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Title: Seasonal Relationship Between The Digestive Enzyme Activity Of Laminarinase And Ingestion Rate Of Acartia clausii

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The relationship between the digestive enzyme activity of laminarinase and ingestion rate of the copepod Acartia clausii at five food concentrations of Thalassiosira weissflogii were investigated in a series of experiments using copepods collected from Yaquina Bay, Oregon during 1982 and 1983. Copepods were acclimated to these five food concentrations and filtered seawater for three days in the laboratory. Following this interval, 24-hour grazing experiments were performed to determine the ingestion rates of the copepods at these food concentrations. Laminarinase activities of the copepods from all food levels and filtered seawater were determined following the conclusion of these grazing experiments.

Ingestion rates for Acartia clausii increased approximately linearly with food concentrations below 2.5×10^6 um^3/ml and reached a maximum rate at food concentrations above this level. Ivlev equation fits to the data were statistically the same for experiments conducted with animals collected during fall and winter months, with a maximum

ingestion rate for the combined data of 10.5×10^6 um^3/copepod/day. The maximum ingestion rates increased by about a factor of 1.5 for experiments conducted during spring and summer months.

Copepod laminarinase activity in individual experiments remained relatively constant at all food concentrations for five days, and decreased only for starved individuals. There was no significant correlation between laminarinase activity and ingestion rate in the majority of experiments. Therefore, this enzyme does not appear to be a useful index of ingestion rate in short-term experiments. The level of copepod laminarinase activity was found to vary seasonally. The highest activities were found during spring months (April 1982) and decreased to low levels during the fall and winter.

The maximum ingestion rate for A. clausii was positively correlated with the level of laminarinase activity. Thus, this enzyme appears to be an index of the maximum ingestive capacity of this copepod. Presumably the level of digestive enzyme activity represents a physiological adjustment in the rate of food processing in response to biological or physical factors operating over time intervals in excess of five days for A. clausii. The time required for changes in digestive enzyme levels may be related to the time required for production and rearrangement of specific enzyme-producing cells in the mid-gut.

Seasonal Relationship Between the Digestive Enzyme Activity of Laminarinase and Ingestion Rate of *Acartia clausii*

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Redacted for privacy

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Redacted for privacy

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Introduction

An understanding of trophic relations among marine organisms remains one of the fundamental goals of marine biologists. Because of the enormous complexity of oceanic ecosystems and the large numbers of species involved the trophic dynamics approach seeks to understand this system by grouping organisms with similar life histories and feeding habits into trophic levels and formulating certain generalizations regarding rates and amounts of energy transferred between these groups. Ultimately, given a sufficient comprehension of these relationships, marine biologists would like to be able to predict the production of species of interest and especially those organisms which have economic importance to man.

The initial input of energy into oceanic ecosystems is solar radiation which is converted by phytoplankton into organic matter. As this potential energy is passed to successively higher trophic levels energy is lost from the system through respiration and the excretion of organic compounds; thus the number of trophic levels supported at a given location depends upon the efficiency of energy transport between lower trophic levels and the magnitude of initial energy conversion by the primary producers. Since species of interest to man frequently occupy higher trophic levels, our ability to accurately determine their production depends to a great extent on initial estimates of the magnitude of energy transfer at lower trophic levels. Several mathmatical models of marine communities, particularly the lower trophic levels represented by plankton, have been formulated to accomplish this task (e.g. Riley, 1963; Steele, 1974; Landry, 1976;

Steele and Frost, 1977; Steele and Mullin, 1977). Such models require accurate descriptions of the rates of feeding, growth, metabolism, and production of dominant species within marine ecosystems and their relationship to changes in enviromental factors. In oceanic food webs, calanoid copepods constitute prominant pathways for energy flow between primary producers and the larger predatory species of zooplankton and nekton (Frost, 1972). Copepods are one of the main components of the plankton and are frequently the largest group, both numerically and in terms of biomass, found in surface waters. Therefore, a detailed knowledge of the grazing impact of herbivorous copepods is required before we can successfully apply the techniques of trophic dynamics to oceanic ecosystems.

Many studies have been devoted to examining the feeding behavior of marine planktonic copepods; however, attempts to quantify the grazing impact of these organisms on the phytoplankton community have had only limited success. One reason for this difficulty is the apparent complexity of the feeding response. Copepod species have different mouthpart structures and feeding capabilities (Anraku and Omori, 1963; Itoh, 1970; Nival and Nival, 1976; Schnack, 1981; Vanderploeg and Ondricek-Fallscheer, 1982; Dexter, 1983), and thus it has proven difficult to generalize on grazing activity. Even within the category of predominantly herbivorous copepods there appear to be differences in feeding strategies regarding particle selectivity or lack of it, and differences in the food capture process (Alcarez et al., 1980; Rosenberg, 1980; Koehl and Strickler, 1981; Paffenhofer et al., 1982; Strickler, 1982; Yule and Crisp, 1983). The issue of particle selection, in particular, makes generalization of particle

removal in herbivorous copepods extremely difficult. Particle selection based on particle size, particle abundance, particle type and/or 'taste' has all been documented (see Conover and Huntley, 1980; Frost, 1980; and Kerfoot, 1980 for recent reviews of filter feeding and particle capture in copepods).

Another issue which hampers our ability to evaluate the grazing impact of copepods on phytoplankton is the uncertainty involved in extrapolation of laboratory-derived grazing rates to field situations. There are many problems associated with estimating the natural rate of any process from laboratory data and this is especially true for feeding relationships. Factors known to affect the laboratory measurement of grazing rates include temperature, the size of the experimental container, the duration of the experiment, the illumination levels, the concentration and age of the phytoplankton cells used as food, the length of time animals are preconditioned to the food source, and the method used to obtain the grazing rates (see Anraku, 1964 and Mullin, 1967 for a discussion of these effects). In recognition of these problems, several investigators recently have attempted to obtain more 'natural' grazing rates by measuring the consumption of natural particle assemblages by copepods collected simultaneously with the particles (Poulet, 1973; Boyd et al., 1980; Dagg et al., 1980; O'Conners et al., 1980; Huntley, 1981). These quasi-field studies eliminate the problems of artificial food sources and concentrations; however, they still retain the problems of confinement, illumination, and manipulation imposed on the animals before and/or during the feeding period. These difficulties point up the need for techniques of determining copepod feeding rates

which eliminate, or at least greatly minimize, the handling time and separation of animals from their food source.

One approach appears to meet the above criteria; measurement of the activities of selected digestive enzymes and the concomitant relationships of these activities to the amount of food ingested by the animals. If the relationship between digestive enzyme activity and ingestion rate can be determined, the grazing rates of copepods in the field could easily be determined by measuring enzyme activities from collected zooplankton samples. Such a technique would eliminate all of the problems discussed above; that is, grazing rate measurements would not occur under artificial conditions, and the need for time-consuming feeding experiments and excessive manipulation of the animals would be eliminated. This method would, however, still leave unanswered the question of what the animals were feeding on, but this could be determined by other techniques such as examination of gut contents.

The enzyme approach to determining ingestion rates in marine copepods had its beginnings with the work of Mayzaud and Conover (1976). These authors measured the activities of several digestive enzymes in mixed zooplankton samples during the summer and fall of 1974, and examined the relationships of these enzyme activities to the biochemical composition of the particulate matter on which zooplankton were presumably feeding. They found that the activities of amylase, α and β glucosidases, β galactosidases, and acidic and alkaline proteases were all significantly correlated with the variations in abundance of the particulate matter. In a later paper, Mayzaud and Poulet (1978) found that over the course of a year five species of

neritic copepods exhibited a linear relationship between feeding rates and naturally occurring particulate matter concentrations, and that digestive enzyme levels of the copepod population also varied linearly on a seasonal basis. This seemed to indicate that copepods acclimate to changes in the biochemical composition and concentration of their food supply and that grazing rates could be related to the activities of digestive enzymes (the acclimation hypothesis). In support of this relationship, Samain et al. (1981) found that the grazing rate of Artemia on the same phytoplankton species was highly modified when chemical composition of the cells was different. The different observed ingestion rates, induced by the different chemical composition of the cells, was balanced by the regulation of the digestive enzymes amylase and trypsin; both enzymes varied directly with the proportion of substrate ingested. In addition, Cox (1981) and Cox and Willason (1981) showed for Euphausia pacifica and Calanus pacificus that the digestive enzyme laminarinase is substrate-inducible in the grazers with a relatively short lag time; that is, enzyme activities rise and fall over a period of a day or so in proportion to the concentrations of chrysolaminarin (leucosin) in the grazers diet. More recently, Cox et al. (1982) demonstrated a positive correlation between estimated grazing rates and laminarinase activity for Calanus pacificus in a region along the southern California coast.

The results of these studies provided solid evidence for the possibility of determining in situ grazing rates from measurements of digestive enzyme activity, and prompted the study described in this thesis. To furthur quantify relationships between enzyme activity and

ingestion rate a series of experiments was initiated to elucidate seasonal relationships between these variables, at different food levels, for the neritic copepod Acartia clausii. Acartia clausii is a small calanoid copepod, ranging from 0.9 to 1.4 mm in length. It was chosen for this study because it is one of the dominant copepod species found within estuarine systems and along the Oregon coast. Within the Yaquina Bay estuary it is usually present year round. Typical winter abundances in the lower portion of this estuary are less than 10 per cubic meter, while mid-summer abundances are 1000 to 10,000 per cubic meter (Frohlander et al. (1973). The digestive enzyme laminarinase, or β-1, 3-glucanohydrolase, was chosen for this study because it is apparently unique to herbivores among marine planktonic zooplankton, and its specific substrate, chrysolaminarin (β-1, 3 glucan) is unique to phytoplankton (Cox, 1981). Chrysolaminarin is not only unique to phytoplankton, but is fairly widespread and abundant as a storage product in marine phytoplankton (Beattie et al., 1961; Ford and Percival, 1965; Percival and McDowell, 1967; Handa, 1969; Handa and Tominaga, 1969; Handa and Yanagi, 1969; Handa, 1970; Allan et al., 1972; Haug and Myklestad, 1973). Chrysolaminarin occurs in both soluble and insoluble forms, together comprising up to 90% of the ash-free dry weight of phytoplankton (Myklestad, 1974). Although other types of polysaccharide storage products are found in phytoplankton groups such as the dinoflagellates and some Chlorophyceae (Stewart, 1974; Parsons et al., 1977), these starch-like carbohydrates are usually minor constituents in comparison with β-1,3 glucan concentrations from mixed phytoplankton samples (Mayzaud and Mayzaud, 1981; Gaudy and Boucher,

1983).

The term laminarinase does not refer to a single enzyme, but rather describes a group of carbohydrases which hydrolyse -D-1,3 glucans; the name arose because laminarin was used as the test substrate by initial investigators (Bull and Chesters, 1966; Chesters and Bull, 1963a). Polysaccharide degradation may be achieved by (1) endwise removal of a monomer from the chain end; (2) endwise removal of a short chained oligosaccharide (usually the disaccharide) from the chain end; and (3) random cleavage of the molecule (Bull and Chesters, 1966). The terms exo- and endohydrolysis are applied to methods (1) - (2) and to (3), respectively. Exolaminarinase is of type (1) since it removes terminal glucose units. The laminarinase complex can contain different proportions of these exo- and endoenzymes in different species of micro-organisms and fungi (Chesters and Bull, 1963b; Nelson et al., 1963; Muchmore et al., 1969), and this results in different pH and temperature optima for the activities of the enzyme complexes in these species (Chesters and Bull, 1963c). Although the various proportions of these enzyme components in marine copepod laminarinases has not been investigated, differences among species may explain the differences in pH optima reported by different investigators. In this study the activity of the enzyme complex, laminarinase, was measured by the production of glucose from the substrate laminarin, because although different organisms may differ in the exact composition of the multienzyme system the endproduct of substrate degradation is glucose in all cases.

Thus the goals of this study were to determine if a relationship exists between ingestion rate and laminarinase activity for Acartia

clausii, and to determine if grazing rates can be predicted from enzyme measurements as suggested by the acclimation hypothesis.

Materials and Methods

Animal Collections

Acartia clausii were collected from the Oregon State University Marine Science Center dock on Yaquina bay, Oregon. Sampling was usually begun a few hours before high tide and concluded at or before low tide, depending on the apparent number of copepods captured. Prior to June 1983 animals were collected using a half-meter net with a 64 um mesh inner lining (500 um mesh outer protective lining). After this time a 202 um mesh net with a 0.25 sq. meter opening was used. The copepods were collected by pumping seawater through a 5 cm diameter hose into the partially submerged net, using a Pacer pump run by a three horsepower Briggs & Stratton engine. After an appropriate interval the net was rinsed down while still in the water and the cod end placed immediately into a bucket of seawater from the depth of sampling. The temperature of the water was noted and the cod end removed from the net and all contents poured into insulated 8 liter containers. The containers were cleaned of any settled detritus, topped off with seawater, and transported back to the laboratory at Oregon State University. Once in the laboratory the containers were placed in a walk-in coldroom adjusted to the measured ambient temperature of the bay. They were kept overnight, and animal sorting was initiated the following day. The dates of animal collections and the ambient temperatures recorded for the bay on these dates are presented in Table 1.

Table 1 Dates of animal collections from the Marine Science Center dock on lower Yaquina Bay, Oregon and the ambient water temperatures to the nearest 0.5 °C recorded for these dates.

Collection Date	Ambient Temperature (°C)
March 19, 1982	10.0
April 7, 1982	10.0
June 23, 1982	10.0
July 22, 1982	10.0
September 20, 1982	10.0
October 8, 1982	13.0
November 9, 1982	13.0
December 16, 1982	12.0
February 28, 1983	11.0
June 6, 1983	10.5
July 5, 1983	14.0
September 29, 1983	10.0

Experimental Setup

Groups of 70 adult Acartia clausii females were sorted into 7 cm diameter clear acrylic cylinders lined on one end with 232 um mesh. These "cages" were placed inside one liter flasks containing 700 ml of 0.8-um filtered seawater. Sorting continued until 11 groups of 70 A. clausii had been placed in the experimental flasks. Throughout this process the animals were kept at the temperature of the coldroom by holding all flasks in a temperature-controlled water bath. Upon completion of the sorting the flasks were randomly assigned to five groups (eventually to become five different food levels) and a control: two flasks were assigned to each future food level and a single flask to a zero food level containing only filtered seawater.

In all experiments the centric diatom Thalassiosira weissflogii (= T. fluviatilis) was used as the sole food source for the copepods. This diatom was obtained from batch cultures grown in F/2 nutrients and vitamins (Strickland and Parsons, 1972) under the same temperature and light conditions at which the copepods were maintained. The approximate food concentrations used in these experiments are shown in Table 2. Prior to July 1982 the food levels used were B - F; after this time all experiments were run at levels A - E.

The food levels listed in Table 2 were obtained by diluting portions of the batch cultures with 0.8 um-filtered seawater. The system used to determine cell concentrations was a model ZBi Coulter counter fitted with a 70 um aperture. A sensitivity setting of 32 and a lower threshold setting of 7 were employed. The Coulter counter was

Table 2 Experimental conditions used during the acclimation interval of these experiments. All experiments utilized Thalassiosira weissflogii as the food source for the adult Acartia clausii females. The food concentrations shown are the approximate concentrations used. The actual food concentrations used were within 5% of these values.

Food Level	T. weissflogii (10^6 um^3/ml)	Flask Vol. (ml)	# Copepods	# Flasks
0	0.0	700	70	1
A	0.5	700	70	2
B	1.0	700	70	2
C	2.5	700	70	2
D	5.0	700	70	2
E	7.5	700	70	2
F	10.0	700	70	2

interfaced to a Coulter P64 size-distribution analyzer and a PDP-8e minicomputer and a teletype terminal. The Coulter counter determines particle concentration by monitoring the interruption of an electrical current conducted through the seawater as particles pass through the aperture, and therefore measures particle volume displacement. Particle number is also determined from the number of discrete electrical pulses measured in a known volume of seawater. This system determines the size of particles passing through the aperature by calculating the diameter of a sphere with a volume equal to that displaced by each particle (equivalent spherical diameter). Based on the calculation of equivalent spherical diameter, the particle volumes are assigned to one of 64 size channels by the Coulter P64 size-distribution analyzer. The mean particle size of these channels was calculated as a linear multiple of the channel number and Coulter sensitivity, and was based on a calibration using plastic beads of known size for the aperture and sensitivity setting used. With the Coulter setting used in this study, values in channels less than 7 were attributed to "electronic noise", and the total particle volume in channels 7 through 64 was taken as the concentration of phytoplankton in the sample measured.

Animal Acclimation Interval

This portion of the experimental protocol was initiated by filling 10 one-liter flasks with 700 ml of filtered seawater and T. weissflogii at the appropriate concentrations listed in Table 2. Two flasks were used for each of the five food levels. The time was noted

and the cages containing the copepods were transferred from the filtered seawater into the food medium. The animals in the control (zero food level) were transferred to an equal volume of filtered seawater. All containers were then placed in a flow-through water bath, in the walk-in coldroom, under constant cool-white fluorescent lighting (approximately 60 uE/m^2/sec). The cages in the flasks were connected to a horizontal bar positioned above the flasks; this bar was connected to a small motor which raised and lowered the cages through the water 6 to 7 times every 15 minutes. This motion provided a well-mixed phytoplankton suspension and minimized sinking of the cells. Initial tests of this system showed that sinking and accumulation of cells on the mesh of the cages were minimal in the range of phytoplankton concentrations used in these experiments. The copepods were kept in these different food concentrations for three days following this initial setup. During this acclimation period the cell concentrations were measured in all flasks approximately every 12 hours with the Coulter counter, and the cages were transferred at this time to 700 ml of fresh food medium containing the appropriate concentration of T. weissflogii. During the 12 hour intervals between medium changes, grazing by the copepods reduced phytoplankton concentrations in the flasks; however, the decrease in cell concentration was usually less than 10 or 15% of the initial food level and there was never any overlap between concentration ranges among the five food levels. The food level for each of the flasks during the acclimation period was calculated in the following manner. The mean of the measurements of initial cell concentrations in each of the flasks was determined as well as the mean of the final cell

concentrations before medium changes. The mean of these two values for each flask was recorded as the concentration of phytoplankton to which the animals were acclimated during this period.

Grazing Experiment

After the three day acclimation period a 24 hour grazing experiment was performed to obtain ingestion rates for A. clausii at each food level. The procedure followed in these experiments consisted of the following steps. Initially, the concentration of T. weissflogii in a stock batch culture was measured with the Coulter counter and eight liters of the highest food level (F or E) was prepared by diluting the culture with 0.8 um filtered and autoclaved seawater. An equal volume of filtered seawater to be used for dilutions was placed in a separate container. One-quarter-strength nutrients and vitamins (F/8) was added to both of these containers. In addition, 10 umoles/liter ammonia (as NH_4NO_3) were added to both containers to eliminate or reduce the effects of ammonia excreted by the copepods during the grazing experiment. Next, three 20 ml samples from the highest food level (food stock) were placed in small vials and 50 adult A. clausii females from each of the highest-acclimation-level flasks were sorted into two of the vials. After sorting was completed three separate samples were removed from the food stock, the time was recorded, and the cell concentration in each was measured on the Coulter counter by making at least five replicate counts on each sample. Immediately after finishing these counts three 700 ml aliquots from the food stock were placed in

separate one-liter flasks. Next, three grazing cages were placed in flasks containing 700 ml of filtered seawater and the vials with the copepods were poured into two of the cages. The vial with no copepods was added to the third cage. These cages were then carefully placed into the flasks containing the same food concentration to which the animals had been acclimated. The flask containing no animals served as a control to measure cell growth during the experiment. The three flasks were placed in the walk-in coldroom and the cages were connected to the stirring mechanism as described earlier. All the conditions of temperature and lighting were identical to those used during the acclimation period. The above procedure was then repeated for the next food level by diluting the initial food stock with a portion of the above prepared filtered seawater until the concentration of the next food level was attained (either E or D). This process continued until all five food levels had been set up.

