater (Dagg and Grill, 1980; Baars and Oosterhuis, 1984; Madin and Cetta, 1984; Murtaugh, 1984; 1985; Kiørboe *et al.*, 1985; Kiørboe and Tiselius, 1987). If correct, this would indicate that the gut fluorescence method

underestimates the GER during active feeding. The experiments described in this chapter were designed to test whether the evacuation rates of feeding and non-feeding copepods were different. In addition, because GERs were measured after copepods had fed at four different initial food levels, these experiments allowed examination of the relationship between GERs and food concentration.

Methods

Zooplankton were collected 5 to 16 km west of the entrance to Yaquina Bay, Oregon (44°37'N, 124°04'W) from June 1986 through May 1987. Oblique tows were made with a 0.7 m plankton net fitted with 333 or 500-μm mesh and a 10-liter Plexiglass cod-end. The cod-end contents were diluted with surface seawater, transported to the laboratory, and placed in a 10 °C coldroom. Groups of 20 adult female *Calanus marshallae* were sorted into 1-liter beakers containing acrylic cylinders covered on one end with 750-μm mesh; the cylinders were elevated off the bottom of the beakers by acrylic rings glued to the underside of the mesh. This arrangement allowed copepods to be rapidly transferred to alternative food concentrations, and separated the copepods from their fecal pellets which passed through the mesh to the bottom of the flasks. The initial protocol for the three types of gut clearance rate experiments conducted in this study were similar; i.e., copepods were kept in filtered seawater for 24 hours prior to the start of an experiment, transferred to 700 ml of food medium, and allowed to feed for three hours before starting measurements of their gut evacuation rate. Four concentrations (nominally 500, 1000, 2000, and 4000 cells ml^{-1}) of the centric diatom *Thalassiosira weissflogii* were used as food in the experiments. Cell concentrations were measured with a Coulter model ZBI particle counter equipped with a 100-μm aperture. All experiments took place under continuous low light (10-20 $\mu E\ m^{-2}\ sec^{-1}$) at 10 °C.

Gut evacuation rates using gut fluorescence as a tracer:

The decline of gut pigment fluorescence through time was measured as one tracer of food evacuation. The sampling times varied somewhat in different experiments; however, the times most often used were 0, 5, 10, 15, 20, 25, 30, 45, 60, 90, and 1440 min following transfer from the food suspension to filtered seawater. For each time point, the copepods were rinsed briefly with filtered seawater, transferred to a glass grinding tube and homogenized in cold 90% acetone. The fluorescence of the filtrate was measured, before and after acidification, with a Turner Designs model 10 fluorometer equipped for chlorophyll detection (F4T5 lamp, Corning 5-60 excitation filter, Corning 3-66 reference filter, and Corning 70 and 16 emission filters). The concentration of gut pigments per copepod was determined using the following equations:

$$\frac{ng\ Chl\text{-}a}{Copepod} = K\left(\frac{\tau}{\tau-1}\right)(F_0-F_a)\left(\frac{v}{n}\right) \qquad (2\text{-}1)$$

$$\frac{ng\ Chl\text{-}a\ eq.\ wt.}{Copepod} = K\left(\frac{\tau}{\tau-1}\right)(\tau F_a-F_0)\left(\frac{v}{n}\right) \qquad (2\text{-}2)$$

where K is the calibration factor [ng chl-*a* l^{-1} (fluorescence unit)$^{-1}$], τ is the acid ratio for chlorophyll-*a*, F_0 is the initial fluorescence, F_a is the fluorescence after acidification, v is the extract volume, and n is the number of copepods used. Total gut pigment was calculated as the sum of chlorophyll-*a* (equation 2-1) and

pheopigments (equation 2-2), expressed in units of chlorophyll-*a* equivalent weight. All gut fluorescence values were corrected for the background fluorescence of copepods starved for 24 hours.

Gut evacuation rates using ^{68}Ge as a tracer:

The second set of experiments used a radioactive tracer, 68-germanium, to measure GERs of *Calanus marshallae*. This isotope is taken up by diatoms as germanic acid and along with silicon is incorporated into diatom frustules (Azam *et al.*, 1973; 1981; Rivkin, 1986). It has a half-life of 287 days and decays by electron capture to 68-gallium, a nuclide with a half-life of 68 min. This isotope, in turn, decays to 68-zinc by electron capture (10%) and positron (β^+) emission (90%) (Lederer and Shirley, 1978). The maximum energy of the β^+ emitted by the decay of ^{68}Ga is 1.89 MeV; it is this decay product which was detected using liquid scintillation techniques.

Thalassiosira weissflogii were labelled by growing cells in one liter batch cultures containing f/2 (Guillard and Ryther, 1962) nutrient levels (100 μM Si) and an initial molar ratio of ^{68}Ge:Si equal to 1.2×10^{-6}. The initial activity of the medium was 55 μCi liter^{-1} [0.12 μmol of Ge added in the form of $^{68}Ge(OH)_4$]. In preliminary experiments, mean cell volume and growth rates decreased for cultures with Ge:Si ratios greater than 10^{-3}; however, at lower ratios growth rates and cell volumes were identical to those in cultures containing no germanium.

After *Calanus marshallae* had fed for three hours on a given concentration of labelled *Thalassiosira weissflogii*, the decline in copepod radioactivity was measured through time after transferring the animals either to filtered seawater or to an identical concentration of unlabelled cells. The sampling times most often used were 0, 4, 8, 12, 16, 20, 30, 45, 60, 90, and 1440 min following transfer from the labelled food suspension. Labelled food concentrations were obtained by diluting aliquots of the radioactive stock cultures with filtered seawater and determining cell concentration with a Coulter model ZBI particle counter. To check for potential dilution of the label during the experiment, several replicate volumes of the experimental food mixture were filtered through GF/F filters at the start and conclusion of each experiment. No significant change in activity per cell occurred during the experiments. The copepods removed for each time interval were rinsed with filtered seawater and transferred individually to a liquid scintillation vial. At the end of the experiment, 1.0 ml of tissue solubilizer (Protosol, New England Nuclear Corp.) was added to each vial and the vials were kept at 55 °C for 24 hours. Following this interval, the vials were allowed to cool and 10 ml of either Aquasol (New England Nuclear) or Econofluor (New England Nuclear) liquid scintillation cocktail were added to each vial. After a delay of 24 hours to ensure that ^{68}Ga was in equilibrium with ^{68}Ge (Rivkin, 1986), and to eliminate sample chemiluminescence, the radioactivities of the samples (dpm) were counted on a Beckman Instruments Inc. model 1800 liquid scintillation counter. All samples were corrected for quench and background radiation. The mean

activity of copepods kept either in filtered seawater or in unlabelled food medium for 24 hours was subtracted from all samples.

Gut evacuation rate calculation:

The concentration of gut pigment (total chlorophyll *a* equivalent weight) and the mean ^{68}Ge activity (dpm), measured at each time point, were expressed as a percentage either of the gut concentration or of the mean activity measured at time zero. GER was then calculated by fitting the data to the exponential decay model:

$$S_t = S_0 e^{-Rt} \qquad (2-3)$$

where S_0 is the initial level of gut contents (100%), S_t is the percentage of gut contents remaining at time t, and R is the instantaneous evacuation rate with units of min^{-1}. The data from each experiment were fit to this model using the Gauss method of nonlinear regression which uses a Taylor series expansion to approximate the nonlinear regression model and then employs least squares to estimate the parameters (Neter *et al.*, 1983). Nonlinear regression methods provided better fits to the data than those obtained from linear regression of log-transformed data.

Results

Table II.1 shows the collection dates and GERs of *Calanus marshallae* calculated by fitting the exponential model to data collected during the initial 90 minutes of each experiment. Despite the fact that experiments utilized copepods collected at various times of the year, and that initial gut tracer concentrations varied between experiments, GERs within treatments varied by less than a factor of 1.5 and were not statistically different (F-test, $p > 0.05$). Apparently, when subjected to the same experimental conditions, the fraction of gut material lost per unit time does not differ markedly for *Calanus marshallae* collected at different times of the year. This result allowed the pooling of experiments conducted at different times of the year, to facilitate comparisons between treatments. Fits to the exponential model for the pooled data for each of the three types of gut evacuation rate experiments conducted are shown in Fig. II.1.

Comparison of non-feeding copepod GERs:

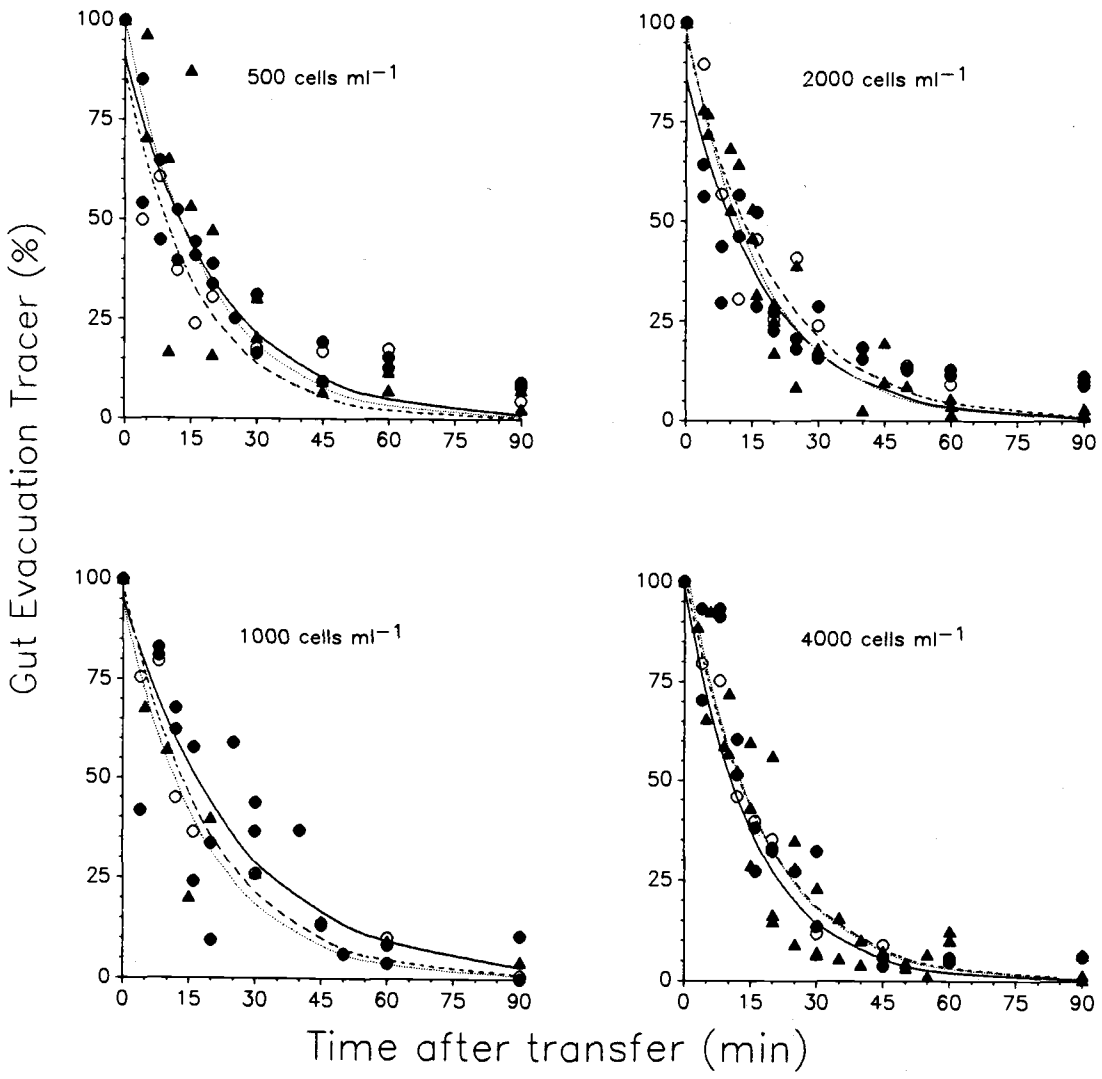
The two tracers of copepod gut evacuation used in this study (pigment fluorescence and 68-germanium activity) are associated with separate components of a diatom cell, and therefore conceivably could have been measuring different rates of evacuation through the gut. To verify that both tracers move along the gut at similar rates, and thus can be used interchangeably, evacuation rates of

Table II.1. Gut evacuation rates (GER ± SE) of *Calanus marshallae* following transfer from initial to final food concentrations (cells ml-1) or to filtered seawater (fsw). N is the sample size. In ^{68}Ge-tracer experiments initial food was ^{68}Ge-labelled *Thalassiosira weissflogii* and final food was unlabelled cells. Initial gut pigment (chl a equivalent wt) for ^{68}Ge-tracer experiments were calculated using a conversion factor of 4.37 pg pigment cell^{-1} measured for *T. weissflogii*, and mean specific activity of cells sampled at start and finish of each experiment. R^2 is the coefficient of determination for fits to the exponential decline model.

Collection date	Gut tracer	Food conc		Specific activity	GER	R^2	(N)	Initial gut pigment
		initial	final	(dis min^{-1})	(% min^{-1} ± SE)			(ng copepod^{-1})
29. May 1987	pigment	564	fsw		3.91 ± 1.57	0.6837	(9)	0.74
29. May 1987	pigment	572	fsw		5.59 ± 1.25	0.9030	(8)	1.29
4. Nov. 1986	^{68}Ge	556	510	0.755	4.98 ± 0.83	0.8794	(11)	3.33
24. Mar. 1987	^{68}Ge	496	517	0.514	4.64 ± 0.79	0.9115	(10)	0.71
1. Apr. 1987	^{68}Ge	493	fsw	0.620	6.08 ± 1.33	0.8449	(10)	1.20
29. May 1987	pigment	983	fsw		5.45 ± 1.00	0.9102	(9)	5.23
4. Nov. 1986	^{68}Ge	1056	1112	0.789	3.60 ± 0.52	0.9133	(12)	3.36
27. Mar. 1987	^{68}Ge	941	973	0.574	4.90 ± 1.78	0.6844	(10)	0.89
1. Apr. 1987	^{68}Ge	1009	fsw	0.700	5.10 ± 0.60	0.9578	(10)	4.11
16. Sept. 1986	pigment	2072	fsw		6.72 ± 1.20	0.8793	(12)	5.34
9. Mar. 1987	pigment	2114	fsw		4.87 ± 0.78	0.9292	(9)	10.70
29. Apr. 1987	pigment	2127	fsw		5.98 ± 0.72	0.9639	(9)	11.78
26. Aug. 1986	^{68}Ge	1998	1995	0.574	5.65 ± 0.89	0.8775	(12)	7.78
9. Sept. 1986	^{68}Ge	2022	2061	0.590	5.05 ± 1.12	0.7968	(12)	6.24
8. Aug. 1986	^{68}Ge	2060	fsw	0.732	5.07 ± 0.80	0.8850	(12)	3.66
24. June 1986	pigment	4076	fsw		7.81 ± 0.59	0.9735	(14)	9.19
1. July 1986	pigment	4229	fsw		5.35 ± 0.60	0.9370	(16)	14.74
9. Mar. 1987	pigment	4007	fsw		5.19 ± 0.94	0.9021	(9)	16.15
4. Nov. 1986	^{68}Ge	4014	4051	0.749	5.82 ± 0.86	0.9243	(10)	11.42
27. Mar. 1987	^{68}Ge	3989	4031	0.652	8.38 ± 1.62	0.8909	(10)	10.12
1. Apr. 1987	^{68}Ge	4055	fsw	0.853	5.72 ± 0.50	0.9775	(10)	6.55

Figure II.1. Decline of gut pigment (△···△) and decline of 68-germanium following transfer to either filtered seawater (○--○) or to unlabelled cells (●—●) at four concentrations of *Thalassiosira weissflogii*. Curves are nonlinear regression fits to $S_t = S_0e^{-Rt}$ for the pooled initial 90 min of data for each type of experiment (see text).

Figure II.1


500 cells ml^{-1}
2000 cells ml^{-1}
1000 cells ml^{-1}
4000 cells ml^{-1}
Gut Evacuation Tracer (%)
Time after transfer (min)
0
25
50
75
100
0
15
30
45
60
75
90

non-feeding copepods for each tracer were compared at the four different initial food concentrations (Table II.2). The GERs of both tracers were statistically the same (t-test, $p < 0.05$) at all food levels, indicating that gut pigment and ^{68}Ge-labelled diatom frustules were not egested at different rates.

GERs of feeding versus non-feeding copepods:

Mean GERs of feeding and non-feeding copepods at each food concentration were calculated by fitting the exponential model to the pooled data for each type of experiment. Rates were calculated for both the initial 20 and 90 minutes of the experiments (Table II.3). There was no detectable difference (t-test, $p < 0.05$) between GERs of feeding and non-feeding copepods calculated over either interval. GERs calculated over 90 minute intervals, however, tended to be lower than rates calculated for the initial 20 minutes of these experiments for both feeding and non-feeding copepods. The average decrease in rates between 20 and 90 min for non-feeding copepods (7.23%) was roughly half that observed for feeding copepods (16.27%).

GER versus food concentration:

The inability to discriminate between GERs of feeding and non-feeding copepods, as measured in these experiments, indicates that if gut evacuation rate does vary with food concentration, the time required to effect changes is in excess of one gut passage time. Figure II.2 shows the short-term (20 min) GERs of

Table II.2. Comparison of gut evacuation rates (GER) of non-feeding *Calanus marshallae* measured using two separate tracers (gut pigment fluorescence and ^{68}Ge activity) at four different food concentrations. N is the number of data points. Rates shown are best fits to exponential model using pooled initial 90 min of data following transfer to filtered seawater from all replicate experiments at a given food concentration. R^2 is the coefficient of determination for fits to the exponential model; ns: not significantly different for $\alpha = 0.05$.

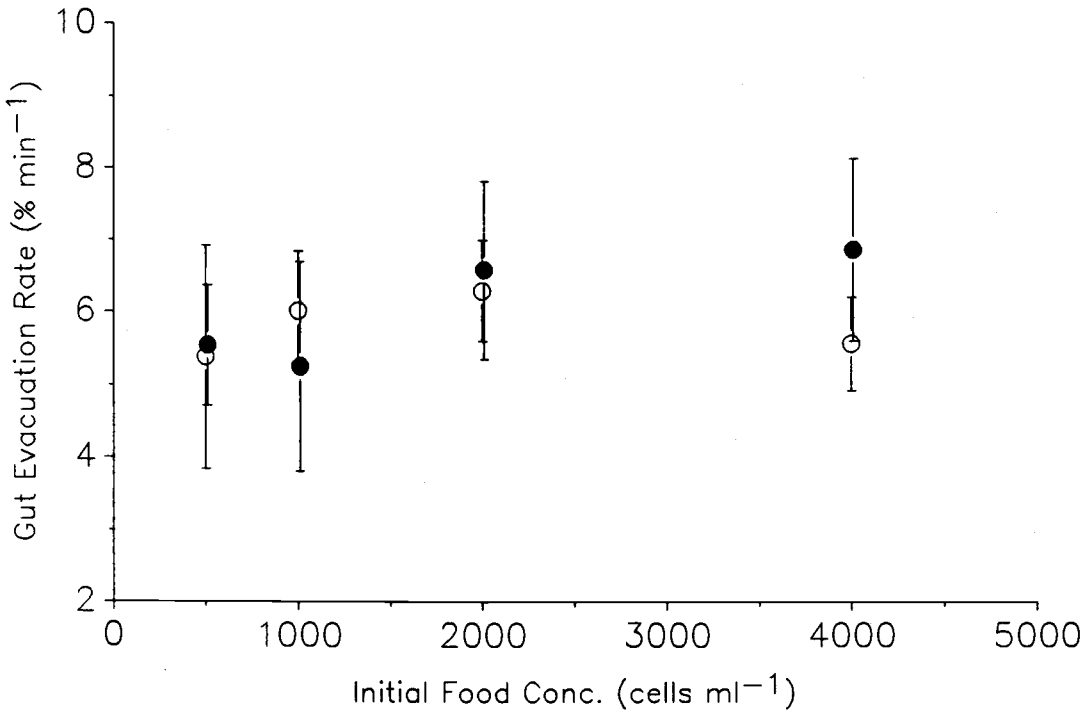
Food conc (cells ml^{-1})	Gut tracer	GER (% min^{-1} ± SE)	R^2	(N)	Significance
500	pigment	5.59 ± 1.35	0.7292	(17)	ns
	^{68}Ge	6.08 ± 1.33	0.8449	(10)	
1000	pigment	5.45 ± 1.00	0.9102	(9)	ns
	^{68}Ge	5.10 ± 0.60	0.9578	(10)	
2000	pigment	5.77 ± 0.54	0.9037	(30)	ns
	^{68}Ge	5.07 ± 0.80	0.8850	(12)	
4000	pigment	5.93 ± 0.47	0.9132	(39)	ns
	^{68}Ge	5.72 ± 0.50	0.9775	(10)	

Table II.3. Gut evacuation rates of feeding and non-feeding *Calanus marshallae* calculated by fitting the exponential model to the initial 20 and 90 minutes following transfer to unlabelled cells or filtered seawater. R^2 is the coefficient of determination obtained by fitting the exponential model to (N) measurements of gut tracer concentration made during the two intervals shown.

Food Conc. (cells ml^{-1})	Experiment Type	20 min Gut Evacuation Rate			90 min Gut Evacuation Rate		
		(% min^{-1} ± SE)	R^2	N	(% min^{-1} ± SE)	R^2	N
500	Non-feeding	5.38 ± 1.54	0.5027	(16)	4.84 ± 0.86	0.7458	(27)
	Feeding	5.54 ± 0.84	0.8280	(12)	4.80 ± 0.55	0.8945	(21)
1000	Non-feeding	6.01 ± 0.83	0.8766	(11)	5.24 ± 0.39	0.9649	(19)
	Feeding	5.25 ± 1.44	0.6271	(12)	3.87 ± 0.73	0.7634	(22)
2000	Non-feeding	6.29 ± 0.70	0.8348	(21)	5.58 ± 0.44	0.8977	(42)
	Feeding	6.58 ± 1.24	0.7618	(12)	5.32 ± 0.69	0.8343	(24)
4000	Non-feeding	5.56 ± 0.64	0.8171	(24)	5.88 ± 0.38	0.9257	(49)
	Feeding	6.86 ± 1.27	0.7847	(12)	6.43 ± 1.00	0.8434	(20)

Figure II.2. Gut evacuation rates (± SE) of feeding (●) and non-feeding (○) *Calanus marshallae* measured after 3 hr at four concentrations of *Thalassiosira weissflogii*. Rates were calculated by fitting the pooled initial 20 min of data for each type of experiment to the exponential decline model.

Figure II.2


10
8
6
4
2
Gut Evacuation Rate (% min^{-1})
0
1000
2000
3000
4000
5000
Initial Food Conc. (cells ml^{-1})

feeding and non-feeding *Calanus marshallae* measured after three hours of feeding at the four food concentrations used in my experiments. There is no difference (F-test, $p < 0.05$) between the short-term GERs measured at the different food concentrations. The 90 minute GERs (not shown) increase by a factor of 1.2 and 1.3, respectively, for feeding and non-feeding copepods between 500 and 4000 cells ml^{-1}. Despite this trend, linear regression of the data indicates the slope is not significantly different (t-test, $p < 0.05$) from zero for either feeding or non-feeding copepods.

Discussion

The calculation of GER depends on the model applied to evaluate the experimental data. Most studies, including this one, have shown that gut contents decrease exponentially with time, thus supporting use of the exponential model (Mackas and Bohrer, 1976; Kiørboe *et al.*, 1982; Dagg and Wyman, 1983; Simard *et al.*, 1985; Tande and Båmstedt, 1985; Christoffersen and Jespersen, 1986; Bautista *et al.*, 1988). If removal of gut contents truly occurs exponentially when a copepod is transferred to filtered seawater, the proportion of gut contents egested per unit time remains constant, but the amount of material lost per unit time declines as gut contents are depleted. Some investigators have suggested that the exponential decline of gut contents is an artifact of using non-feeding animals, since copepods may slow their rate of egestion when placed in an environment devoid of food (Dagg and Grill, 1980; Kiørboe *et al.*,1985). In my study, however, the loss of gut contents for both feeding and non-feeding copepods declined exponentially. This agrees with results obtained in other studies of feeding copepods (Christoffersen and Jespersen, 1986; Kiørboe and Tiselius, 1987). In these previous studies, however, copepods were transferred at the start of an experiment to a food source different in some respect from the initial food type. My data show that exponential decline still occurs when the food type is the same throughout an experiment.

GERs traditionally have been measured using non-feeding copepods because of the difficulty involved in trying to determine rates for actively feeding animals. Attempts to determine GERs for feeding copepods are complicated by dilution and mixing processes which take place in the gut. In this study it was assumed that GERs of feeding copepods could be estimated by short-term (20 min) measurements of the rate of gut tracer loss following transfer to a non-labelled food source. This assumption appears reasonable given the way in which food is processed and transported within the copepod gut. Mixing of ingested material is confined primarily to the anterior diverticulum and vascular region of the midgut. Once ingested material passes into the posterior region of the midgut little mixing occurs and the material is tightly packed within a fecal pellet and enclosed in a peritrophic membrane (Ong and Lake, 1969; Nott *et al.*, 1985). Following egestion of the fecal pellet, material from the anterior region of the midgut is dispersed into the posterior region by a brief episode characterized by several peristaltic contractions and the process of pellet formation begins again (Gauld, 1957). This description suggests that when copepods are transferred from labelled to unlabelled food at the start of a gut evacuation rate experiment, the initial loss of material will consist primarily of labelled material present in the posterior region of the midgut at the time of transfer. Thus short-term measurements of label evacuation should be only slightly biased by tracer dilution, and are therefore reasonable estimates of the true GER of feeding copepods.

There were no detectable differences between GERs of feeding and non-feeding copepods calculated using data collected during the initial 20 minutes of these experiments. Because of the increasing effects of tracer dilution with time, however, one would expect that GERs of feeding copepods would decline with time and therefore rates of non-feeding copepods would appear faster when calculated over longer intervals. Comparison of rates calculated over 20 and 90 minute time intervals (Table II.3) does indicate that GERs of feeding copepods decreased to a greater extent than those of non-feeding copepods. In addition, although rates were not detectably different, GERs of non-feeding copepods tended to be higher than rates for feeding animals at all but the highest food concentration in the 90-min experiments. It may be that effects of tracer dilution are too subtle to detect unequivocally, given the short duration and variability associated with gut evacuation rate experiments.

There are only a few studies in which GERs of feeding and non-feeding copepods have been compared, and the conclusions reached are not in agreement. Head (1988) compared GERs of feeding and non-feeding *Pseudocalanus* by measuring the rate of loss of unlabelled pigment following transfer of animals from unlabelled *Thalassiosira weissflogi* to either ^{14}C-labelled cells or filtered seawater. In agreement with my study, evacuation rates calculated over the first 15 minutes were indistinguishable. Christoffersen and Jespersen (1986) measured the evacuation rate of *Eudiaptomus graciloides* by transferring animals that had been feeding on *Scenedesmus* to both yeast and filtered seawater, and then following the

decline of gut fluorescence. They also found no difference between the evacuation rate of feeding and non-feeding copepods. Kiørboe and Tiselius (1987) also measured GERs of feeding copepods by monitoring the decline of gut fluorescence following transfer to a non-fluorescent food source. *Acartia tonsa* was allowed to feed on "excess" concentrations of *Rhodomonas baltica* [equivalent spherical diameter (ESD) of 6.5 μm], and then was transferred to either filtered seawater or to a suspension (2000-4000 cells ml^{-1}) of the heterotrophic flagellate *Oxyrrhis marina* (ESD of 18 μm). GERs of feeding and non-feeding copepods were the same during the initial 30 minutes following transfer, but thereafter the evacuation rate of copepods in filtered seawater decreased to half that of feeding animals. However, given the large size difference between the two cells provided as food in this study, and the apparent failure to match initial and final food concentrations, perhaps these results should be interpreted with caution. In the third study, Tsuda and Nemoto (1987) calculated the gut passage time of feeding *Pseudocalanus minutus* using an equation derived from Mackas and Bohrer (1976). With this equation one obtains the gut passage time by dividing the copepod's gut pigment content by its ingestion rate and multiplying this result by the volume-specific pigment content of the cells offered. The gut passage time of feeding copepods measured using this equation was longer than that of non-feeding copepods by a factor of 1.3 to 2.6.