Thus for each food level there were two replicate grazer flasks containing 50 A. clausii and one control flask without animals. For each of the five food levels the starting time of the experiment was taken as the mean of the times at which the three samples, containing the food stock, were run on the Coulter counter. The initial phytoplankton concentrations for each food level were similarly taken as the mean of the three measured cell concentrations for these samples (expressed in terms of total cell volume, 10^6 um^3/ml).

After 24 hours the grazing experiment was concluded by measuring cell concentrations on at least three samples from each flask with the Coulter counter. After the counts from each food level were completed

the animals in each grazing flask were counted and any dead copepods were removed. The data set for the grazing experiment, from which all subsequent calculations were made, was thus composed of the number of copepods alive at the end of the experiment, the volume of medium used in each flask (700 ml), the particle counts (total cell volume/ml and total cell number/ml) in the control and grazer flasks at each food level, and the initial and final times of these measurements for each flask. All cell concentration and time values were taken as the means of at least three separate samples measured for each flask. The cell concentration in each sample was determined by making at least five replicate counts of the sample with the Coulter counter, using the same settings and methods described previously for the acclimation period.

Ingestion Rate Calculations

The equations used to calculate ingestion rates for each grazer flask are listed in Table 3. These equations were developed from the basic production equation (Kremer and Nixon, 1978; Steele and Frost, 1977):

$$1/N(dN/dt) = a - r - e - w - g - s$$

where N = phytoplankton population size, t = time, and the phytoplankton specific rates are as follows: a = assimilation, r = respiration, e = excretion, w = dilution, g = grazing, and s = sinking losses (Donaghay, 1980). Under the conditions used in these experiments w and s were zero, and the (a - r - e) portion of the equation is set equal to k, the phytoplankton growth rate. Using the

Table 3 Grazing equations (from Donaghay, 1980).

Input Variables	Symbol		Equation	Units
Initial Control Concentration	C_i			um^3/ml
Initial Grazer Concentration	G_i			um^3/ml
Final Control Concentration	C_f			um^3/ml
Final Grazer Concentration	G_f			um^3/ml
Initial Control Time	T_{C0}			day
Initial Grazer Time	T_{G0}			day
Final Control Time	T_{Cf}			day
Final Grazer Time	T_{Gf}			day
Volume of Food Medium	V			ml
Animal Number per Flask	A			number
Output				
Control Growth Rate	k_c	=	$\ln(C_f/C_i)/(T_{Cf} - T_{C0})$	day^{-1}
Apparent Growth Rate	k_a	=	$\ln(G_f/G_i)/(T_{Gf} - T_{G0})$	day^{-1}
Grazing Rate	k_g	=	$k_c - k_a$	day^{-1}
Mean Time in Grazing Period	T^*	=	$(T_{Gf} + T_{G0})/2$	day
Exponential Mean Biomass	EMB	=	$G_i(e^{k_a(T^* - T_{G0})})$	um^3/ml
Total Grazing Flux Loss	GFL	=	$k_g(EMB)V$	um^3/day
Ingestion Rate	IR	=	GFL/A	$um^3/copepod/day$

notation presented in Table 3, the measured growth rate in control flasks (containing no copepods) was denoted k_c. The apparent growth rate in each grazer flask was called k_a, which included the effects of copepod grazing as well as phytoplankton growth. The difference between these two rates, k_g, is the estimated grazing rate over the duration of the experiment. The three equations used to calculate these rates assume that phytoplankton growth and copepod grazing are exponential processes over the course of an experiment. This assumption has been tested previously with A. clausii under the same experimental conditions used in these experiments (Donaghay, 1980; Dexter, 1983), and appears to be valid providing the grazing experiments are run with log-phase phytoplankton provided with adequate nutrients under constant non-saturating light levels, and with copepods that have been acclimated to the phytoplankton concentrations used in the experiment.

Laminarinase Activity and Protein Analysis

After the conclusion of the grazing experiment two groups of 20 A. clausii from each grazing flask and the flask containing filtered seawater (zero food level) were sorted into small vials containing 20 ml of the remaining food medium. Each group of copepods was collected on a 25 mm diameter Nuclepore filter and transferred to a glass homogenizing tube with a pair of fine forceps. A 0.5 ml volume of 0.25 M phosphate buffer, made isotonic with seawater by adding NaCl, was added to the grinding tube, and the mixture was homogenized for two minutes. From the resulting homogenate, 200 ul

was removed for analysis of laminarinase activity and an equal volume for measurement of protein concentration. Both subsamples were placed in polypropylene test tubes and frozen at -20°C for 24 or 48 hours before continuing the analysis. Preliminary tests had shown no loss in enzyme activity in samples frozen at this temperature for 48 hours.

Prior to November 1982 (6 experiments) the phosphate grinding buffer used was adjusted to a pH of 5.0. After this time (6 experiments) a pH 5.8 phosphate buffer was employed. The initial buffer pH was chosen to allow comparisons between this study and other reports of copepod laminarinase activity in which a phosphate buffer at pH 5.0 was utilized (Mayzaud and Conover, 1976; Cox, 1981; Cox et al., 1983). The maximum enzyme activity of laminarinase from A. clausii in this study occurred at pH 5.8. Therefore, in order to increase the enzyme activity of the sample sizes used, especially that of the starved copepods, a pH of 5.8 was adopted. To facilitate comparisons between these groups of experiments a study was conducted with A clausii to determine the ratio of laminarinase activity at the two pH values. This ratio (pH 5.8/pH 5.0) was 1.863 (SD = 0.466, n = 11) and was used to convert enzyme activities measured at pH 5.0 to equivalent pH 5.8 laminarinase activities. At present the gut pH of live copepods is unknown. The pH of digestive juice from other Crustacea varies between 5.0 and 7.5 (Bond, 1934; Mayzaud and Mayzaud, 1981), therefore, the choice of a pH within this range for digestive enzyme work is somewhat arbitrary and the conditions producing a maximum laminarinase activity were adopted for this study.

The procedures used to determine laminarinase activity were adapted from Vacquier (1971). After 24 hours the aliquot for enzyme

analysis, 200 ul, was thawed and mixed with 1 ml of laminarin (from Laminaria digitata, CalBiochem) in 0.25 M phosphate buffer adjusted to a pH of 5.0 or 5.8. The concentration of laminarin used was 3.0 mg/ml, which is sufficient to saturate enzyme activity (Cox, 1981); thus, all measurements represented a determination of V_{max}. After incubation of the mixture at 37°C for 100 minutes the reaction was stopped by placing the samples in an ice bath and by the addition of 500 ul of 0.3 M $ZnSO_4$ and 500 ul of 0.3 M $Ba(OH)_2$. The samples were then centrifuged at 12,000 rpm for 15 minutes to precipitate the protein, and 1 ml of supernatant was removed to a polypropylene test tube for determination of glucose concentration. Glucose concentration was determined by incubating the samples at 37°C for 30 minutes after adding a glucose oxidase - peroxidase reagent (Sigma Tech. Bull. No. 510) and measuring the color development of the samples on a model 70 Bausch & Lomb spectrophotometer at a wavelength of 420 nm using 1 cm cells. The absorbance of the samples was corrected for the absorbance of blanks run with the samples, and the amount of glucose produced was determined by comparison with glucose standards. Laminarinase activities were expressed as ug glucose produced per copepod per minute at 37°C.

The aliquot for protein analysis, 200 ul, was thawed after 48 hours and analyzed for protein content using the method of Lowry et al. (1951). The samples were incubated for 30 min at room temperature following the addition of Folin - Ciocalteu reagent, and the absorbances of the samples were measured on a spectrophotometer at 750 nm. The absorbances of the samples were corrected by the absorbances of blanks run concurrently with the samples. The protein

concentrations were determined by comparison with bovine serum albumin standards. The protein concentrations were expressed as ug protein per copepod and were used to express enzyme activities on a per unit protein basis (ug glucose produced/mg protein/hr at 37°C).

In addition to these experiments a single experiment was run to follow changes in laminarinase activity with time at three food concentrations and in filtered seawater. Acartia clausii females were collected from Yaquina Bay during October 1981 and placed in the cold room at 10°C. Three groups of approximately 200 adult A. clausii females were placed in one-liter flasks containing 900 ml of a Thalassiosira weissflogii suspension adjusted to cell volume concentrations corresponding to levels C, D, and E (2.5, 5.0, 7.5 x 10^6 um^3/ml). A fourth group of 200 individuals was placed in a similar volume of filtered seawater. The food concentrations were re-established every 12 hours as described above for the acclimation interval. Every 24 hours for five days three groups of 10 copepods were removed from each of the four flasks and the laminarinase activity of the copepods was determined as described above.

Results

Ingestion Rates

Ingestion rates for the Acartia clausii females for each experiment were calculated on a cell volume basis (10^6 um^3/animal/day) and plotted against the calculated exponential mean cell biomass (10^6 um^3/ml) in each grazing flask. The general shape of the functional response curves for these experiments showed that ingestion rates usually became saturated at food concentrations less than 2.5 x 10^6 um^3/ml; therefore, a curvilinear model was chosen to describe these results. Initially, the Ivlev (1955) equation as modified by Parsons et al. (1967) was fit to the data for each experiment. This equation takes the form:

$$I = I_m(1 - e^{-K(x - p_0)},$$

where I is the ingestion rate, I_m is the maximum ingestion rate, K is a constant, x is the concentration of phytoplankton (exponential mean biomass), and p_0 is the food concentration at which feeding ceases (the so-called threshold concentration). The three parameters in this nonlinear equation (I_m,K,p_0) were found by using a program which employed the Gauss-Newton method of nonlinear regression as modified by Hartley (1961). This method uses a Taylor series expansion to approximate the nonlinear regression model with linear terms, and then employs ordinary least squares to estimate the parameters. Iteration of these steps generally leads to a solution

for the nonlinear regression parameters. Convergence of parameters was obtained for all experiments except for the experiment conducted on April 7, 1982, and in this case convergence failed because of the large increase in ingestion rates observed at the highest food level.

The results of this analysis showed that for all experiments the 95% confidence intervals for the parameter p_0 either included the origin or were negative. Because a negative threshold food concentration is undefined for this model the parameter p0 was eliminated and the standard Ivlev (1955) equation was fit to all experiments (Figs. 1 - 6). The Ivlev equation has the form:

$$I = I_m(1 - e^{-Kx}),$$

where all the terms are identical to those described above. The two parameters (I_m,K) were obtained using the modified Gauss-Newton program described above. The values of these parameters for all experiments and their 95% confidence intervals are presented in Table 4.

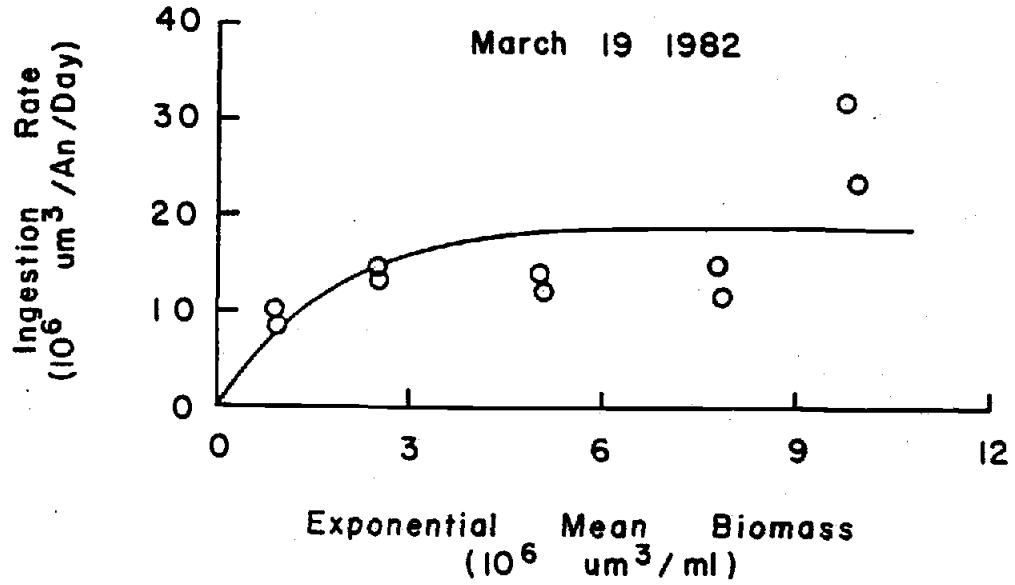
To determine if ingestion rate curves differed for these experiments, the Ivlev fits for each experiment were compared using an F test which tests for equality of the variances of two or more regression models (Neter and Wasserman, 1974). If the error terms in the regression models being compared had equal variances as determined by the F test, then the regression models were from the same "population" of models, and could be comapared. All experiments with the exception of those in April 1982 and March 1982 had statistically equal variances ($p < .05$) and were included in this analysis.

Table 4 Ivlev equation parameters for the ingestion rate data for each experiment and the standard deviation and 95% confidence intervals for these parameters. I_m is the maximum ingestion rate, K is a constant, and r^2 is the coefficient of determination for the Ivlev fits to the data for each experiment. Equation parameters could not be determined for the April 7, 1982 experiment (see text).

Experiment Date	r^2	I_m	Std. Dev.	95% C.I.	K	Std. Dev.	95% C.I.
March 19, 1982	0.250	18.19	2.82	(11.69, 24.69)	0.62	0.39	(-0.28, 1.52)
June 23, 1982	0.590	16.77	0.55	(15.50, 18.03)	1.69	0.34	(0.91, 2.48)
July 22, 1982	0.649	13.71	1.07	(11.24, 16.18)	1.70	0.50	(0.54, 2.86)
September 20, 1982	0.200	3.50	0.49	(2.36, 4.63)	1.17	0.62	(-0.25, 2.59)
October 8, 1982	0.762	10.72	0.59	(9.34, 12.09)	1.88	0.41	(0.93, 2.84)
November 9, 1982	0.815	10.28	0.41	(9.32, 11.23)	1.79	0.31	(1.08, 2.49)
December 16, 1982	0.274	10.95	1.04	(8.55, 13.36)	1.71	0.73	(0.02, 3.40)
February 28, 1983	0.955	11.09	0.27	(10.46, 11.72)	1.27	0.12	(0.99, 1.54)
June 6, 1983	0.850	19.74	3.34	(12.03, 27.45)	0.28	0.10	(0.04, 0.53)
July 5, 1983	0.910	19.78	0.70	(18.16, 21.39)	1.46	0.20	(0.99, 1.93)
September 29, 1983	0.704	9.79	0.57	(8.45, 11.14)	1.61	0.42	(0.61, 2.61)

Figure 1 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on March 19, 1982 and April 7, 1982. The centric diatom Thalassiosira weissflogii was provided as the food source during these experiments. The ingestion rates are shown versus the exponential mean biomass (10^6 um^3/ml) of cell concentration in each grazing flask and were calculated using the equations shown in Table 3. The data for the March 19, 1982 experiment was fit using the Ivlev equation ($I = I_m(1 - e^{-Kx})$). The values of these parameters are shown in Table 4. The April 7, 1982 experiment could not be fit using the Ivlev equation (see text for details).

Figure 1


March 19 1982
Ingestion Rate
(10^6 um^3/An/Day)
40
30
20
10
0
0
3
6
9
12
Exponential Mean Biomass
(10^6 um^3/ml)

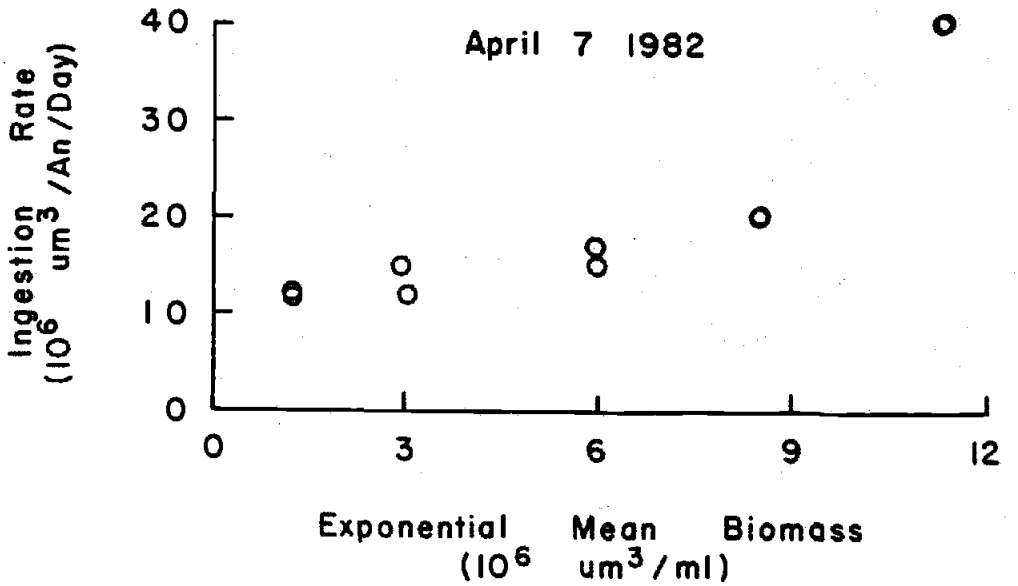
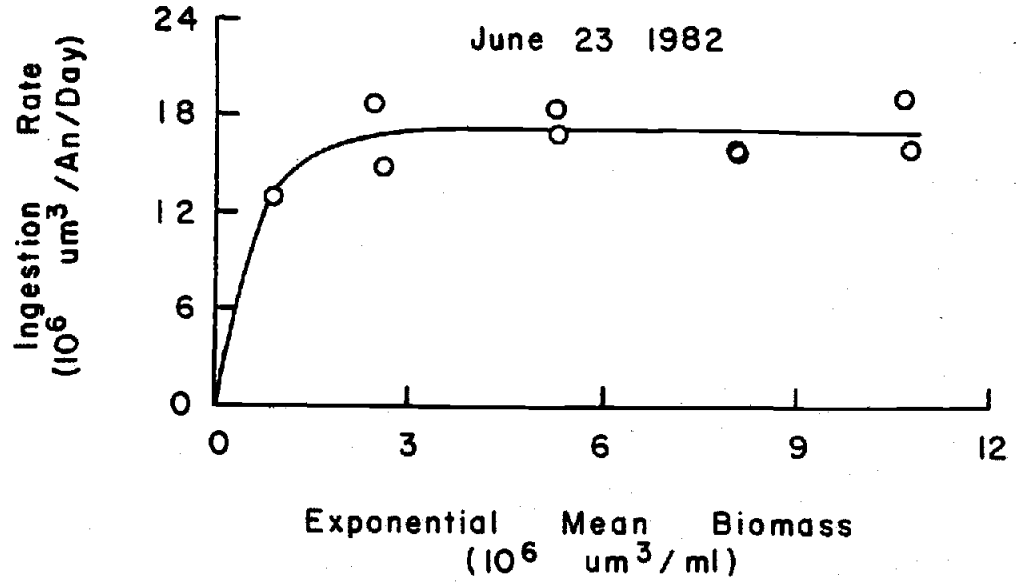

April 7 1982
Ingestion Rate
(10^6 um^3/An/Day)
40
30
20
10
0
0
3
6
9
12
Exponential Mean Biomass
(10^6 um^3/ml)

Figure 2 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on June 23, 1982 and July 22, 1982. The centric diatom Thalassiosira weissflogii was provided as the food source during these experiments. The ingestion rates are shown versus the exponential mean biomass (10^6 um^3/ml) of cell concentration in each grazing flask and were calculated using the equations shown in Table 3. The data from each experiment were fit using the Ivlev equation ($I = I_m(1 - e^{-Kx})$. The values of these parameters are shown in Table 4.