The lack of agreement between the four studies cited above may indicate that control of GER differs among copepod species. However, as indicated above,

GERs of feeding copepods which are measured following transfer to a food source different from the initial source (Christoffersen and Jespersen, 1986; Kiørboe and Tiselius, 1987) should be interpreted with caution. Although there is no consensus regarding response of digestive enzymes to changes in food quality or quantity, at least some copepod species alter digestive enzyme levels in response to these factors, and require a period of acclimation to the new food source before enzyme levels stabilize (Mayzaud, 1986). It is possible, therefore, that GERs may vary during transition to a different food source, especially if the new food source differs greatly in terms of biochemical composition. The procedure used by Tsuda and Nemoto (1987) to measure GERs of feeding copepods has the advantage of not requiring transfer of copepods to different food sources; however, calculation of gut passage time by this technique requires the measurement of ingestion rate. Thus, while this method may be useful for investigating factors affecting GER, its use depends upon the validity of the ingestion rates obtained.

The final topic investigated in these experiments was the effect of food concentration on GER. Within the range of food concentrations examined (500 to 4000 cells ml^{-1}) there was no significant change in the GER of *Calanus marshallae*. Copepods were acclimated to the different food concentrations for three hours prior to starting the experiments. Thus the lack of change in GERs should be interpreted as implying that if a relationship between GER and food concentration exists for this *C. marshallae*, an acclimation period in excess of three hours is required for noticeable changes to occur. Other studies have also found

that GERs remain constant over certain ranges in food concentration. Wang and Conover (1986) reported that GERs of *Temora longicornis* were similar between 0.5 and 2 mm^3 $liter^{-1}$ of *Thalassiosira weissflogii* ($\approx$ 500 to 2000 cells ml^{-1}), but at higher food levels ($>$ 4 mm^3 $liter^{-1}$) evacuation rates increased. Dagg and Walser (1987) found that the GER of *Neocalanus plumchrus* decreased sharply in *T. weissflogii* concentrations less than 4 μg chl $liter^{-1}$ ($\approx$ 1000 cells ml^{-1}), but remained constant (averaging 4.27 % min^{-1}) above this food concentration. The lack of agreement regarding the relationship between GER and food concentration may reflect differences in experimental design, especially acclimation times, or indicate that different copepod species have evolved different strategies for regulating food processing.

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Chapter III

Gut Evacuation Rates and Herbivorous Grazing of Copepods in the Northeast Central Pacific Ocean: Seasonal variation and the relationship to copepod body size.

Abstract

Gut evacuation rates (GERs) of the dominant herbivorous copepods near 33°N, 139°W were measured during four seasonal VERTEX cruises conducted between July 1987 and May 1988. Rates of the majority of copepod species and developmental stages on each cruise did not vary significantly with time of day, or or among locations separated by as much as 225 km. GERs did vary seasonally. The extent of seasonal changes varied for different species, however, in many cases by a factor of 2. Seasonal changes in temperature and copepod body size accounted for 64% of observed variation in gut evacuation rates for all species. GERs decreased with body size and ranged from 7.43 to 0.50 % min^{-1}. The best fit to these data was with the power function, GER = aL^b, using total body length as the independent variable (L). The exponent (b) was the same for all cruises (-1.27), and appeared to be independent of temperature, species composition and food concentration. The magnitude of (a) tended to increase with temperature, although differences in (a) between cruises where GERs were measured at identical temperatures suggested that the value of this coefficient depended on factors besides temperature.

Short-term ingestion rates calculated during the four cruises also increased with body size. Ingestion, corrected for assumed 33% losses of gut pigment, ranged from 0.13 to 9.30 ng chl-*a* $copepod^{-1}$ hr^{-1}. Comparison of these rates, after conversion to carbon units using a C:Chl ratio of 80, to estimated metabolic

requirements showed that herbivorous grazing rates for most species were not sufficient to meet metabolic demands. This suggests that most copepod species were feeding omnivorously. To meet estimated metabolic requirements, carnivorous food intake would have had to exceed herbivorous consumption for many copepod species.

Introduction

The gut fluorescence method, which provides estimates of *in situ* herbivorous grazing rates, has been used with increasing frequency since its introduction by Mackas and Bohrer (1976). The method has proved popular because zooplankton feeding occurs prior to capture, in the animal's natural environment, thereby avoiding the problems associated with measurement of grazing rates in artificial laboratory settings (e.g. Mullin, 1967) and ambiguities associated with extrapolation of such rates to the field. Two quantities must be measured for this method: pigment concentration (chlorophyll-*a* and its degradation products) in the guts of freshly captured zooplankton, and the gut evacuation rate (GER) of food in the gut. Multiplication of these two quantities gives the average ingestion rate for the period of time preceding capture required for evacuation of gut contents (Mackas and Bohrer, 1976).

Application of the gut fluorescence method has become more complicated in recent years as investigations have shown that some variable fraction of gut pigment may not, at times, be detected by fluorescence (e.g. Conover *et al.*, 1986; Kiørboe and Tiselius, 1987; Lopez *et al.*, 1988; Pasternak and Drits, 1988). In addition, GER may vary as a function of several other factors. Several studies have demonstrated that GERs increase with temperature (Kiørboe *et al.*, 1982; Dagg and Wyman, 1983; Christoffersen and Jespersen, 1986; Dam and Peterson, 1988), and other workers have found, or suggested, that evacuation rates vary with

ambient food concentration (Dagg and Walser, 1987; Tsuda and Nemoto, 1987), the level of gut fullness (Baars and Oosterhuis, 1984; Wang and Conover, 1986; Ellis and Small, 1989), food type or quality (Nicolajsen *et al.*, 1983; Baars and Helling, 1985; Head and Harris, 1987; Clarke *et al.*, 1988; Head, 1988), and time of day (Arashkevich, 1977; Baars and Oosterhuis, 1984; Head, 1986).

The potential for GER to vary suggests that this rate should be measured at the same time, and under the same conditions, as gut pigment measurements when determining ingestion rates (Dagg and Walser, 1987). However, often it is desirable to extrapolate results beyond the immediate area of collection, or to attempt some prediction of future grazing intensity. The uncertainty of such predictions will depend, in part, on the dynamic range over which GER can vary for a given species. Models formulated to predict GERs would facilitate estimation of *in situ* ingestion rates determined by the gut fluorescence method. Development of predictive models will require functions describing GER in terms of the variables that effect changes in the rate of food passage. In this study, GERs were measured for the dominant pigment-containing copepods found in the Northeast Pacific Ocean near 33°N, 139°W to examine both short-term and seasonal variability. The changes observed were examined with respect to variation in body size and temperature and a descriptive model was formulated incorporating these two parameters.

Measurements of GER were also combined with measured gut pigment concentrations to estimate in situ herbivorous ingestion rates. These rates were

compared to estimates of respiration rates to evaluate whether herbivorous feeding was adequate to meet estimated respiratory demands.

Methods

Copepod GERs, dry weights, and length measurements were determined for animals collected during four cruises in the central Northeast Pacific Ocean near the VERTEX seasonal station (33°N, 139°W, Fig. III.1). All experiments took place under low light, in a flow-through seawater chamber, at the temperature measured (± 1°C) for the upper mixed layer of the water column (Table III.1). Zooplankton were collected from the upper water column during 20 to 30 min tows with two 0.7 m diameter plankton nets equipped with 202 or 333 μm mesh. The contents of both cod-ends were combined, quickly diluted, and living material decanted through 2000 μm mesh into a partially filled container of filtered seawater. This volume was divided into three size fractions (202-500 μm, 500-1000 μm, and 1000-2000 μm) by collecting animals on successively smaller mesh. One size group was selected for each experiment, given 3 rinses in filtered seawater to remove particulates, and then gently washed off the mesh into a beaker of filtered seawater. Roughly equal aliquots of these zooplankton were poured into acrylic cylinders containing 0.2 μm filtered seawater. The base of these cylinders were covered with 335 μm mesh (containment-mesh), and rested 1 cm off the bottom of 1 liter beakers within the flow-through seawater chamber. This arrangement allowed animals to be rapidly removed from the filtered seawater for processing, and provided a barrier between animals and their fecal material. Copepods were removed from the filtered seawater at the following times: 0, 5,

Figure III.1. Collection locations of zooplankton used in gut evacuation rate experiments.

Figure III.1

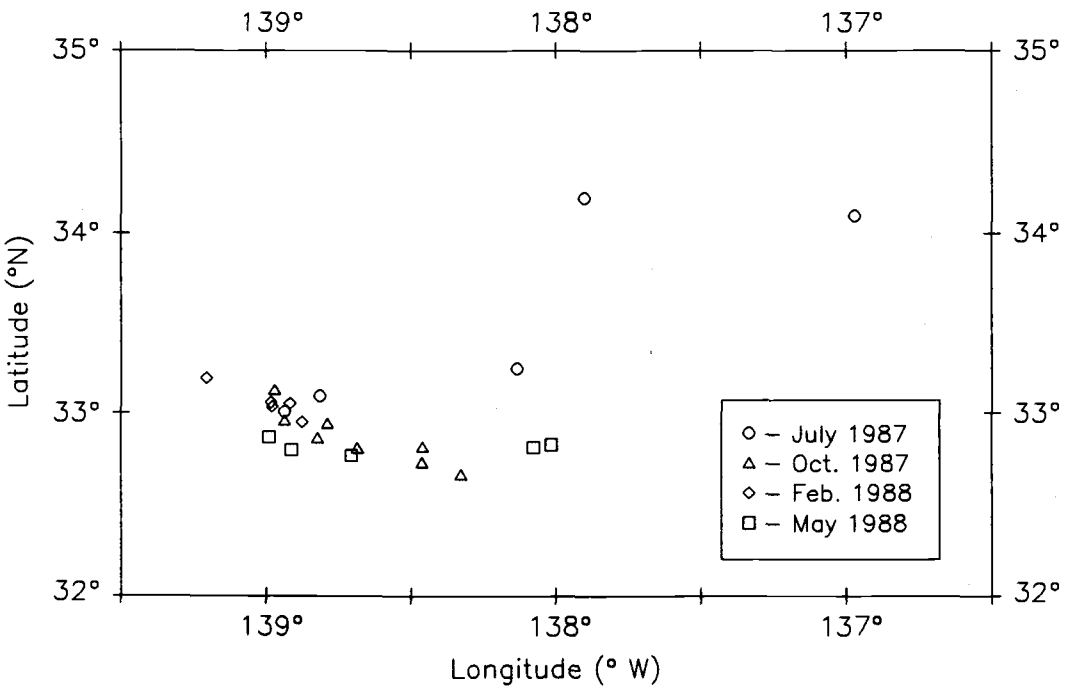

139°
138°
137°
35°
34°
33°
32°
Latitude (°N)
Longitude (° W)
○ – July 1987
△ – Oct. 1987
◇ – Feb. 1988
□ – May 1988

Table III.1. Experiment dates and temperatures at which gut evacuation rates were measured for copepods collected near 33°N, 139°W.

VERTEX Cruise #	Experiment Dates	Temperature (°C)
IV	July 10-16, 1987	20
V	Oct. 23-29, 1987	20
VI	Feb. 2-7, 1988	17
VII	May 9-13, 1988	18

10, 15, 20, 30, 45, 60, and 90 minutes. Animals were rinsed off the containment-mesh onto small pieces of mesh, placed into petri dishes, covered with aluminum foil, and frozen at -20°C. The period of time from collection to removal of the time-0 sample was approximately 5 minutes.

In the laboratory, each frozen sample was thawed in the dark and abundant copepod stages picked from the thawed sample using a Wild M8 dissecting scope operating at low light intensity. Copepods were selected on the basis of the following criteria: (1) only species and stages which could be quickly identified were utilized to permit rapid processing of samples; (2) only copepod stages which, by virtue of numbers present and/or gut pigment levels, provided a fluorescent signal above background levels were analyzed; and (3) to minimize bias arising from inclusion of animals which died prior to or during experiments, only intact copepods with undamaged appendages were selected for analysis. The number of individuals analyzed from each sample varied for different copepod species; the number chosen was based on availability and the number necessary to give an adequate fluorescence signal. For each time point copepods were rinsed briefly with filtered seawater, transferred to a glass grinding tube, and homogenized in cold 90% acetone. The filtrate fluorescence was measured, before and after acidification, with a Turner Designs model 10 fluorometer equipped for chlorophyll detection (F4T5 lamp, Corning 5-60 excitation filter, Corning 3-66 reference filter, and Corning 70 and 16 emission filters). Gut pigment concentration was calculated using the following equations:

$$\frac{ng\ Chl\text{-}a}{Copepod} = \dot{K}\left[\frac{\tau}{\tau-1}\right](F_0-F_a)\left[\frac{v}{n}\right] \qquad (3\text{-}1)$$

$$\frac{ng\ Chl\text{-}a\ eq.\ wt.}{Copepod} = K\left[\frac{\tau}{\tau-1}\right](\tau F_a-F_0)\left[\frac{v}{n}\right] \qquad (3\text{-}2)$$

where K is the calibration factor [ng chl-*a* l^{-1} (fluorescence unit)$^{-1}$], τ is the acid ratio for chlorophyll-*a*, F_0 is the initial fluorescence, F_a is the fluorescence after acidification, v is the extract volume, and n is the number of copepods. Total gut pigment (chlorophyll-*a* equivalent weight) was calculated as the sum of equations (3-1) and (3-2).

Gut evacuation rates were calculated by fitting each copepod's gut pigment data to the exponential decay model using the Gauss method of nonlinear regression (Neter *et al.*, 1983):

$$S_t = S_0 e^{-Rt} \qquad (3\text{-}3)$$

where S_0 is the initial level of gut contents, S_t is the gut pigment remaining at time t, and R is the instantaneous gut evacuation rate with units of min^{-1}. GERs tended to decline once gut pigment levels decreased to roughly 80 - 90% of initial levels. Previous work (Ellis and Small, 1989) indicated that evacuation rates calculated for the initial period of gut pigment loss in starving animals were identical to rates of continuously feeding animals; therefore, GERs were calculated from the initial decline of gut contents. Following techniques adopted in other studies, this interval (usually 90 min) was determined by examining semilog plots of gut pigment versus time in filtered seawater and excluding later time points which

deviated from the initial linear decrease (Kiørboe and Tiselius, 1987; Dam and Peterson, 1988).

Assumptions regarding the stoichiometry of conversion of chlorophyll to its degradation products in the copepod gut have been reexamined recently (e.g. Helling and Baars, 1985; Conover *et al.*, 1986; Pasternak *et al.*, 1987). It now appears that the assumption of 100% molar conversion of chlorophyll-*a* to pheophorbide-*a* (Shuman and Lorenzen, 1975) may not be correct. Several studies have determined that a variable fraction (0 - 99.9%) of ingested chlorophyll is "lost", either assimilated or degraded to a non-fluorescent product which escapes detection, during passage through the gut. A survey of the literature (Table III.2) indicates that with the exception of the work by Conover *et al.* (1986) apparent losses of gut pigments range from 0 to 60.3%. The high losses reported by Conover *et al.* (1986) are thought to be atypical of herbivorous copepods (Kiorboe and Tiselius, 1987) and may have been due to fragmentation of fecal pellets which resulted in loss of pigment to the medium (Lopez *et al.*, 1988). The mechanism responsible for pigment losses has not been determined; however, if degradation time is much shorter than gut residence time, as might be the case for chemical or enzymatic destruction of pigment, most pigment loss will have already occurred prior to animal capture. Only the most recently ingested material would be subject to degradation and this apparent loss of pigment should not greatly bias calculations of GERs. Calculation of ingestion rates, however, will be underestimated as a result of chlorophyll losses because initial measurement of pigment will not include

Table III.2. Estimates of the percentage of pigment lost during gut passage for various species of zooplankton.

Species	% Pigment Loss (± SE)	Range	N	Food Source	Reference
Acartia tonsa	11.3 ± 4.1	(0.6 - 24.1)	6	*Thalassiosira fluviatilis*	Kiørboe & Tiselius (1987)
Calanus finmarchicus	32.9 ± 7.6	(0.0 - 52.4)	6	Natural particulates	Helling & Baars (1985)
C. glacialis	90.4 ± 0.4	(90.0 - 90.8)	2	*Thalassiosira* sp.	Conover *et al.*, (1986)
C. hyperboreus	97.5 ± 1.4	(93.4 - 99.9)	4	*Thalassiosira* sp.	Conover *et al.*, (1986)
	60.3 ± 19.1	(41.2 - 79.3)	2	?	Head (pers. comm.) cited in Lopez *et al.*, (1988)
C. pacificus	45.1 ± 13.8	(0.0 - 92.0)	7	*Gymnodinium splendens*	Lopez *et al.*, (1988)
	19.7 ± 27.8	(0.0 - 39.3)	2	*Phaeodactylum tricornutum*	Pasternak & Drits (1988)
	4.0		1	Natural particulates	Pasternak & Drits (1988)
	38.0 ± 1.8	(37.0 - 92.0)	11	?	Hassett & Landry (unpubl. data) cited in Dam & Peterson (1988)
C. pacificus and *C. marshallae*	36.3 ± 2.6	(28.0 - 48.0)	7	*Coscinodiscus angstii*	Shuman & Lorenzen (1975)
Euphausia pacifica	22.0		1	*Coscinodiscus angstii*	Shuman & Lorenzen (1975)
Euphausia sp. and *Neocalanus cristatus* *N. plumchrus*	20.0		1	*Coscinodiscus angstii*	Shuman & Lorenzen (1975)
Neocalanus plumchrus	11.0	≈(0 - 70)	57	*Thalassiosira weissflogii*	Dagg & Walser (1987)
Pleuromamma sp.	34.8 ± 8.1	(26.4 - 42.7)	3	Natural particulates	Pasternak & Drits (1988)
Pseudocalanus sp.	40.0		1	*Dunaliella tertiolecta*	Shuman & Lorenzen (1975)
	37.9 ± 5.3	(16.0 - 54.0)	7	Epontic algae	Head (1988)
Temora longicornis	45.0 ± 2.9	(40.0 - 59.0)	5	?	Dam (unpubl. data) cited in Dam & Peterson (1988)
Undinula darwini	0.0		1	Natural particulates	Pasternak & Drits (1988)
Weighted Mean	26.5	(0.0 - 97.5)	124		

any material destroyed or assimilated in the gut prior to capture. In this study ingestion rates were calculated using the equation suggested by Wang and Conover (1986):

$$I = \frac{RP}{(1-b)} \qquad (3\text{-}4)$$

where I is the ingestion rate (ng Pigment copepod^{-1} hr^{-1}), R is the gut evacuation rate (hr^{-1}), P is measured gut pigment (ng chl-*a* equivalents copepod^{-1}), and b is the fractional loss of total pigment in the digestive process (in this study assumed to be 0.33).

Ingestion rates of pigment were converted to carbon by multiplying ingested pigment by a carbon:chlorophyll ratio of 80. Carbon:chlorophyll ratios for the seasonal VERTEX cruises were determined from the slope of regressions of particulate organic carbon (POC) on Chl-*a* for water samples collected above the photic zone. The slope of the regression line is interpreted as the average C:Chl ratio of organic matter associated with pigment, and the intercept is the average amount of carbon derived from detritus and zooplankton present in the POC sample (Banse, 1977). Carbon:chlorophyll ratios (i.e., the slopes of regressions of POC on Chl-*a*) for the different cruises were quite variable, ranging from 36 to 117. Ingestion rates were converted to a carbon basis using a value of 80, which is approximately the mean of POC:chl-*a* ratios measured for particulate matter collected during the different cruises. Calculation of carbon ingestion rates using this approach makes the assumption that gut pigment represents the remains of

living phytoplankton and that detritus is selected against or comprises an insignificant fraction of the diet.

A portion of the zooplankton collected for gut evacuation experiments was frozen and used to determine total body length, cephalothorax length, and dry weight of copepod species for which GERs were measured. The extra frozen samples from all experiments on a given cruise were pooled to obtain adequate numbers of animals for these measurements. Total length, measured from the head to the end of the caudal rami, and cephalothorax length were measured for a maximum of 25 individuals with a Wild M8 dissecting scope. Dry weights were determined by rinsing groups of animals briefly with distilled water, drying the animals at 60°C for 4 days on tared pieces of aluminum foil, then measuring weights on a Perkin-Elmer Model AD22 autobalance. In some cases inadequate numbers of animals were obtained for reliable determination of dry weight. In these cases dry weights were estimated from the equation:

$$W = (5.729)L^{3.023} \qquad (3\text{-}5)$$

where W is dry weight (μg copepod^{-1}) and L is cephalothorax length (mm). The coefficients were determined by linear regression of log-transformed data for copepod species from all cruises ($R^2 = 0.9005$, $n = 46$).

Results

Species identification

Seventeen species of copepods, representing nine families within the order Calanoida, met the criteria necessary for determination of GERs (Table III.3). These copepods were the dominant species containing gut pigment within the 202-2000 μm sieve fraction in the study area. They ranged in size from 0.97 to 6.61 mm total length (Table III.4), from 0.80 to 5.86 mm cephalothorax length (Table III.5), and from 0.60 to 280.00 μg dry weight. The abundance of copepod species and their developmental stages varied at different times of year, resulting in differences between cruises in the numbers and species of copepods used in experiments. Apparent diversity was greatest in October 1987 when evacuation rates were measured for 14 species of copepods, while in February 1988 only 6 species were sufficiently abundant for measurements. *Calanus tenuicornis*, *Neocalanus gracilis*, *Pleuromamma abdominalis*, and *P. gracilis* were the only copepod species for which GERs were measured on all four cruises.

Table III.3 also lists other copepods whose rates of gut food passage could not be determined using the gut fluorescence technique because they did not meet the three criteria for analysis. *Calanus lighti* and *Undinula darwini* contained sufficient quantities of gut pigment for analysis, 1.404 and 0.927 ng pigment copepod^{-1}, respectively, but were too scarce in samples to permit calculations of gut evacuation rate. *Lucicutia* sp. and *Corycaeus* sp. could not be rapidly

Table III.3. List of copepod species identified within the study area. (*) indicates species for which gut evacuation rates were measured.

Species
Calanoida
Acartiidae
**Acartia danae* Giesbrecht
Aetideidae
Euchirella curticauda Giesbrecht
**Undeucheata plumosa* Giesbrecht
Calanidae
Calanus lighti Bowman
**Calanus tenuicornis* Dana
**Nannocalanus minor* Claus f. *major*
**Nannocalanus minor* Claus f. *minor*
**Neocalanus gracilis* Dana
**Neocalanus robustior* Giesbrecht
Calocalanidae
**Calocalanus pavo* Dana
**Mecynocera clausii* Thompson
Candaciidae
Candacia bipinnata Giesbrecht
Candacia ethiopica Dana
**Paracandacia bispinosa* Claus
Centropagiidae
**Centropages violaceus* Claus
Eucalanidae
**Eucalanus crassus* Giesbrecht
**Eucalanus elongatus* Claus
Euchaetidae
Euchaeta media Giesbrecht
Lucicutiidae
**Lucicutia flavicornis* Giesbrecht

Table III.3. (Continued)

Species
Calanoida
Metridiidae
**Pleuromamma abdominalis* Lubbock
**Pleuromamma gracilis* Claus
**Pleuromamma xiphias* Giesbrecht
Cyclopoida
Corycaeidae
Corycaeus speciosus Dana
Corycaeus sp.
Oithonidae
Oithona sp.
Oncaeidae
Oncaea conifera Giesbrecht
Oncaea mediterranea Claus
Oncaea venusta Philippi
Sapphirinidae
Sapphirina stellata Giesbrecht

Table III.4. Total length (mm ± std error) of selected copepod species from the study area.

Species	Stage	July 1987	Oct. 1987	Feb. 1988	May 1988
Acartia danae	CVIf	1.257 ± 0.012	1.129 ± 0.009	1.250 ± 0.013	1.231 ± 0.014
Calanus tenuicornis	CVIf	1.925 ± 0.028	1.905 ± 0.017	1.971 ± 0.055	1.944 ± 0.012
	CV	1.626 ± 0.021		1.597 ± 0.063	
Calocalanus pavo	CVIf		1.106 ± 0.004	1.290 ± 0.074	
Centropages violaceus	CVIf	1.991 ± 0.018		2.084 ± 0.016	
Eucalanus crassus	CVIf		3.940 ± 0.050		
	CVIm		3.604		
	CIVm		2.891		
	CIII		2.386 ± 0.013		
	CII		1.815 ± 0.013		
	CI		1.418 ± 0.007		
Eucalanus elongatus	CVIf		6.613 ± 0.043		
	CVIm		4.733 ± 0.019		
	CVf		5.155 ± 0.027		
	CVm		3.688 ± 0.017		
	CIVf		3.897 ± 0.016		
	CIVm		2.878 ± 0.013		
	CIII		2.218 ± 0.026		

Table III.4. Total length (mm ± std error) of selected copepod species from the study area.

Species	Stage	July 1987	Oct. 1987	Feb. 1988	May 1988
Lucicutia flavicornis	CVIf	1.534 ± 0.036	1.552 ± 0.012	1.620 ± 0.076	1.563 ± 0.009
	CVIm	1.584 ± 0.142	1.465 ± 0.010		
Mecynocera clausii	CVIf	0.965 ± 0.009	0.973 ± 0.004	0.984 ± 0.006	1.003 ± 0.005
Nannocalanus minor f. major	CVIf	2.334 ± 0.012	2.297 ± 0.018	2.103 ± 0.062	
	CVIm	1.970 ± 0.006	1.973 ± 0.009		
	CV		1.769 ± 0.012		
Nannocalanus minor f. minor	CVIf	1.912 ± 0.020		1.673 ± 0.047	1.850 ± 0.024
	CVIm	1.720 ± 0.017			
Neocalanus gracilis	CVIf	3.345 ± 0.018	3.192 ± 0.027	3.223 ± 0.016	3.381 ± 0.034
	CV		2.563 ± 0.027		
Neocalanus robustior	CVIf	4.376 ± 0.031	4.386 ± 0.026	4.220 ± 0.021	4.514
	CV		3.274 ± 0.017		3.410
	CIV		2.409 ± 0.015		2.583 ± 0.022
	CIII		1.909 ± 0.011	1.921 ± 0.011	2.028 ± 0.034
	CII		1.510 ± 0.009	1.557 ± 0.017	
Paracandacia bispinosa	CVIf	1.910 ± 0.012		1.880 ± 0.015	2.020 ± 0.018

Table III.4. Total length (mm ± std error) of selected copepod species from the study area.