Figure 2


June 23 1982
Ingestion Rate
(10^6 um^3 /An/Day)
24
18
12
6
0
0
3
6
9
12
Exponential Mean Biomass
(10^6 um^3 / ml)

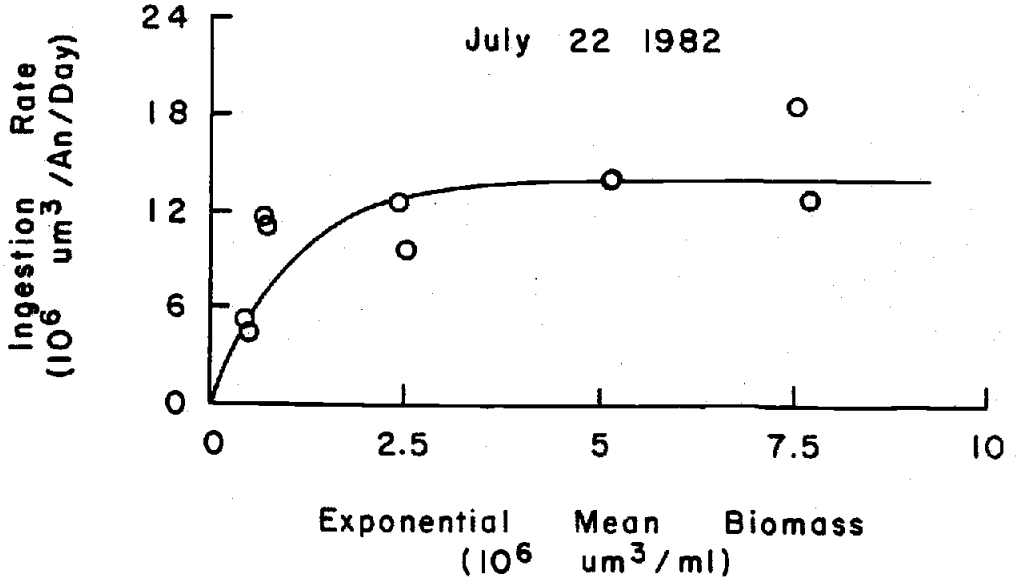
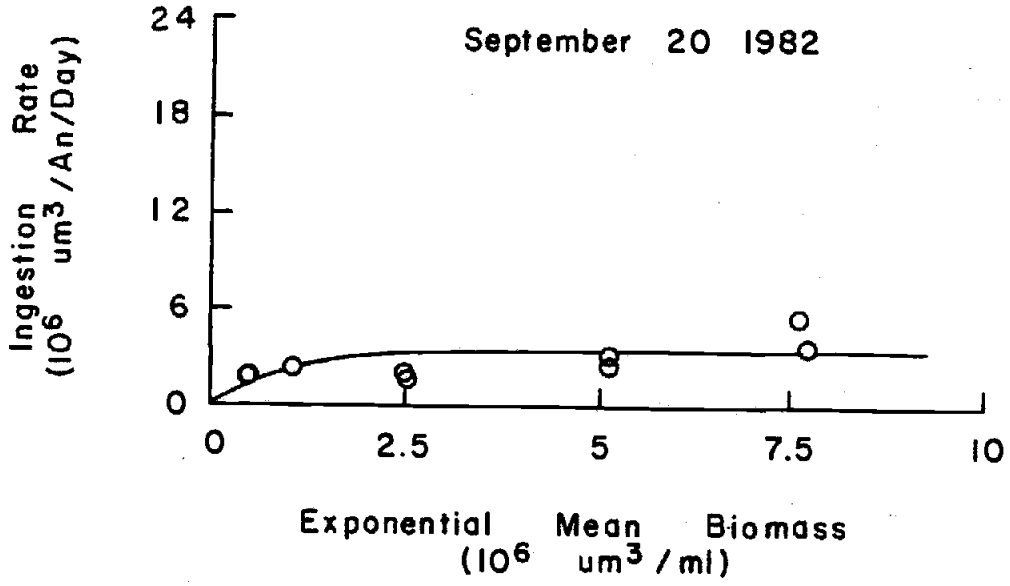

July 22 1982
Ingestion Rate
(10^6 um^3 /An/Day)
24
18
12
6
0
0
2.5
5
7.5
10
Exponential Mean Biomass
(10^6 um^3 / ml)

Figure 3 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on September 20, 1982 and October 8, 1982. The centric diatom Thalassiosira weissflogii was provided as the food source during these experiments. The ingestion rates are shown versus the exponential mean biomass (10^6 um^3/ml) of cell concentration in each grazing flask and were calculated using the equations shown in Table 3. The data from each experiment were fit using the Ivlev equation ($I = I_m(1 - e^{-Kx})$. The values of these parameters are shown in Table 4.

Figure 3


September 20 1982
Ingestion Rate
(10^6 um^3/An/Day)
24
18
12
6
0
0
2.5
5
7.5
10
Exponential Mean Biomass
(10^6 um^3/ml)

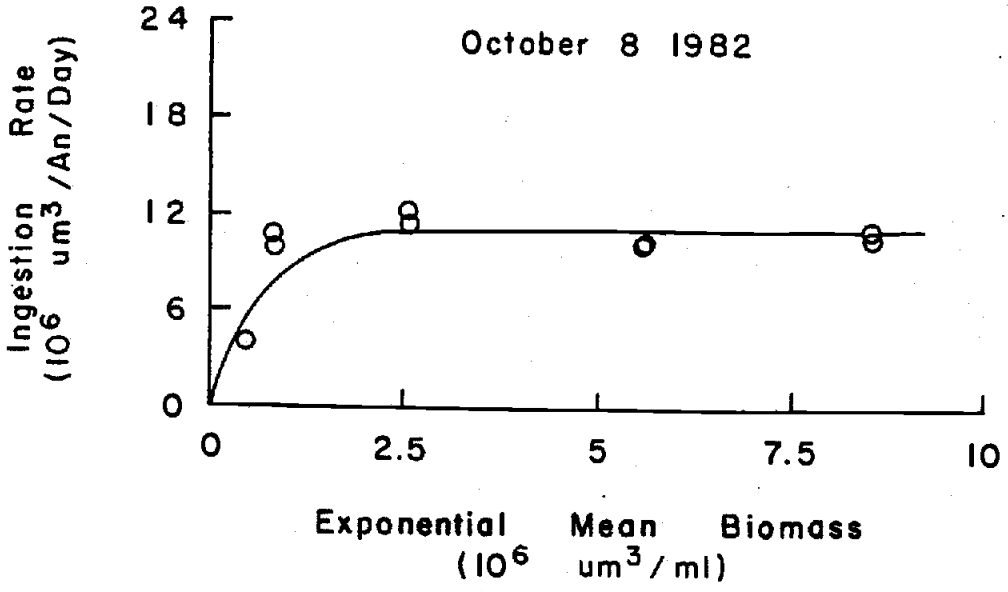
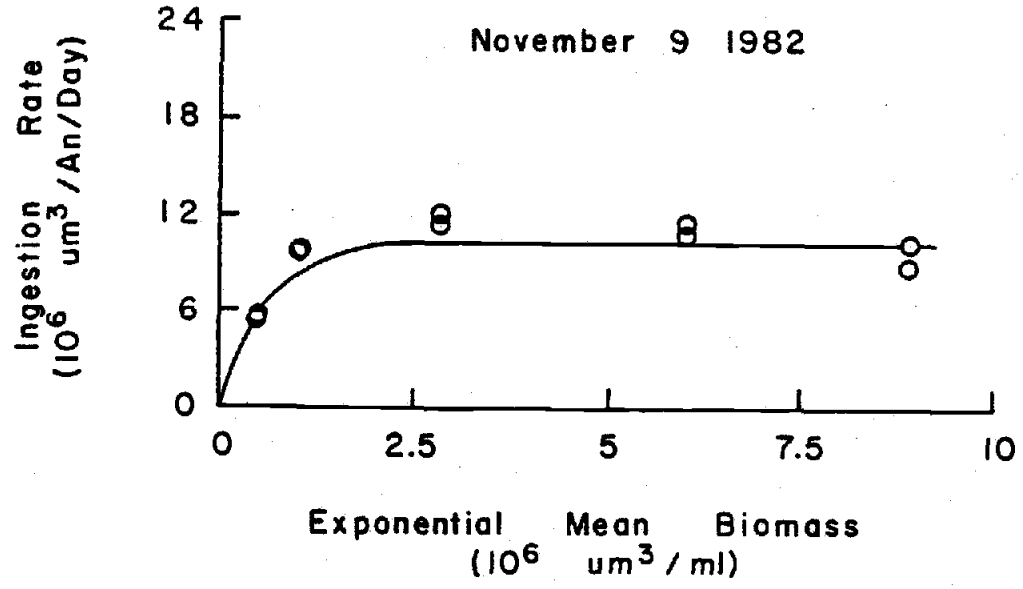

October 8 1982
Ingestion Rate
(10^6 um^3/An/Day)
24
18
12
6
0
0
2.5
5
7.5
10
Exponential Mean Biomass
(10^6 um^3/ml)

Figure 4 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on November 9, 1982 and December 16, 1982. The centric diatom Thalassiosira weissflogii was provided as the food source during these experiments. The ingestion rates are shown versus the exponential mean biomass (10^6 um^3/ml) of cell concentration in each grazing flask and were calculated using the equations shown in Table 3. The data from each experiment were fit using the Ivlev equation ($I = I_m(1 - e^{-Kx})$). The values of these parameters are shown in Table 4.

Figure 4


November 9 1982
Ingestion Rate
(10^6 um^3 /An/Day)
24
18
12
6
0
0
2.5
5
7.5
10
Exponential Mean Biomass
(10^6 um^3 / ml)

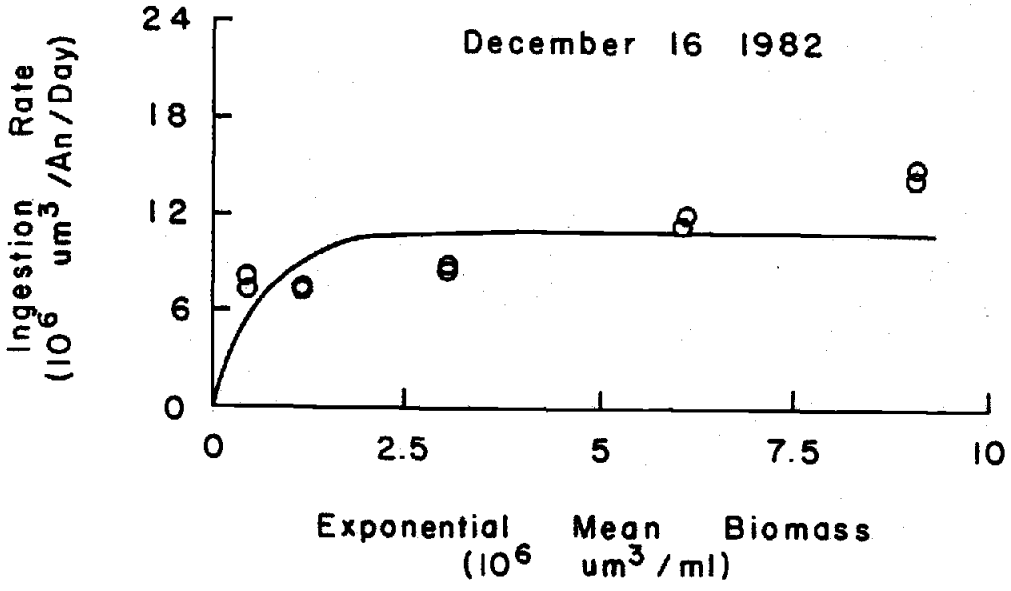
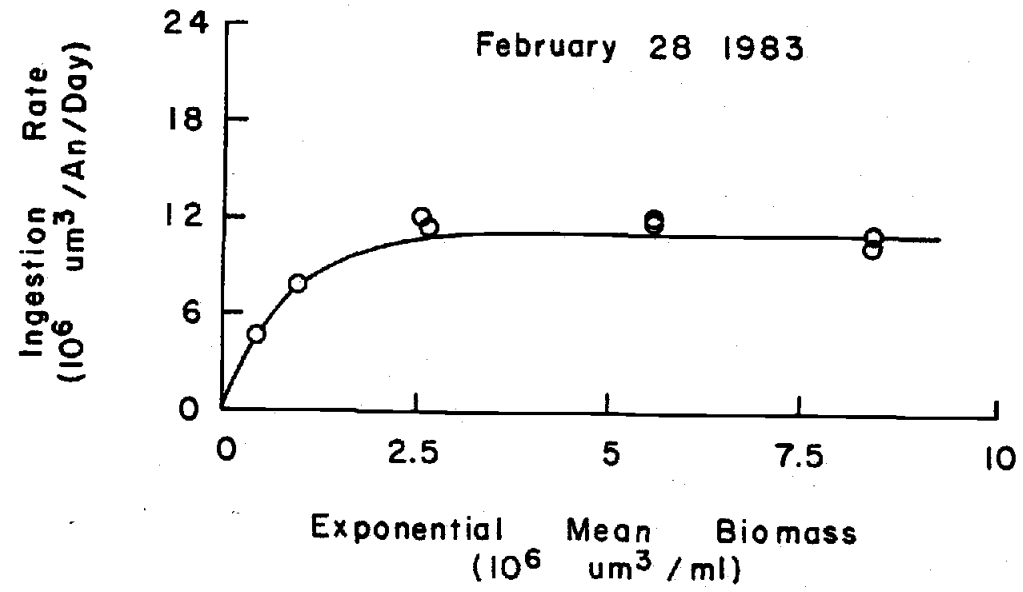

December 16 1982
Ingestion Rate
(10^6 um^3 /An/Day)
24
18
12
6
0
0
2.5
5
7.5
10
Exponential Mean Biomass
(10^6 um^3 / ml)

Figure 5 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on February 28, 1983 and June 6, 1983. The centric diatom Thalassiosira weissflogii was provided as the food source during these experiments. The ingestion rates are shown versus the exponential mean biomass (10^6 um^3/ml) of cell concentration in each grazing flask and were calculated using the equations shown in Table 3. The data from each experiment were fit using the Ivlev equation ($I = I_m(1 - e^{-Kx})$). The values of these parameters are shown in Table 4.

Figure 5


February 28 1983
Ingestion Rate
(10^6 um^3/An/Day)
24
18
12
6
0
0
2.5
5
7.5
10
Exponential Mean Biomass
(10^6 um^3/ml)

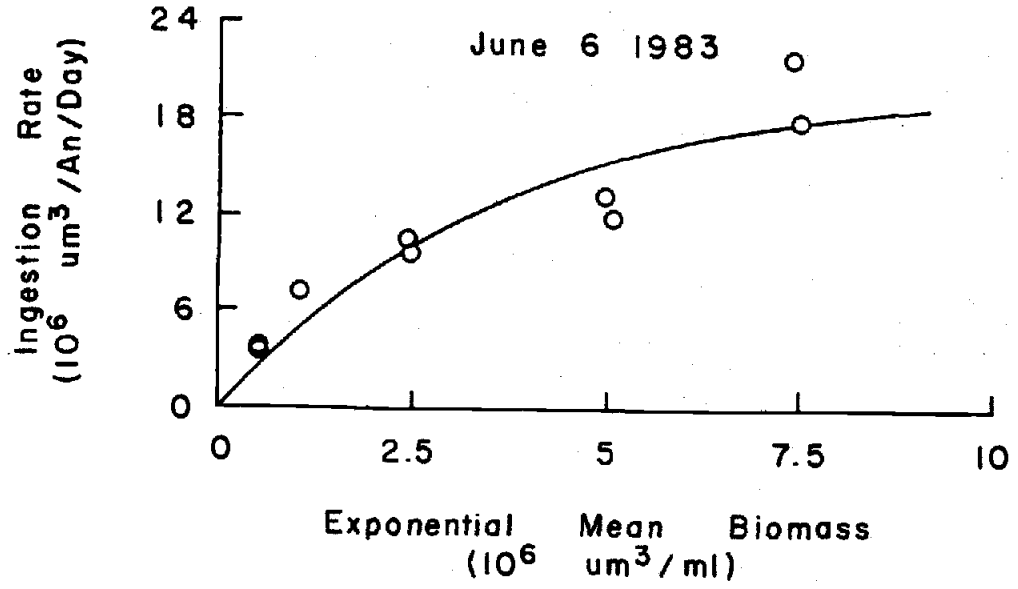
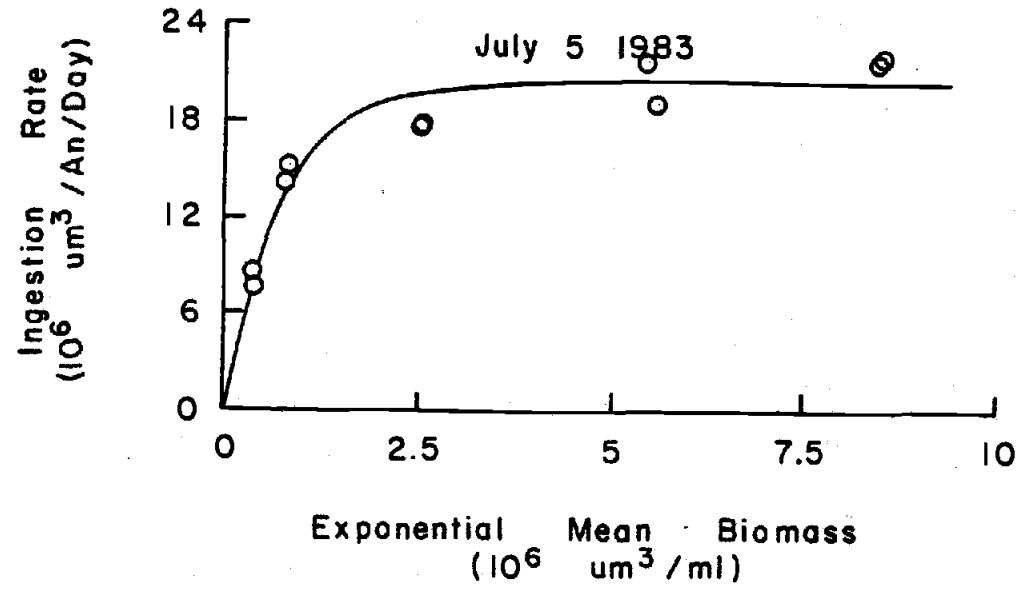
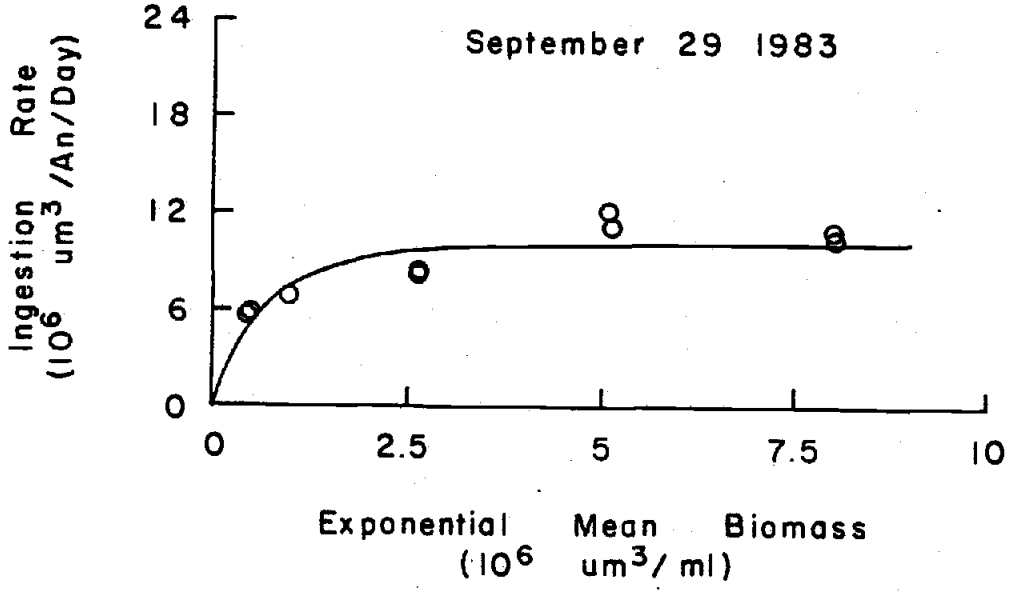

June 6 1983
Ingestion Rate
(10^6 um^3/An/Day)
24
18
12
6
0
0
2.5
5
7.5
10
Exponential Mean Biomass
(10^6 um^3/ml)

Figure 6 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on July 5, 1983 and September 29, 1983. The centric diatom Thalassiosira weissflogii was provided as the food source during these experiments. The ingestion rates are shown versus the exponential mean biomass (10^6 um^3/ml) of cell concentration in each grazing flask and were calculated using the equations shown in Table 3. The data from each experiment were fit using the Ivlev equation ($I = I_m(1 - e^{-Kx})$). The values of these parameters are shown in Table 4.