Species	Stage	July 1987	Oct. 1987	Feb. 1988	May 1988
Pleuromamma abdominalis	CVIf	3.360 ± 0.046	3.475 ± 0.054	3.431 ± 0.029	3.459 ± 0.050
	CVIm	3.400 ± 0.030	3.534 ± 0.025	3.361 ± 0.026	3.881 ± 0.023
Pleuromamma gracilis	CVIf	2.058 ± 0.011	2.001 ± 0.012	2.101 ± 0.045	2.039 ± 0.014
	CVIm	1.863 ± 0.015	1.853 ± 0.009	1.950 ± 0.012	1.902 ± 0.029
Pleuromamma xiphias	CVIf	4.529 ± 0.030	4.831 ± 0.021	4.510 ± 0.051	5.025 ± 0.018
	CVIm	4.197 ± 0.281			4.895 ± 0.138
	CV	3.382 ± 0.016	3.406 ± 0.050		3.495 ± 0.061
Undeuchaeta plumosa	CVIf	3.796 ± 0.019			

Table III.5. Cephalothorax length (mm ± std error) of selected copepod species from the study area.

Species	Stage	July 1987	Oct. 1987	Feb. 1988	May 1988
Acartia danae	CVIf	0.973 ± 0.005	0.858 ± 0.006	0.951 ± 0.009	0.932 ± 0.010
Calanus tenuicornis	CVIf	1.486 ± 0.017	1.433 ± 0.012	1.490 ± 0.009	1.467 ± 0.008
	CV	1.273 ± 0.014		1.227 ± 0.005	
Calocalanus pavo	CVIf		0.923 ± 0.005	0.934 ± 0.011	
Centropages violaceus	CVIf	1.529 ± 0.018		1.595 ± 0.014	
Eucalanus crassus	CVIf		3.439 ± 0.047		
	CVIm		2.970		
	CIVm		2.495		
	CIII		2.088 ± 0.012		
	CII		1.589 ± 0.010		
	CI		1.243 ± 0.008		
Eucalanus elongatus	CVIf		5.861 ± 0.012		
	CVIm		4.147 ± 0.014		
	CVf		4.607 ± 0.021		
	CVm		3.284 ± 0.016		
	CIVf		3.482 ± 0.009		
	CIVm		2.588 ± 0.013		
	CIII		1.986 ± 0.022		

Table III.5. Cephalothorax length (mm ± std error) of selected copepod species from the study area.

Species	Stage	July 1987	Oct. 1987	Feb. 1988	May 1988
Lucicutia flavicornis	CVIf	1.001 ± 0.033	0.984 ± 0.010	0.967 ± 0.006	0.929 ± 0.008
	CVIm	0.965 ± 0.153	0.902 ± 0.007		
Mecynocera clausii	CVIf	0.798 ± 0.006	0.797 ± 0.003	0.820 ± 0.005	0.814 ± 0.005
Nannocalanus minor f. major	CVIf	1.877 ± 0.016	1.771 ± 0.010	1.703 ± 0.042	
	CVIm	1.565 ± 0.005	1.496 ± 0.008		
	CV		1.383 ± 0.010		
Nannocalanus minor f. minor	CVIf	1.565 ± 0.013		1.337 ± 0.052	1.497 ± 0.018
	CVIm	1.350 ± 0.004			
Neocalanus gracilis	CVIf	2.724 ± 0.018	2.511 ± 0.030	2.631 ± 0.012	2.614 ± 0.021
	CV		2.020 ± 0.015		
Neocalanus robustior	CVIf	3.585 ± 0.026	3.381 ± 0.018	3.458 ± 0.019	3.485
	CV		2.609 ± 0.014		2.770
	CIV		1.915 ± 0.011		2.052 ± 0.014
	CIII		1.517 ± 0.009	1.563 ± 0.013	1.584 ± 0.022
	CII		1.217 ± 0.007	1.240 ± 0.008	
Paracandacia bispinosa	CVIf	1.524 ± 0.009		1.541 ± 0.015	1.579 ± 0.027

Table III.5. Cephalothorax length (mm ± std error) of selected copepod species from the study area.

Species	Stage	July 1987	Oct. 1987	Feb. 1988	May 1988
Pleuromamma abdominalis	CVIf	2.350 ± 0.033	2.330 ± 0.035	2.349 ± 0.017	2.336 ± 0.035
	CVIm	2.399 ± 0.016	2.362 ± 0.012	2.361 ± 0.028	2.495 ± 0.023
Pleuromamma gracilis	CVIf	1.403 ± 0.008	1.302 ± 0.010	1.382 ± 0.006	1.332 ± 0.008
	CVIm	1.236 ± 0.009	1.163 ± 0.006	1.215 ± 0.006	1.193 ± 0.019
Pleuromamma xiphias	CVIf	3.230 ± 0.029	3.287 ± 0.013	3.192 ± 0.017	3.356 ± 0.021
	CVIm	3.031 ± 0.198			3.410 ± 0.167
	CV	2.422 ± 0.009	2.261 ± 0.017		2.393 ± 0.033
Undeuchaeta plumosa	CVIf	3.148 ± 0.012			

identified to the species level. The remaining species listed in the taxa *Aetideidae*, *Candaciidae*, *Euchaetidae*, and *Cyclopoida* contained low and variable levels of pigment and thus were not suitable for the gut fluorescence technique.

Gut evacuation rates

Spatial and Temporal Variability: The gut evacuation rate (GER) experiments conducted on each cruise took place over a period of several days using animals collected at different times and from different locations along the cruise track (Tables III.6, III.7, III.8 and III.9). To determine whether GERs differed significantly for copepods collected over the temporal and spatial intervals used in these experiments, GERs were compared using the Tukey-Kramer test for unplanned comparisons (Sokal and Rohlf, 1981). In July 1987 GER measurements were repeated for five species (*Acartia danae*, *Nannocalanus minor f. minor*, *Neocalanus gracilis*, *Pleuromamma abdominalis*, and *P. gracilis*) over a period of 7 days, at different times of night, at locations separated by a maximum distance of 225 km (Table III.6). GERs did not differ significantly ($p > 0.05$) between experiments for any of these copepods; coefficients of variation ranged from 5.3 to 27.4%. Repeated measurements of nighttime GERs also were not significantly different for developmental stages of *Calanus tenuicornis* (CVI and CV), or male and female *Pleuromamma gracilis* CVI collected over a six day interval in February 1988 (coefficient of variation range: 6.3 to 14.2%; Table III.8). In May 1988, only one of the nine copepods examined in multiple experiments,

Table III.6. Gut evacuation rates (GER ± SE), initial gut pigment (chl-*a* equiv. wt. ± SE), and ingestion rates (ng pigment ind^{-1} h^{-1}) adjusted for an assumed 33% loss of pigments (see text) for copepods collected July 10-16 1987. Initial gut pigment concentrations are the Y-intercepts from least square fits to the exponential decline model. r^2 is the coefficient of determination for fits to this model. Collection times are given in Pacific Standard Time. (*) - dry weights estimated from a regression of cephalothorax length versus dry weight for species within the study area. All experiments took place at 20°C.

Species	Stage	Dry wt. (μg ind^{-1})	GER (% min^{-1})	Inital Pigment (ng ind^{-1})	r^2	Adjusted Ingestion Rate	Collection Time	Collection Date	Collection Location
Acartia danae	CVIf	3.694	5.37 ± 1.31	0.197 ± 0.026	0.8468	0.95 ± 0.26	01:51	07/15/87	33.009°N 138.937°W
			4.48 ± 0.87	0.162 ± 0.019	0.9248	0.65 ± 0.15	03:07	07/16/87	33.095°N 138.817°W
			4.93 ± 2.13	0.190 ± 0.053	0.6718	0.84 ± 0.43	04:25	07/10/87	34.095°N 136.974°W
Calanus tenuicornis	CVIf	18.968*	1.65 ± 0.19	0.155 ± 0.006	0.9583	0.23 ± 0.03	05:21	07/11/87	33.247°N 138.134°W
	CV	11.983*	2.94 ± 1.50	0.974 ± 0.217	0.4674	2.56 ± 1.43	01:51	07/15/87	33.009°N 138.937°W
Centropages violaceus	CVIf	14.000	2.51 ± 0.97	0.257 ± 0.057	0.7687	0.58 ± 0.26	03:07	07/16/87	33.095°N 138.817°W
Lucicutia flavicornis	CVIf	5.746*	1.91 ± 0.89	0.351 ± 0.087	0.7893	0.60 ± 0.32	03:07	07/16/87	33.095°N 138.817°W
Nannocalanus minor f. minor	CVIf	18.700	1.57 ± 0.58	0.166 ± 0.015	0.7902	0.23 ± 0.09	18:26	07/15/87	34.194°N 137.903°W
			2.70 ± 1.19	0.138 ± 0.021	0.6494	0.33 ± 0.16	04:25	07/10/87	34.095°N 136.974°W
			1.99 ± 0.72	0.136 ± 0.018	0.7377	0.24 ± 0.09	05:21	07/11/87	33.247°N 138.134°W
Neocalanus gracilis	CVIf	118.118	1.43 ± 0.29	1.457 ± 0.117	0.8674	1.87 ± 0.41	01:51	07/15/87	33.009°N 138.937°W
			1.34 ± 0.38	1.299 ± 0.120	0.7198	1.56 ± 0.46	03:07	07/16/87	33.095°N 138.817°W
			1.54 ± 0.31	0.633 ± 0.044	0.8407	0.87 ± 0.19	05:21	07/11/87	33.247°N 138.134°W
Pleuromamma abdominalis	CVIf	120.356	0.83 ± 0.13	0.913 ± 0.050	0.8895	0.68 ± 0.11	01:51	07/15/87	33.009°N 138.937°W
			0.86 ± 0.16	0.960 ± 0.046	0.8515	0.74 ± 0.14	03:07	07/16/87	33.095°N 138.817°W
			0.92 ± 0.06	0.604 ± 0.008	0.9904	0.50 ± 0.03	05:21	07/11/87	33.247°N 138.134°W
	CVIm	80.679*	0.87 ± 0.13	1.117 ± 0.055	0.9281	0.87 ± 0.14	01:51	07/15/87	33.009°N 138.937°W

Table III.6. (Continued)

Species	Stage	Dry wt. (μg ind^{-1})	GER (% min^{-1})	Inital Pigment (ng ind^{-1})	r^2	Adjusted Ingestion Rate	Collection		
							Time	Date	Location
Pleuromamma gracilis	CVIf	22.888	1.95 ± 0.32	0.440 ± 0.028	0.9034	0.77 ± 0.14	01:51	07/15/87	33.009°N 138.937°W
			1.30 ± 0.22	0.246 ± 0.013	0.8977	0.29 ± 0.05	04:25	07/10/87	34.095°N 136.974°W
			1.36 ± 0.25	0.232 ± 0.014	0.8622	0.28 ± 0.06	05:21	07/11/87	33.247°N 138.134°W
	CVIm	16.442	1.21 ± 0.22	0.197 ± 0.012	0.8761	0.21 ± 0.04	01:51	07/15/87	33.009°N 138.937°W
			0.94 ± 0.18	0.131 ± 0.005	0.8606	0.11 ± 0.02	04:25	07/10/87	34.095°N 136.974°W
			0.87 ± 0.18	0.120 ± 0.006	0.8453	0.09 ± 0.02	05:21	07/11/87	33.247°N 138.134°W
Undeuchaeta plumosa	CVIf	280.000	0.50 ± 0.15	0.785 ± 0.051	0.6552	0.35 ± 0.11	01:51	07/15/87	33.009°N 138.937°W

Table III.7. Gut evacuation rates (GER ± SE), initial gut pigment (chl-*a* equiv. wt. ± SE), and ingestion rates (ng pigment ind^{-1} h^{-1}) adjusted for an assumed 33% loss of pigments (see text) for copepods collected October 23-29 1987. Initial gut pigment concentrations are the Y-intercepts from least square fits to the exponential decline model. r^2 is the coefficient of determination for fits to this model. Collection times are given in Pacific Standard Time. (*) - dry weights estimated from a regression of cephalothorax length versus dry weight for species within the study area. All experiments took place at 20°C.

Species	Stage	Dry wt. (μg ind^{-1})	GER (% min^{-1})	Inital Pigment (ng ind^{-1})	r^2	Adjusted Ingestion Rate	Collection		
							Time	Date	Location
Calanus tenuicornis	CVIf	8.000	1.12 ± 0.38	0.275 ± 0.013	0.8122	0.28 ± 0.09	00:18	10/27/87	32.806°N 138.685°W
			1.63 ± 0.20	0.400 ± 0.016	0.9702	0.58 ± 0.07	01:00	10/29/87	32.661°N 138.327°W
			1.75 ± 0.44	0.354 ± 0.026	0.7749	0.56 ± 0.14	01:59	10/25/87	32.866°N 138.823°W
Calocalanus pavo	CVIf	1.550	6.78 ± 4.93	0.025 ± 0.007	0.5900	0.15 ± 0.12	17:58	10/27/87	32.816°N 138.460°W
Eucalanus crassus	CIII	46.692	3.07 ± 0.70	0.826 ± 0.079	0.8156	2.27 ± 0.56	20:48	10/27/87	32.729°N 138.482°W
			2.60 ± 0.54	0.504 ± 0.050	0.8605	1.17 ± 0.27	00:18	10/27/87	32.806°N 138.685°W
			3.18 ± 1.16	0.595 ± 0.096	0.7188	1.69 ± 0.68	00:19	10/26/87	32.961°N 138.935°W
			2.96 ± 1.07	0.824 ± 0.227	0.7957	2.18 ± 0.99	01:00	10/29/87	32.661°N 138.327°W
			3.12 ± 0.34	0.377 ± 0.015	0.9629	1.05 ± 0.12	01:59	10/25/87	32.866°N 138.823°W
			2.38 ± 0.61	0.507 ± 0.054	0.8180	1.08 ± 0.30	06:19	10/23/87	32.130°N 138.972°W
	CII	10.538	5.58 ± 0.73	0.056 ± 0.007	0.9554	0.28 ± 0.05	20:48	10/27/87	32.729°N 138.482°W
			3.51 ± 0.73	0.467 ± 0.047	0.8846	1.47 ± 0.34	00:18	10/27/87	32.806°N 138.685°W
			4.00 ± 0.74	0.519 ± 0.056	0.9204	1.86 ± 0.40	06:19	10/23/87	32.130°N 138.972°W
	CI	4.917	6.62 ± 1.92	0.160 ± 0.022	0.9154	0.95 ± 0.30	15:03	10/27/87	32.943°N 138.788°W
			7.43 ± 1.13	0.160 ± 0.013	0.9426	1.06 ± 0.18	20:48	10/27/87	32.729°N 138.482°W
Eucalanus elongatus	CVIf	229.250	1.09 ± 0.58	2.412 ± 0.330	0.5003	2.35 ± 1.29	00:19	10/26/87	32.961°N 138.935°W
			2.17 ± 0.87	1.115 ± 0.140	0.7953	2.17 ± 0.91	01:00	10/29/87	32.661°N 138.327°W
			1.05 ± 0.50	2.405 ± 0.235	0.5293	2.26 ± 1.10	06:19	10/23/87	32.130°N 138.972°W
	CVIm	87.992	0.49 ± 0.08	0.986 ± 0.031	0.9194	0.43 ± 0.07	00:18	10/27/87	32.806°N 138.685°W
			0.94 ± 0.35	0.970 ± 0.112	0.6281	0.82 ± 0.32	00:19	10/26/87	32.961°N 138.935°W
			1.41 ± 0.13	1.419 ± 0.047	0.9789	1.79 ± 0.08	06:19	10/23/87	32.130°N 138.972°W

Table III.7. (Continued)

Species	Stage	Dry wt. (μg ind^{-1})	GER (% min^{-1})	Inital Pigment (ng ind^{-1})	r^2	Adjusted Ingestion Rate	Collection		
							Time	Date	Location
Eucalanus elongatus	CVf	84.514	1.55 ± 0.41	1.431 ± 0.111	0.8317	1.99 ± 0.55	00:18	10/27/87	32.806°N 138.685°W
			1.96 ± 0.67	1.344 ± 0.198	0.7712	2.36 ± 0.88	00:19	10/26/87	32.961°N 138.935°W
			1.09 ± 0.38	0.975 ± 0.089	0.7583	0.95 ± 0.34	06:19	10/23/87	32.130°N 138.972°W
	CVm	27.847	1.22 ± 0.39	0.518 ± 0.048	0.7089	0.57 ± 0.19	00:19	10/26/87	32.961°N 138.935°W
			1.14 ± 0.36	0.881 ± 0.077	0.8220	0.90 ± 0.30	06:19	10/23/87	32.130°N 138.972°W
	CIVf	19.545	1.53 ± 0.50	0.630 ± 0.075	0.7538	0.86 ± 0.30	00:18	10/27/87	32.806°N 138.685°W
			2.13 ± 0.74	0.951 ± 0.183	0.8042	1.81 ± 0.34	00:19	10/26/87	32.961°N 138.935°W
			1.52 ± 0.32	0.638 ± 0.060	0.9259	0.87 ± 0.20	06:19	10/23/87	32.130°N 138.972°W
	CIVm	11.200	2.41 ± 0.64	0.342 ± 0.036	0.8513	0.74 ± 0.21	00:18	10/27/87	32.806°N 138.685°W
			2.76 ± 0.64	0.610 ± 0.071	0.8938	1.51 ± 0.39	00:19	10/26/87	32.961°N 138.935°W
Lucicutia flavicornis	CVIf	7.328	3.58 ± 0.92	0.057 ± 0.004	0.8846	0.18 ± 0.05	17:58	10/27/87	32.816°N 138.460°W
Mecynocera clausii	CVIf	0.581	5.80 ± 4.07	0.047 ± 0.027	0.5782	0.24 ± 0.22	17:58	10/27/87	32.816°N 138.460°W
Nannocalanus minor f. major	CVIf	52.250	2.57 ± 0.78	0.228 ± 0.035	0.8871	0.53 ± 0.18	15:03	10/27/87	32.943°N 138.788°W
	CV	21.286	3.31 ± 1.96	0.044 ± 0.021	0.4311	0.13 ± 0.10	15:03	10/27/87	32.943°N 138.788°W
Neocalanus gracilis	CVIf	96.750	2.04 ± 0.60	1.616 ± 0.270	0.9352	2.95 ± 1.00	00:18	10/27/87	32.806°N 138.685°W
			1.23 ± 0.18	0.859 ± 0.032	0.9829	1.58 ± 0.14	01:59	10/25/87	32.866°N 138.823°W
			2.86 ± 0.77	1.880 ± 0.195	0.8479	4.81 ± 1.39	06:19	10/23/87	32.130°N 138.972°W
	CV	47.977*	2.38 ± 0.54	1.073 ± 0.097	0.8809	2.29 ± 0.56	06:19	10/23/87	32.130°N 138.972°W
Neocalanus robustior	CV	103.971*	3.05 ± 0.62	0.674 ± 0.103	0.9278	1.84 ± 0.47	00:18	10/27/87	32.806°N 138.685°W
			2.20 ± 0.48	0.491 ± 0.049	0.9396	0.97 ± 0.23	01:00	10/29/87	32.661°N 138.327°W

Table III.7. (Continued)

Species	Stage	Dry wt. (μg ind^{-1})	GER (% min^{-1})	Inital Pigment (ng ind^{-1})	r^2	Adjusted Ingestion Rate	Collection		
							Time	Date	Location
Pleuromamma abdominalis	CVIf	112.244	1.55 ± 0.47	0.957 ± 0.074	0.8420	1.33 ± 0.42	00:18	10/27/87	32.806°N 138.685°W
			2.45 ± 0.31	1.402 ± 0.091	0.9564	3.08 ± 0.44	00:19	10/26/87	32.961°N 138.935°W
			1.92 ± 0.58	1.606 ± 0.168	0.7824	2.76 ± 0.88	01:00	10/29/87	32.661°N 138.327°W
			2.34 ± 0.52	2.612 ± 0.243	0.8422	5.47 ± 1.32	06:19	10/23/87	32.130°N 138.972°W
	CVIm	121.167	1.79 ± 0.99	1.375 ± 0.291	0.4893	2.20 ± 1.31	00:18	10/27/87	32.806°N 138.685°W
			2.11 ± 0.36	1.973 ± 0.135	0.9076	3.73 ± 0.71	01:00	10/29/87	32.661°N 138.327°W
			1.21 ± 0.29	1.774 ± 0.161	0.8686	1.92 ± 0.49	06:19	10/23/87	32.130°N 138.972°W
Pleuromamma gracilis	CVIf	14.592	2.97 ± 0.31	0.344 ± 0.015	0.9729	0.91 ± 0.10	00:18	10/27/87	32.806°N 138.685°W
			2.60 ± 0.43	0.492 ± 0.040	0.9371	1.15 ± 0.21	01:00	10/29/87	32.661°N 138.327°W
			1.93 ± 0.56	0.627 ± 0.064	0.7514	1.08 ± 0.33	01:59	10/25/87	32.866°N 138.823°W
			2.30 ± 0.68	0.742 ± 0.096	0.8074	1.53 ± 0.49	06:19	10/23/87	32.130°N 138.972°W
	CVIm	10.873	2.26 ± 0.37	0.293 ± 0.025	0.9384	0.59 ± 0.11	20:48	10/27/87	32.729°N 138.482°W
			2.47 ± 0.31	0.329 ± 0.015	0.9644	0.73 ± 0.10	01:00	10/29/87	32.661°N 138.327°W
			2.29 ± 0.23	0.363 ± 0.016	0.9723	0.74 ± 0.08	01:59	10/25/87	32.866°N 138.823°W
Pleuromamma xiphias	CVIf	197.586	1.72 ± 0.26	4.061 ± 0.220	0.9514	6.26 ± 1.00	00:18	10/27/87	32.806°N 138.685°W
			1.38 ± 0.46	4.663 ± 0.508	0.6828	5.76 ± 2.02	00:19	10/26/87	32.961°N 138.935°W
			0.84 ± 0.16	5.078 ± 0.261	0.9020	3.82 ± 0.75	01:00	10/29/87	32.661°N 138.327°W
			1.06 ± 0.58	9.798 ± 1.419	0.6455	9.30 ± 5.26	06:19	10/23/87	32.130°N 138.972°W
	CV	45.625	3.17 ± 0.43	1.853 ± 0.099	0.9593	5.26 ± 0.77	00:19	10/26/87	32.961°N 138.935°W
			1.13 ± 0.19	1.488 ± 0.071	0.9357	1.51 ± 0.26	01:00	10/29/87	32.661°N 138.327°W

Table III.8. Gut evacuation rates (GER ± SE), initial gut pigment (chl-*a* equiv. wt. ± SE), and ingestion rates (ng pigment ind^{-1} h^{-1}) adjusted for an assumed 33% loss of pigments (see text) for copepods collected February 2-7 1988. Initial gut pigment concentrations are the Y-intercepts from least square fits to the exponential decline model. r^2 is the coefficient of determination for fits to this model. Collection times are given in Pacific Standard Time. (*) - dry weights estimated from a regression of cephalothorax length versus dry weight for species within the study area. All experiments took place at 17°C.

Species	Stage	Dry wt. (μg ind^{-1})	GER (% min^{-1})	Inital Pigment (ng ind^{-1})	r^2	Adjusted Ingestion Rate	Collection		
							Time	Date	Location
Acartia danae	CVIf	4.922*	4.92 ± 1.27	0.093 ± 0.013	0.9554	0.41 ± 0.35	19:14	02/05/88	33.196°N 139.206°W
Calanus tenuicornis	CVIf	9.410	0.95 ± 0.25	0.565 ± 0.041	0.7259	0.48 ± 0.13	00:10	02/03/88	33.036°N 138.980°W
			1.17 ± 0.64	0.246 ± 0.026	0.7866	0.26 ± 0.14	00:48	02/07/88	32.951°N 138.876°W
			1.05 ± 0.19	0.497 ± 0.025	0.8976	0.47 ± 0.09	01:06	02/04/88	33.060°N 138.984°W
			1.01 ± 0.18	0.520 ± 0.029	0.8962	0.47 ± 0.09	02:30	02/02/88	33.054°N 138.919°W
	CV	6.500	2.13 ± 0.23	0.494 ± 0.022	0.9735	0.94 ± 0.11	00:10	02/03/88	33.036°N 138.980°W
			2.33 ± 0.72	0.387 ± 0.049	0.7026	0.81 ± 0.27	02:30	02/02/88	33.054°N 138.919°W
Lucicutia flavicornis	CVIf	7.042	1.80 ± 0.58	0.631 ± 0.056	0.8294	1.02 ± 0.25	02:30	02/02/88	33.054°N 138.919°W
Neocalanus gracilis	CVIf	89.200	0.84 ± 0.10	0.868 ± 0.033	0.9762	0.65 ± 0.08	00:48	02/07/88	32.951°N 138.876°W
Pleuromamma abdominalis	CVIf	82.600	1.07 ± 0.12	1.288 ± 0.047	0.9549	1.23 ± 0.15	00:48	02/07/88	32.951°N 138.876°W
Pleuromamma gracilis	CVIf	18.605	1.02 ± 0.11	0.741 ± 0.022	0.9415	0.68 ± 0.08	00:10	02/03/88	33.036°N 138.980°W
			1.28 ± 0.35	0.347 ± 0.031	0.7181	0.40 ± 0.11	00:48	02/07/88	32.951°N 138.876°W
			1.00 ± 0.04	0.691 ± 0.008	0.9938	0.62 ± 0.03	02:30	02/02/88	33.054°N 138.919°W
	CVIm	14.311	1.66 ± 0.13	0.500 ± 0.016	0.9794	0.74 ± 0.06	01:06	02/04/88	33.060°N 138.984°W
			1.51 ± 0.20	0.379 ± 0.018	0.9256	0.51 ± 0.07	02:30	02/02/88	33.054°N 138.919°W

Table III.9. Gut evacuation rates (GER ± SE), initial gut pigment (chl-*a* equiv. wt. ± SE), and ingestion rates (ng pigment ind^{-1} h^{-1}) adjusted far an assumed 33% loss of pigments (see text) for copepods collected May 9-13 1988. Initial gut pigment concentrations are the Y-intercepts from least square fits to the exponential decline model. r^2 is the coefficient of determination for fits to this model. Collection times are given in Pacific Standard Time. (*) - dry weights estimated from a regression of cephalothorax length versus dry weight for species within the study area. All experiments took place at 18°C.