Figure 6


July 5 1983
Ingestion Rate
(10^6 um^3 /An/Day)
24
18
12
6
0
0
2.5
5
7.5
10
Exponential Mean Biomass
(10^6 um^3 /ml)


September 29 1983
Ingestion Rate
(10^6 um^3 /An/Day)
24
18
12
6
0
0
2.5
5
7.5
10
Exponential Mean Biomass
(10^6 um^3/ ml)

Comparisons showed that ingestion rate curves for October 1982, November 1982, December 1982, February 1983, and September 1983 were statistically the same ($p < .05$) and could be treated as a single data set. However, the ingestion rate curves for June 1982, July 1982, September 1982, June 1983 and July 1983 were statistically different ($p < .05$) from each other and could not be combined. Thus it was readily apparent that the ingestion rates for A. clausii at identical food concentrations varied seasonally. With the exception of the September 20, 1982 experiment, ingestion rates during the fall and winter months remained relatively low and constant. During the summer months ingestion rates were more variable; however, the maximum ingestion rates attained (I_m) during these months were consistently higher than fall and winter experiments by about a factor of one and one-half or two.

Ingestion Rate versus Laminarinase Activity

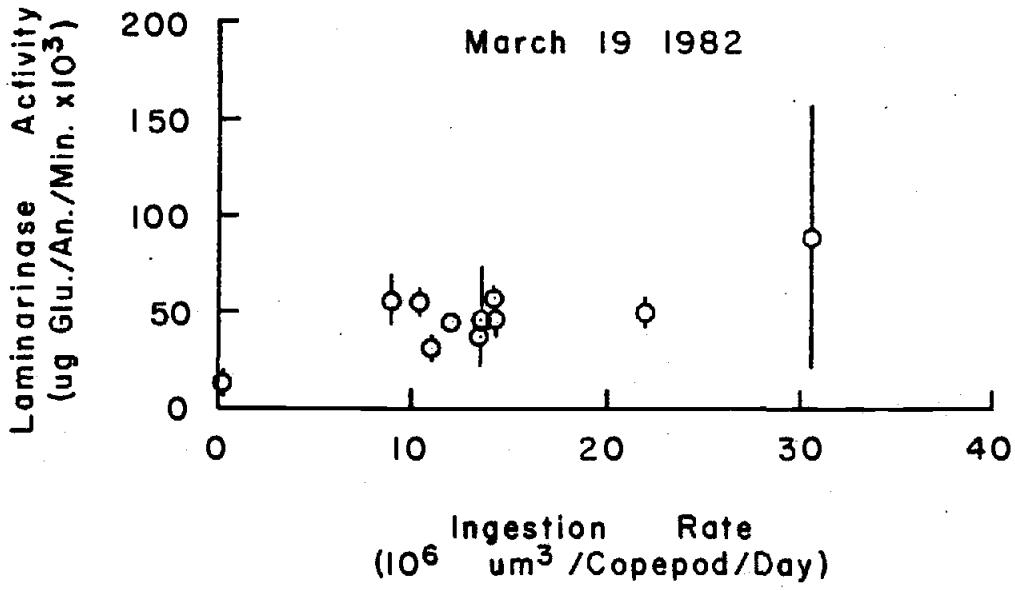
Laminarinase activities expressed on a per animal basis (LA = ug glucose/copepod/minute) and total animal protein (LP = ug glucose/mg protein/hour), are shown in Figs. 7 - 18 as functions of ingestion rate. The Spearman rank correlation test (Steel and Torrie, 1980) was used to determine if a significant correlation existed between laminarinase activity and ingestion rate at the five food concentrations used in this study (Table 5). A significant positive correlation between LA and ingestion rate occurred in only three experiments: June 1982, February 1983, and July 1983. There was no significant relationship between these parameters for the remaining

Table 5 Spearman rank correlation values for comparisons between laminarinase activity and ingestion rate. LA refers to laminarinase activity expressed as ug glucose produced/ copepod/minute. LP refers to laminarinase activity expressed as ug glucose produced/mg protein/hour. The level of significance is indicated as follows: 0.05 = (*), 0.01 = (**), 0.001 = (***).

Experiment Date	LA	LP
March 19, 1982	0.23	-0.25
April 7, 1982	-0.28	-0.59
June 23, 1982	0.64*	-0.36
July 22, 1982	0.54	0.46
September 20, 1982	-0.38	-0.41
October 8, 1982	0.52	0.17
November 9, 1982	-0.58	-0.78**
December 16, 1982	0.11	-0.14
February 28, 1983	0.76*	0.48
June 6, 1983	0.24	-0.88***
July 5, 1983	0.77**	0.89***
September 29, 1983	-0.40	-0.50

Figure 7 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on March 19, 1982 versus the laminarinase activity of the copepods expressed as ug glucose/animal/minute x 10^3 and as ug glucose/mg protein/hour x 10^{-2}. The error bars shown are the standard deviations of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask. The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 7


March 19 1982
Laminarinase Activity
(ug Glu./An./Min. x10³)
200
150
100
50
0
0
10
20
30
40
Ingestion Rate
(10⁶ um³ /Copepod/Day)

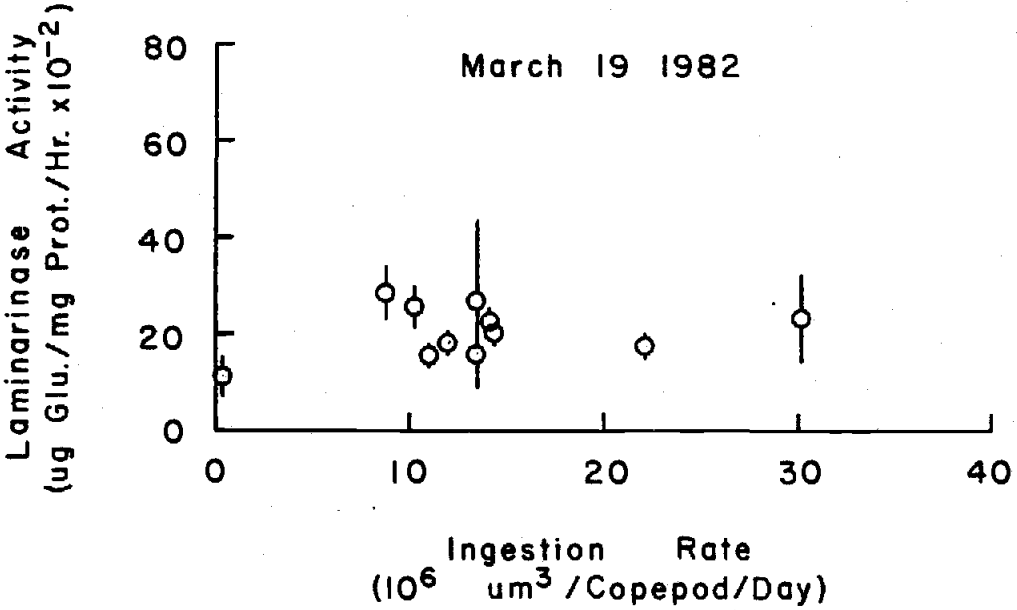
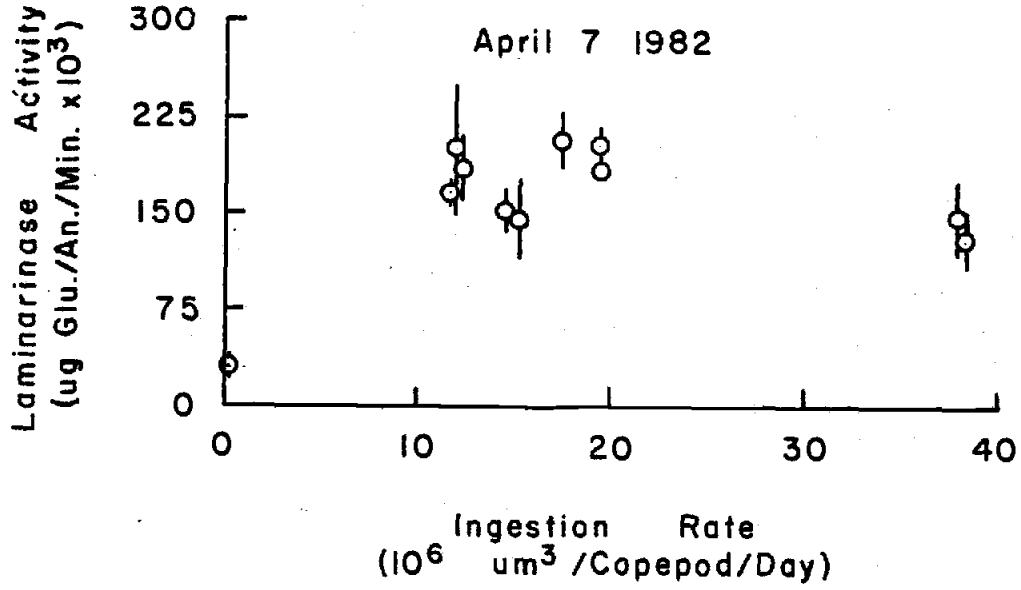

March 19 1982
Laminarinase Activity
(ug Glu./mg Prot./Hr. x10⁻²)
80
60
40
20
0
0
10
20
30
40
Ingestion Rate
(10⁶ um³ /Copepod/Day)

Figure 8 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on April 7, 1982 versus the laminarinase activity of the copepods expressed as ug glucose/animal/minute x 10^3 and as ug glucose/mg protein/hour x 10^{-2}. The error bars shown are the standard deviations of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask. The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 8


Laminarinase Activity
(ug Glu./An./Min. x10³)
300
225
150
75
0
April 7 1982
0
10
20
30
40
Ingestion Rate
(10⁶ um³ /Copepod/Day)

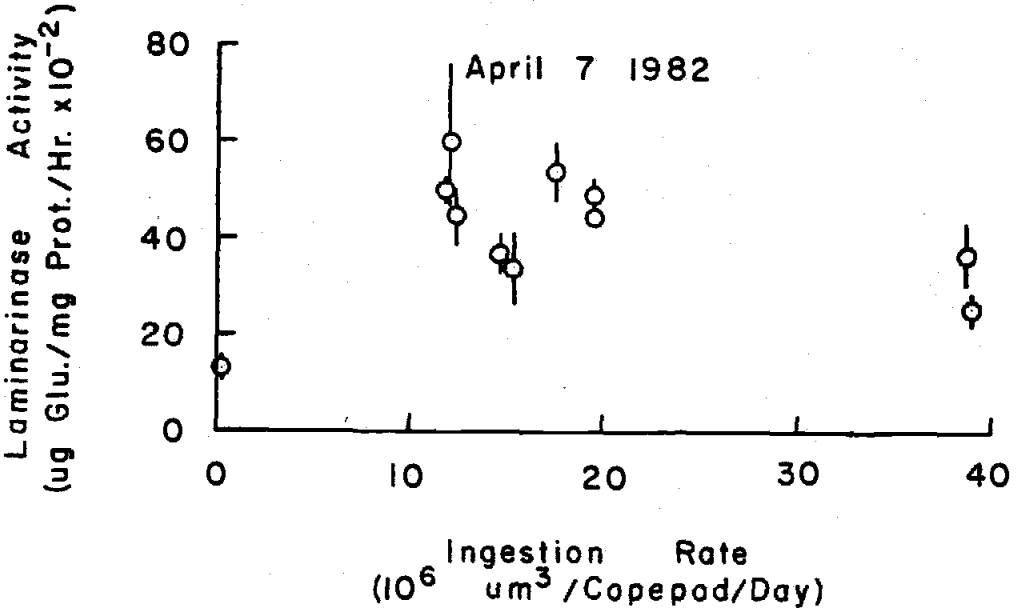
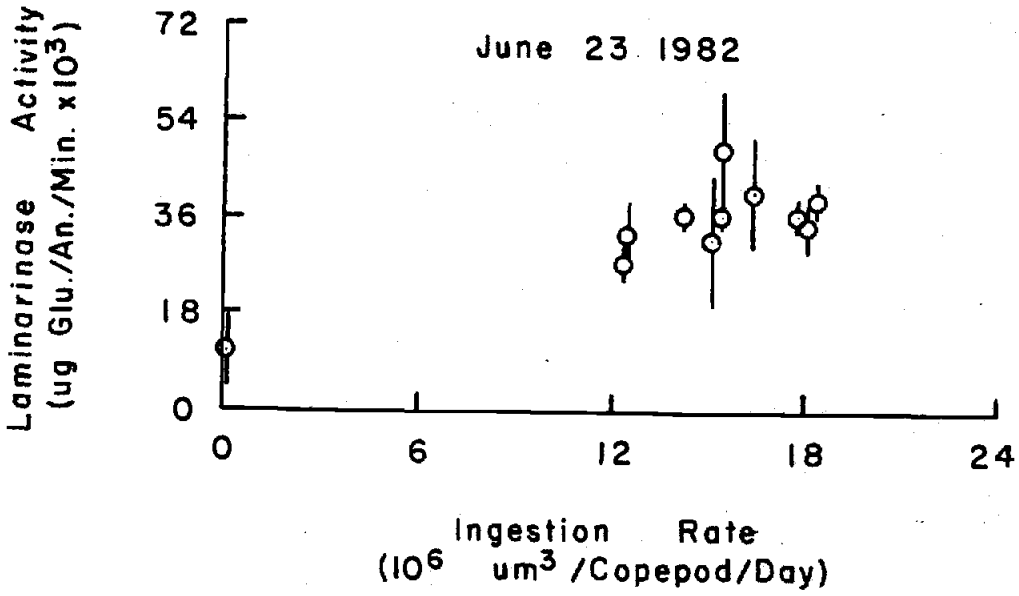

Laminarinase Activity
(ug Glu./mg Prot./Hr. x10⁻²)
80
60
40
20
0
April 7 1982
0
10
20
30
40
Ingestion Rate
(10⁶ um³ /Copepod/Day)

Figure 9 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on June 23, 1982 versus the laminarinase activity of the copepods expressed as ug glucose/animal/minute x 10^3 and as ug glucose/mg protein/hour x 10^{-2}. The error bars shown are the standard deviations of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask. The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 9


Laminarinase Activity
(ug Glu./An./Min. x10³)
72
54
36
18
0
June 23 1982
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

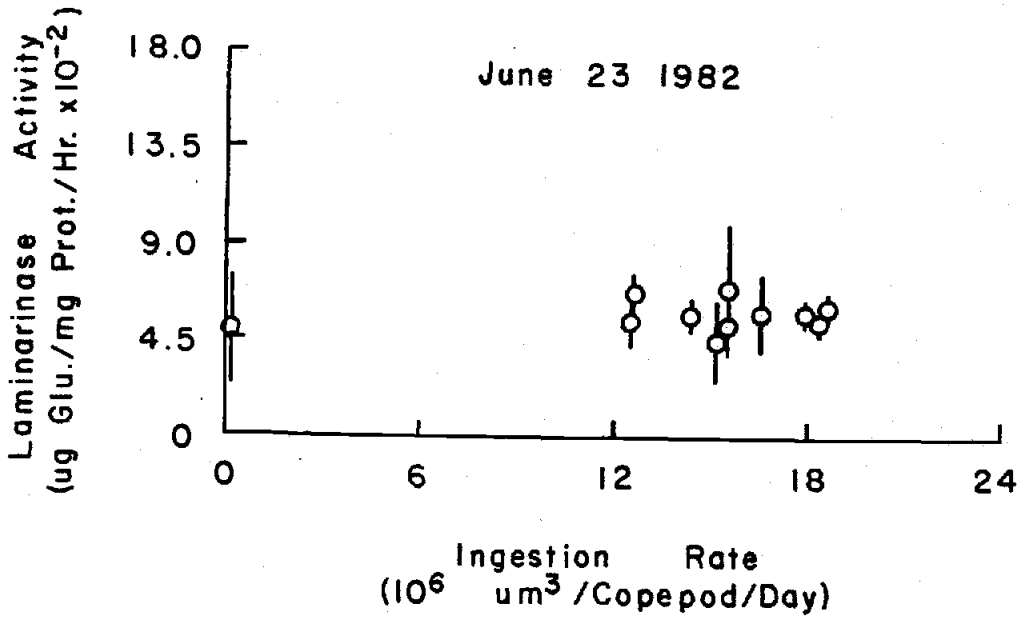
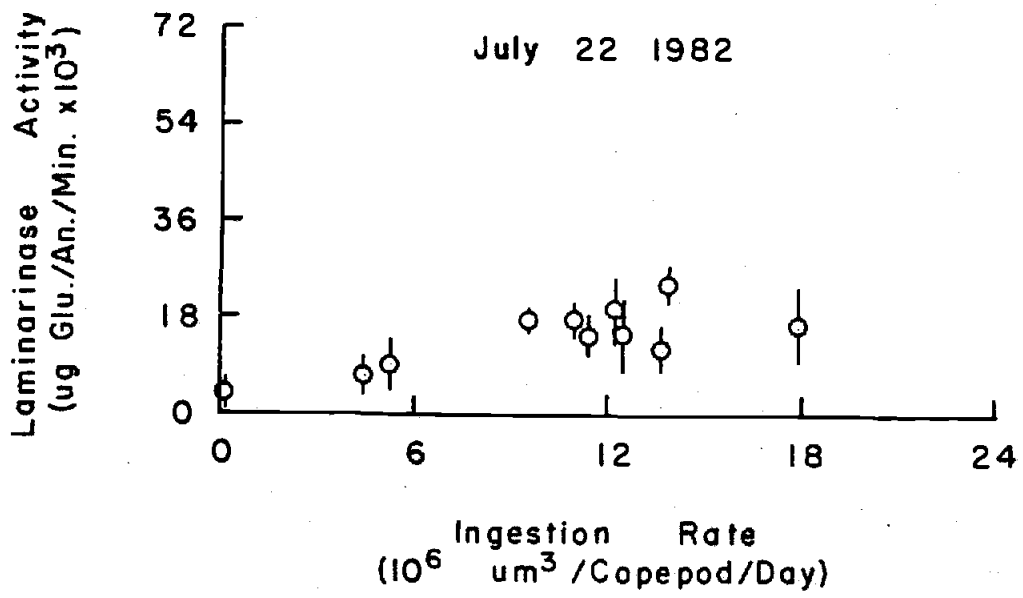