Species	Stage	Dry wt. (μg ind^{-1})	GER (% min^{-1})	Inital Pigment (ng ind^{-1})	r^2	Adjusted Ingestion Rate	Collection		
							Time	Date	Location
Acartia danae	CVIf	3.533	4.03 ± 0.34	0.072 ± 0.003	0.9784	0.26 ± 0.02	00:07	05/13/88	32.811°N 138.077°W
			4.37 ± 0.75	0.059 ± 0.005	0.9621	0.23 ± 0.04	00:20	05/10/88	32.796°N 138.914°W
Calanus tenuicornis	CVIf	10.700	1.79 ± 0.40	0.279 ± 0.019	0.8990	0.45 ± 0.10	00:00	05/09/88	32.868°N 138.990°W
			0.99 ± 0.15	0.382 ± 0.017	0.9087	0.34 ± 0.05	00:05	05/11/88	32.764°N 138.705°W
			0.94 ± 0.29	0.336 ± 0.026	0.7970	0.28 ± 0.09	00:20	05/10/88	32.796°N 138.914°W
			1.52 ± 0.27	0.291 ± 0.020	0.8904	0.40 ± 0.08	02:30	05/09/88	32.868°N 138.990°W
Mecynocera clausii	CVIf	0.731	3.76 ± 0.62	0.039 ± 0.002	0.9770	0.13 ± 0.02	02:30	05/09/88	32.868°N 138.990°W
Nannocalanus minor f. minor	CVIf	21.778	0.96 ± 0.51	0.183 ± 0.024	0.4392	0.16 ± 0.09	00:07	05/13/88	32.811°N 138.077°W
			1.36 ± 0.27	0.201 ± 0.013	0.8494	0.24 ± 0.05	00:20	05/10/88	32.796°N 138.914°W
Neocalanus gracilis	CVIf	111.400	1.70 ± 0.47	0.988 ± 0.102	0.8714	1.50 ± 0.44	02:15	05/13/88	32.827°N 138.015°W
			1.54 ± 0.37	1.636 ± 0.144	0.8309	2.26 ± 0.58	03:00	05/10/88	32.805°N 138.958°W
Neocalanus robustior	CIV	50.311*	2.43 ± 0.61	0.419 ± 0.042	0.8544	0.91 ± 0.37	03:00	05/10/88	32.805°N 138.958°W
	CIII	23.007*	2.78 ± 1.64	0.260 ± 0.055	0.8212	0.65 ± 0.41	03:00	05/10/88	32.805°N 138.958°W
Paracandacia bispinosa	CVIf	39.950	2.18 ± 0.74	0.148 ± 0.020	0.6467	0.29 ± 0.11	00:05	05/11/88	32.764°N 138.705°W
Pleuromamma abdominalis	CVIf	80.399	1.49 ± 0.58	1.474 ± 0.195	0.5743	1.97 ± 0.81	00:00	05/09/88	32.868°N 138.990°W
			0.74 ± 0.10	1.484 ± 0.055	0.9273	0.98 ± 0.14	02:15	05/13/88	32.827°N 138.015°W
			1.36 ± 0.52	1.174 ± 0.145	0.7487	1.43 ± 0.57	03:00	05/10/88	32.805°N 138.958°W

Table III.9. (Continued)

Species	Stage	Dry wt. (μg ind^{-1})	GER (% min^{-1})	Inital Pigment (ng ind^{-1})	r^2	Adjusted Ingestion Rate	Collection		
							Time	Date	Location
Pleuromamma gracilis	CVIf	17.280	1.64 ± 0.53	0.690 ± 0.072	0.7872	1.01 ± 0.34	00:00	05/09/88	32.868°N 138.990°W
			1.30 ± 0.05	0.651 ± 0.007	0.9958	0.76 ± 0.03	00:07	05/13/88	32.811°N 138.077°W
			1.69 ± 0.16	0.630 ± 0.022	0.9649	0.95 ± 0.10	00:20	05/10/88	32.796°N 138.914°W
			1.45 ± 0.22	0.400 ± 0.019	0.9268	0.52 ± 0.08	02:15	05/13/88	32.827°N 138.015°W
			1.84 ± 0.20	0.395 ± 0.017	0.9600	0.65 ± 0.08	02:30	05/09/88	32.868°N 138.990°W
			1.55 ± 0.33	0.666 ± 0.052	0.9010	0.92 ± 0.21	03:00	05/10/88	32.805°N 138.958°W
	CVIm	12.487	1.54 ± 0.30	0.325 ± 0.021	0.8664	0.45 ± 0.09	00:07	05/13/88	32.811°N 138.077°W
			1.69 ± 0.24	0.368 ± 0.019	0.9168	0.56 ± 0.08	00:20	05/10/88	32.796°N 138.914°W
			1.45 ± 0.39	0.246 ± 0.023	0.8300	0.32 ± 0.09	02:30	05/09/88	32.868°N 138.990°W
			2.34 ± 0.58	0.438 ± 0.029	0.8428	0.92 ± 0.24	03:00	05/10/88	32.805°N 138.958°W
Pleuromamma xiphias	CVIf	165.272	0.57 ± 0.18	2.721 ± 0.152	0.8374	1.39 ± 0.44	02:15	05/13/88	32.827°N 138.015°W
			1.45 ± 0.26	3.550 ± 0.093	0.9440	4.61 ± 0.84	03:00	05/10/88	32.805°N 138.958°W
	CV	60.250	1.44 ± 0.33	1.195 ± 0.101	0.8198	1.54 ± 0.38	00:00	05/09/88	32.868°N 138.990°W

Pleuromamma xiphias CVI, had GERs which differed significantly for experiments. Measured rates differed by a factor of 2.5 for *P. xiphias* CVI collected near the same time of night (3 days apart) from stations separated by 88 km (Table III.9). Evacuation rates of 3 other species collected from the same two stations, *Pleuromamma abdominalis*, *P. gracilis* and *Neocalanus gracilis*, were not significantly different, although both *Pleuromamma* species showed the same trend of lower rates at the May 10th collection location. Similar results were obtained in October 1987. GERs measured at different times and locations were not significantly different ($p > 0.05$) for all species and developmental stages, except *P. xiphias* CV and male *Eucalanus elongatus* CVI (Table III.7). Rates measured for these two species varied by a factor of 3 between experiments. While it is not possible to separate temporal and spatial components of variation in these data, GERs did change for *E. elongatus* collected at different times of night, with the highest values measured near dawn and lowest near midnight. Experiments with *E. elongatus* collected at the same time of night (October 26 and 27 experiments) at stations 29 km apart were indistinguishable. Unlike *E. elongatus*, GERs of *P. xiphias* CV collected at approximately the same time of night were significantly different. The two experiments conducted with this copepod occurred 3 days apart at stations separated by 99 km.

Variation With Body Size: Except for the three cases mentioned above, intraspecific GERs were not statistically different for groups of animals collected at different times and/or locations on a given cruise. Yet evacuation rates did vary

between species by over an order of magnitude and were inversely correlated with body size. The lowest evacuation rate, O.50 % min-1, was measured for the 3.8 mm copepod *Undeuchaeta plumosa* CVI, while the highest GER, 7.43 % min^{-1}, was measured for *Eucalanus crassus* CI which had a total length of 1.4 mm.

Evacuation rates from each cruise were plotted against body size and tested for goodness-of-fit to linear, logarithmic, exponential, and power models. The data were best fit by the power function $G = aX^b$, where G is GER (% min^{-1}), a and b are coefficients, and X is one of the three indices of body size measured: total length, cephalothorax length, or dry weight. Figures III.2 and III.3 show the fits to this model [Log(G) = bLog(X) + Log(a)] obtained for total length and dry weight. Model I linear regressions of GERs versus all indices of body size were significant ($p < 0.05$) for all cruises. Using total length as the independent variable explained a greater proportion of the variation in GERs (54 - 73%) than did either cephalothorax length or dry weight (Table III.10). Least-squares estimates for the coefficient b, obtained by fitting data from each cruise to the log-transformed power function, were statistically the same (analysis of covariance, $p > 0.05$), regardless of which index of body size was used as the independent variable. Values of b for the pooled data from all cruises were -0.85, -0.69, or -0.27 using total length, cephalothorax length, and dry weight as the independent variable, respectively. All regressions of GER versus body size were highly significant ($p < 0.001$) for the pooled data.

Figure III.2. Gut evacuation rates (GER) versus copepod total length (L) for the four cruises. The lines shown are least squares fits to Log (GER) = Log a + b Log(L). The data shown are means for copepod species and developmental stages where rates were measured in more than one experiment. Error bars are standard errors.

Figure III.2

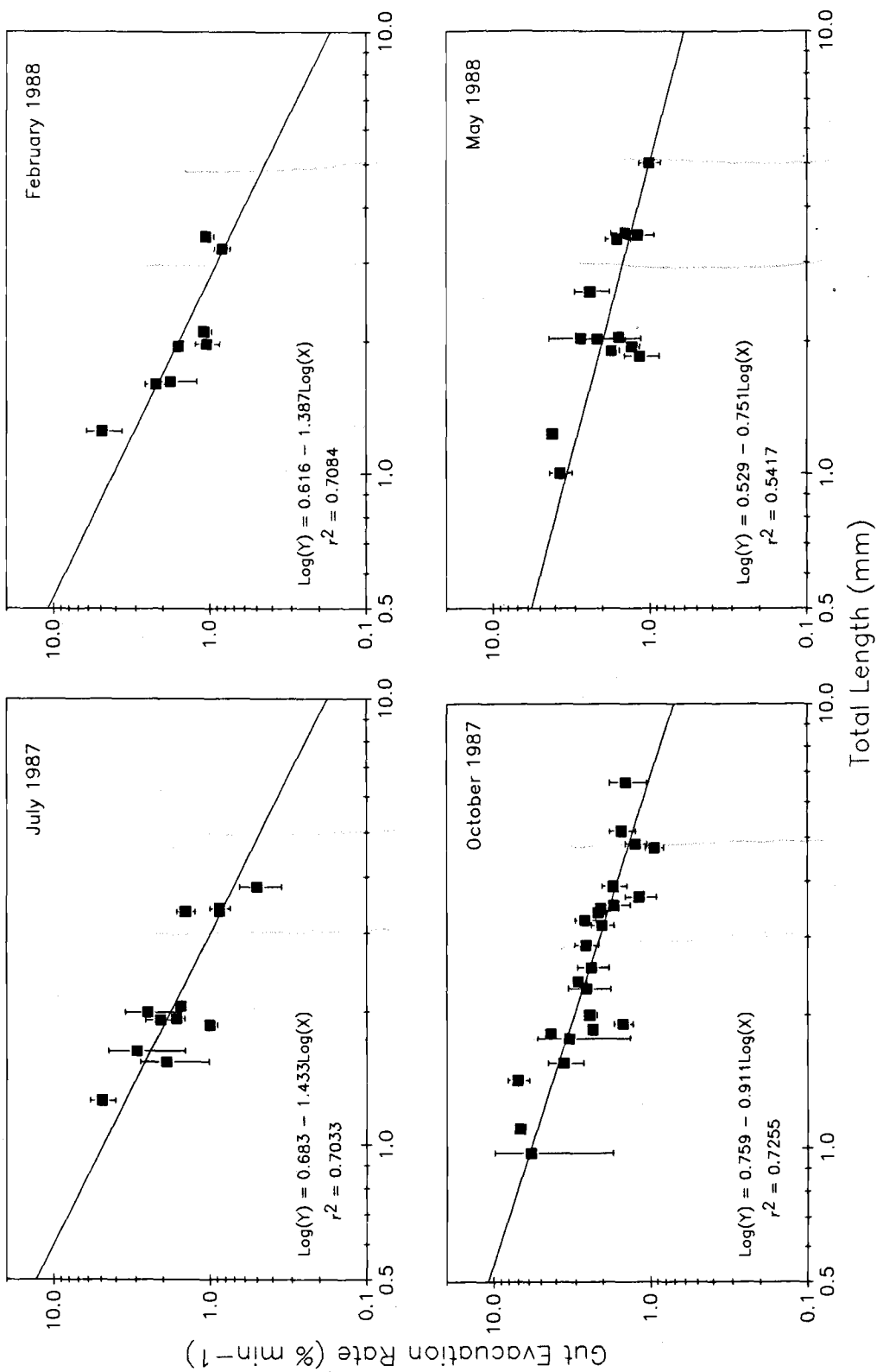

February 1988
Log(Y) = 0.616 – 1.387Log(X)
r2 = 0.7084
May 1988
Log(Y) = 0.529 – 0.751Log(X)
r2 = 0.5417
July 1987
Log(Y) = 0.683 – 1.433Log(X)
r2 = 0.7033
October 1987
Log(Y) = 0.759 – 0.911Log(X)
r2 = 0.7255
Gut Evacuation Rate (% min–1)
Total Length (mm)
10.0
1.0
0.1
0.5

Figure III.3. Gut evacuation rates (GER) versus copepod dry weight (W). The lines shown are least squares fits to Log(GER) = b Log(W) + Log(a). The data shown are means for copepod species and developmental stages where rates were measured in more than one experiment. Error bars are standard errors.

Figure III.3

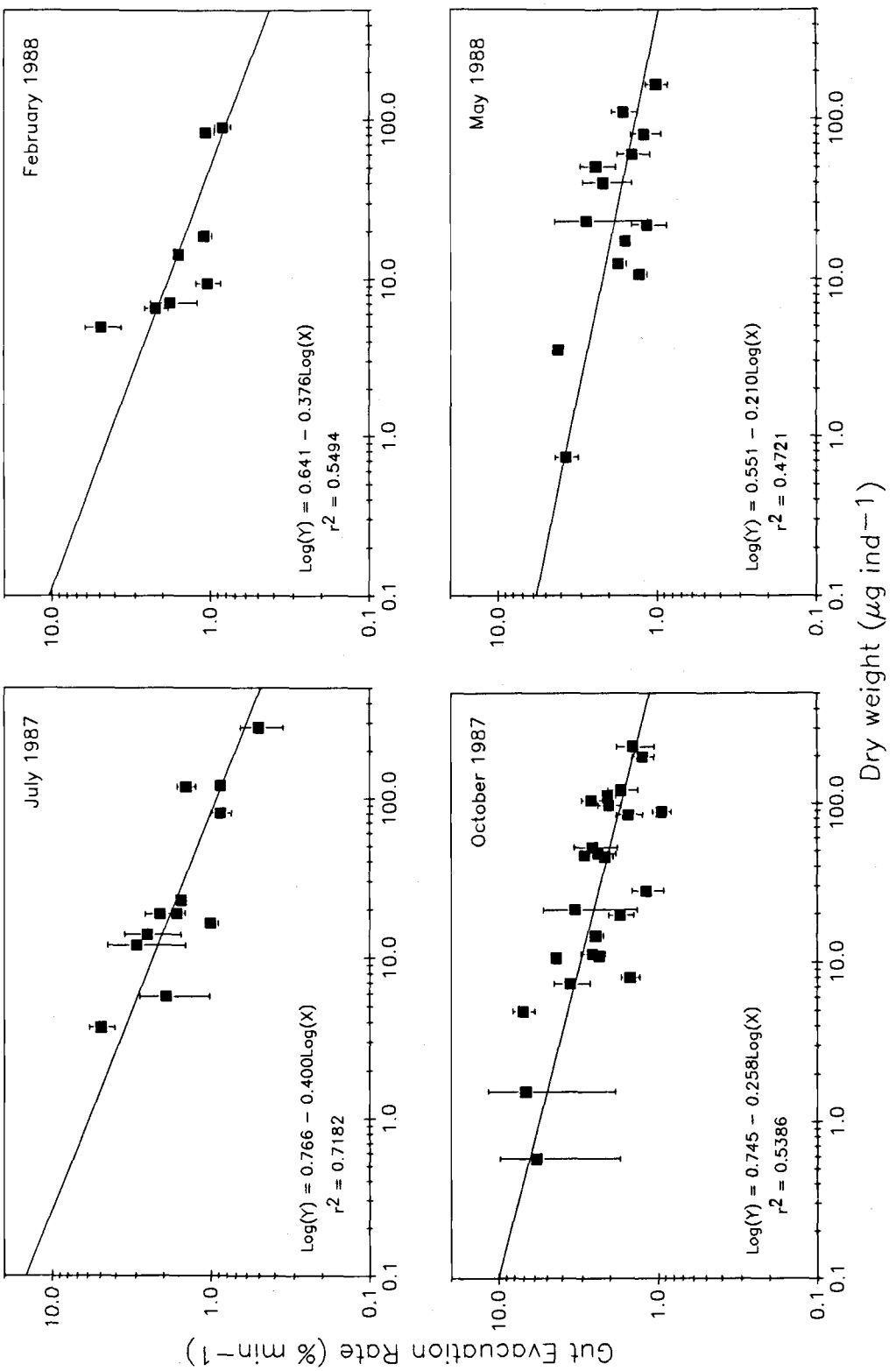

February 1988
Log(Y) = 0.641 – 0.376Log(X)
r2 = 0.5494
May 1988
Log(Y) = 0.551 – 0.210Log(X)
r2 = 0.4721
July 1987
Log(Y) = 0.766 – 0.400Log(X)
r2 = 0.7182
October 1987
Log(Y) = 0.745 – 0.258Log(X)
r2 = 0.5386
Gut Evacuation Rate (% min−1)
Dry weight (μg ind−1)
0.1
1.0
10.0
100.0

Table III.10. Summary of regression statistics for analysis of relationship between gut evacuation rate (G, % min-1) and body size (W), where W is either: (A) total length (mm), (B) cephalothorax length (mm), or (C) dry weight (μg). The linear model of the allometric equation, log(G) = log(a) + b log(W), and model I regression methods were used for finding a, b, and r2, the coefficient of determination. n is the sample size. The linear model of the allometric equation, log(G) = log(u) + v log(W), and model II geometric mean regression methods (Ricker, 1973) were used for finding u and v. The 95% confidence intervals (C.I.) for v were calculated according to Ricker (1975).

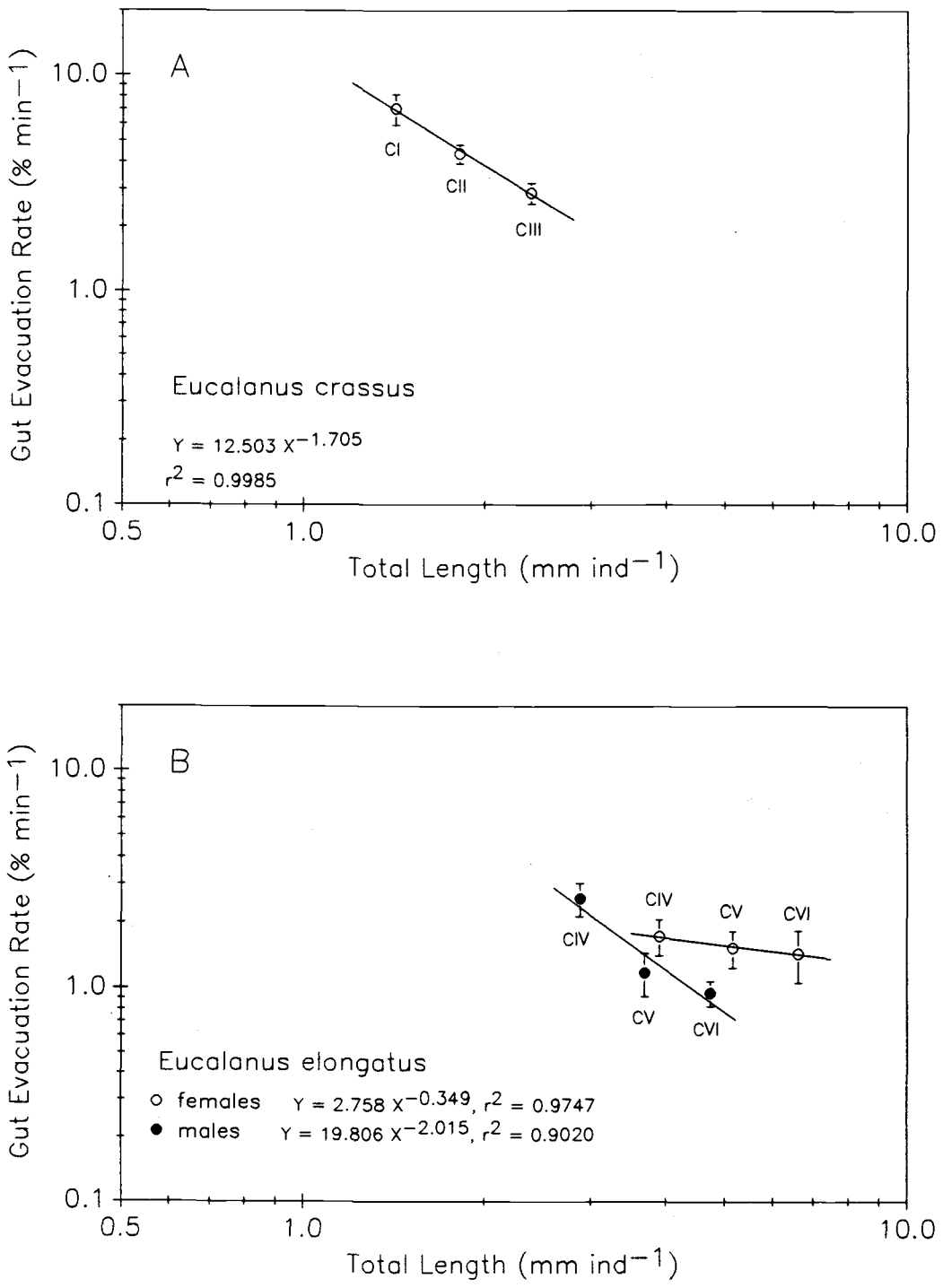
Cruise Date	Temperature (°C)	Model I Regression			Model II Regression			n
		a	b	r^2	u	v	95% C.I. for v	
A. TOTAL LENGTH								
Feb 1988	17	4.13	-1.39	0.7084	4.98	-1.65	-2.77 , -0.98	8
May 1988	18	3.38	-0.75	0.5417	4.20	-1.02	-1.58 , -0.66	13
July 1987	20	4.82	-1.43	0.7033	5.99	-1.71	-2.49 , -1.18	12
Oct 1987	20	5.74	-0.91	0.7255	6.69	-1.07	-1.35 , -0.85	24
Pooled		3.99	-0.85	0.4414	5.75	-1.27	-1.55 , -1.04	57
B. CEPHALOTHORAX LENGTH								
Feb 1988	17	2.34	-1.16	0.5892	2.65	-1.51	-2.76 , -0.83	8
May 1988	18	2.69	-0.76	0.4749	3.19	-1.10	-1.75 , -0.69	13
July 1987	20	2.82	-1.21	0.5691	3.43	-1.60	-2.51 , -1.03	12
Oct 1987	20	4.20	-0.79	0.6179	4.92	-1.01	-1.32 , -0.77	24
Pooled		2.87	-0.69	0.3317	3.84	-1.20	-1.50 , -0.97	57
C. DRY WEIGHT								
Feb 1988	17	4.37	-0.38	0.5494	6.34	-0.51	-0.96 , -0.27	8
May 1988	18	3.55	-0.21	0.4721	4.87	-0.31	-0.49 , -0.19	13
July 1987	20	5.83	-0.40	0.7182	7.33	-0.47	-0.68 , -0.33	12
Oct 1987	20	5.56	-0.26	0.5386	7.52	-0.35	-0.48 , -0.26	24
Pooled		4.53	-0.27	0.4438	6.95	-0.40	-0.49 , -0.33	57

GERs were measured for several developmental stages of *Eucalanus crassus* and *E. elongatus*, permitting analysis of the intraspecific relationship between GERs and body size for these species. As was the case for the pooled data described above, total length was the best predictor of gut evacuation rate. Least-squares fit of average GERs of *E. crassus* (copepodite stages CI, CII, and CIII) to the power function using total length as the independent variable described 99.85% of the observed variation in evacuation rates (Fig. III.4A). The exponent (b) (-1.705 $\pm$ 0.138) was higher than that calculated for the pooled data. *E. elongatus* GERs also decreased with increasing total length in more advanced developmental stages (CIV, CV, and CVI); however, differences were observed between males and females in these developmental stages (Figure III.4B). Males showed a greater change in evacuation rate per increment of body size (b = -2.015) than did females (b = -0.348). Male copepodite stages CV and CVI also had lower GERs than those expected for females of the same size.

Statistical analysis of the relationship between GERs and body size presented thus far has utilized Model I regression techniques, which assume that the independent variable is under the control of the investigator and is measured without error. Several investigators have stressed the need to utilize model II regression techniques when analyzing morphometric data as this technique does not require that the independent variable be controlled and error-free (Ricker, 1973; 1975; Huntley and Boyd, 1984). Laws and Archie (1981) have published examples of studies in which incorrect conclusions were reached when model I

Figure III.4. Least squares fits of mean gut evacuation rates (GER) and total length (L) to the power function $GER = aL^b$. Error bars are standard errors. A. *Eucalanus crassus* copepodite stages CI, CII, and CIII. B. *Eucalanus elongatus* male and female copepodite stages CIV, CV, and CVI.

Figure III.4


A
10.0
1.0
0.1
0.5
1.0
10.0
Gut Evacuation Rate (% min^{-1})
Total Length (mm ind^{-1})
CI
CII
CIII
Eucalanus crassus
Y = 12.503 X$^{-1.705}$
r^2 = 0.9985
B
CIV
CV
CVI
Eucalanus elongatus
females Y = 2.758 X$^{-0.349}$, r^2 = 0.9747
males Y = 19.806 X$^{-2.015}$, r^2 = 0.9020

regressions were performed on morphometric data. To avoid this problem, data were also analyzed using model II geometric mean regression techniques (Table III.10). The conclusions reached are identical to those stated earlier; i.e., there were no significant differences between slopes for the different cruises. The pooled slopes (v) for the functional relationship between GER and body size increase using geometric mean regression; the values obtained were -1.27 for total length, -1.20 for cephalothorax length, and -0.40 for dry weight.

While the slopes (b or v) of log-log plots of GERs versus copepod body size were the same for all cruises, GERs did vary between cruises. Adjusted mean GERs (adjusted for a common body size) differed significantly between the four cruises (ANCOVA: Table III.11). The regression intercepts shown in Table III.10 indicate that GERs were highest in October, and that rates decreased for other cruises in the order: July, February, and May, respectively.

Temperature Dependence: Differences in the temperature (17 to 20°C) at which GERs were measured on these cruises provides one potential explanation for variation between cruises. Figure III.5 shows the GER predicted for a 2.35 mm copepod (the average total length for all data) for each cruise plotted against experimental temperature. Predicted GERs were calculated using the geometric regression coefficients obtained for each cruise (Table III.10). By comparing GERs predicted for the same total length, this evaluation of temperature attempts to minimize the confounding effects of body size. Interpretation of the data presented in Figure III.5 is ambiguous given the disparity between rates calculated

Table III.11. Analysis of covariance tables for comparison of gut evacuation rates (GERs) measured on the four cruises. GERs were fit to the model Log(GER) = Log(a) + bLog(W) where the independent variable W was either: A. total length, B. cephalothorax length, or C. dry weight. df is degrees of freedom; SS is sum of squares; MS is mean square error; F is the F-statistic; ** indicates $p < 0.01$.