Laminarinase Activity
(ug Glu./mg Prot./Hr. x10⁻²)
18.0
13.5
9.0
4.5
0
June 23 1982
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

Figure 10 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on July 22, 1982 versus the laminarinase activity of the copepods expressed as ug glucose/animal/minute x 10^3 and as ug glucose/mg protein/hour x 10^{-2}. The error bars shown are the standard deviations of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask. The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 10


Laminarinase Activity
(ug Glu./An./Min. x10³)
72
54
36
18
0
July 22 1982
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

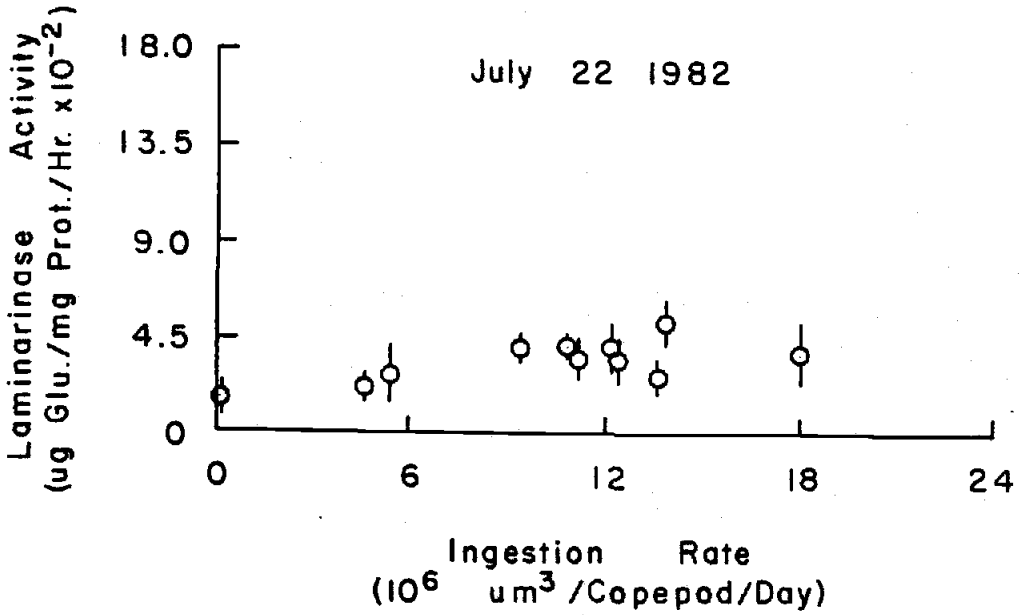
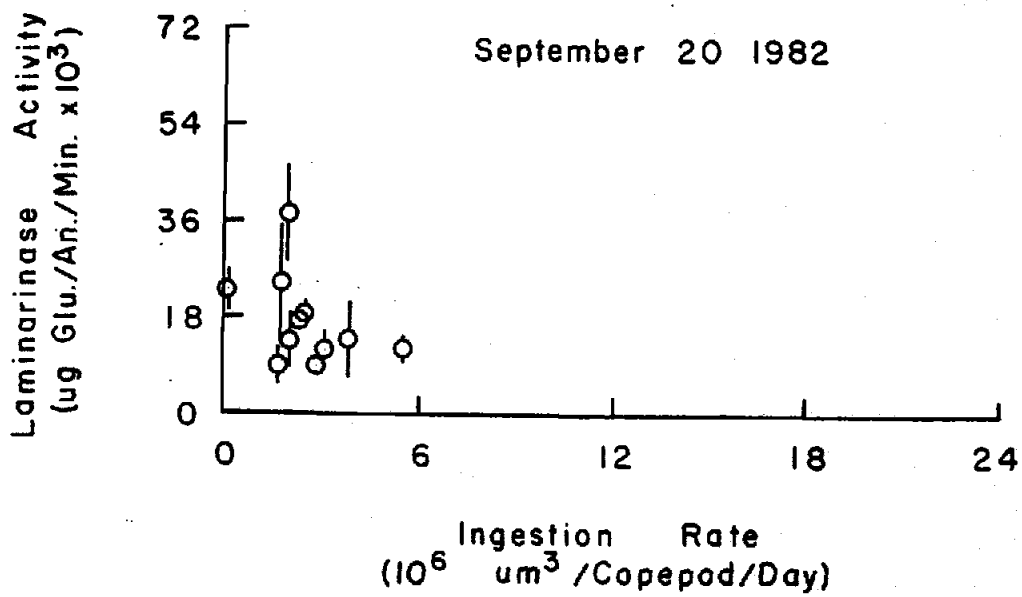

Laminarinase Activity
(ug Glu./mg Prot./Hr. x10⁻²)
18.0
13.5
9.0
4.5
0
July 22 1982
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

Figure 11 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on September 20, 1982 versus the laminarinase activity of the copepods expressed as ug glucose/animal/minute x 10^3 and as ug glucose/mg protein/hour x 10^{-2}. The error bars shown are the standard deviations of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask. The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 11


Laminarinase Activity
(ug Glu./An./Min. x10³)
72
54
36
18
0
September 20 1982
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

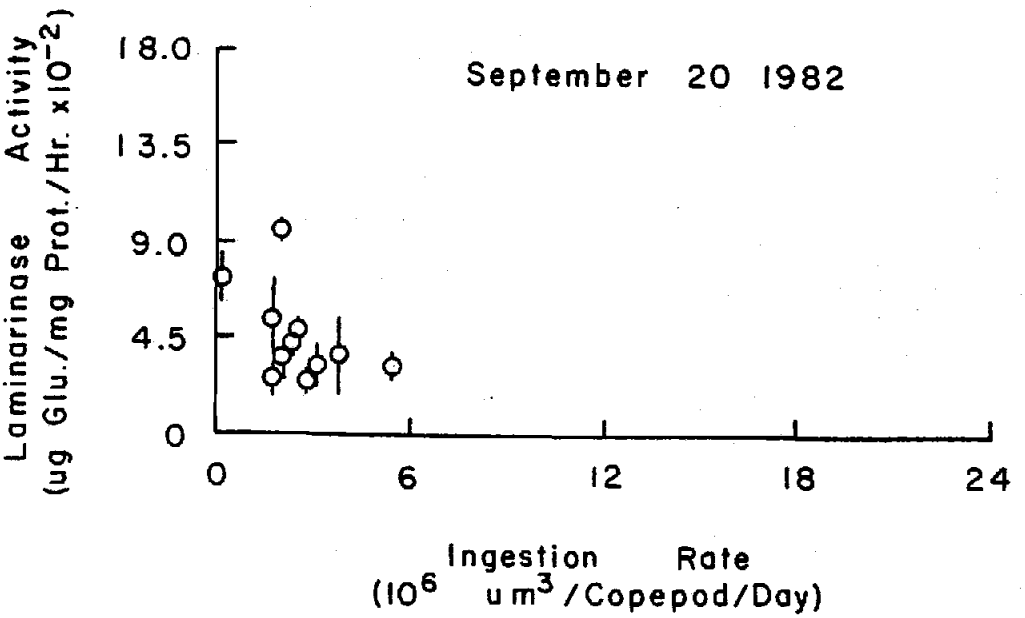
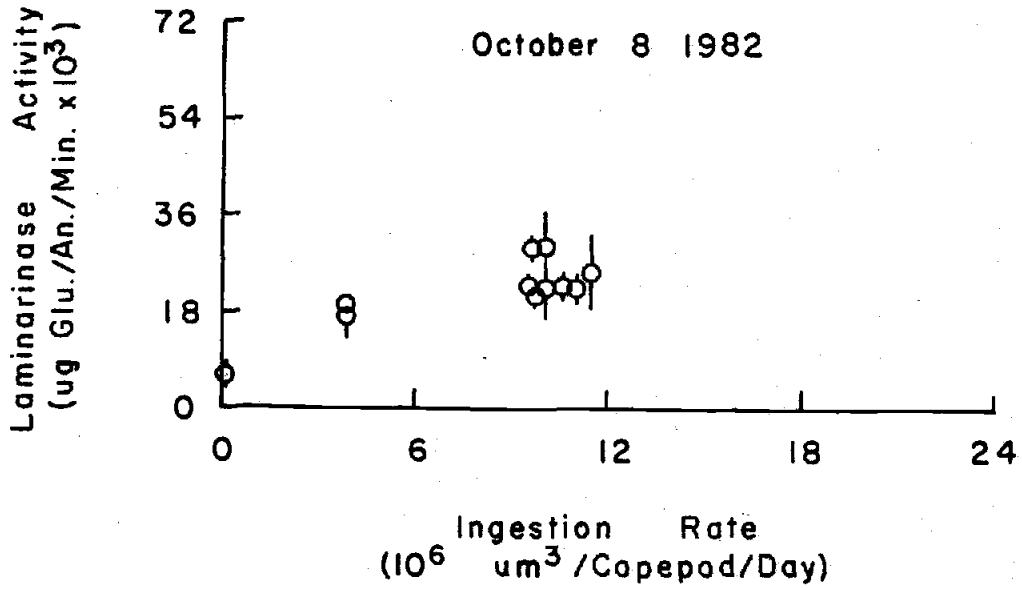

Laminarinase Activity
(ug Glu./mg Prot./Hr. x10⁻²)
18.0
13.5
9.0
4.5
0
September 20 1982
0
6
12
18
24
Ingestion Rate
(10⁶ u m³ /Copepod/Day)

Figure 12 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on October 8, 1982 versus the laminarinase activity of the copepods expressed as ug glucose/animal/minute x 10^3 and as ug glucose/mg protein/hour x 10^{-2}. The error bars shown are the standard deviations of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask. The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 12


Laminarinase Activity
(ug Glu./An./Min. x10³)
72
54
36
18
0
October 8 1982
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

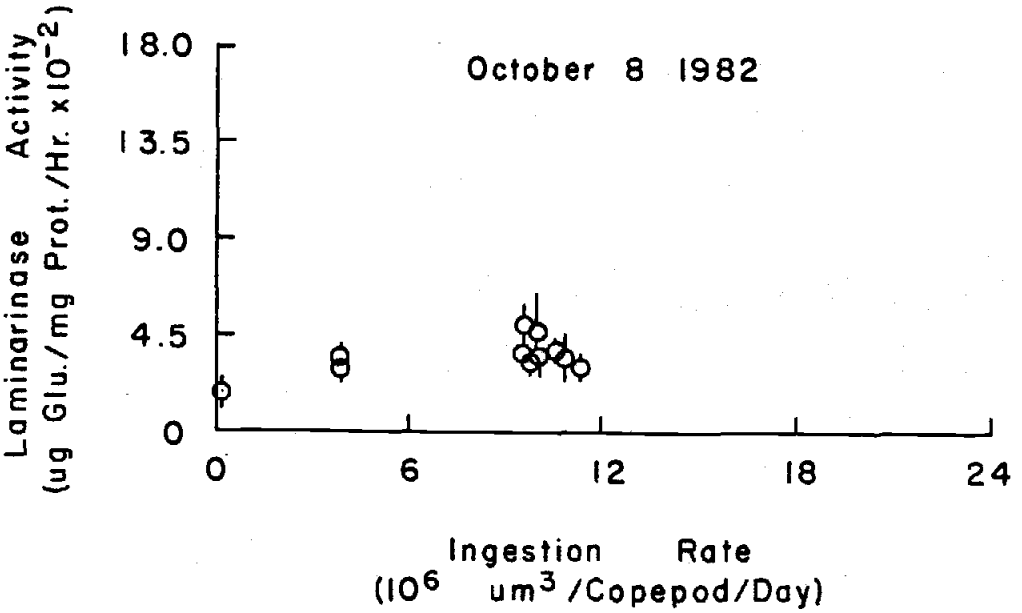
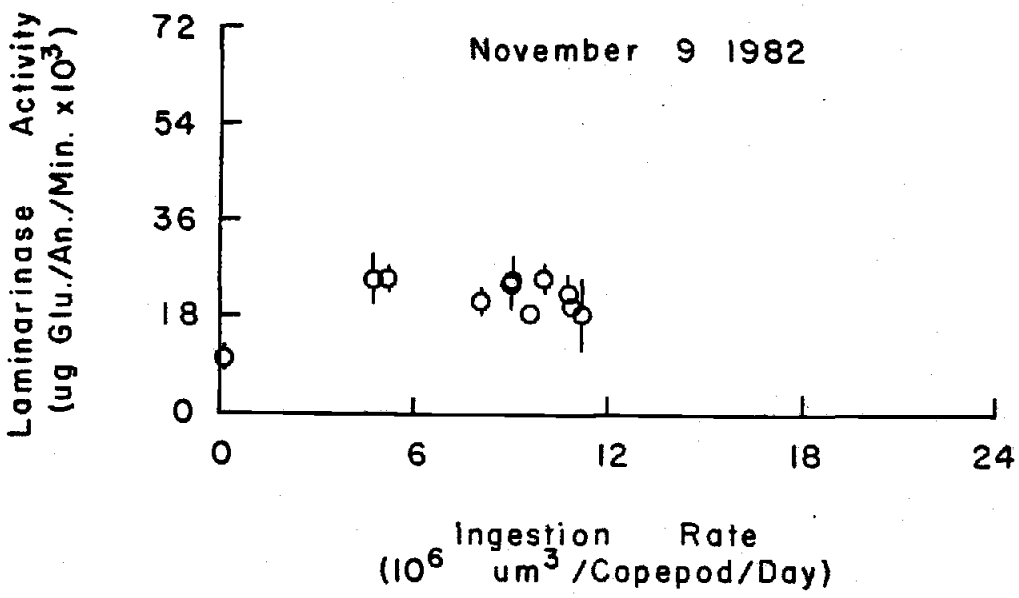

Laminarinase Activity
(ug Glu./mg Prot./Hr. x10⁻²)
18.0
13.5
9.0
4.5
0
October 8 1982
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

Figure 13 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on November 9, 1982 versus the laminarinase activity of the copepods expressed as ug glucose/animal/minute x 10^3 and as ug glucose/mg protein/hour x 10^{-2}. The error bars shown are the standard deviations of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask. The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 13


Laminarinase Activity
(ug Glu./An./Min. x10³)
72
54
36
18
0
November 9 1982
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

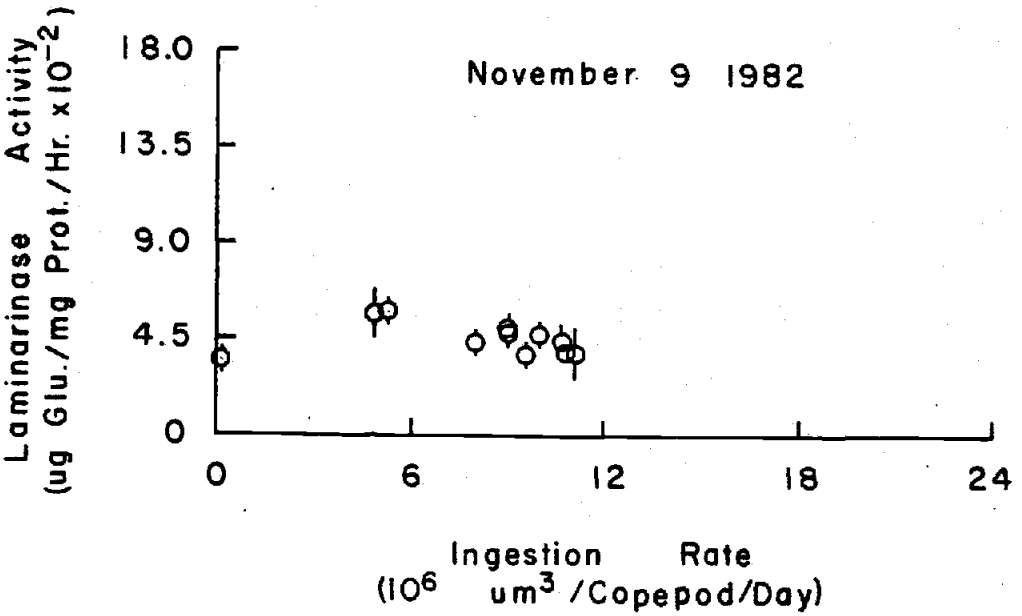
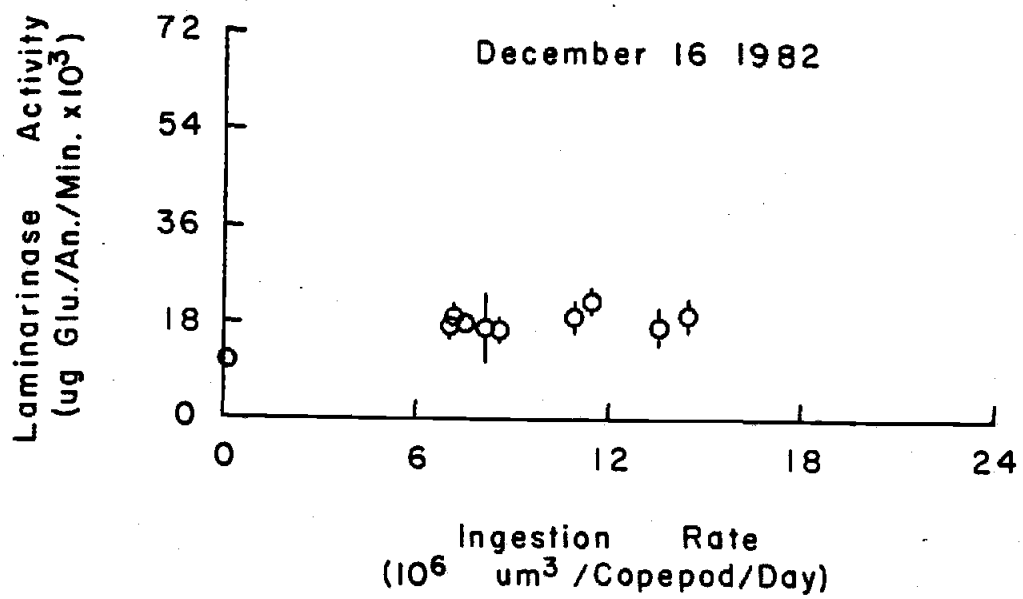

Laminarinase Activity
(ug Glu./mg Prot./Hr. x10⁻²)
18.0
13.5
9.0
4.5
0
November 9 1982
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

Figure 14 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on December 16, 1982 versus the laminarinase activity of the copepods expressed as ug glucose/animal/minute x 10^3 and as ug glucose/mg protein/hour x 10^{-2}. The error bars shown are the standard deviations of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask. The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 14


Laminarinase Activity
(ug Glu./An./Min. x10³)
72
54
36
18
0
December 16 1982
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