A. Total length

Source of variation	df	SS	MS	F
Cruise GERs	3	0.8247	0.2749	14.576 **
Error	54	1.0184	0.0189	

B. Cephalothorax length

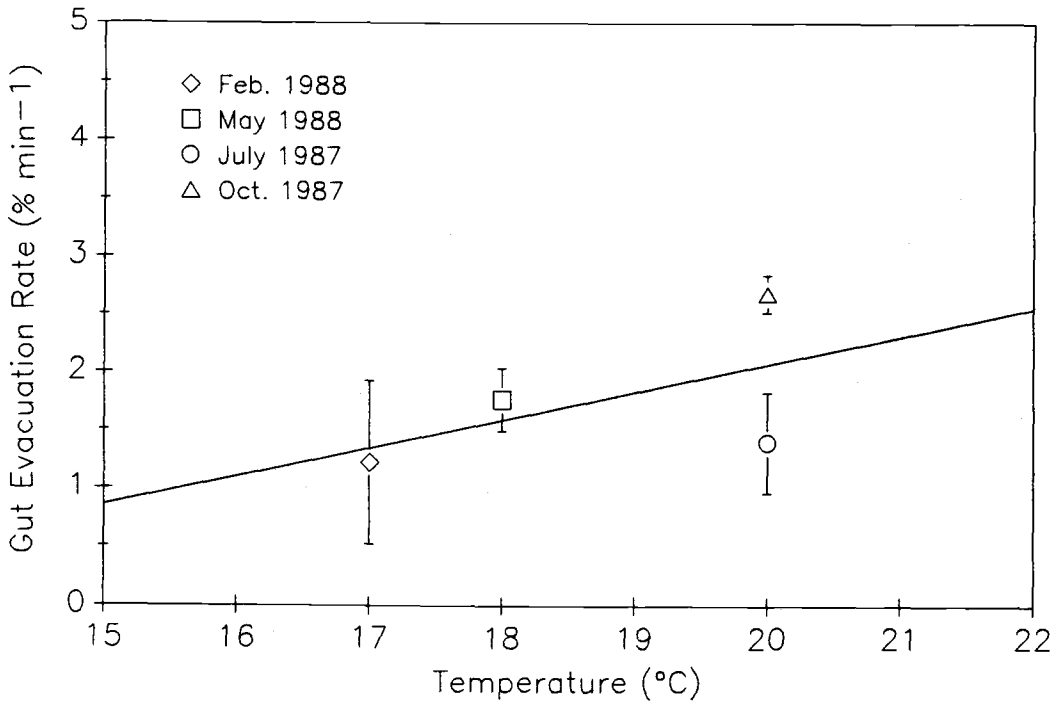
Source of variation	df	SS	MS	F
Cruise GERs	3	0.9123	0.3041	12.707 **
Error	54	1.2923	0.0239	

C. Dry weight

Source of variation	df	SS	MS	F
Cruise GERs	3	0.5147	0.1716	7.019 **
Error	54	1.3198	0.0244	

Figure III.5. Mean gut evacuation rates (GER) normalized to a copepod total length of 2.35 mm (the overall mean copepod length for all species and cruises) for each cruise versus experimental temperature. Error bars are standard errors. The line shown is a least-squares fit to the data: $Y = 0.24(X)-2.77$, $r^2 = 0.3097$.

Figure III.5


Gut Evacuation Rate (% min−1)
Temperature (°C)
◇ Feb. 1988
□ May 1988
○ July 1987
△ Oct. 1987
0
1
2
3
4
5
15
16
17
18
19
20
21
22

for the two 20 °C cruises. There were no differences between estimated GERs for the February, May and July cruises; yet if the July data are excluded, the data show a strong temperature effect. If the average of the predicted GERs for the July and October cruises is used as an estimate of the 20 °C GER, the Q_{10} calculated between 17 and 20°C is 4.61 [i.e., $(1.93/1.22)^{(10/(20-17)}$].

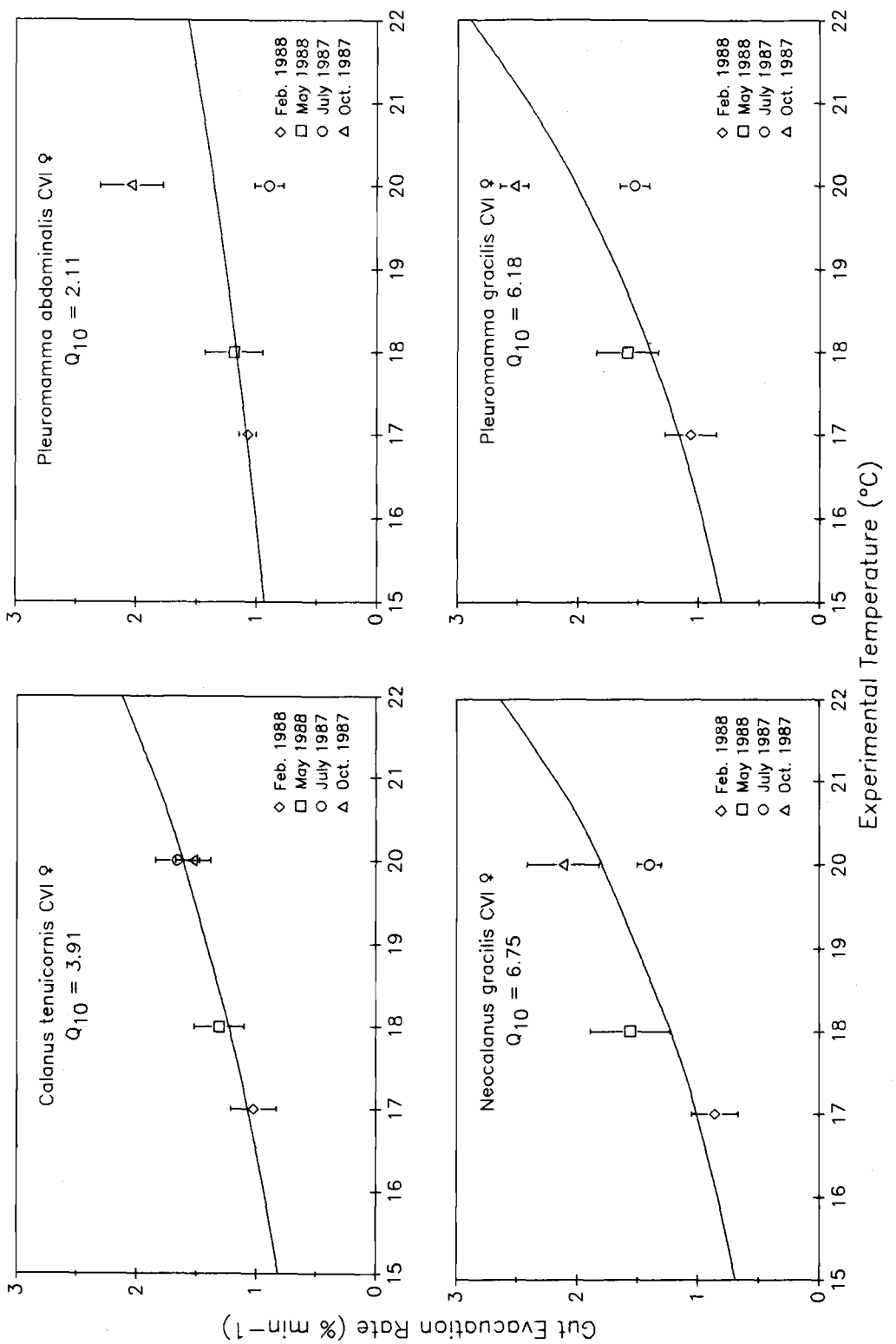
Similar patterns were observed for individual species. Figure III.6 shows mean GERs of four species, ranging in size from 1.9 to 3.4 mm total length, plotted against temperature. An attempt was made to separate the effects of temperature from those of body size on GERs by normalizing each species GER to its average seasonal total length. Adjusted GERs were calculated using the equation below:

$$G_{adj} = G_m \left[\frac{L}{L_{ave}} \right]^{\nu} \qquad (3\text{-}6)$$

where G_{adj} is the adjusted GER (% min^{-1}), G_m is the rate actually measured, L is each species total length (mm) measured for each cruise, L_{ave} is the average seasonal total length, and ν is the geometric regression slope (-1.27) for the pooled data (Table III.10). The adjustments for body size only resulted in slight changes in GERs as (L/L_{ave}) only ranged between 0.964 to 1.037. Evacuation rates of *Calanus tenuicornis*, *Neocalanus gracilis*, *Pleuromamma abdominalis*, and *P. gracilis* tended to increase with temperature (Fig. III.6); however, with the exception of *Calanus tenuicornis*, the rates measured in July at 20 °C were

Figure III.6. Gut evacuation rates of *Calanus tenuicornis*, *Neocalanus plumchrus*, *Pleuromamma abdominalis*, and *P. gracilis* versus temperature. GERs were adjusted to each species mean total length (see text). The curves shown are least squares fits of adjusted GERs versus temperature (T) to the exponential model $GER = a(e^{cT})$. Error bars are standard errors.

Figure III.6


Pleuromamma abdominalis CVI ♀
Q_{10} = 2.11
Pleuromamma gracilis CVI ♀
Q_{10} = 6.18
Calanus tenuicornis CVI ♀
Q_{10} = 3.91
Neocalanus gracilis CVI ♀
Q_{10} = 6.75
◇ Feb. 1988
□ May 1988
○ July 1987
△ Oct. 1987
Gut Evacuation Rate (% min⁻¹)
Experimental Temperature (°C)

substantially lower than those measured in October at the same temperature. Q_{10} values calculated between 17 and 20 °C, using values obtained by fitting the adjusted GERs to the exponential model, GER = $a(e^{cT})$, ranged from 2.11 for *Pleuromamma abdominalis* to 6.75 for *P. gracilis*.

Variation with gut fullness: The differences between July and October GERs indicate that parameters in addition to body size and temperature must play some role in controlling rates of food passage through the gut. Possible choices include: gut fullness, food concentration, food quality, the size and digestibility of particles consumed, digestive enzyme activity, endogenous rhythms of grazing activity, and frequency of feeding episodes. Data collected in this study allow some examination of the first alternative: the level of food in the gut. A plot of GER versus initial gut pigment concentration for several copepod species shows that GERs remain unchanged at different concentrations of gut pigment (Fig. III.7). If the majority of material in the gut of these copepods consists of material associated with pigment, then these data imply that GERs are independent of the amount of food in the gut. However, if these copepods were feeding omnivorously, differences in gut pigment might be unrelated to the volume of material in the gut. Constancy of GERs at different pigment levels might indicate volume of food in the gut was constant for these experiments and the proportion of plant matter ingested varied. This issue cannot be resolved in the absence of some measure of the total gut contents.

Figure III.7. Gut evacuation rates versus initial gut pigment for several species of copepod. Error bars are standard errors. July 1987 (○), October 1987 (△), February 1988 (◇), May 1988 (□).

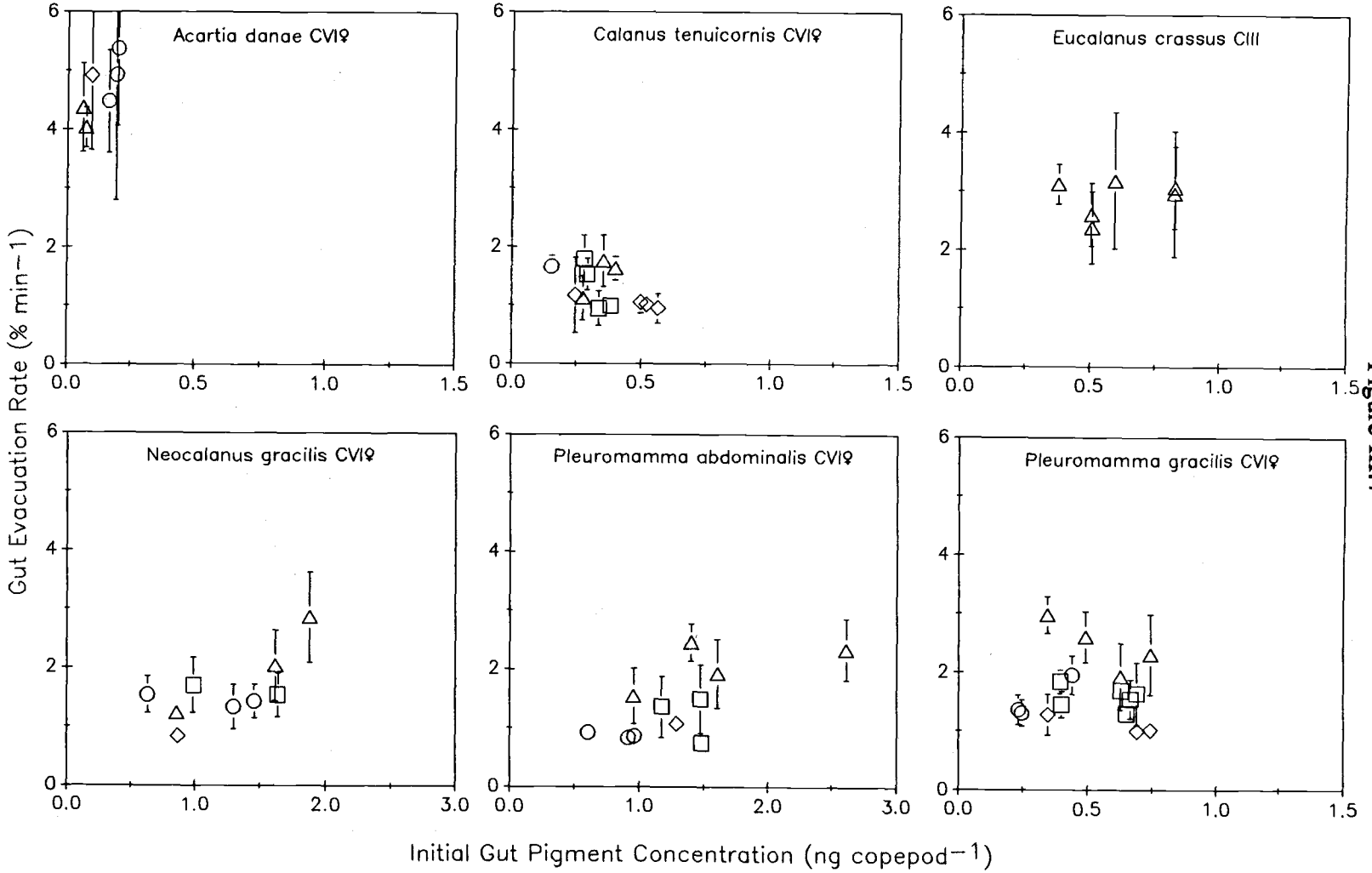

Acartia danae CVI♀
Calanus tenuicornis CVI♀
Eucalanus crassus CIII
Neocalanus gracilis CVI♀
Pleuromamma abdominalis CVI♀
Pleuromamma gracilis CVI♀
Gut Evacuation Rate (% min−1)
Initial Gut Pigment Concentration (ng copepod−1)

Figure III.7

Predictive Model: The amount of variation in GERs which could be attributed solely to temperature and body size differences of copepods collected in this study was estimated by fitting the data from all cruises to two different models which expressed GER as a power function of copepod body size and either a linear (equation 3-7) or exponential (equation 3-8) function of temperature.

$$GER = (aT + c)W^b \quad (3\text{-}7)$$

$$GER = (ae^{cT})W^b \quad (3\text{-}8)$$

where GER is the predicted gut evacuation rate (% min^{-1}) measured at temperature T °C for a copepod of body size W, and a, b, and c are coefficients. Coefficients of determination for fits to both models were almost identical (Table III.12), with the exponential model (equation 3-8) giving a slightly higher value. For both models, using total body length as the index of body size provided the best fit to the data, explaining 64% of the observed variation (Table III.12 and Fig. III.8). Dry weight and cephalothorax length were less successful predictors of GER, explaining 56 and 48% of the variation, respectively (Table III.12). The fit of all data to a power function using total length as the independent variable accounted for 44% of the variance in GERs (Table III.10). Therefore, adding temperature as a variable accounted for an additional 20% of the observed variation in GERs.

Gut Pigment Concentrations

As mentioned on page 31, there is considerable controversy regarding the

Table III.12. Nonlinear regression coefficients (a,b,c) for A) the model $G = (ae^{bT})W^c$, and B) the model $G = (aT + c)W^b$, where G is gut evacuation rate (% min^{-1}), T is experimental temperature (°C), and W is either copepod total length (TotLength), cephalothorax length (CTLength), or dry weight (Dwt).

A.

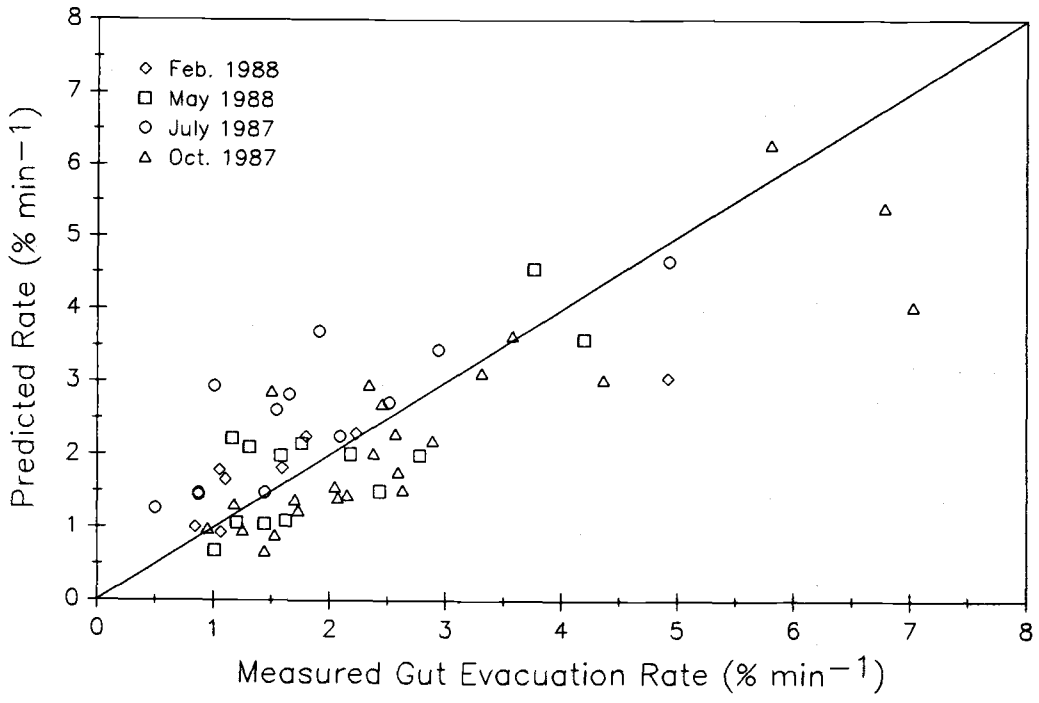
W	a ± SE	b ± SE	c ± SE	r^2
TotLength (mm)	0.3503 ± 0.2929	0.1428 ± 0.0422	-1.1730 ± 0.1248	0.6364
CTLength (mm)	0.2228 ± 0.2235	0.1461 ± 0.0512	-1.0216 ± 0.1591	0.4768
Dwt (μg)	0.3876 ± 0.3655	0.1351 ± 0.0478	-0.2836 ± 0.0324	0.5634

B.

W	a ± SE	b ± SE	c ± SE	r^2
TotLength (mm)	0.7134 ± 0.2117	-1.1734 ± 0.1249	-8.1880 ± 3.9755	0.6351
CTLength (mm)	0.5190 ± 0.1679	-1.0130 ± 0.1589	-6.2500 ± 3.2010	0.4728
Dwt (μg)	0.6498 ± 0.2254	-0.2830 ± 0.0325	-7.2337 ± 4.2573	0.5627

Figure III.8. Measured gut evacuation rates versus those predicted from the model $G = (ae^{cT})W^b$, where G is the predicted GER (% min^{-1}), W is copepod total length (mm), T is temperature (°C), and a, b, and c are least squares coefficients.

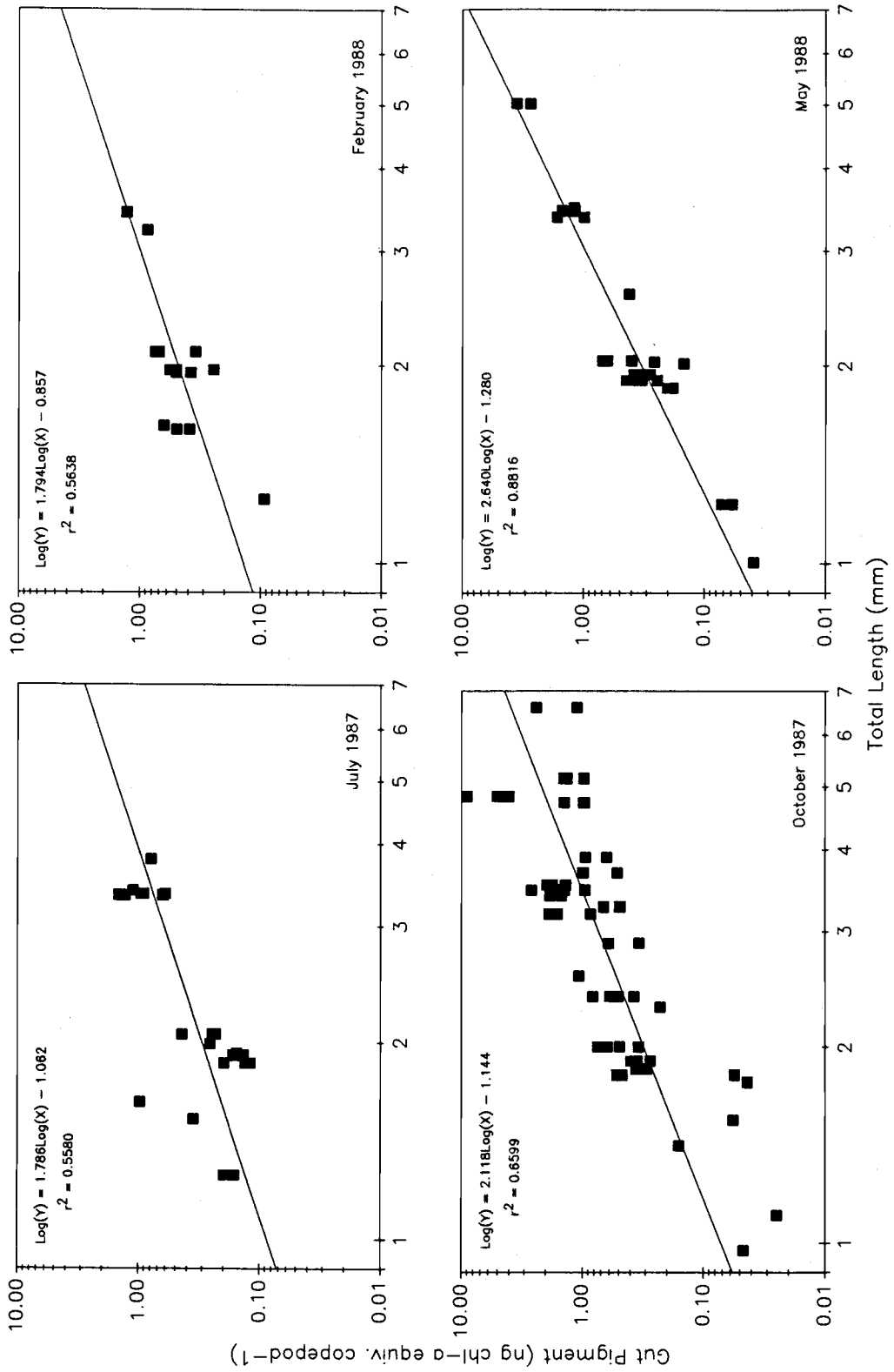
Figure III.8


Feb. 1988
May 1988
July 1987
Oct. 1987
Predicted Rate (% min−1)
Measured Gut Evacuation Rate (% min−1)
0
1
2
3
4
5
6
7
8

accurate measurement of copepod gut pigment concentrations because it appears that some variable fraction may be assimilated or converted to derivatives which are not detectable by fluorometric means (see references in Table III.2). In this section gut pigment values refer to concentrations actually measured; the issue of "pigment loss" will be treated later (see ingestion rate section). Gut pigment concentrations (chl-*a* equivalent weight) increased with copepod body size, ranging between 0.03 and 9.80 ng ind^{-1} (Fig. III.9). Values greater than 2.0 ng ind^{-1} were measured in only three species: *Eucalanus elongatus* CVI, *Pleuromamma abdominalis* CVI, and *P. xiphias* CVI. Unlike trends observed for GERs, significant temporal and spatial variation in gut pigment content were observed for most copepods. Virtually all zooplankton collections occurred at night, therefore diel patterns of gut fullness cannot be determined. However, trends exhibited by different species can be compared. In July, *Neocalanus gracilis*, *P. abdominalis*, and *P. gracilis* had maximal or near-maximal gut pigment levels near the onset of sampling (1:51 am) and significantly lower levels (Tukey-Kramer test, $p < 0.05$) closer to sunrise (5:21 am). Gut pigment concentrations of *Nannocalanus minor f. minor* exhibited a similar pattern, although the change in pigment levels was not statistically significant. *Acartia danae* showed a different pattern with gut pigment levels varying little between collection times (Table III.6). In October there was no overall temporal pattern for all species, although many copepods had highest gut pigment levels near dawn (6:19 am, Table III.7). In February and May (Tables III.8 and III.9) experiments were confined to a three hour interval between

Figure III.9. Gut pigment concentrations of copepods collected during the four cruises plotted against copepod total length.

Figure III.9


Log(Y) = 1.794Log(X) – 0.857
r2 = 0.5638
February 1988
Log(Y) = 2.640Log(X) – 1.280
r2 = 0.8816
May 1988
Log(Y) = 1.786Log(X) – 1.082
r2 = 0.5580
July 1987
Log(Y) = 2.118Log(X) – 1.144
r2 = 0.6599
October 1987
10.00
1.00
0.10
0.01
1
2
3
4
5
6
7
Gut Pigment (ng chl–a equiv. copepod–1)
Total Length (mm)

midnight and 3:00 am to minimize variability arising from differences in collection time. Gut pigment concentrations varied significantly for copepods collected from different locations on these cruises, indicating that spatial as well as temporal variation in grazing activity occurred within the region of study.

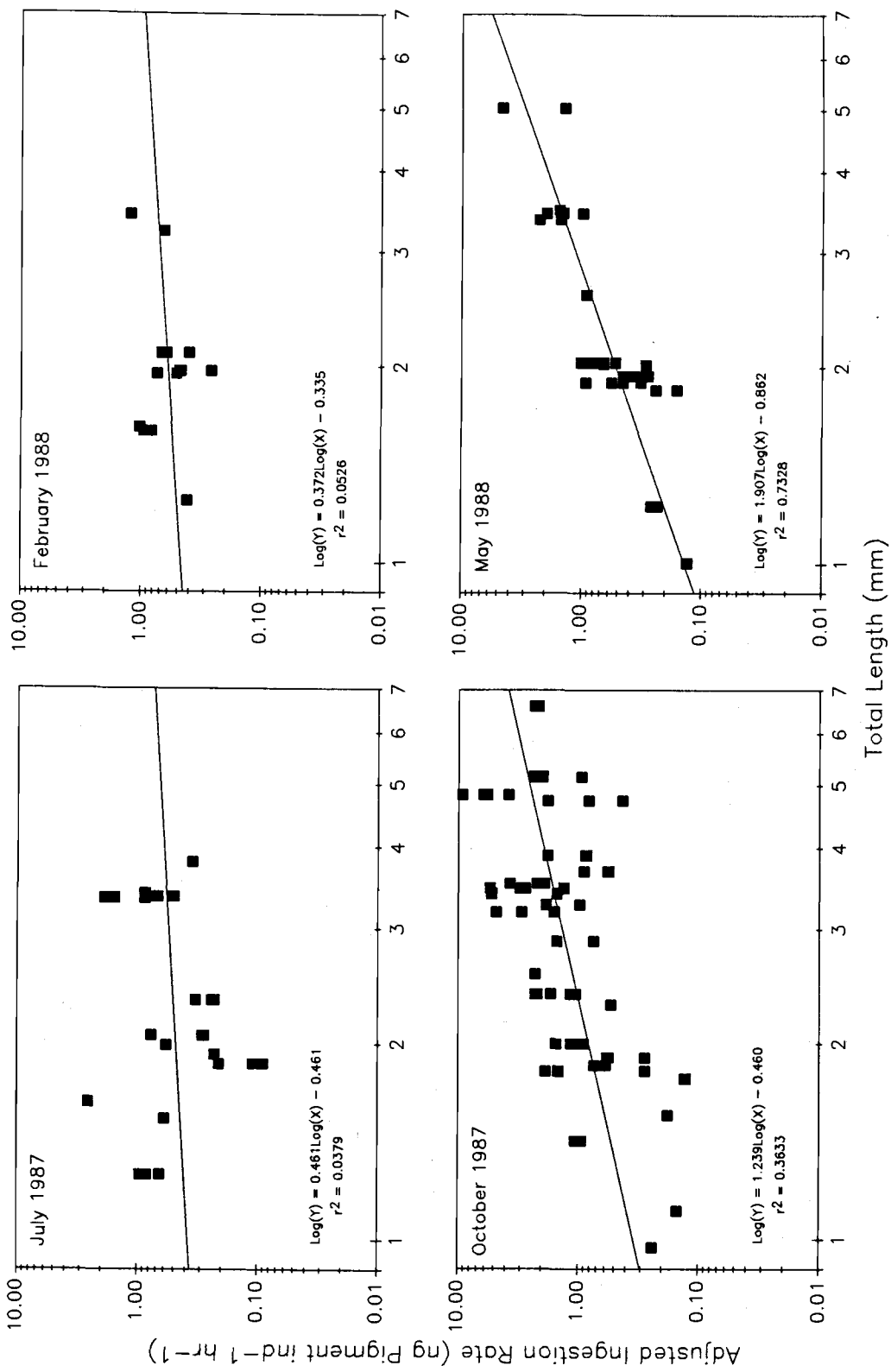
Ingestion Rates

Hourly ingestion rates (ng pigment ind^{-1} hr^{-1}) were calculated by multiplying gut evacuation rates (hr^{-1}) by initial gut pigment (ng chl-*a* equiv. wt ind^{-1}) concentrations adjusted for assumed "losses" of gut pigment. The fraction of gut pigment not detected by fluorescence (pigment loss) for copepods in this study is unknown; however, all studies examining this issue have reported some incidence of pigment loss (Table III.2). Therefore, gut pigment concentrations were increased by 33% to correct for non-detected pigment assumed to have been assimilated or converted to non-fluorescent derivatives in the gut. This correction factor is near the median (34.8%) and weighted mean (26.5%) of values shown in Table III.2 and agrees with corrections applied in at least one other study (Dam and Peterson, 1988). It is also near the value of 34.8% reported by Pasternak and Drits (1988) for *Pleuromamma* sp., which is the only reported value for a copepod species included in my study.