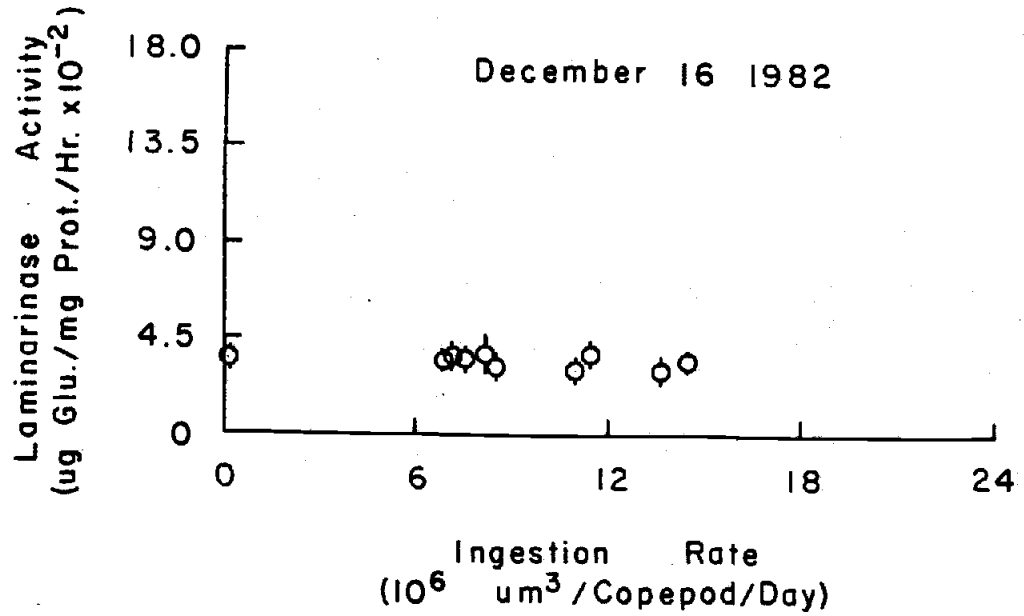
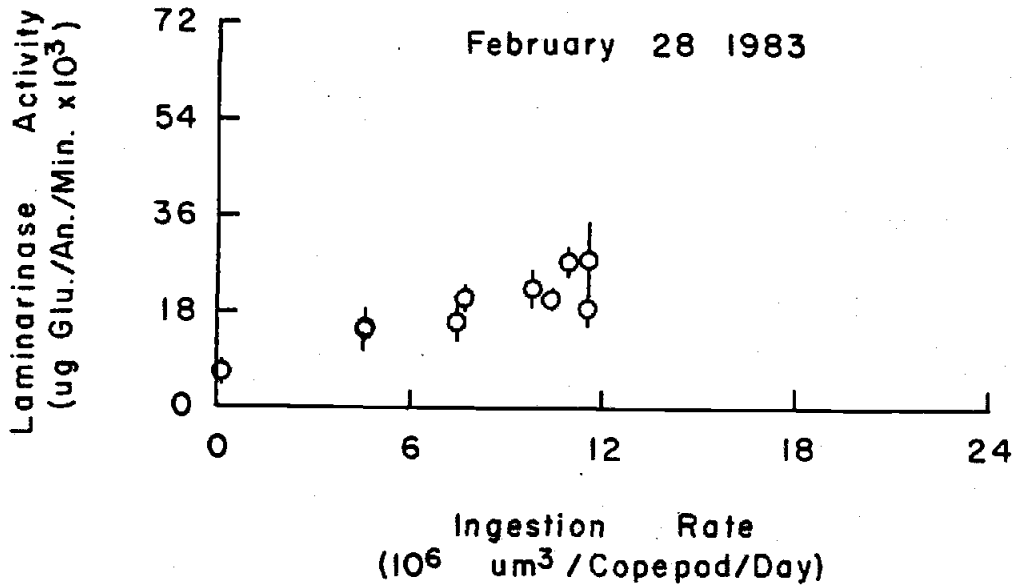

Laminarinase Activity
(ug Glu./mg Prot./Hr. x10⁻²)
18.0
13.5
9.0
4.5
0
December 16 1982
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

Figure 15 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on February 28, 1983 versus the laminarinase activity of the copepods expressed as ug glucose/animal/minute x 10^3 and as ug glucose/mg protein/hour x 10^{-2}. The error bars shown are the standard deviations of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask. The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 15


Laminarinase Activity
(ug Glu./An./Min. x10³)
72
54
36
18
0
February 28 1983
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

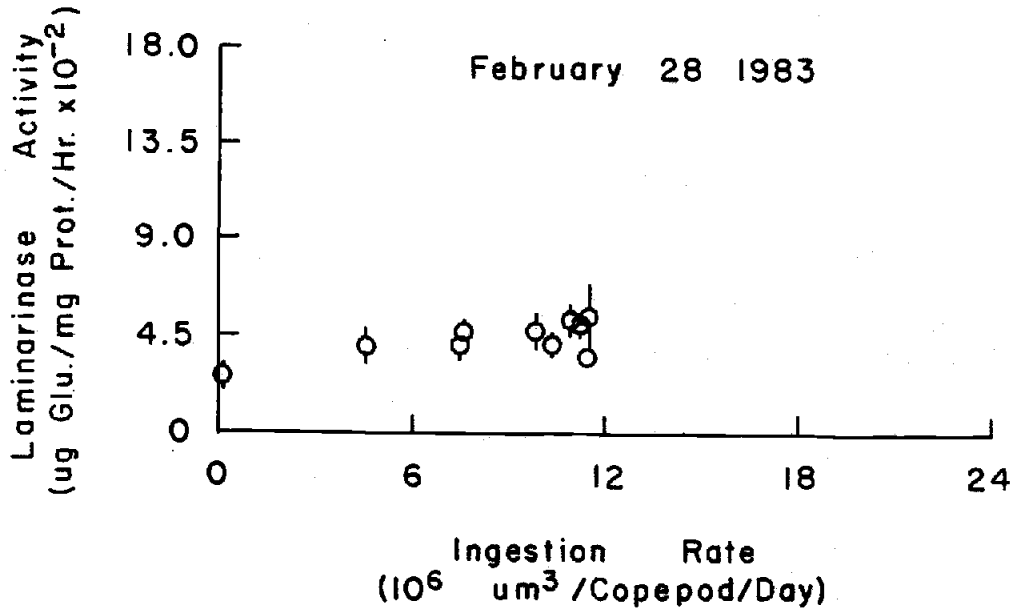
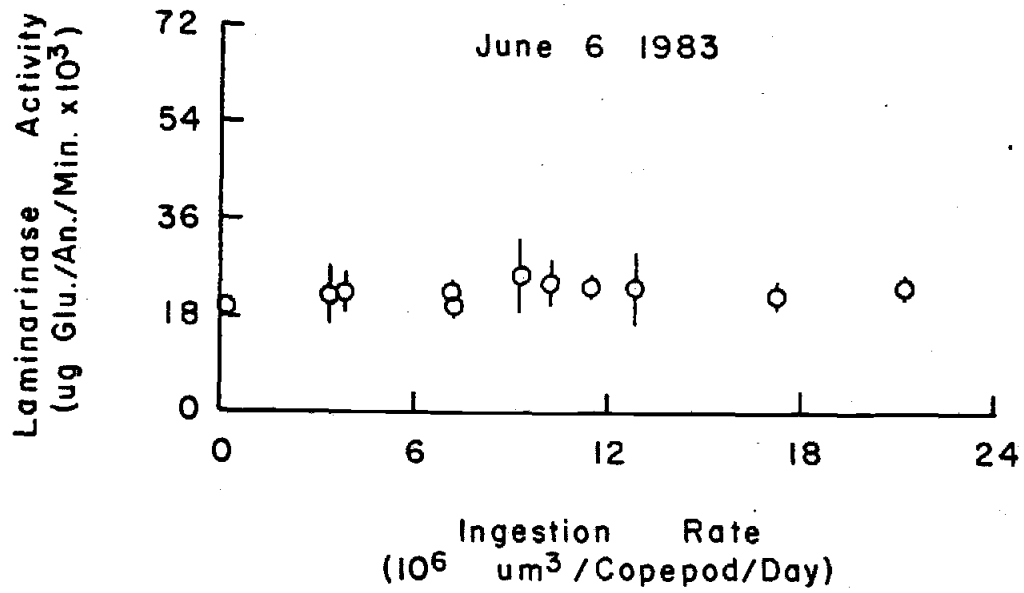

Laminarinase Activity
(ug Glu./mg Prot./Hr. x10⁻²)
18.0
13.5
9.0
4.5
0
February 28 1983
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

Figure 16 Ingestion rates (10^6 um3/copepod/day) for adult Acartia clausii females collected on June 6, 1983 versus the laminarinase activity of the copepods expressed as ug glucose/animal/minute x 10^3 and as ug glucose/mg protein/hour x 10^{-2}. The error bars shown are the standard deviations of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask. The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 16


Laminarinase Activity
(ug Glu./An./Min. x10³)
72
54
36
18
0
June 6 1983
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

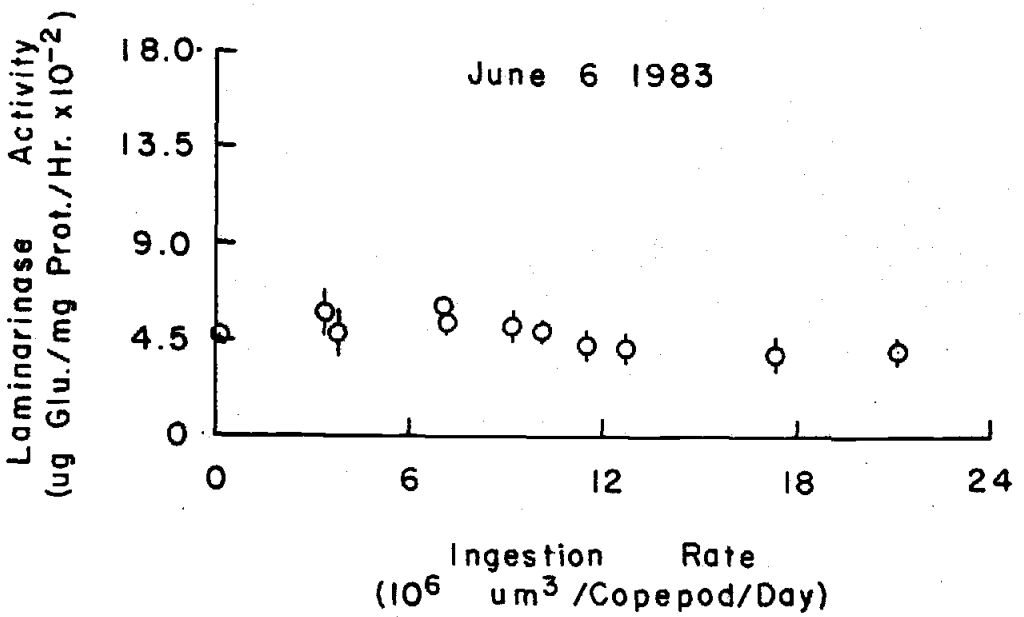
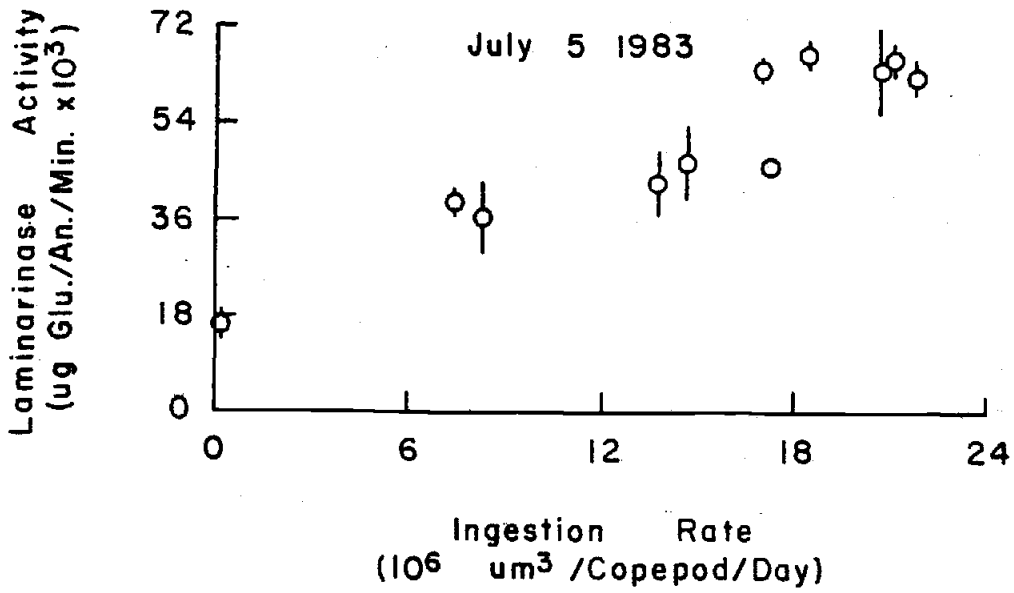

Laminarinase Activity
(ug Glu./mg Prot./Hr. x10⁻²)
18.0
13.5
9.0
4.5
0
June 6 1983
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

Figure 17 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on July 5, 1983 versus the laminarinase activity of the copepods expressed as ug glucose/animal/minute x 10^3 and as ug glucose/mg protein/hour x 10^{-2}. The error bars shown are the standard deviations of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask. The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 17


July 5 1983
Laminarinase Activity (ug Glu./An./Min. x10³)
72
54
36
18
0
0
6
12
18
24
Ingestion Rate (10⁶ um³ /Copepod/Day)

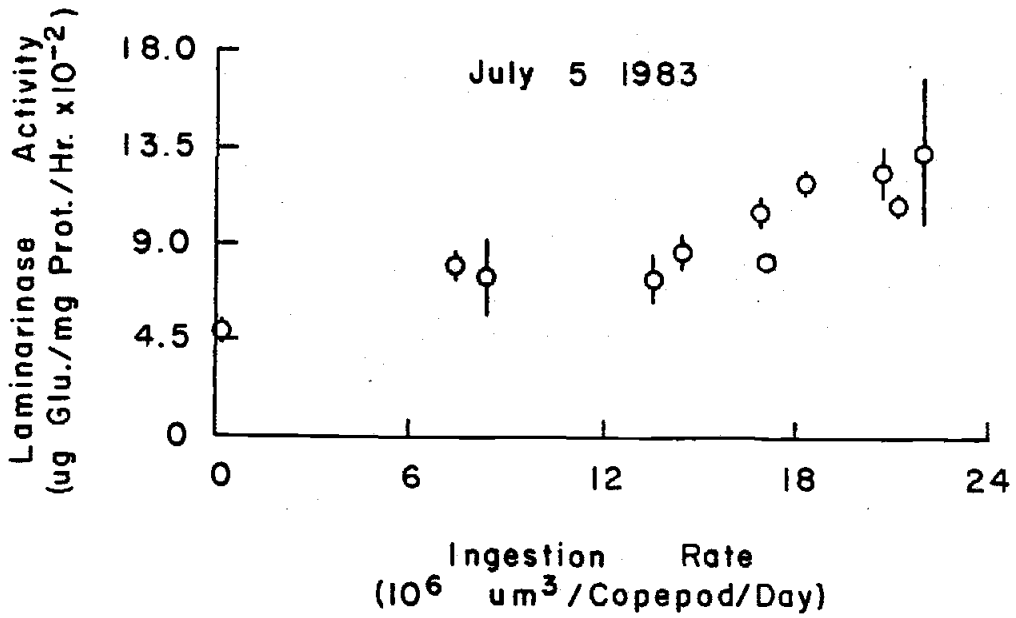
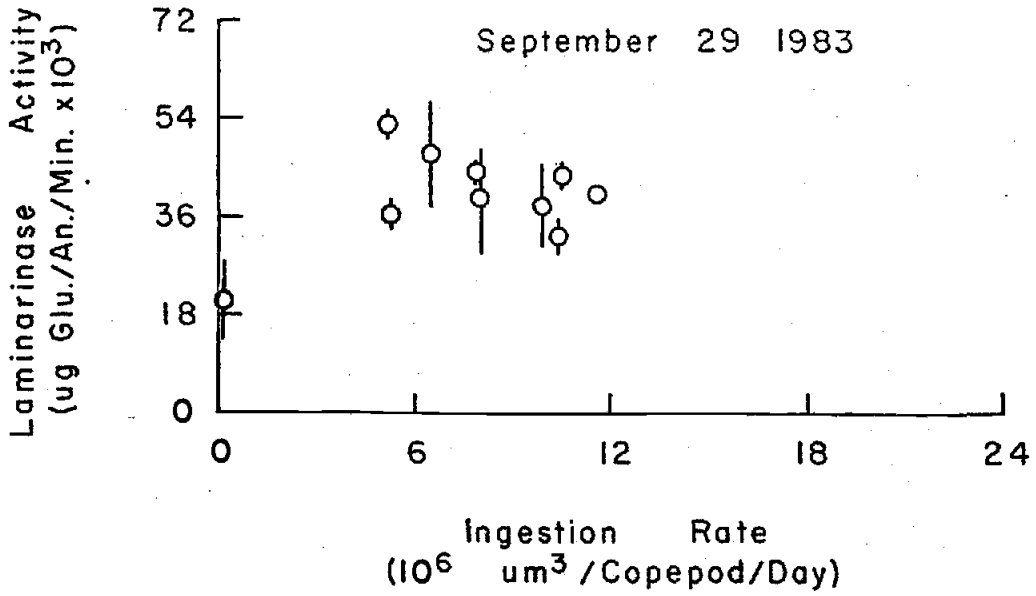
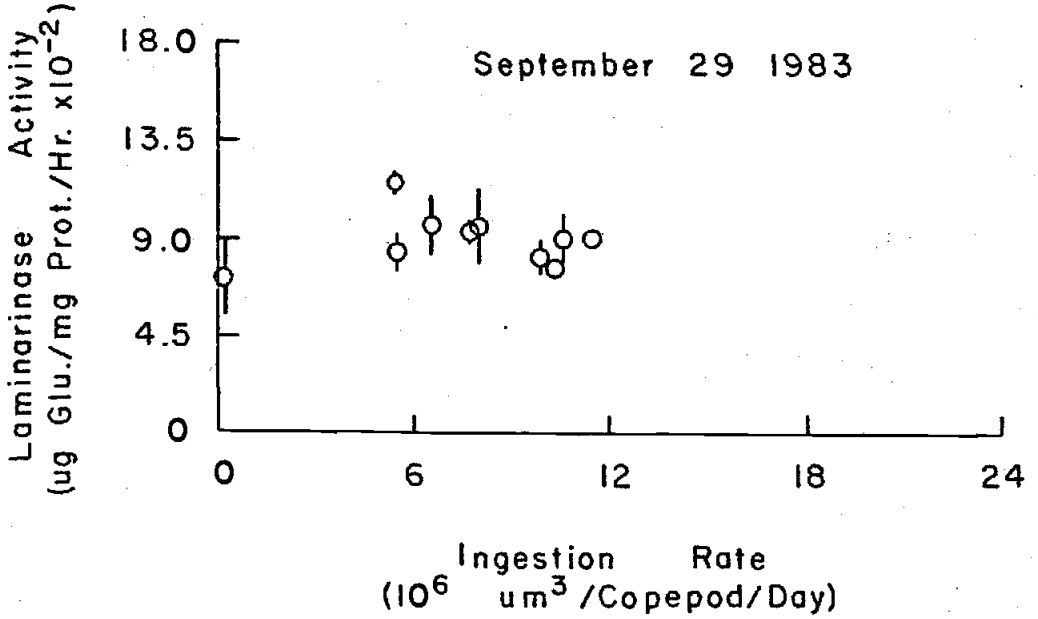

July 5 1983
Laminarinase Activity (ug Glu./mg Prot./Hr. x10⁻²)
18.0
13.5
9.0
4.5
0
0
6
12
18
24
Ingestion Rate (10⁶ um³ /Copepod/Day)

Figure 18 Ingestion rates (10^6 um^3/copepod/day) for adult Acartia clausii females collected on September 29, 1983 versus the laminarinase activity of the copepods expressed as ug glucose/animal/minute x 10^3 and as ug glucose/mg protein/hour x 10^{-2}. The error bars shown are the standard deviations of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask. The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 18


Laminarinase Activity
(ug Glu./An./Min. x10³)
72
54
36
18
0
September 29 1983
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)


Laminarinase Activity
(ug Glu./mg Prot./Hr. x10⁻²)
18.0
13.5
9.0
4.5
0
September 29 1983
0
6
12
18
24
Ingestion Rate
(10⁶ um³ /Copepod/Day)

nine experiments. When laminarinase activity expressed in terms of total copepod protein (LP) was compared with ingestion rate, a somewhat different pattern was observed. The majority of experiments had negative correlation coefficients (Table 5), but only two of these negative coefficients were significant (for experiments in November 1982 and June 1983). One experiment (July 1983) showed a significant positive correlation between LP and ingestion rate.

The different patterns of significance observed, depending on the units used to express laminarinase activity, appeared to occur because copepods acclimated to the lowest food levels (levels A and B) often had lower protein concentrations than copepods acclimated to higher food concentrations (levels C, D, E, and F). Spearman rank correlation coefficients for copepod protein concentration versus acclimation food concentration (Table 6) were positive in all but two experiments and were significant for five of the experiments. The relatively low protein concentrations in animals at low food levels yielded relatively high LP values. In addition, animals at low food levels usually had the lowest ingestion rates (Figs. 1 - 6). Conversely, animals at high food levels often had relatively high protein concentrations, relatively low LP values, and relatively high ingestion rates. This combination of effects produced the many negative correlations between LP and ingestion rates that were observed for most of the experiments (Table 5). However, it must be remembered that only two of these negative correlations were statistically significant. Non-significance indicated no statistical correlation between LP and ingestion rate, an indication also borne out by visual examination of Figs. 7, 8, 9, 11, 14, and 18.

Table 6 Spearman rank correlation values for comparisons between laminarinase activity expressed as ug glucose produced/copepod/minute (LA) and acclimation food concentration, and between the protein concentration of *Acartia clausii* (PRO) and acclimation food concentration. The level of significance is indicated as follows: 0.05 = (*), 0.01 = (**), 0.001 = (***).

Experiment Date	LA	PRO
March 19, 1982	-0.06	0.52
April 7, 1982	-0.36	0.71*
June 23, 1982	0.65*	0.78*
July 22, 1982	0.41	0.72*
September 20, 1982	-0.72*	-0.61
October 8, 1982	0.85**	0.25
November 9, 1982	-0.64*	0.45
December 16, 1982	0.14	0.61
February 28, 1983	0.63	0.68*
June 6, 1983	0.25	0.91***
July 5, 1983	0.90***	0.53
September 29, 1983	-0.49	-0.07

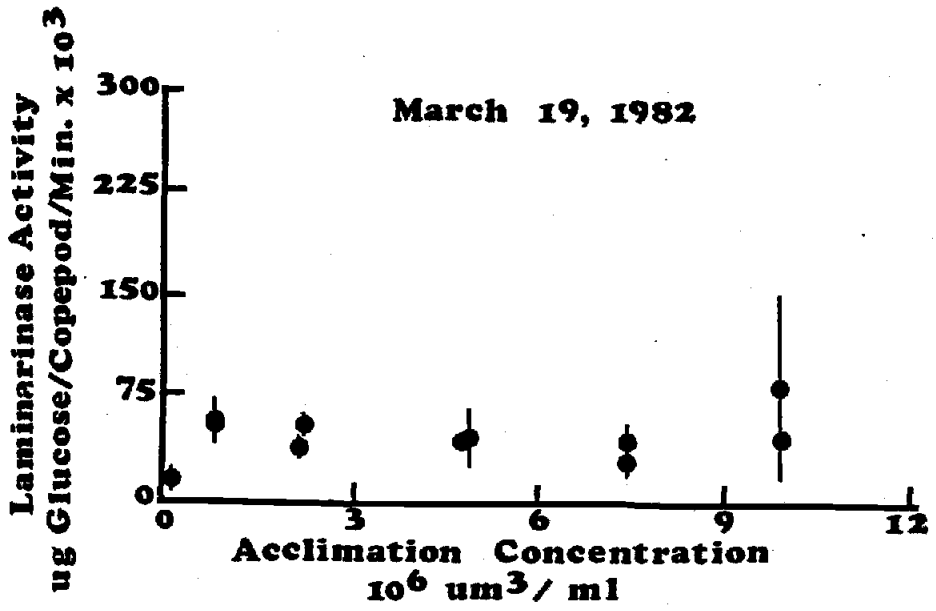
There also were experiments which showed a negative correlation between animal-based laminarinase activity (LA) and ingestion rate (Table 5), but none of the negative correlation coefficients were statistically significant. The three significant positive correlations between LA and ingestion rate did not follow a seasonal pattern; thus, while two of these significant values were found in summer months, the third was found in February. Moreover, not all of the summer (July, 1982 and June 1983) correlations were significant, though all were positive. These results point up the problems associated with comparing enzyme activities for copepods acclimated to different food concentrations when the activities are expressed in terms of non-specific substrates such as the total animal or total protein. To obtain a valid specific enzyme activity the results should be expressed on the basis of total protein content of the enzyme present in the copepods. The lack of a significant relationship between LA and ingestion rate for the majority of experiments, and the negative correlations between LP and ingestion rate, suggests that Acartia clausii conserves laminarinase and utilizes other protein reserves when acclimated at low food concentrations.

Laminarinase Activity versus Acclimation Food Concentration

Relationships between the laminarinase activity (ug glucose/copepod/minute) of Acartia clausii and the five food levels (plus zero food level) to which the animals were acclimated before experimentation, are shown in Figs. 19 - 24. The Spearman rank

Figure 19 Laminarinase activities (ug glucose/copepod/minute x 10^3) of adult Acartia clausii females collected on March 19, 1982 and April 7, 1982 versus the concentration of Thalassiosira weissflogii to which the copepods were maintained at during the three day acclimation interval. The error bars shown are the standard deviation of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask (see text for details). The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 19


March 19, 1982
Laminarinase Activity
ug Glucose/Copepod/Min. x 10³
300
225
150
75
0
0
3
6
9
12
Acclimation Concentration
10⁶ um³/ ml

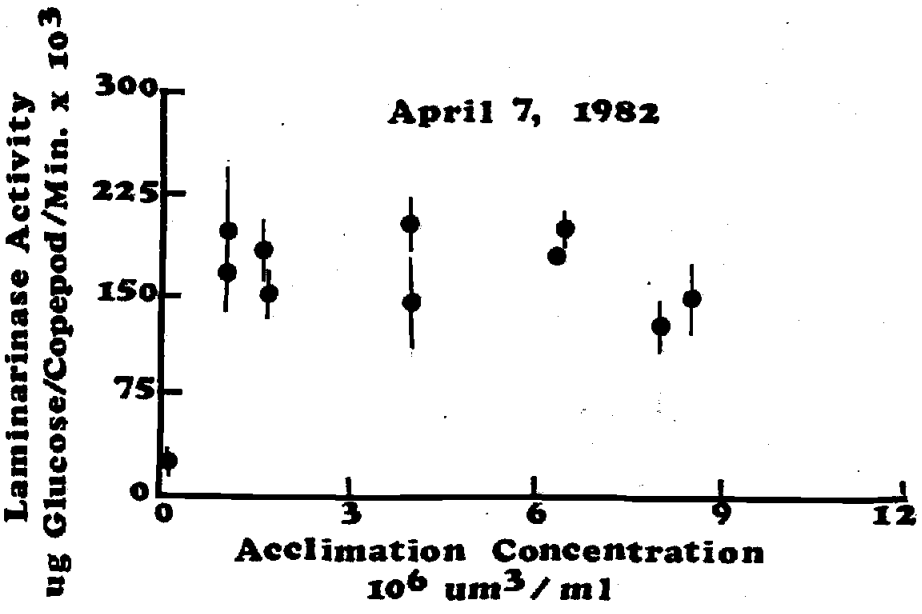
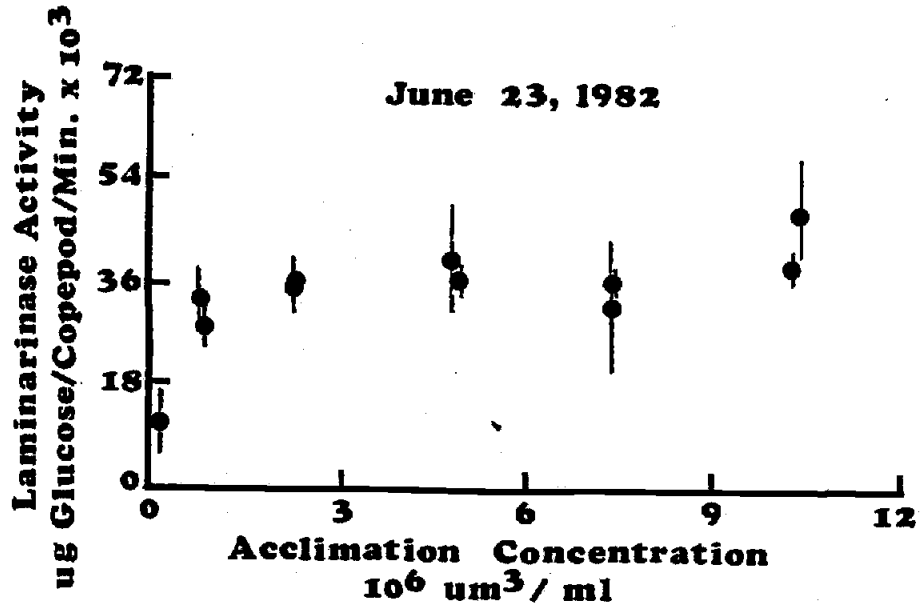

April 7, 1982
Laminarinase Activity
ug Glucose/Copepod/Min. x 10³
300
225
150
75
0
0
3
6
9
12
Acclimation Concentration
10⁶ um³/ ml

Figure 20 Laminarinase activities (ug glucose/copepod/minute x 10^3) of adult Acartia clausii females collected on June 23, 1982 and July 22, 1982 versus the concentration of Thalassiosira weissflogii to which the copepods were maintained at during the three day acclimation interval. The error bars shown are the standard deviation of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask (see text for details). The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 20


June 23, 1982
Laminarinase Activity
ug Glucose/Copepod/Min. x 10³
72
54
36
18
0
0
3
6
9
12
Acclimation Concentration
10⁶ um³/ ml

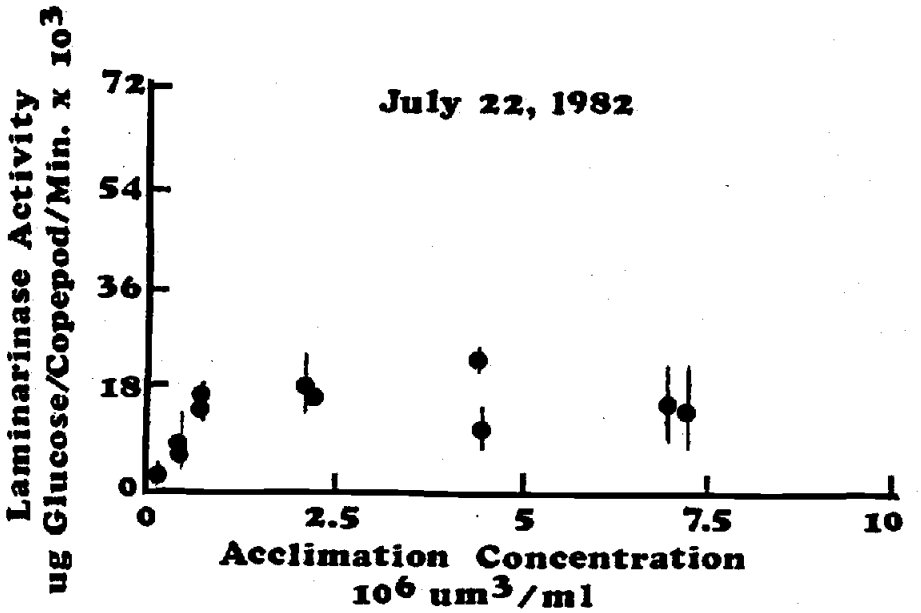
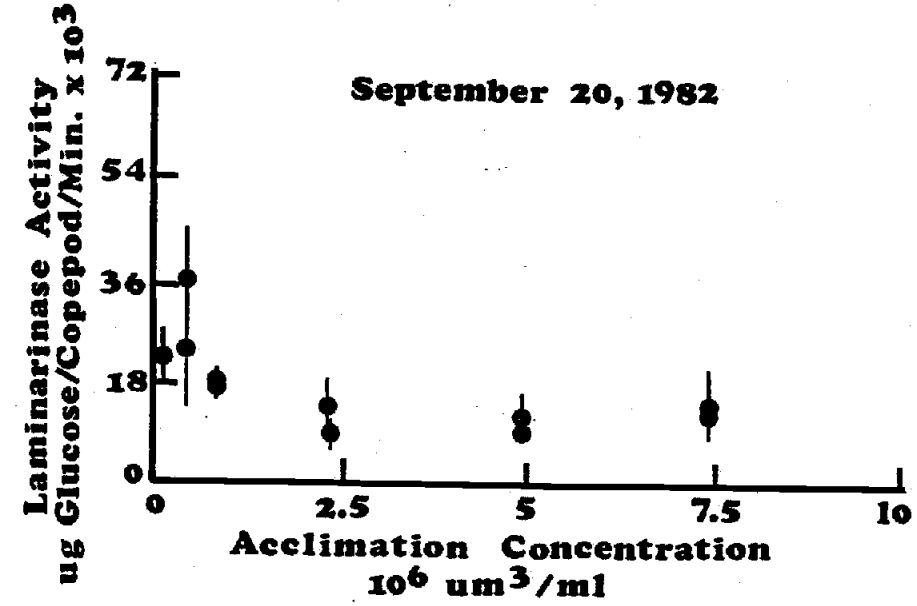

July 22, 1982
Laminarinase Activity
ug Glucose/Copepod/Min. x 10³
72
54
36
18
0
0
2.5
5
7.5
10
Acclimation Concentration
10⁶ um³/ml

Figure 21 Laminarinase activities (ug glucose/copepod/minute x 10^3) of adult Acartia clausii females collected on September 20, 1982 and October 8, 1982 versus the concentration of Thalassiosira weissflogii to which the copepods were maintained at during the three day acclimation interval. The error bars shown are the standard deviation of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask (see text for details). The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 21


September 20, 1982
Laminarinase Activity
ug Glucose/Copepod/Min. x 10³
72
54
36
18
0
0
2.5
5
7.5
10
Acclimation Concentration
10⁶ um³/ml

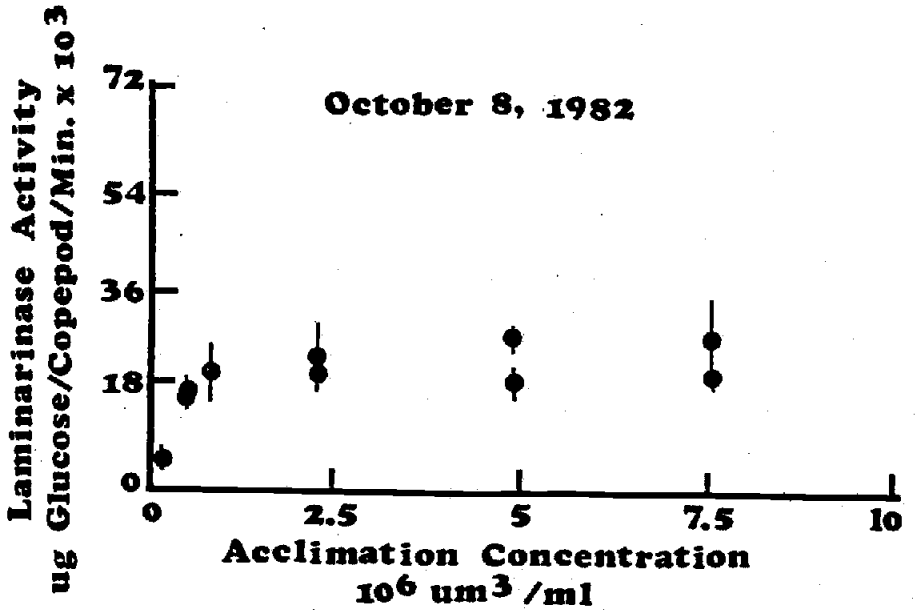
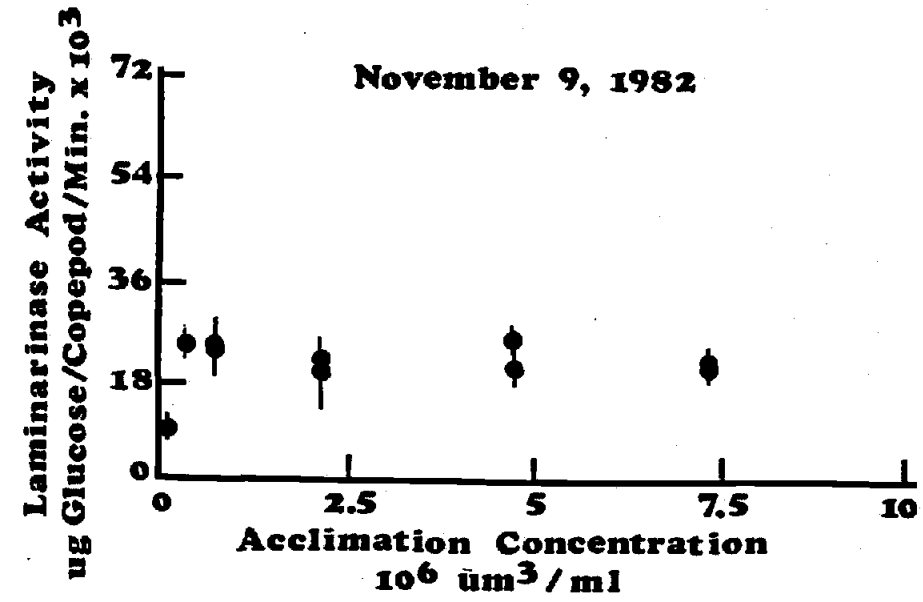

October 8, 1982
Laminarinase Activity
ug Glucose/Copepod/Min. x 10³
72
54
36
18
0
0
2.5
5
7.5
10
Acclimation Concentration
10⁶ um³/ml

Figure 22 Laminarinase activities (ug glucose/copepod/minute $x^{-}10^{3}$) of adult Acartia clausii females collected on November 9, 1982 and December 16, 1982 versus the concentration of Thalassiosira weissflogii to which the copepods were maintained at during the three day acclimation interval. The error bars shown are the standard deviation of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask (see text for details). The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 22