Adjusted ingestion rates of pigment varied by almost two orders of magnitude (0.13 to 9.30 ng chl-*a* equiv. $copepod^{-1}$ hr^{-1}) for copepods analyzed in these experiments (Fig. III.10). Temporal and spatial patterns of ingestion rates as

Figure III.10. Adjusted ingestion rates (I) calculated for copepods collected on the four cruises plotted against copepod total length (L). The lines shown are least squares fits to $Log(I) = bLog(L) + Log(a)$.

Figure III.10



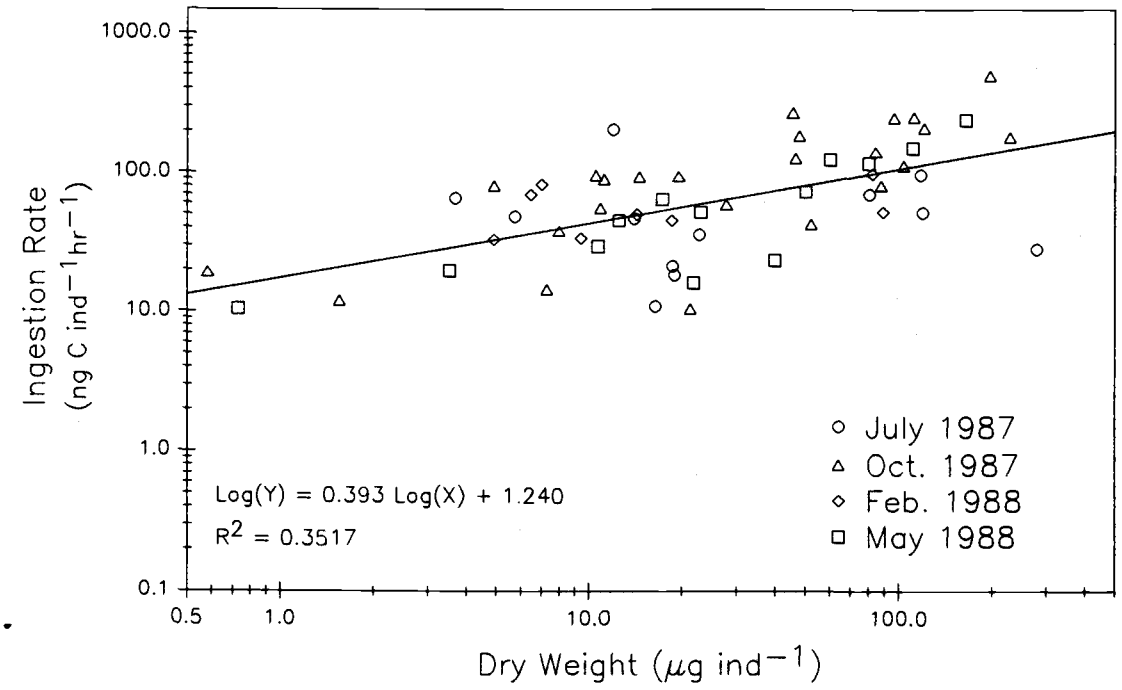
a function of body size followed the same trends as gut pigments (Tables III.6, III.7, III.8, and III.9). This result is a consequence of intraspecific gut evacuation rates showing only minor changes when measured at different times and locations, while gut pigment levels varied significantly for animals collected at different times and locations. Patterns of pigment ingestion rate versus copepod total length differed on these cruises (Fig. III.10). There was no significant change in ingestion rate with increasing body length in July and February, while in October and May pigment ingestion rates increased significantly with copepod total length.

The number of experiments conducted with different species varied on these cruises; therefore, to facilitate comparisons a mean ingestion rate was calculated for each species. Mean chlorophyll ingestion rates were converted to herbivorous grazing rates expressed in carbon units using a carbon:chlorophyll ratio of 80 (see methods). Mean herbivorous ingestion rates of carbon increased with copepod body size and ranged from a low of 10.4 to a high of 502.8 ng C ind^{-1} hr^{-1} (Fig. III.11). (Figure III.11 shows ingestion rates plotted against copepod dry weight rather than total length, as weight is more common in the literature as an index of body size). Grazing rates were highest in October, during which the overall mean rate (125.6 ng C ind^{-1} hr^{-1}) was 2.2 times greater than in July and February, and 1.7 times greater than the mean rate measured in May.

Carbon assimilation rates were calculated for all species by assuming that 70% of ingested carbon was assimilated. Measurements of copepod assimilation efficiencies generally range between 50 and 98% (Raymont, 1983). While it is

Figure III.11. Mean carbon ingestion rates calculated assuming copepods are feeding herbivorously. A carbon:chlorophyll ratio of 80 was used to convert ingestion rates of pigment to carbon units.

Figure III.11



recognized that assimilation efficiencies can vary, general physiological models developed for copepods have often assumed a value of 0.7 (e.g., Steele 1974; Huntley and Boyd, 1984). Conover (1978) calculated a mean of 0.7 (n = 104, SD = 0.16) for assimilation efficiencies reported in the literature. Carbon assimilation rates were compared to respiration rates (ng C $ind^{-1}hr^{-1}$), predicted from an equation expressing respiration of subtropical copepods as a function of dry weight [Ikeda (1974) as modified by Huntley and Boyd (1984)], in order to evaluate whether measured herbivorous grazing rates were sufficient to meet the respiratory requirements of the copepod species in these experiments. Figure III.12A shows that herbivorous ingestion rates for most species were apparently too low to satisfy estimated respiratory demands. Copepods with ingestion rates exceeding estimated respiratory demands on at least one cruise included *Acartia danae*, *Calanus tenuicornis* CV, *Mecynocera clausii*, *Eucalanus crassus* CII and CI, *E. elongatus* CIVm, *Lucicutia flavicornis*, *Pleuromamma gracilis* CVIf, and *P. xiphias* CV. Percentages of respired carbon potentially derived from herbivorous grazing ranged from a low of 4% for *Undeuchaeta plumosa* CVI to a high of 277% for *C. tenuicornis* CV (Table III.13). Percentages tended to decline with increasing developmental stage for *E. crassus*, *E. elongatus*, and *P. xiphias*. Patterns between cruises varied for different species, with some copepods showing large fluctuations in the proportion of respiration accounted for by herbivorous grazing between cruises (e.g. *A. danae*, *L. flavicornis*, *P. gracilis* CVIf, and *P. xiphias* CV).

Figure III.12. Comparison between rates of carbon assimilation and estimated respiration assuming copepods are (A) feeding herbivorously and (B) feeding omnivorously (see text). The equation for the line estimating respiration (R, ngC $copepod^{-1}hr^{-1}$) as a function of body size (W) is from Huntley and Boyd (1984): $Log(R) = 0.685*Log(W) + 0.976$

Figure III.12

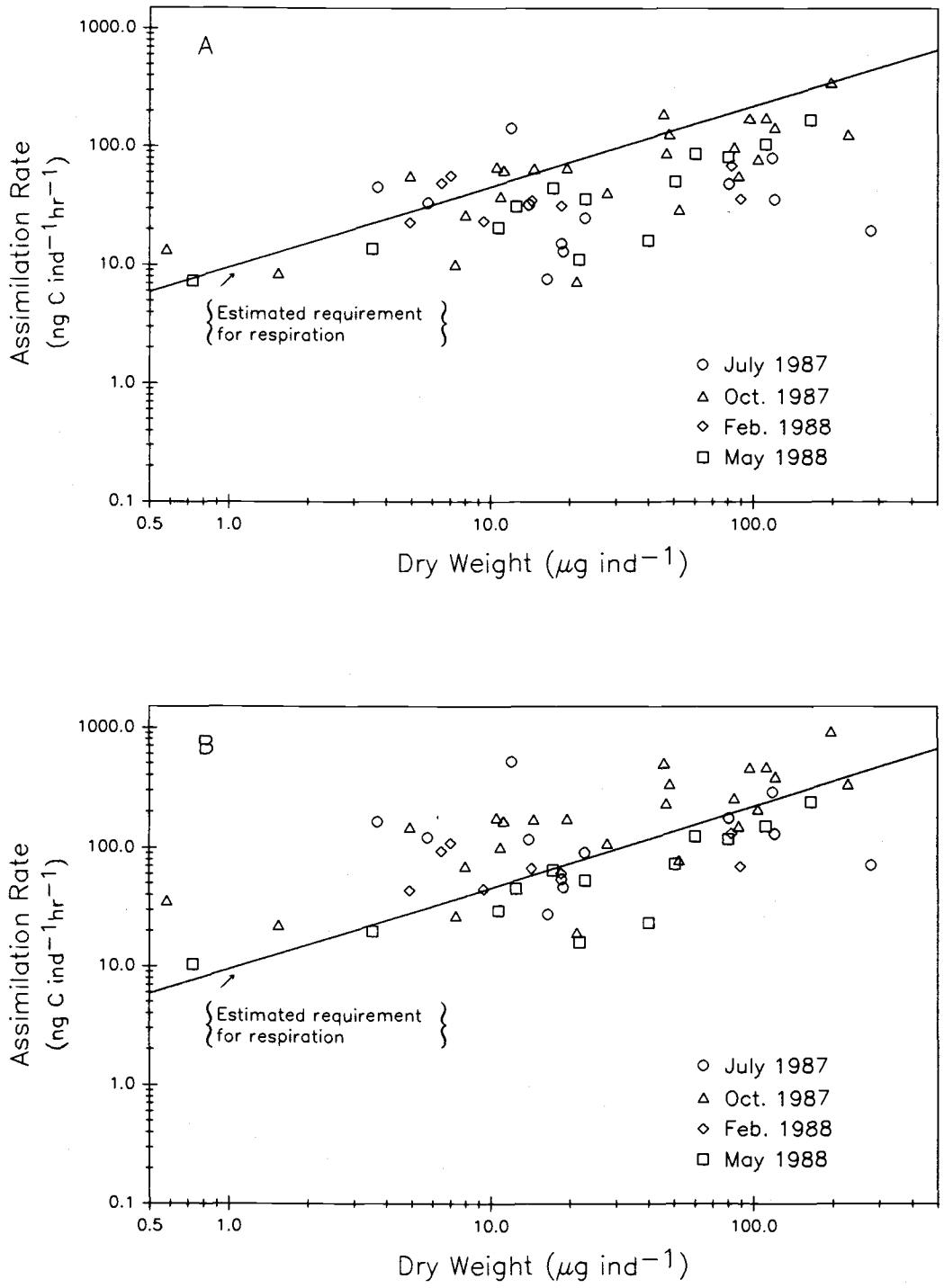


Table III.13. Estimation of the percentage of respired carbon potentially derived from ingestion of phytoplankton for copepod species at different times of year. Respiration rates (μg C copepod^{-1} hr^{-1}) were calculated using Ikeda's (1974) equation as modified by Huntley and Boyd (1984) expressing respiration as a function of copepod dry weight for subtropical zooplankton. Ingestion rates were corrected for assumed 33% loss of gut pigment and converted to carbon using a C:Chl ratio of 80. Calculations assume that 70% of ingested carbon was assimilated.

Species	Stage	July 1987	Oct. 1987	Feb. 1988	May 1988
Acartiidae					
Acartia danae	CVIf	197		116	61
Aetideidae					
Undeuchaeta plumosa	CVIf	4			
Calanidae					
Calanus tenuicornis	CVIf	18	67	53	43
	CV	277		144	
Nannocalanus minor f. major	CVIf		21		
	CV		9		
Nannocalanus minor f. minor	CVIf	21			15
Neocalanus gracilis	CVIf	32	81	18	44
	CV		96		
Neocalanus robustior	CV		34		
	CIV				37
	CIII				45

Table III.13 (Continued)

Species	Stage	July 1987	Oct. 1987	Feb. 1988	May 1988
Calocalanidae					
Calocalanus pavo	CVIf		66		
Mecynocera clausii	CVIf		206		270
Candaciidae					
Paracandacia bispinosa	CVIf				14
Centropagiidae					
Centropages violaceus	CVIf	56			
Eucalanidae					
Eucalanus crassus	CIII		67		
	CII		142		
	CI		200		
Eucalanus elongatus	CVIf		32		
	CVIm		28		
	CVf		50		
	CVm		45		
	CIVf		91		
	CIVm		127		

Table III.13 (Continued)

Species	Stage	July 1987	Oct. 1987	Feb. 1988	May 1988
Lucicutiidae					
Lucicutia flavicornis	CVIf	107	27	158	
Metridiidae					
Pleuromamma abdominalis	CVIf	14	74	36	43
	CVIm	25	58		
Pleuromamma gracilis	CVIf	31	110	46	67
	CVIm	12	79	60	59
Pleuromamma xiphias	CVIf		99		54
	CV		146		55

The calculation of herbivorous grazing rates as described above neglects carbon associated with detrital particles and zooplankton. To evaluate the potential importance of these food items in meeting estimated respiratory demands, assimilation rates were calculated from ingestion rates converted to carbon using ratios of POC:total pigment (chl-*a* equiv. wt.) integrated over the upper 150 m of the water column for each cruise (Fig. III.12B). The integrated C:pigment ratios were 290, 212, 153, and 115 for July, October, February, and May, respectively. Ingestion rates calculated in this manner assume copepods were feeding omnivorously and non-selectively across the entire range of particle sizes collected in bottle casts. While this assumption clearly departs from reality, the fact that these assimilation rates exceed estimated respiratory needs for most species (Fig III.12B) suggests that most copepods included in this study must feed on animal matter and/or detritus in addition to phytoplankton to meet respiratory requirements.

Discussion

Gut evacuation rates

Constancy of rates: When GERs are used to calculate short-term ingestion rates by the gut fluorescence technique they are usually assumed to be constant for the species of interest and independent of time of day (Baustista *et al.*, 1988; Tiselius, 1988). Rates measured for copepods collected within a limited area are often assumed representative of extended areas, or are applied to animals collected at other times of year (Nicolajsen *et al.*, 1983). This study provides a good test of these assumptions as GERs were measured at different times of year and times of day for copepods collected at locations separated by 10's to 100's of kilometers. In general, the data support the notion that gut evacuation rates are a relatively conservative characteristic of copepod feeding behavior, at least over a period of several days to weeks. The vast majority of species and developmental stages for which multiple experiments were conducted showed no significant differences in GERs for experiments conducted at different times of night, or at different locations, over a period of several days. However, GERs did vary by about a factor of 2 for copepods collected at different times of year (e.g. Fig. III.7) and seasonal changes in temperature and copepod body size could not account for all of the observed variation (Fig. III.6.).

Spatial variation: Collections of animals for experiments performed on each

cruise were generally separated by tens of kilometers, although collection sites in July 1987 were more dispersed, in one case separated by 225 km (Fig. III.1). Statistical comparisons of evacuation rates for the copepod species and developmental stages collected at all sites showed only 3 instances in which rates differed significantly. In two of these cases, involving *Pleuromamma xiphias* CVI (May 1988, Table III.9) and *P. xiphias* CV (October 1987, Table III.7), collection times were similar, but locations were separated by approximately 88 and 99 km, respectively. During February and July intraspecific GERs did not vary significantly despite the greater spatial distances between collections in July.

A few other studies have reported significant coarse-scale (Haury *et al.*, 1978) variation in GER. Head (1986) found that *Calanus glacialis* CV evacuation rates differed twofold for animals collected at the same time of day at stations separated by ca. 110 km in the Arctic Ocean. GERs of *C. glacialis* (CIV and CV), of *C. hyperboreus* (CIII, CIV, and CV), and of *Metridia longa* CVI also differed significantly between stations separated by similar distances in the Parry Channel, Arctic Ocean (Head *et al.*, 1988). Underlying causes for spatial differences between GERs of individual copepod species are not known, although animal history, and patchiness in food concentration and/or food quality, can be suggested by analogy with studies of spatial variation in feeding intensity (e.g. Hayward, 1980). Unfortunately, these explanations cannot be evaluated with the data collected in this study. It is interesting to note, however, that both studies cited above also found that GER differences among locations were only observed

for a few of the developmental stages or copepod species present. Therefore, the factors that do influence the relatively uncommon changes in GER appear to effect different responses both within and between species.

Diurnal variation: Gut evacuation experiments were conducted primarily between sunset and dawn in this study and, with one exception (male *Eucalanus elongatus*, Table III.7), rates measured at different times were not significantly different. Few studies have investigated whether GERs vary for animals collected at different times of day and the conclusions reached are equivocal. For example, Head (1986) reported that evacuation rates of *Calanus hyperboreus* CIV and *C. glacialis* CV did not change for animals collected at different times, while rates of *C. hyperboreus* CIII and CV did vary significantly between sampling times. Arashkevich (1977) examined digestion durations (= gut residence times) of several tropical copepods collected at different times of day and reported that digestion durations did not fluctuate for the majority of species, several of which were present in my study: *Nannocalanus minor*, *Neocalanus gracilis*, and *Pleuromamma xiphias*. The two exceptions mentioned by Arashkevich (1977), *Eucalanus attenuatus* and *Acartia tonsa*, had gut transit times which tended to increase in daylight.

Since my experiments took place almost exclusively at night, the possibility that GERs decreased during daylight hours cannot be excluded. The few daytime collections showed that most species were either absent, or present in greatly

reduced numbers, making experiments difficult to conduct during daylight hours. *Eucalanus crassus* CI was the only copepod for which day-night comparisons were available (Table III.7), and GERs were statistically the same. The rationale for assuming that GERs may decrease during daylight hours appears to be based on two observations of copepod feeding behavior: (1) that many copepod species exhibit diel changes in feeding intensity with most species showing increased levels of gut fullness during the night (Head *et al.*, 1984; Harris and Malej, 1986; Stearns, 1986; Bautista *et al.*, 1988; Ohman, 1988; Tiselius, 1988; Dagg *et al.*, 1989); and (2) that when copepods are placed in filtered seawater gut evacuation rates decrease with time as gut contents decrease (Baars and Oosterhuis, 1984; Christoffersen and Jespersen, 1986; Bautista *et al.*, 1988; Ellis and Small, 1989). The inference drawn from these observations is that GER is dependent on gut fullness and the lower levels observed during daylight hours probably result in decreased GERs.

Dependence on gut fullness: Gut evacuation rates of copepod species generally appear to be independent of gut pigment level (Fig. III.7), at least over the relatively small range of gut pigment concentrations observed in most species during the night. A few species appeared to show slight increases in GER as gut pigment levels increased (e.g. *Neocalanus gracilis* and *Pleuromamma abdominalis* in Fig. III.7), while GERs of others decreased slightly at higher levels of gut pigment (e.g., *P. gracilis* in October and *Calanus tenuicornis*, in Fig. III.7).

Neither of these trends were statistically significant. Results obtained in other studies also show no consensus regarding the dependency of GERs on the amount of food in the gut. Various reports show gut evacuation rates increasing (Baars and Oosterhuis, 1984; Head, 1988), decreasing (Wang and Conover, 1986), or showing no relation (Head and Harris, 1987; Head *et al.*, 1988) with increasing gut pigment levels. Dagg and Walser (1987) reported that GERs of *Neocalanus plumchrus* increased with gut pigment concentration and ambient food level below 3.5-4.0 μg chl l^{-1} and remained constant above this level. *Calanus glacialis* showed a similar saturation response, with GERs increasing with gut pigment level up to ca. 1 ng chl ind^{-1} and remaining constant at higher gut levels (Head, 1986).

The lack of consistent patterns between GERs and gut pigment levels for copepods in my study and others may be due in part to the fact that copepods are ingesting varying amounts of non-pigmented material. Most copepods included in my study can be considered as omnivores (Wickstead, 1962; Mullin, 1966; 1967; Arashkevich, 1969; Timonin, 1971; Hayward, 1980; Paffenhöfer and Knowles, 1980; Raymont, 1983), with the carnivorous component of the diet probably varying with prey abundance and encounter frequency. Comparisons of GERs at different initial gut pigment levels therefore do not necessarily indicate differences in gut fullness. The apparent independence of GERs and gut pigment level observed in this study may only indicate that copepods had full guts containing variable proportions of gut pigment. Both studies cited above as showing no relation between GERs and gut pigment level (i.e., Head and Harris, 1987; Head

et al., 1988) also involved field collected copepods which may have consumed non-pigmented material and thus rendered gut pigment an unreliable index of gut fullness. This explanation, however, cannot explain the variable responses observed in laboratory studies in which copepods are fed phytoplankton cultures (Wang and Conover, 1986; Dagg and Walser, 1987). In these cases gut pigment is a direct measure of gut fullness.

Variation with body size: While GERs for the most part did not vary significantly for a particular developmental stage and sex of copepod collected at different times and locations, rates did vary by over an order of magnitude (0.50 - 7.43 % min^{-1}) among copepod species, and differed between sexes and among developmental stages within species. Most of the variance between GERs could be accounted for by differences in copepod body size, with rates tending to decrease with increasing body weight or length. Similar changes in GERs with body size have been observed for developmental stages or weight classes of other zooplankton species (Heyraud, 1979; Tande and Båmstedt, 1985; Head *et al.*, 1988).

Notable exceptions to the overall inverse trend between GERs and body size were the differences observed between males and females. Males tended to have lower evacuation rates than females of the same developmental stage despite smaller body size. This pattern was seen for *E. elongatus* stages CV and CVI (Fig III.4B) and for adult stages of *Pleuromamma abdominalis* and *P. gracilis*. Similar

sex-related differences between GERs have been reported for *Acartia grani* by Baustista *et al.* (1988).

The general inverse relationship between GERs and copepod body size was approximated by the allometric equation, $G = aW^b$. This equation has been used to describe the weight dependence of several other physiological processes of copepods, including respiration (e.g. Ikeda, 1978; 1985; Uye and Yashiro, 1988), nitrogen and phosphate excretion (Ikeda and Mitchell, 1982; Vidal and Whitledge, 1982), ingestion (Mullin and Brooks, 1976; Ikeda, 1977; Huntley and Boyd, 1984), and assimilation (Huntley, 1988), and provided the best fit to the data obtained in my study. Depending upon which measure of body size (W) was used, this model accounted for 33 - 44% of the variance in GERs for the combined data collected on all cruises (Table III.10). For the two species of *Eucalanus* the fit to this equation was much better, describing 99.8% of the variance between gut evacuation rates of *E. crassus* stages CI-CIII (Fig. III.4A) and greater than 90% of the variance between developmental stages CIV-CVI of male or female *E. elongatus* (Fig. III.4B).

The best fit to the allometric equation for GERs was obtained using total body length as the index of body size; use of cephalothorax length or dry weight resulted in lower coefficients of determination. The improved fit for total length is probably a consequence of copepods with similar cephalothorax lengths having variable urosome lengths. Since the urosome contains the distal portion of the midgut and the hindgut, total length (= cephalothorax + urosome) is a better

correlate of gut length than is cephalothorax length. It seems reasonable to expect some degree of correlation between gut residence time and gut length since digestion and packaging of fecal material occur as food is transported along the gut. The lower correlation obtained when using dry weight as the index of body size may result from seasonal variations in lipid storage which increase the variability of body weights associated with a given gut length. Lipid concentrations may have varied considerably for copepods collected on these cruises as levels in subtropical copepods are quite variable, ranging from 8 to 60% of dry weight (Sargent and Henderson, 1986), and can exhibit short-term as well as seasonal fluctuations (Lee and Hirota, 1973; Lee *et al.*, 1974). Use of lipid-free dry weight as a measure of body size would improve the correlation with gut evacuation rates if this interpretation is correct.

Regardless of which measure of body size was used, the slopes of log-log plots of GERs versus body size were statistically the same for groups of copepods collected at different times of year (Table III.10). In addition to time of year, several other parameters varied between cruises, including temperature, species composition, and perhaps food type and quality. The constancy of slopes despite these changes suggests that the relationship observed between gut evacuation rate and body size may apply to zooplankton assemblages in other oceanic environments. Since intercepts varied between cruises, however, a test of this hypothesis is difficult. Its evaluation requires measurements of GERs and body size for several copepods species collected within a given region over a relatively

short period of time (several days). A survey of the literature indicates that most investigators have measured GERs for only a small number of copepod species, or developmental stages, and that frequently the size of animals used in experiments is not reported (Appendix). A limited comparison can be made, however, with evacuation rates measured for copepodite stages of *Calanus glacialis* (CIV, CV, and CVI) and *C. finmarchicus* (CV and CVI) at -1 °C in the Barents Sea by Tande and Båmstedt (1985). Fitting the data for both species, which range from ca. 82 to 509 μg C in body size, to the allometric equation using Model II regression techniques gives a value of -0.41 for v, very close to the -0.40 obtained in my study despite the almost 20°C difference in temperatures. The results obtained also show good agreement with similar studies investigating the relationship between body size and GER in fish. As observed for copepods, evacuation of food occurs exponentially for many species of fish (Jobling *et al.*, 1977). GERs of dab (*Limanda*) were observed to vary as fish weight raised to the -0.386 power (Jobling *et al.*, 1977), while Flowerdew and Grove (1979) reported a value of -0.364 for turbot (*Scophthalmus maximus*), and Pandian (1967) calculated a value of -0.41 for Pacific tarpon (*Megalops cyprinoides*).

Theoretical considerations: Although only limited comparisons can be made within the copepod literature for the dependency of GERs on body size, by examining theoretical expectations regarding the relationship between rates of food passage and body size it is possible to assess whether the constancy and magnitude

of the regression slopes appear reasonable. An equation expressing gut evacuation rates as a function of body weight can be derived by making certain assumptions regarding food processing in copepods and by making analogies with models of gut evacuation and food processing in fish (Fänge and Grove, 1979; Jobling, 1981; Holmgren *et al.*, 1983; Grove, 1986). In deriving this equation, I assume that digestive processes in the gut operate in a manner which optimizes the net gain of energy and nutrients from ingested food items (Penry and Jumars, 1986; 1987). Thus the residence time of food items in the gut should not exceed the time interval necessary to digest and assimilate products from food items entering the gut. I also assume that digestive enzymes are not limiting in the gut. Nott *et al.* (1985) has suggested that the supply of B-cells which release hydrolytic enzymes into the lumen of the gut, and are broken down during feeding, could be exhausted after a few hours of feeding and limit the duration of the digestive cycle. To ensure digestive enzymes are not limiting, I assume that animals do not feed during the interval necessary to replenish the supply of B-cells in the digestive epithelium. In addition, it is assumed that the rate at which food is digested in the gut is proportional to the surface area of food exposed to digestive enzymes, and for purposes of simplification, that food in the gut can be modeled as a bolus of material whose surface area is the site of food digestion.

Since surface area increases as volume raised to the ⅔ power, the change in the volume of the food bolus in the gut (V) with time (t) due to digestion can be expressed as:

$$\frac{dV}{dt} = -kV^{2/3} \tag{3-9}$$

where k is the instantaneous digestion rate (Fänge and Grove, 1979). The negative sign indicates that volume is reduced with increasing time. If digestion is complete within a time interval t_d, and if after this interval the reduced volume of food V_d is egested, then integration of equation (3-9) gives:

$$t_d = \left[\frac{3V_0^{1/3}}{k}\right] \tag{3-10}$$

where V_0 is the initial volume of food in the gut and t_d is the time required to empty the gut, or the gut evacuation time (GET). When loss of food from the gut occurs exponentially the reciprocal of the GER represents the amount of time required to eliminate 1/e = 63% of the initial volume of material in the gut (Mackas and Burns, 1986). Therefore equation (3-10) can be written as:

$$GER = \left[\frac{1}{t_d}\right] = k' V_0^{-1/3} \tag{3-11}$$

Finally, if it is assumed that gut volume is proportional to body weight (W), and that initially the same proportion of the gut is filled with food for animals of different weight, then an equation relating GER and body weight can be expressed as:

$$GER = aW^{-1/3} \tag{3-12}$$

Since copepod body weight was proportional to length raised to the 3.19 power (calculated from equation (3-5), but using model II techniques to yield $\nu = 3.19$)

when data from all species and cruises were combined, equation (3-12) can be rewritten in terms of total length (L):

$$GER = aL^{-1.05} \tag{3-13}$$

Both of the exponents derived in equations (3-12) and (3-13) are slightly lower than the values calculated for the combined data (-0.40 and -1.27), although they lie within the 95% confidence intervals calculated for the individual cruises (Table III.10). The lower theoretical values may be a consequence of the assumptions used to derive the equations. For example, it was assumed that food in the gut was a bolus of material with digestive enzymes acting only on the surface of this volume. This abstraction is probably not valid given that material in the midgut is mixed by peristaltic contractions (Gauld, 1957; Ong and Lake, 1969), which presumably allows digestive enzymes to act on individual food items in the gut. If material in the gut is viewed as consisting of separate food items, the surface area exposed to digestive enzymes is greater than predicted in equation (3-9) and digestive rate should increase as a function of the number and surface area of particles in the gut. This idea can be expressed mathematically by dividing the initial volume of food in the gut (V_0) into n particles of similar shape and volume (V_i), i.e. $V_0 = nV_i$. Substituting this expression into equation (3-11) gives:

$$GER = \left(k' V_0^{-1/3}\right) = \left[k'(nV_i)^{-1/3}\right] = \left(k' n^{-1/3} V_i^{-1/3}\right) \tag{3-14}$$

This equation indicates that GER should decrease as the number of food particles or the volume of individual food items in the gut increases.

The size of food particles (i.e., V_i) eaten by zooplankton does tend to increase with copepod body size. However, each copepod species can consume a range of particle sizes, and the selection of food items is dependent on several factors including food concentration, food quality, mouthpart morphology, as well as the behavioral and sensory responses of the copepods (Anraku and Omori, 1963; Donaghay and Small, 1979; Paffenhöfer *et al.*, 1982; Cowles and Strickler, 1983; Buskey, 1984; Greene and Landry, 1985). Because of the complexity and number of factors that effect the size of particles consumed by copepods, it is not possible at this time to refine equation (3-13), by expressing the term V_i as a function of copepod body size, and formulate an equation relating GER, copepod body size, and the size of consumed food items. Nevertheless, the fact that weight exponents are reasonably close to predicted values when food is treated as a bolus of material suggests that this approximation is not unreasonable, and that the proportionally greater surface area of food exposed to the action of digestive enzymes of smaller versus larger copepods provides an explanation for trends observed with body size in this study.

Temperature: Experimental temperatures varied between 17 and 20 °C on different cruises, and given the reported temperature dependency of GER (Kiørboe *et al.*, 1982; Dagg and Wyman, 1983; Christofferson and Jespersen, 1986; Dam and Peterson, 1988) temperature may have accounted for some portion of the variation not explained by changes in body size. With few exceptions, the highest

GERs were measured during October at 20 °C and the lowest rates during February at 17 °C. Despite this apparent trend with temperature, correlations with temperature were poor for many species because July GERs, which were also measured at 20 °C, were only slightly higher than February values. For some copepods seasonal changes in body size appeared to account for the differences observed between July and October GERs. Copepods collected in July were generally larger than the same species collected in October. Apparently the decrease in rates arising from larger body size offset the increase expected by higher temperatures. The results obtained for *Calanus tenuicornis* appear to support this interpretation. Total length of *C. tenuicornis* was similar in July and October and measured GERs for these cruises showed good agreement.

If the mean of July and October evacuation rates are used as the best estimate of 20°C rates, the data imply that GERs are strongly dependent on temperature, with Q_{10} for individual species ranging from 2.11 for *Pleuromamma abdominalis* to 6.75 for *P. gracilis* (Fig III.6). Q_{10} values of this magnitude have been reported in other studies; for example, Christoffersen and Jespersen (1986) reported a Q_{10} of 4.1 for *Eudiaptomus graciloides*, and Dagg and Wyman (1983) reported a value of 5.4 for *Neocalanus plumchrus*. However, as noted by these latter authors, these values seem unreasonably high and probably indicate more data are needed over a larger range of temperatures to adequately evaluate the temperature dependency of gut evacuation rates. Other studies have found that evacuation rates were less dependent on temperature. Kiorboe *et al.* (1982)

reported a Q_{10} of 3.3 for *Centropages hamatus* and Dam and Peterson (1988) pooled their own data for *Temora longicornis* along with data for other species, including those cited above, and found that gut evacuation rates increased linearly with temperature (-1 to 19.5°C) with a Q_{10} of 2.21.

It is also possible that October GERs were higher in response to factors not measured in this study, and that evacuation rates of copepods included in my study are independent of temperature when measured over seasonal time spans. The seasonal range of temperature in near-surface water was small, and animals may have acclimated to the presumably slowly changing temperatures over this small range. In agreement with this proposition, Baars and Oosterhuis (1984) found no relation between gut passage time and ambient temperature for several copepod species collected at different times of year in the North Sea. Similarly, Batchelder (1986) found that GERs were not related to temperature for *Metridia pacifica* collected at different times of year. My results indicate that, with the October data excluded, there was no temperature effect on gut evacuation rate.

Food quality: Seasonal shifts in food quality, or types of food consumed by zooplankton, have also been suggested as effecting changes in rates of gut evacuation (Nicolajsen *et al.*, 1983; Baars and Helling, 1985; Head and Harris, 1987). Although evidence supporting this contention is limited, it might account for the higher GERs measured for copepods in October as well as some portion of the variation in GERs measured at different locations within cruises.

Conclusions regarding the dependency of GERs on food quality in this study, and others, are difficult to reach because of uncertainty regarding the composition of material actually ingested by particular species, and what indices of ingested material should be measured to determine its food quality. Generally a food can be considered to be of "higher quality" if its consumption promotes increased growth or fecundity in comparison to other food sources. Usually some measure of N, either PON or protein, is used to assess food quality because dead cells and detritus, both depleted in N, are ingested at greatly reduced rates in comparison with other food sources (Paffenhöfer and Strickland, 1970; Heinle *et al.*, 1977; Starkweather and Bogdan, 1980; Paffenhöfer and Van Sant, 1985; Conover *et al.*, 1988), and because recent work has suggested that the grazing strategy of copepods may be to maximize nitrogenous ingestion (Cowles *et al.*, 1988). Even more problematic than determination of what index of food quality should be measured, is the issue of what copepods are actually consuming. Consumption of food items in proportion to their abundance describes a nonselective feeding strategy, and while some species apparently feed in this manner (e.g. Turner and Tester, 1989), many do not (Frost, 1980). Thus, elemental or biochemical analyses of total particulate matter, or even specific size fractions, are not necessarily representative of the material actually ingested. Because of these difficulties, field studies have been unable to provide definitive evidence that GERs are dependent on food quality.

Laboratory studies avoid the uncertainty of what food items are being

consumed and can therefore more adequately address the complexity of food quality issues. Comparison of GERs, or gut residence times, of copepods fed different phytoplankton species do not show substantial differences (Arashkevich, 1977; Batchelder, 1986). Comparisons of GERs of copepods fed natural particulates versus cultures (Dagg and Walser, 1987) or other food sources of presumed higher quality (epontic algae, Head, 1988), appear to show reduced GERs on natural particulate food. A strategy of reducing rates of food passage through the gut, presumably to allow more complete digestion and absorption of nutrients in response to consumption of lower quality food, appears to differ from results obtained by Clarke *et al.* (1988) for *Euphausia superba*. They found that fecal egestion rates increased as the percentage organic content of fecal pellets decreased. The inference drawn Clarke *et al.* (1988) was that GERs increase as food quality decreases. These two strategies may not be mutually exclusive. Head and Harris (1987) have suggested that the advantage of either to the copepod may depend on food concentration, with the former strategy being preferential at low food concentrations.

Investigation of food quality as a potential source of variation of GERs in my studies, particularly between the July and October experiments which took place at the same temperature, suffers from all of the uncertainties mentioned above. Integrated ratios of particulate carbon (POC) to particulate nitrogen (PON) for the upper water column were similar on both cruises (Table III.14A), and although POC:Chl-*a* and PON:Chl-*a* ratios were higher in July than October the assessment

Table III.14. POC:Chl-*a*, PON:Chl-*a*, and POC:PON weight ratios (mg/m2) for particulate matter on seasonal VERTEX cruises IV - VII. (A) Integrated over the upper 150 m of the water column. (B) Measured at the depth (m) of the chlorophyll maximum. (C) Measured at the depth of maximum primary production (PP max.).

A. Integrated over upper 150m

VERTEX Cruise	Date	POC / Chl-*a*	PON / Chl-*a*	POC / PON
IV	July 1987	320	52	6.14
V	Oct. 1987	253	38	6.63
VI	Feb. 1988	162	28	5.81
VII	May 1988	162	24	6.84

B. At the Chlorophyll maximum

VERTEX Cruise	Date	Chl max. Depth	POC / Chl-*a*	PON / Chl-*a*	POC / PON
IV	July 1987	100	235	37	6.44
V	Oct. 1987	60	183	32	5.70
VI	Feb. 1988	20	152	24	6.23
VII	May 1988	150	88	15	5.82

C. At the Primary production maximum

VERTEX Cruise	Date	PP max. Depth	POC / Chl-*a*	PON / Chl-*a*	POC / PON
IV	July 1987	10	495	75	6.63
V	Oct. 1987	10	457	57	8.00
VI	Feb. 1988	10	134	23	6.23
VII	May 1988	25	314	41	7.63

of these differences in terms of food quality is unclear. Changes in these ratios may have arisen from altered species assemblages, changes in average pigment content per cell, or differences in the proportion of plant to animal matter in collected samples. Comparison of integrated ratios will not be valid if copepods are feeding at discrete depths, where the quality of particulate matter may differ substantially from the average for the water column. Several studies have reported that vertical distributions of zooplankton tend to coincide with the chlorophyll maximum (Anderson *et al.*, 1972; Mullin and Brooks, 1972; Hobsen and Lorenzen, 1972; Youngbluth, 1975; Haury, 1976, Ortner *et al.*, 1980; Townsend *et al.*, 1984), while others have reported that zooplankton abundance coincides more closely with the depth of maximum primary productivity (Lorenzen, 1967; Venrick *et al.*, 1973; Longhurst, 1976; Herman *et al*, 1981; Herman, 1983; Herman and Platt, 1983; Cowles *et al.*, 1987). Table III.14B and C show ratios for particulate matter at depths corresponding to the chlorophyll and primary production maximum. Comparisons of these ratios show distinct differences between July and October. At both depths the ratios of POC:Chl-*a* and PON:Chl-*a* were higher in July than October. Ratios of POC:PON were similar at both depths in July (6.44 versus 6.63), while in October this ratio was substantially higher at the productivity maximum (8.00) than at the chlorophyll maximum (5.70). The depths at which individual copepod species were feeding on these cruises is unknown; however, nighttime biomass of 202-2000 μm zooplankton was higher at the primary production maximum than at the chlorophyll maximum (2.11

versus 1.50 mg dry wt m^{-3} in July, and 1.79 versus 1.54 mg dry wt m^{-3} in October) for both cruises. If a decision on food quality is based solely on the basis of nitrogen, the lower C:N ratio and higher PON:Chl-*a* ratio in July at the depth of maximum carbon fixation (relative to October ratios) may indicate that lower GERs measured in July were associated with ingestion of higher quality food, as suggested by the Clarke *et al.* (1988) results.

Predictive model: By expressing GERs as a power function of body size, and either a linear or exponential function of temperature, 64% of the seasonal variation among different species and stages could be explained. Exponential (equation 3-7) and linear (equation 3-8) models both provided roughly equivalent descriptions for the temperature dependency of gut evacuation rates, although the coefficient of determination was slightly greater for the exponential model. The inability to distinguish between these two models is not unexpected given the small range of temperatures used in this study. Most investigations have used the exponential model to describe the temperature dependence of GER (Kiørboe *et al.* 1982; Dagg and Wyman, 1983; Christofferson and Jesperson, 1986). However, Dam and Peterson (1988) found that a linear model provided the best fit to their data for *Temora longicornis* when GERs were measured at ambient temperatures at different times of year.

Comparisons of GERs predicted from either the exponential (ET) or linear (LT) temperature model are generally in poor agreement with rates measured at

similar temperatures for copepods collected from other oceanic regions. For example, Dam and Peterson (1988) measured a GER of 3.50 % min^{-1} for *Temora longicornis* at 17 °C. However, GERs predicted by the ET and LT models for a 35 ug copepod (Dam, 1986) at 17 °C are 1.41 and 1.39 % min^{-1}, respectively. Similarly, Kiørboe *et al.* (1982) reported a GER of 3.92 % min^{-1} for *Centropages hamatus* (10.4 μg dry wt) at 15 °C, while the ET model predicts a GER of 1.51 % min^{-1}, and the LT model a value of 1.30 % min^{-1}.

The lack of agreement between model predictions and GERs measured for copepods from different oceanic habitats may occur because copepods are acclimated physiologically to different temperature ranges. Comparisons of temperature dependency of physiological rates for animals residing in habitats with different temperature ranges often show that temperature-rate curves for cold-acclimated organisms are shifted towards lower temperatures, so that their rates are higher at a given temperature than values measured for similar sized organisms acclimated to warmer temperatures (Prosser and Brown, 1962). The relatively high GER measured at 17 °C for *Temora longicornis* collected from Long Island Sound (Dam and Peterson, 1988) and at 15 °C for *Centropages typicus* collected from the North Sea (Kiørboe *et al.*, 1982) were both measured near the upper limit of temperatures experienced by these animals in the field. The low GERs predicted by the ET or LT models for these copepods is consistent with the idea that a copepod acclimated to a particular seasonal temperature range will have a higher GER near the upper limit of its temperature range than will a similar sized

copepod for which the experimental temperature is near the lower range of seasonally experienced values.

The GER of a particular species of copepod probably can vary in response to forcing functions only within finite limits. These limits most likely reflect constraints imposed by gut morphology and digestive mechanisms that presumably operate to optimize the net gain of energy from ingested food items (Penry and Jumars, 1986; 1987). If this is the case, and temperature acclimation of GER does occur for copepods from different habitats, one would expect to find similar ranges of GERs for copepods from different oceanic habitats. A survey of the literature indicates that GERs do overlap extensively for copepods from different regions (see Appendix). Rates reported for tropical species range from 0.80 to 4.44 % min^{-1} (Arashkevich, 1977; Pasternak and Drits, 1988); rates of subtropical species (0.50 to 7.43 % min^{-1}) show a similar range (Kleppel *et al.*, 1985; Bautista *et al.*, 1988; Pasternak and Drits, 1989; Peterson *et al.*, 1990b; this study), as do values reported for temperate (0.65 to 8.00 % min^{-1}) (Dagg and Grill, 1980; Dam and Peterson, 1988; Tsuda and Nemoto, 1988; Dagg *et al.*, 1989; Ellis and Small, 1989), subarctic (0.43 to 4.76 % min^{-1}) (Kiorboe *et al.*, 1982; Dagg and Wyman, 1983; Kiorboe *et al.*, 1985; Simard *et al.*, 1985; Batchelder, 1986; Mackas and Burns, 1986; Wang and Conover, 1986; Head and Harris, 1987; Tiselius, 1988), and arctic species (0.03 to 6.00 % min^{-1}) (Tande and Båmstedt, 1985; Head, 1986; 1988; Head *et al.*, 1988; Hansen *et al.*, 1990). These results suggest that the empirical model of GER developed in my study may be applicable only for

subtropical copepods. Similar relationships between GER, body size, and temperature presumably would apply to copepods in other temperature regimes; however, the GER for a particular body size would be shifted relative to my data set to reflect the different seasonal range of temperatures.

There have been few other attempts to formulate predictive models of copepod gut evacuation rates. One exception is the study by Dam and Peterson (1988). These authors reported that linear regression of GER on temperature explained 75% of the seasonal variation among rates measured by *Temora longicornis*, and 72% of the variance when published rates of other copepods (mainly temperate and subarctic species) were included in their analysis. Their multi-species regression equation predicts a 5-fold increase in GER over a temperature range from -1 to 19 °C. Unfortunately, the published data do not include information on the seasonal variation of *T. longicornis* body size, so it is not possible to assess whether including this variable would have reduced the amount of unexplained variation.

The Dam and Peterson (1988) multi-species regression included GERs for copepods with dry weights that differed by more than an order of magnitude. By omitting body size as a variable, the use of this model implicitly assumes that GERs are independent, or only minimally affected by body size. This contradicts the results obtained in my study, which show that GER is strongly dependent on body size. For example, the GERs measured at 20 °C during October 1987 for abundant stages of 13 species of copepods ranging from 1.5 to 229 μg dry weight

varied 7-fold. Thus the variation of GERs observed at a single temperature, for different sized copepods, exceeded the range of GERs predicted by the Dam and Peterson (1988) regression for a 20 °C span of temperatures.

Ingestion Rates

Variation with body size: Ingestion rates (I) of pigment tended to increase with copepod total length, although the increase was statistically significant only for animals collected during October and May cruises (Fig. III.10). Comparison of these results with other studies which have examined the relation between body size and feeding rate is complicated by the fact that ingestion rates calculated in my study only measure feeding on phytoplankton. The total consumption of food by copepods was most likely underestimated (see below), and the proportion of phytoplankton in the diet may vary with copepod size. Most studies examining relationships between feeding rates and body size in copepods have expressed their results in terms of copepod dry weight. Slopes of log-log plots of ingestion rate versus body weight obtained in most studies tend to range between 0.5 and 0.85. For example, Ikeda (1977) reported a value of 0.623 for the weight exponent of tropical copepods, Nival and Nival (1976) obtained a value of 0.778 by combining data from several species, and Paffenhöfer (1971) calculated a value of 0.768 for different developmental stages of *Calanus helgolandicus*. All of these results are reasonably near the mean value of 0.80 $\pm$ 0.14 calculated by combining results

from several studies on relationships between ingestion rate and body size in poikilotherms (Peters, 1983). Mullin and Brooks (1976) reported that the weight exponent varied with food concentration for *Calanus pacificus*; ingestion rates were proportional to $W^{.35}$ at food concentrations below 57 μg C l^{-1}, and proportional to $W^{.70}$ at higher food concentrations. Particulate organic carbon (POC) concentrations never exceeded 50 μg C l^{-1} during the four cruises conducted in my study. The weight exponent calculated for the multi-species assemblage was 0.393 (Fig. III.11), which is near Mullin and Brook's value for low food concentrations. However, if the fraction of total food consumed consisting of pigmented material declined for larger copepods (as suggested by Table III.12), this slope would increase had ingestion rates been measured for both pigmented and non-pigmented components of the diet.

Comparison to estimated requirements for respiration: Herbivorous ingestion rates for all but a few species were not adequate to meet estimated metabolic requirements (Table III.13). This same result has been observed in several other studies of herbivorous grazing in copepods. For example, Simard *et al.* (1985) found that grazing rates of *Calanus finmarchicus* in the St Lawrence estuary, measured by gut fluorescence techniques, did not meet estimated energy requirements for respiration. Dagg and Grill (1980) reported that only 10 of 41 ingestion rates of *Centropages typicus* exceeded metabolic requirements in the New York Bight. Mullin and Brooks (1976) reported that at 25 of the 61 locations

sampled off southern California in April, and at 5 of 12 locations sampled in June, *Calanus pacificus* ingestion rates were below respiratory requirements. Dagg *et al.* (1980) reported similar results, with ingestion exceeding metabolic requirements for copepods off the coast of Peru in only 12 of 90 feeding experiments. In the subarctic Pacific, Dagg and Walser (1987) reported that herbivorous ingestion rates of *Neocalanus plumchrus* were consistently below rates needed to balance metabolic requirements in May 1984. In my study several factors conceivably could have contributed to this result, including: (1) episodic feeding which resulted in a temporary imbalance between food consumption and respiration rates; (2) underestimation of gut pigment concentrations; (3) phytoplankton C:Chl ratios exceeded the value of 80 used to convert pigment to carbon units; (4) assimilation efficiencies were higher than 0.70; and/or (5) copepods were consuming non-chlorophyllous material not detected by the gut fluorescence technique.

Measured ingestion rates might have been insufficient to meet estimated metabolic needs if at the time grazing rates were measured respiration and assimilation were temporarily out of balance. Many studies have observed diel changes in copepod grazing (e.g. Mackas and Bohrer, 1976; Dagg and Wyman, 1983; Head *et al.*, 1984; Welschmeyer *et al.*, 1984; Head *et al.*, 1985; Kiφrboe *et al.*, 1985; Kleppel *et al.*, 1985; Simard *et al.*, 1985; Christoffersen and Jespersen, 1986; Harris and Malej, 1986; Stearns, 1986; Head and Harris, 1987; Baustista *et al.*, 1988) and presumably there are periods of the 24-hr day when food intake is not sufficient to meet respiratory requirements and animals must rely on reserves

accumulated during periods of active feeding. Ingestion rates measured for copepods on VERTEX cruises took place almost exclusively at night, and while gut contents of some species have shown maximum values during the daylight (e.g. Kiørboe *et al.*, 1985), the most common pattern observed in studies cited above was nighttime maxima in gut pigment concentrations. Hayward (1980) reported that calanoid copepods from the North Pacific central gyre, including the three species of *Pleuromamma* and *Nannocalanus minor* found in my study, tended to have maximal gut contents at night. Therefore, it seems reasonable to assume that measured gut pigment levels were near maximum, or at least above the daily average, for most of the copepod species in this study. Assimilation rates calculated near the times of maximal grazing activity would be expected to exceed respiratory requirements to allow accumulation of reserves for use at other times of day.

Underestimation of gut pigment concentrations could have resulted from animals egesting some portion of their gut contents during the interval between collection and onset of experiments (Dagg *et al.*, 1989), or as a result of the collection process itself. The extent to which this occurred is unknown; however, it is believed to be of minimal importance as net tows were of relatively short duration (20-30 min) and experiments were begun within 5 min of capture.

Underestimation of gut pigment could also have occurred if pigment losses exceeded the 33% assumed for calculations of ingestion rate. Figure III.12A indicates that in several cases assimilation rates would have needed to increase by

more than a factor of 4 to balance expected respiratory requirements. To achieve this balance the percentage of non-detected pigment would need to exceed 80% of initial values. Although pigment losses of this magnitude have been reported (see Table III.2), only Conover *et al.* (1986) have reported mean losses above 61%. Other authors have suggested that high rates of pigment destruction are not typical of copepods, and may have resulted from fecal pellet fragmentation and loss of pigments during analysis (Kiørboe and Tiselius, 1987; Lopez *et al.*, 1988).

The gut pigment losses that apparently occur over the short intervals it takes food to pass through the gut strongly suggest that destruction of pigment is enzymatic in nature. Reported rates of pigment destruction by physical factors such as photo-oxidation and pH are too slow to account for reported losses (Daley, 1973; Daley and Brown, 1973). The large variability of literature values (0-99%), both within and between species, could be interpreted as arising from differences in the activity or concentration of enzymes in animals having different feeding histories and nutritional requirements. Since the nutritional history of different developmental stages, species, and individuals are likely to vary considerably, the application of a correction factor (33%) near the mean of reported values appears more justified than assuming an extreme value when estimating population grazing rates. Peterson *et al.* (1990a) has suggested that chlorophyll is not digested or reduced to non-fluorescing molecules in copepod guts, and that reports of high losses may be due to methodological problems. These authors constructed pigment budgets for *Calanoides carinatus* which showed pigment recoveries ranging from

85 to 133% (mean = 102.5%, SD = 16). If no loss of pigments occurred during my experiments, the discrepancy between ingestion rates and estimated respiratory requirements would increase. The issue of pigment loss, however, remains unresolved. Penry and Frost (1991) have reported that the fraction of chlorophyll-*a* that is degraded to a colorless product in *Calanus pacificus* can vary with food acclimation and ingestion rate. The fraction of pigment which was degraded was 2-4 times higher for copepods acclimated to high food concentrations (4000 cells ml^{-1}) than for copepods acclimated to low food concentrations (1000 cells ml^{-1}). Given the current state of uncertainty regarding how to deal with the issue of pigment loss, the correction assumed in this study appears reasonable.

Another potential source of error which may have contributed to the calculation of low ingestion rates is the choice of the C:Chl ratio used to convert herbivorous feeding rates to a carbon basis. C:Chl ratios of phytoplankton cultures are quite variable, ranging from 10 to 230 (Eppley, 1968; Platt *et al.*, 1977), with most reported values falling between 30 to 80 (Harris, 1986). Ratios calculated during my study are assumed to represent average ratios for phytoplankton within the photic zone (see methods), and ranged from 36 to 117 with a mean of 80. This mean ratio was used to convert pigment concentration to carbon for all cruises, because regressions used to calculate ratios for each cruise separately were based on limited data sets, and coefficients of determination were low for some of the cruises. However, even if the maximum C:Chl ratio calculated for these cruises (117) had been used it would not have increased most of the ingestion rates

sufficiently to balance predicted metabolic requirements.

Increasing the assimilation efficiency above 0.7 would also decrease the discrepancy between respiratory requirements and ingested carbon. A value of 0.7 is usually considered typical of planktonic herbivores (Huntley and Boyd, 1984); however, higher efficiencies are common especially for animals feeding carnivorously. For example, Corner *et al.* (1976) reported assimilation efficiencies higher than 90% for *Calanus helgolandicus* feeding on *Elminius* nauplii, and Alvarez and Matthews (1975) reported a value of 95% for *Chiridius armatus* feeding on mixed zooplankton. However, even assuming an assimilation efficiency of 100% would not increase assimilation rates enough to meet estimated respiratory requirements for most copepod species in my study.

The assumptions made regarding gut pigment loss, plus the potential errors associated with the C:Chl ratio and assimilation efficiency, all may have contributed to the calculation of low herbivorous ingestion rates for copepods in this study; however, the most likely explanation is that copepods were supplementing their diet by ingesting animal prey and/or detritus. For example, if one still assumes 33% loss of gut pigment and an assimilation efficiency of 0.7, but uses the measured POC:Chl-*a* ratios in Table III.14, carbon ingestion rates could increase by up to a factor of 6.5 (using the highest ratio (495) in Table III.14). Increasing carbon ingestion rates by this magnitude would enable all but 6 copepod species to at least meet metabolic requirements (Table III.13). Paffenhöfer and Knowles (1980) have suggested that omnivorousness is inherent in

most calanoid species, and Hayward (1980) stated that calanoid copepods collected from the North Pacific central gyre, which included several of the species in my study, all tended to be omnivores and food generalists. Landry (1981) expressed the opinion that feeding preferences of pelagic copepods probably form a continuum of behavioral types ranging from a strong preference for phytoplankton to a strong preference for zooplankton prey, and therefore the terms herbivore and carnivore may be artificial in that most species feed omnivorously during all or part of their lifetimes. The morphology of copepod mouthparts, however, does indicate the general type of food copepod species are morphologically best adapted to eat (Anraku and Omori, 1963; Mullin, 1966; Arashkevich, 1969; Arashkevich and Timonin, 1970). Thus, while there are probably no obligate herbivores among calanoid copepods (Mullin, 1966), the proportion of phytoplankton in the diet of species typically considered as herbivores would be expected to be greater than species classified as omnivores or carnivores.

The patterns exhibited by different species in the percentage of respired carbon potentially derived from herbivorous grazing (Table III.13) tend to agree with generally accepted notions regarding feeding preferences of these species. For example, from examination of the morphology of copepod mouthparts and examination of gut contents, copepods within the families Acartiidae, Calanidae, Calocalanidae, and Eucalanidae are considered to feed primarily as herbivores, while members of Centropagiidae, Lucicutiidae, and Metridiidae generally feed omnivorously, and members of Aetideidae and Candaciidae are usually described

as carnivorous (Wickstead, 1962; Anraku and Omori, 1963; Mullin, 1966; 1967; Arashkevich, 1969; Arashkevich and Timonin, 1970; Timonin, 1971, Arashkevich *et al.*, 1982; Raymont, 1983). Species with ingestion rates exceeding estimated respiratory demands in my study included *Acartia clausii*, *Calanus tenuicornis*, *Mecynocera clausii*, *Eucalanus crassus*, and *E. elongatus*, all members of families listed as mainly herbivorous. The omnivorous-tending copepods *Lucicutia flavicornis*, *Pleuromamma gracilis* and *P. xiphias* also had herbivorous ingestion rates exceeding estimated respiratory requirements. However, these species showed rather large fluctuations between cruises, which might reflect switches in the proportion of plant and animal matter being consumed. Switching of feeding preferences has been reported for other species (e.g. Landry, 1981), and Kleppel *et al.* (1988) found that the proportion of gut contents consisting of animal carbon was inversely related to the biomass and productivity of phytoplankton. The copepod with the largest discrepancy between herbivorous ingestion rates and estimated requirements for respiration was *Undeuchaeta plumosa*, a member of the family Aetideidae which consists of species considered to feed predominantly carnivorously.

The data for different developmental stages in this study appear to support the proposition made by Paffenhöfer and Knowles (1980) that at least the late copepodite stages and adults of most marine planktonic calanoids are omnivorous. The fraction of respiration potentially derived from herbivorous grazing declined with increasing developmental stage for *Calanus tenuicornis*, *Eucalanus crassus*,

E. elongatus, and *Pleuromamma xiphias* (Table III.13).

The estimates of herbivorous grazing relative to respiratory demand indicate that the vast majority of material in the guts of many copepod species and developmental stages in my study must have consisted of non-pigmented material. Other studies have reached similar conclusions. For example, Dagg and Walser (1987) calculated that herbivorous ingestion rates of *Neocalanus plumchrus* CV from the subarctic Pacific met only 9 - 36% of respiratory requirements (using an assimilation efficiency of 0.8). Yet, Miller and Nielsen (1988) were able to measure growth for this copepod (carbon specific growth rate of 0.15 day^{-1}), implying that feeding rates must have exceeded respiratory requirements and that most of the gut material must have consisted of non-pigmented material. A recent study by Kleppel *et al.* (1988) also demonstrates the importance of carnivorous feeding for copepods generally considered to feed predominantly as herbivores. In their study, *in situ* carnivorous feeding by *Calanus pacificus* and *Clausocalanus* sp. were determined from the concentrations of plant and animal carotenoids isolated from the guts of copepods. The percentage of microzooplankton in the gut of *C. pacificus* ranged from 93.8 to 99.9% for animals collected at different times of day, while the diet of *Clausocalanus* sp. shifted with time of day, with microzooplankton comprising 0 to 55.3% of gut contents during the night and 88.2 to 98.3% of gut contents during the day.

The widespread occurrence of omnivory among calanoid copepods suggests that in order to estimate more realistic grazing rates, the gut fluorescence technique

should be expanded to incorporate grazing on animal matter. GERs could still be determined using chlorophyll and its derivatives as a tracer of gut food passage, but carbon:pigment ratios representative of material actually being consumed will be required before ingestion can be accurately estimated. The technique by Kleppel *et al.* (1988) determines the zooplankton gut contents by measuring C:carotenoid ratios for phytoplankton and microzooplankton, and measuring carotenoid concentrations in the guts of field captured animals. This method, although labor intensive, has the advantage of including grazing on microzooplankton and could be combined with estimates of gut chlorophyll evacuation rates to obtain more realistic estimates of *in situ* grazing rates of copepods.

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Appendix

Summary of Copepod Gut Evacuation Rates

Reported in the Literature.

Summary of copepod gut evacuation rates (GER; % min^{-1}) reported in the literature. N is the number of experiments; (-) indicates quantity unknown or not available; n.p. = natural particulates; e.a. = epontic algae; p.a. = pelagic algae; C. sp. = Chaetoceros sp.; C.h. = Corethron hystrix; C.p. = Coscinodiscus perforatus; D.b. = Ditylum brightwellii; P.t. = Phaeodactylum tricornutum; R.b. = Rhodomonas baltica; S.t. = Scrippsiella trochoidea; T.w. = Thalassiosira weissflogii = T.w.; T.f. = T. fluviatilis; ; A. = Amphidinium; G. = Gyrodinium; Gm. = Gymnodinium; P. = Prorocentrum; S. = Streptotheca

Species	Stage	Location	Body Size	Temp	GER	N	Food	Concentration	Source
Acartia clausii	CVI	San Juan Islands	.68-.70 mm[a]	13	4.00 ± 0.77[b]	(1)	n.p.	-	Hargis 1977
Acartia grani	CVIf	Alboran Sea	-	22.7	5.30	(1)	n.p.	5-8 μg Chl-a l^{-1}	Bautista *et al.* (1988)
	CVIm	Alboran Sea	-	22.7	4.00	(1)	n.p.	5-8 μg Chl-a l^{-1}	Bautista *et al.* (1988)
Acartia tonsa	CVI	Lab culture	-	13.7	4.65 ± 0.21[c]	(2)	R.b.	-	Kiorboe & Tiselius (1987)
	-	-	-	17-19	1.82[d]	(5)	P.	1 mg l^{-1}	Arashkevich (1977)
	-	-	-	17-19	1.67[d]	(3)	P.	2 mg l^{-1}	Arashkevich (1977)
	-	-	-	17-19	2.70[d]	(2)	P.	10 mg l^{-1}	Arashkevich (1977)
	-	-	-	17-19	2.19 ± 0.51[d,e]	(11)	-	-	Arashkevich (1977)
	CIV-CVI	Los Angeles harbor	-	20	2.90	(1)	n.p.	< 2 μg Chl-a l^{-1}	Kleppel *et al.* (1985)
Acartia sp.	CV-CVI	North Sea	-	10	1.02	(1)	T.f.	> $5x10^6$ $\mu m^3 ml^{-1}$	Tiselius (1988)
Calanoides carinatus	CVIf	Hout Bay, S. Africa	-	15	5.98	(5)	T.w.	1500,8000 cells ml^{-1}	Peterson *et al.* (1990a)
Calanus asutralis	CVIf	~32°S, 17°E	81 μgC	12	4.20[f]	(2)	n.p.		Peterson *et al.* (1990b)
		~32°S, 17°E	81 μgC	15	5.08 ± 0.01[f]	(6)	n.p.		Peterson *et al.* (1990b)
Calanus finmarchicus	CVI	Barents Sea	82 μgC	-1.0	3.20	(1)	n.p.	0.4-9.6 μg Chl-a l^{-1}	Tande & Bamstedt (1985)
		North Sea	94 μgC	5.5	4.56 ± 0.29[g]	(2)	n.p.	0.5-20 μg Chl-a l^{-1}	Kiorboe *et al.* (1985)
		North Sea	-	7-9	4.76	(1)	T.f.	> $5x10^6$ μm^3ml-1	Tiselius (1988)
	CV	Barents Sea	126 μgC	-1.0	1.70	(1)	n.p.	0.5-9.6 μg Chl-a l^{-1}	Tande & Bamstedt (1985)
		St. Lawrence estuary	300 μg dwt	5.0	2.20	(1)	n.p.	< 1.0 μg Chl-a l^{-1}	Simard *et al.* (1985)
Calanus glacialis	CVI	Barents Sea	509 μgC	-1.0	1.60	(1)	n.p.	0.4-9.6 μg Chl-a l^{-1}	Tande & Bamstedt 1985
	CV	Barents Sea	409 μgC	-1.0	1.70	(1)	n.p.	0.4-9.6 μg Chl-a l^{-1}	Tande & Bamstedt 1985
		Barents Sea	-	0.0	1.40	(2)	n.p.	< 900 cells ml^{-1}	Hansen *et al.* 1990

Appendix (Continued).

Species	Stage	Location	Body Size	Temp	GER	N	Food	Concentration	Source
Calanus glacialis	CV	Arctic - Sta. 1	-	-0.5	1.00	(1)	n.p.	-	Head (1986)
		Arctic - Sta. 2	-	-0.5	1.42 ± 0.12[e]	(2)	n.p.	-	Head (1986)
		Arctic - Sta. 3	-	-0.5	0.51 ± 0.32[e]	(5)	n.p.	-	Head (1986)
		Arctic	-	-0.5-2	1.62 ± 0.78[h]	(10)	n.p.	1.5-17 ug Chl-a l^{-1}	Head *et al.* (1988)
	CIV	Barents Sea	162 μgC	-1.0	1.40	(1)	n.p.	0.8-4.3 μg Chl-a l^{-1}	Tande & Bamstedt (1985)
		Arctic	-	-0.5-2	1.73 ± 0.58[h]	(4)	n.p.	1.5-17 ug Chl-a l^{-1}	Head *et al.* (1988)
	CIII	Barents Sea	-	0.0	2.70	(1)	n.p.	< 900 cells ml^{-1}	Hansen *et al.* (1990)
	CII	Barents Sea	-	0.0	1.50	(1)	n.p.	< 900 cells ml^{-1}	Hansen *et al.* (1990)
Calanus hyperboreus	CV	Arctic - Sta. 3	-	-0.5	0.78 ± 0.60[e]	(5)	n.p.	-	Head (1986)
		Arctic	-	-0.5-2	1.10 ± 0.57[h]	(9)	n.p.	1.5-17 μg l^{-1}	Head *et al.* (1988)
	CIV	Arctic - Sta. 1	-	-0.5	1.23	(1)	n.p.	-	Head (1986)
		Arctic - Sta. 2	-	-0.5	1.35 ± 0.20[e]	(3)	n.p.	-	Head (1986)
		Arctic	-	-0.5-2	1.58 ± 0.87[h]	(9)	n.p.	1.5-17 ug l^{-1}	Head *et al.* (1988)
	CIII	Arctic - Sta. 1	-	-0.5	0.83	(1)	n.p.	-	Head (1986)
		Arctic - Sta. 2	-	-0.5	1.37 ± 0.36[e]	(3)	n.p.	-	Head (1986)
		Arctic		-0.5-2	2.18 ± 0.98[h]	(11)	n.p.	1.5-17 ug l^{-1}	Head *et al.* (1988)
Calanus marshallae	CVI	44.62°N, 124.07°W	-	10	5.04 ± 0.84[i]	(5)	T.w.	2.0 μg l^{-1} Chl-a	Ellis & Small (1989)
		44.62°N, 124.07°W	-	10	4.76 ± 0.81[i]	(4)	T.w.	3.6 μg l^{-1} Chl-a	Ellis & Small (1989)
		44.62°N, 124.07°W	-	10	5.56 ± 0.71[i]	(6)	T.w.	6.7 μg l^{-1} Chl-a	Ellis & Small (1989)
		44.62°N, 124.07°W	-	10	6.38 ± 1.36[i]	(6)	T.w.	14.9 μg l^{-1} Chl-a	Ellis & Small (1989)
Calanus pacificus	CVI	48.65°N, 123.50°W	2.0-2.2 mm[a]	12	4.17	(1)	C.p.	10 μg l^{-1} Chl-a	Mackas & Burns (1986)
		47.76°N, 122.83°W	-	-	4.84 ± 1.89[j]	(4)	T.w.	2000 cells ml^{-1}	Dagg *et al.* (1989)
		47.76°N, 122.83°W	-	-	2.62 ± 1.36[k]	(20)	T.w.	2000 cells ml^{-1}	Dagg *et al.* (1989)
		29.48°N, 115.73°W	-	12-13	4.25	(1)	P.t.	1.0 μg l^{-1} Chl-a	Pasternak & Drits (1988)
		29.48°N, 115.73°W	-	12-13	2.51	(1)	P.t.	1.3 μg l^{-1} Chl-a	Pasternak & Drits (1988)
		29.48°N, 115.73°W	-	12-13	2.94	(1)	P.t.	4.8 μg l^{-1} Chl-a	Pasternak & Drits (1988)

Appendix (Continued).

Species	Stage	Location	Body Size	Temp	GER	N	Food	Concentration	Source
Calanus pacificus	CVI	29.48°N, 115.73°W	-	12-13	4.25	(1)	n.p.	-	Pasternak & Drits (1988)
Centropages hamatus	CVI	North Sea	-	1	0.60	(30)	D.b.	> 1.5 $\mu g\ l^{-1}$ chl-a	Kiørboe *et al.* (1982)
		North Sea	15.5 μg dwt	5	1.08	(31)	D.b.	> 1.5 $\mu g\ l^{-1}$ Chl-a	Kiørboe *et al.* (1982)
Centropages hamatus	CVI	North Sea	10.4 μg dwt	10	2.18	(38)	D.b.	> 1.5 $\mu g\ l^{-1}$ Chl-a	Kiørboe *et al.* (1982)
		North Sea	-	11.5	4.00	(1)	T.f.	> 5E6 $\mu m^3\ ml^{-1}$	Tiselius (1988)
		North Sea	10.4 μg dwt	15	3.92	(25)	D.b.	> 1.5 $\mu g\ l^{-1}$ Chl-a	Kiørboe *et al.* (1982)
Centropages typicus	CVI	40.77°N, 72.50°W	16.7 μgC	15	1.11	(1)	C. sp.	high	Dagg & Grill (1980)
Centropages sp.	-	-	-	17-19	0.80[d]	(2)	G.	2 mg l^{-1}	Arashkevich (1977)
	-	-	-	17-19	0.80 ± 0.05[d,e]	(2)	-	-	Arashkevich (1977)
Clausocalanus mastigophorus		-	-	17-19	3.08 ± 0.33[d]	(6)	S.	0.5,1 mg l^{-1}	Arashkevich (1977)
	-	-	-	17-19	4.44 ± 0.70[d,e]	(6)	-	-	Arashkevich (1977)
Eucalanus attenuatus	-	-	-	17-19	1.82[d]	(5)	P.	1 mg l^{-1}	Arashkevich (1977)
	-	-	-	17-19	2.00[d]	(3)	P.	3 mg l^{-1}	Arashkevich (1977)
	-	-	-	17-19	3.33[d]	(2)	P.	10 mg l^{-1}	Arashkevich (1977)
	-	-	-	17-19	2.00 ± 0.53[d,e]	(9)	-	-	Arashkevich (1977)
Eucalanus subtenuis	-	-	-	17-19	2.86[d]	(2)	P.	1 mg l^{-1}	Arashkevich (1977)
	-	-	-	17-19	3.33[d]	(2)	P.	3 mg l^{-1}	Arashkevich (1977)
	-	-	-	17-19	2.50[d]	(1)	Gm.	1.5 mg l^{-1}	Arashkevich (1977)
	-	-	-	17-19	2.86[d]	(2)	S.	1.5 mg l^{-1}	Arashkevich (1977)
	-	-	-	17-19	2.96 ± 0.42[d,e]	(8)	-	-	Arashkevich (1977)
Eurytemora herdmani	-	-	-	-	1.70[l]	(1)	-	-	Mackas & Bohrer (1976)
Metridia longa	CVI	Arctic	-	-0.5-2	0.18 ± 0.12[h]	(4)	n.p.	1.5-17 ug Chl-a l^{-1}	Head *et al.* (1988)

Appendix (Continued).

Species	Stage	Location	Body Size	Temp	GER	N	Food	Concentration	Source
Metridia pacifica	CVI	50.00°N, 145.00°W	-	8.4	2.20	(1)	T.w.	-	Batchelder (1986)
		44.62°N, 124.07°W	-	10.2	2.00 ± 0.57	(2)	T.w.	-	Batchelder (1986)
		50.00°N, 145.00°W	-	12.0	1.70	(1)	T.w.	-	Batchelder (1986)
		44.62°N, 124.07°W	1.5-1.7 mm[a]	12.0	2.78	(1)	C.p.	10 $\mu g\ l^{-1}$ Chl-a	Mackas & Burns (1986)
		48.65°N, 122.50°W	-	13.5	1.40	(1)	C.h.	-	Batchelder (1986)
Nannocalanus minor	-	-	-	17-19	1.33[d]	(3)	P.	1 $mg\ l^{-1}$	Arashkevich (1977)
	-	-	-	17-19	1.38 ± 0.07[d,e]	(3)	-	-	Arashkevich (1977)
Neocalanus cristatus	CV	Bering Sea	5631 µgdwt	8.5	1.83	(1)	n.p.	< 2 μg Chl-a l^{-1}	Dagg & Wyman (1983)
Neocalanus gracilis	CVI	-	-	17-19	3.03[d]	(3)	A.	2 $mg\ l^{-1}$	Arashkevich (1977)
Neocalanus plumchrus	CV	Bering Sea	567 µgdwt	4.0	1.46	(1)	n.p.	< 14 μg Chl-a l^{-1}	Dagg & Wyman (1983)
		Bering Sea	567 µgdwt	7.1	2.78	(1)	n.p.	< 14 μg Chl-a l^{-1}	Dagg & Wyman (1983)
		Bering Sea	567 µgdwt	7.4	3.16	(1)	n.p.	< 14 μg Chl-a l^{-1}	Dagg & Wyman (1983)
		Bering Sea	567 µgdwt	7.7	2.72	(1)	n.p.	< 14 μg Chl-a l^{-1}	Dagg & Wyman (1983)
		Bering Sea	567 µgdwt	9.2	3.88	(1)	n.p.	< 14 μg Chl-a l^{-1}	Dagg & Wyman (1983)
		48.63°N, 123.07°W		8.0	4.27 ± 0.91	(33)	T.w.	> 4 μg Chl-a l^{-1}	Dagg & Walser (1987)
		48.63°N, 123.07°W	-	8.0	1.18	(1)	T.w.	0.33 μg Chl-a l^{-1}	Dagg & Walser (1987)
		50°N, 145°W	-	-	0.94	(5)	n.p.	0.44 μg Chl-a l^{-1}	Dagg & Walser (1987)
Paracalanus parvus	CVI	North Sea	-	10	3.03	(1)	T.f.	> $5x10^6\ \mu m^3 ml^{-1}$	Tiselius (1988)
	CVIf	~ 32°S, 17°E	3.6 µgC	12	4.20[f]	(2)	n.p.	-	Peterson *et al.* (1990b)
		~ 32°S, 17°E	3.6 µgC	15	5.08 ± 0.01[f]	(6)	n.p.	-	Peterson *et al.* (1990b)
Pleuromamma xiphias	-	-	-	17-19	3.57[d]	(3)	S.	3 $mg\ l^{-1}$	Arashkevich (1977)
	-	-	-	17-19	3.64[d,e]	(3)	-	-	Arashkevich (1977)
Pleuromamma sp.	CVI	6.97°N, 135.97°W	-	23-24	1.18 ± 0.38	(3)	n.p.	-	Pasternak & Drits (1988)

Appendix (Continued).

Species	Stage	Location	Body Size	Temp	GER	N	Food	Concentration	Source
Pseudocalanus elongatus	CVI	North Sea	-	10	3.45	(1)	T.f.	> $5x10^6$ $\mu m^3 ml^{-1}$	Tiselius (1988)
Pseudocalanus mimus	CVI	44.62°N, 124.07°W	15.2 µg dwt	7	3.75 ± 0.25	(1)	T.w.	25 µg Chl-a l^{-1}	Ellis (unpubl. data)
		44.62°N, 124.07°W	15.2 µg dwt	10	4.94 ± 0.87	(1)	T.w.	25 µg Chl-a l^{-1}	Ellis (unpubl. data)
Pseudocalanus minutus	CVI	39.33°N, 141.95°E		4.0	1.32	(1)	S.t.	2000 cells ml^{-1}	Tsuda & Nemoto (1987)
Pseudocalanus sp.	-	Arctic	-	-1.5	9.50 ± 1.56[m]	(2)	T.w.	18-24 µg Chl-a l^{-1}	Head (1988)
	-	Arctic	-	-1.5	2.67	(1)	e.a.	~25-30 µg Chl-a l^{-1}	Head (1988)
	-	Arctic	-	-1.5	6.00	(1)	p.a.	~25-30 µg Chl-a l^{-1}	Head (1988)
	CVI-CII	Bedford Basin	6.7 µg dwt	0	0.43	(1)	n.p.	< 3.5 µg l^{-1} chl-a	Head & Harris (1987)
	CVI-CII	Bedford Basin	7.5 µg dwt	2.5	1.98	(1)	n.p.	< 10 µg l^{-1} chl-a	Head & Harris (1987)
Rhincalanus cornutus	-	-	-	17-19	2.50[d]	(2)	-	-	Arashkevich (1977)
Rhincalanus nastus	-	-	-	17-19	2.86[d]	(2)	A.	2 mg l^{-1}	Arashkevich (1977)
	-	-	-	17-19	2.50[d]	(2)	P.	2 mg l^{-1}	Arashkevich (1977)
Scolecithrix danae	-	-	-	17-19	0.83[d]	(2)	P.	1 mg l^{-1}	Arashkevich (1977)
	-	-	-	17-19	0.95 ± 0.19[d,e]	(2)	-	-	Arashkevich (1977)
Temora longicornis	CVI	Long Island Sound	-	0	1.40	(1)	T.w.	4.5 µg Chl-a l^{-1}	Dam & Peterson (1988)
		Long Island Sound	-	1	0.65	(1)	n.p.	10.6 µg Chl-a l^{-1}	Dam & Peterson (1988)
		Long Island Sound	-	3	1.60	(1)	T.w.	5.0 µg Chl-a l^{-1}	Dam & Peterson (1988)
		Bedford Basin	1.038 mm[a]	5	1.74 ± 0.40	(4)	T.w.	8 µg Chl-a l^{-1}	Wang & Conover (1986)
		Bedford Basin	1.038 mm[a]	5	2.11 ± 0.16	(4)	T.w.	16 µg Chl-a l^{-1}	Wang & Conover (1986)
		North Sea	10 µgC	5.5	3.69 ± 1.85[g]	(2)	n.p.	0.5-20 µg Chl-a l^{-1}	Kiorboe *et al.* (1985)
		Long Island Sound	-	6	2.40	(1)	n.p.	2.8 µg Chl-a l^{-1}	Dam & Peterson (1988)
		Long Island Sound	-	6	1.80	(1)	T.w.	5.0 µg Chl-a l^{-1}	Dam & Peterson (1988)
		Long Island Sound	-	6.4	3.10	(1)	n.p.	6.2 µg Chl-a l^{-1}	Dam & Peterson (1988)

Appendix (Continued).

Species	Stage	Location	Body Size	Temp	GER	N	Food	Concentration	Source
Temora longicornis	CVI	Long Island Sound	-	9	3.30	(1)	n.p.	5.0 μg Chl-a l^{-1}	Dam & Peterson (1988)
		Long Island Sound	-	10	3.80	(1)	n.p + T.w.	14.3 μg Chl-a l^{-1}	Dam & Peterson (1988)
		North Sea	-	10	2.86	(1)	T.f.	> $5x10^6$ $\mu m^3 ml^{-1}$	Tiselius (1988)
		Bedford Basin	.989 mm[a]	10	1.69 ± 0.42	(7)	T.w.	8 μg Chl-a l^{-1}	Wang & Conover (1986)
		Bedford Basin	1.038 mm[a]	10	1.26 ± 0.48	(8)	T.w.	8 μg Chl-a l^{-1}	Wang & Conover (1986)
		Long Island Sound	-	11.5	3.05 ± 0.64	(2)	n.p.	2.5,4.1 μg Chl-a l^{-1}	Dam & Peterson (1988)
Temora longicornis	CVI	Long Island Sound	-	13	4.25 ± 0.21	(2)	n.p.	4.0,5.0 μg Chl-a l^{-1}	Dam & Peterson (1988)
		Long Island Sound	-	15	3.9	(1)	n.p.	9.0 μg Chl-a l^{-1}	Dam & Peterson (1988)
		Long Island Sound	-	17	3.50	(1)	n.p.	10.5 μg Chl-a l^{-1}	Dam & Peterson (1988)
Undinula darwini	CVI	7.68°N, 15.38°W	-	23-24	1.26	(1)	n.p.	-	Pasternak & Drits (1988)

a) cephalothorax length
b) estimated by timing first appearance of colored phytoplankton in fecal pellets
c) mean of feeding and non-feeding gut evacuation rates calculated for the initial 30 min.
d) calculated by converting data reported as duration of digestion (= gut passage time)
e) mean for experiments conducted at different times of day
f) mean of rates for *Paracalanus parvus* females and *Calanus asutralis* females and CV and CIV copepodites.
g) mean of rates measured on 7 April and 12 April 1984
h) mean of nighttime rates measured between 28 August and 15 September 1986
i) mean of feeding and non-feeding gut evacuation rates calculated for the initial 90 min.
j) calculated by dividing gut pigment content by the amount of fecal pigment produced during a 6 hr incubation on 9 May 1986.
k) protocol same as above (j) but using animals collected in August 1986.
l) rate estimated by Kiorboe *et al.* (1982)
m) mean of feeding and non-feeding gut evacuation rates calculated for the initial 15 min.