November 9, 1982
Laminarinase Activity
ug Glucose/Copepod/Min. x 10³
72
54
36
18
0
0
2.5
5
7.5
10
Acclimation Concentration
10⁶ um³ / ml

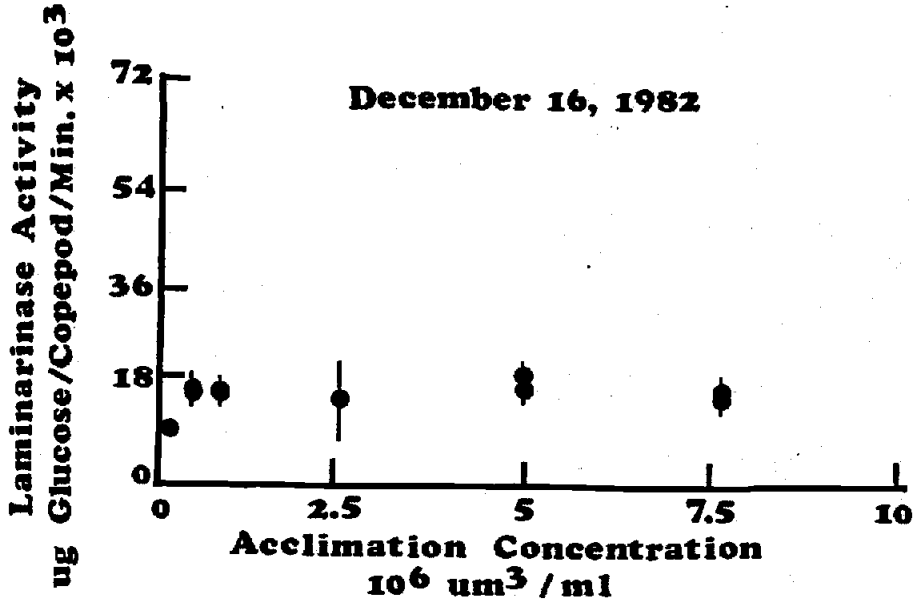
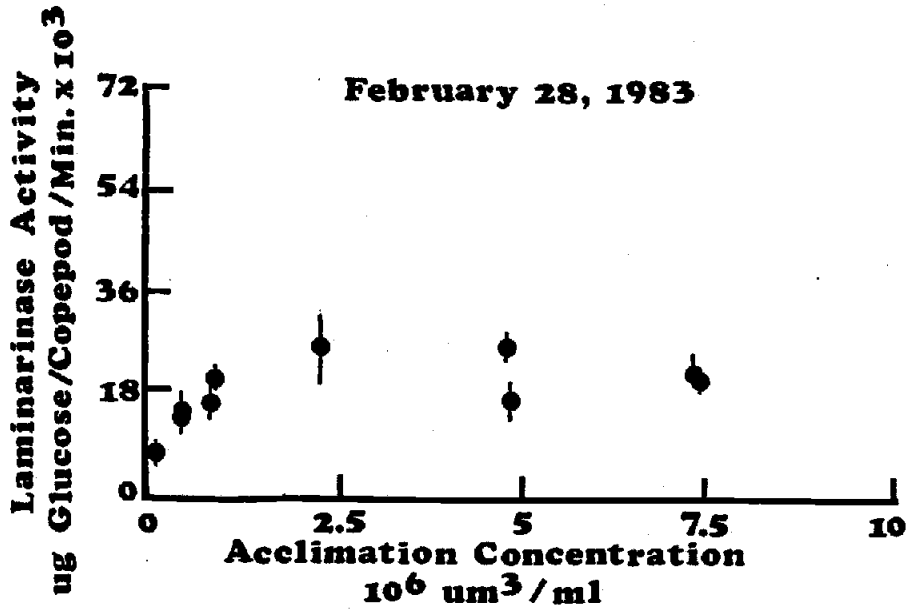

December 16, 1982
Laminarinase Activity
ug Glucose/Copepod/Min. x 10³
72
54
36
18
0
0
2.5
5
7.5
10
Acclimation Concentration
10⁶ um³ / ml

Figure 23 Laminarinase activities (ug glucose/copepod/minute x 10^3) of adult Acartia clausii females collected on February 28, 1983 and June 6, 1983 versus the concentration of Thalassiosira weissflogii to which the copepods were maintained at during the three day acclimation interval. The error bars shown are the standard deviation of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask (see text for details). The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 23


February 28, 1983
Laminarinase Activity
ug Glucose/Copepod/Min. x 10³
72
54
36
18
0
0
2.5
5
7.5
10
Acclimation Concentration
10⁶ um³ / ml

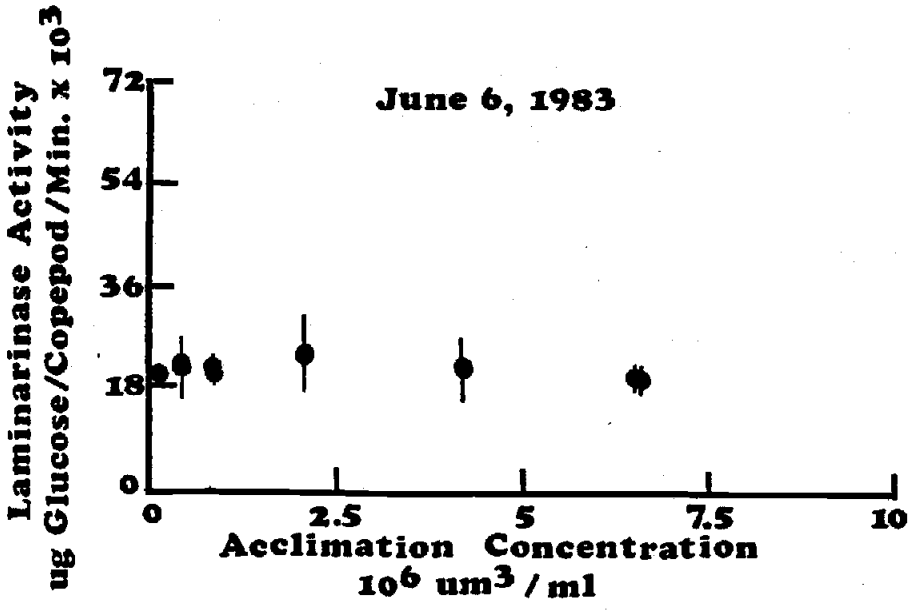
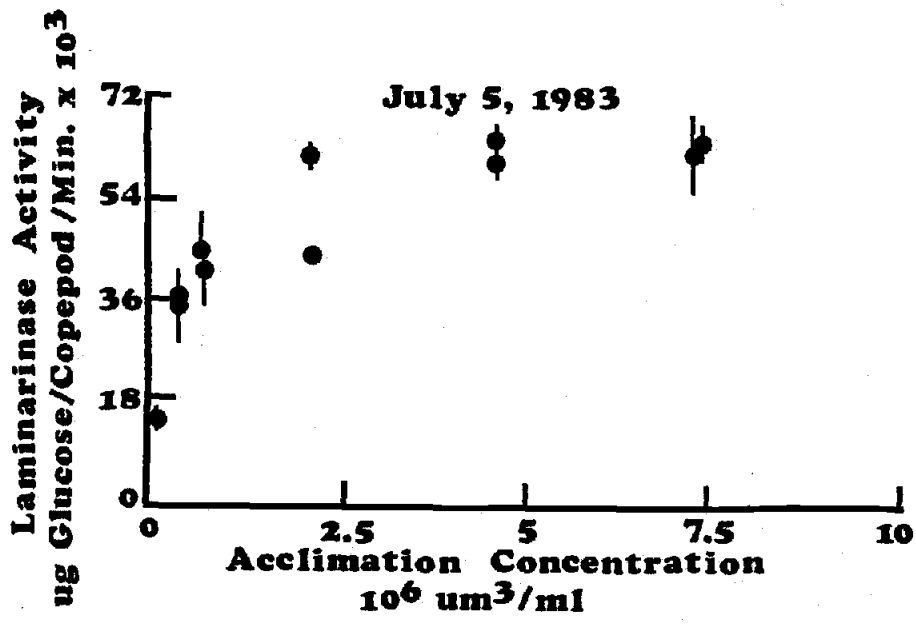
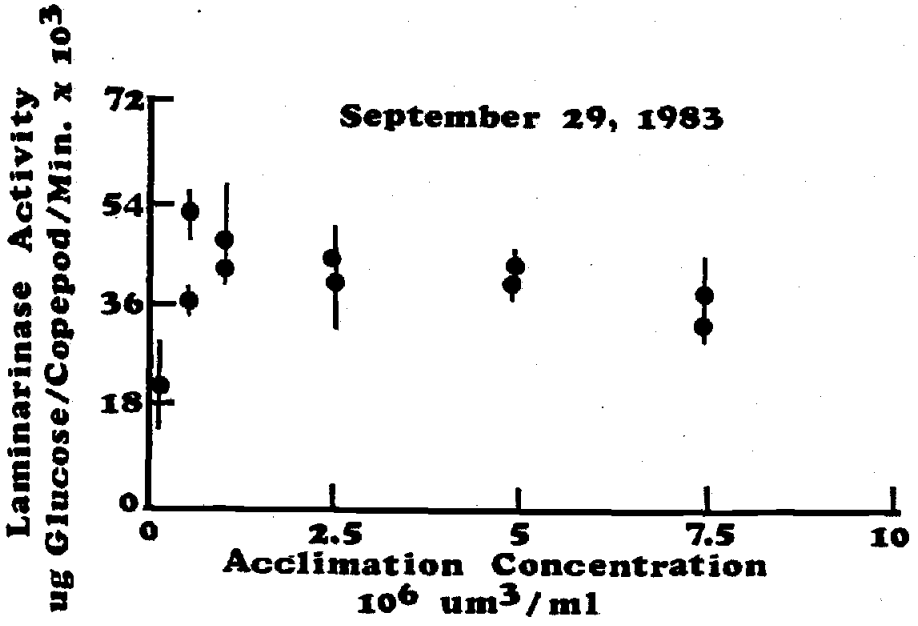

June 6, 1983
Laminarinase Activity
ug Glucose/Copepod/Min. x 10³
72
54
36
18
0
0
2.5
5
7.5
10
Acclimation Concentration
10⁶ um³ / ml

Figure 24 Laminarinase activities (ug glucose/copepod/minute x 10^3) of adult Acartia clausii females collected on July 5, 1983 and September 29, 1983 versus the concentration of Thalassiosira weissflogii to which the copepods were maintained at during the three day acclimation interval. The error bars shown are the standard deviation of the laminarinase activities of two samples of 20 copepods analyzed for each experimental flask (see text for details). The point nearest to the Y-axis in each plot is the enzyme activity of copepods which were starved in filtered seawater throughout the experiment.

Figure 24


July 5, 1983
Laminarinase Activity
ug Glucose/Copepod/Min. x 10³
72
54
36
18
0
0
2.5
5
7.5
10
Acclimation Concentration
10⁶ um³/ml


September 29, 1983
Laminarinase Activity
ug Glucose/Copepod/Min. x 10³
72
54
36
18
0
0
2.5
5
7.5
10
Acclimation Concentration
10⁶ um³/ml

correlation test was used to determine if a significant correlation existed between enzyme activity and food concentration (levels A - F). The results of this test (Table 6) showed that a significant ($p < .05$) positive correlation occurred in three experiments: June 1982, October 1982, and July 1983. Significant negative correlations were found for September 1982 and November 1982, while correlations for the remaining experiments were non-significant.

The largest change in laminarinase activities in these experiments occurred for copepods which were starved in filtered seawater. Enzyme activities were consistently lower (with the exception of September 1982 and June 1983) for starved copepods. Thus, it appears that in these experiments A. clausii for the most part maintained a relatively constant laminarinase activity which was unaffected by either food concentration or ingestion rate, and decreased its digestive enzyme levels only under starvation conditions. The regulation of digestive enzymes for this copepod might therefore be viewed mainly as a switching response. In the presence of food the switch is turned on and laminarinase activities adjust to some constant level. In the absence of food the switch is turned off and enzyme levels drop to some low level which varied depending on the date at which the copepods were collected. This interpretation is supported by the results of an experiment in which Acartia females were placed in three different food concentrations (levels C, D, and E) and filtered seawater, and the laminarinase activity of the copepods was measured daily for five days (Table 7). Laminarinase activities at the three food concentrations were not significantly different from each other or from initial measurements taken at day 1

Table 7 Effects of starvation and food concentration (10^6 um^3/ml) on *Acartia clausii* laminarinase activity (ug glucose/ copepod/minute x 10^3. The copepods were collected on October 30, 1981. Log phase cultures of *Thalassiosira weissflogii* were provided as food.

Time after Capture (days)	n	Mean Laminarinase Activity (± S.D.)	Algal Concentration
1	3	159.0 ± 12.4	7.5
1	3	164.6 ± 2.1	5.0
1	3	145.9 ± 7.5	2.5
1	3	162.7 ± 3.9	0.0
2	3	156.5 ± 8.5	7.5
2	3	155.9 ± 3.9	5.0
2	3	162.7 ± 7.0	2.5
2	3	163.9 ± 1.9	0.0
3	3	148.4 ± 11.4	7.5
3	3	144.7 ± 20.4	5.0
3	3	155.9 ± 2.8	2.5
3	1	109.9	0.0
4	3	105.6 ± 49.7	7.5
4	3	156.5 ± 0.0	5.0
4	3	154.6 ± 8.1	2.5
4	-	-	0.0
5	3	123.6 ± 27.1	7.5
5	3	156.5 ± 3.2	5.0
5	3	157.7 ± 1.1	2.5
5	-	-	0.0

after five days of acclimation to the food concentrations (F-test, $p < 0.05$). Laminarinase activities for copepods placed in filtered seawater were not significantly different from those of copepods kept in the food concentrations for the first two days of the experiment, but dropped to lower levels by the third day. Unfortunately, due to high mortality for copepods kept in filtered seawater, insufficient animals were available for determinations of enzyme activity after the third day of the experiment.

Although laminarinase activities remained relatively constant at different food concentrations and ingestion rates for any given experiment, the level of laminarinase activity differed among experiments throughout the period of study. The seasonal patterns of laminarinase activity for the copepods acclimated to each of the food levels, and for those starved in filtered seawater, are shown in Figs. 25 - 27. Laminarinase activity increased approximately five-fold in April 1982 and then decreased and remained essentially constant until July 1983, when there was a two-fold increase in enzyme activity. The July 1983 enzyme level was apparently maintained through September 1983 by copepods feeding at the lower food concentrations (A and B). The large increase in laminarinase activity observed in the spring of 1982 could not be verified in 1983 as A. clausii was not present in sufficient numbers to allow experiments to be conducted during the spring of 1983.

The results in Figs. 25 - 27 show that A. clausii varies its laminarinase activity seasonally. Enzyme activity apparently is high during spring months and then decreases to low or intermediate levels in the summer. During the fall and winter months enzyme activity is

Figure 25 Laminarinase activities (ug glucose/copepod/minute x 10^3) for Acartia clausii acclimated to food levels E (approximately 7.5 x 10^6 um^3/ml) and D (approximately 5.0 x 10^6 um^3/ml) for all experiments (see text for details).

Figure 25

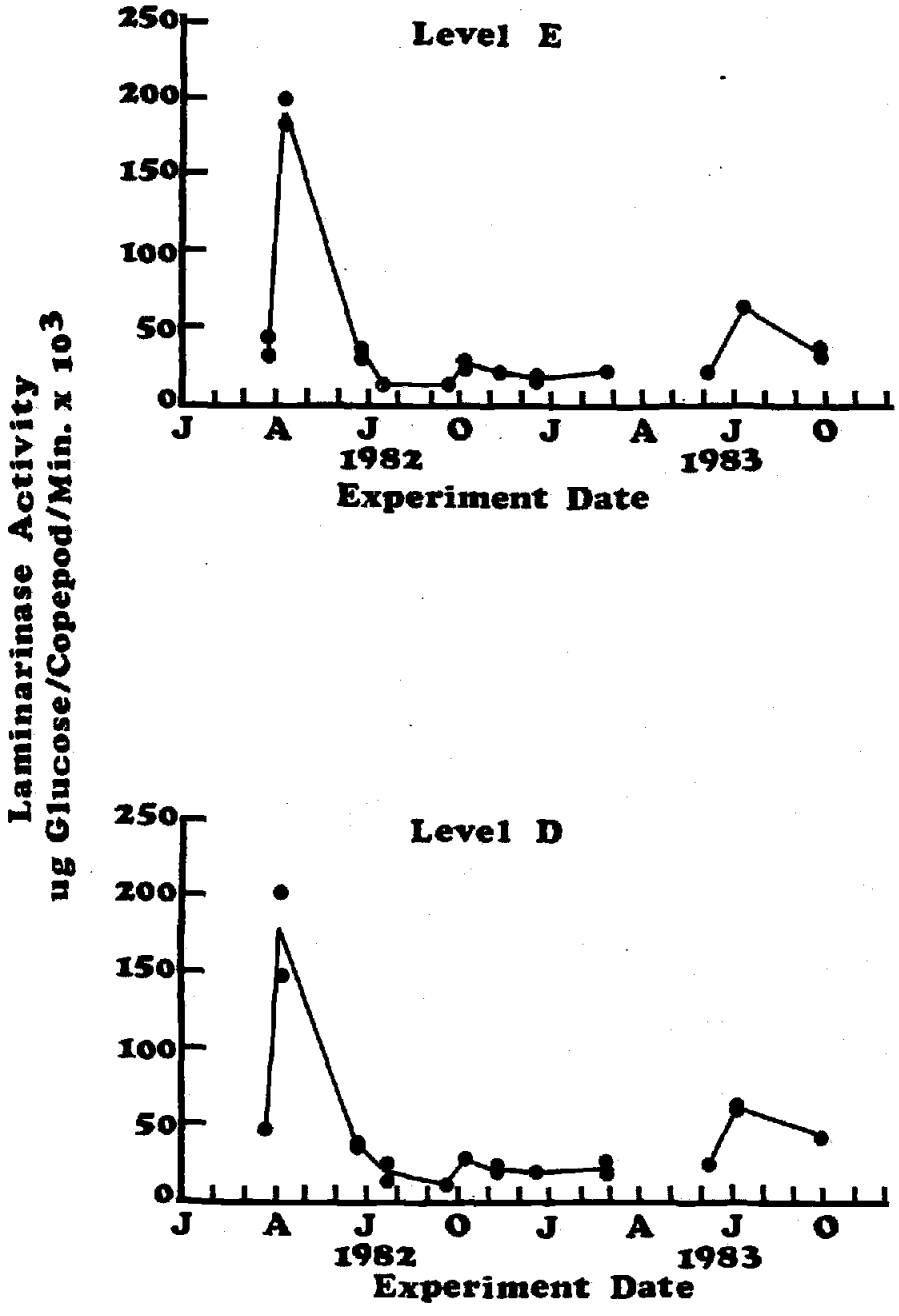

Level E
250
200
150
100
50
0
J A J O J A J O
1982
1983
Experiment Date
Level D
250
200
150
100
50
0
J A J O J A J O
1982
1983
Experiment Date
Laminarinase Activity
ug Glucose/Copepod/Min. x 10³

Figure 26 Laminarinase activities (ug glucose/copepod/minute x 10^3) for *Acartia clausii* acclimated to food levels C (approximately 2.5 x 10^6 um^3/ml) and B (approximately 1.0 x 10^6 um^3/ml) for all experiments (see text for details).

Figure 26

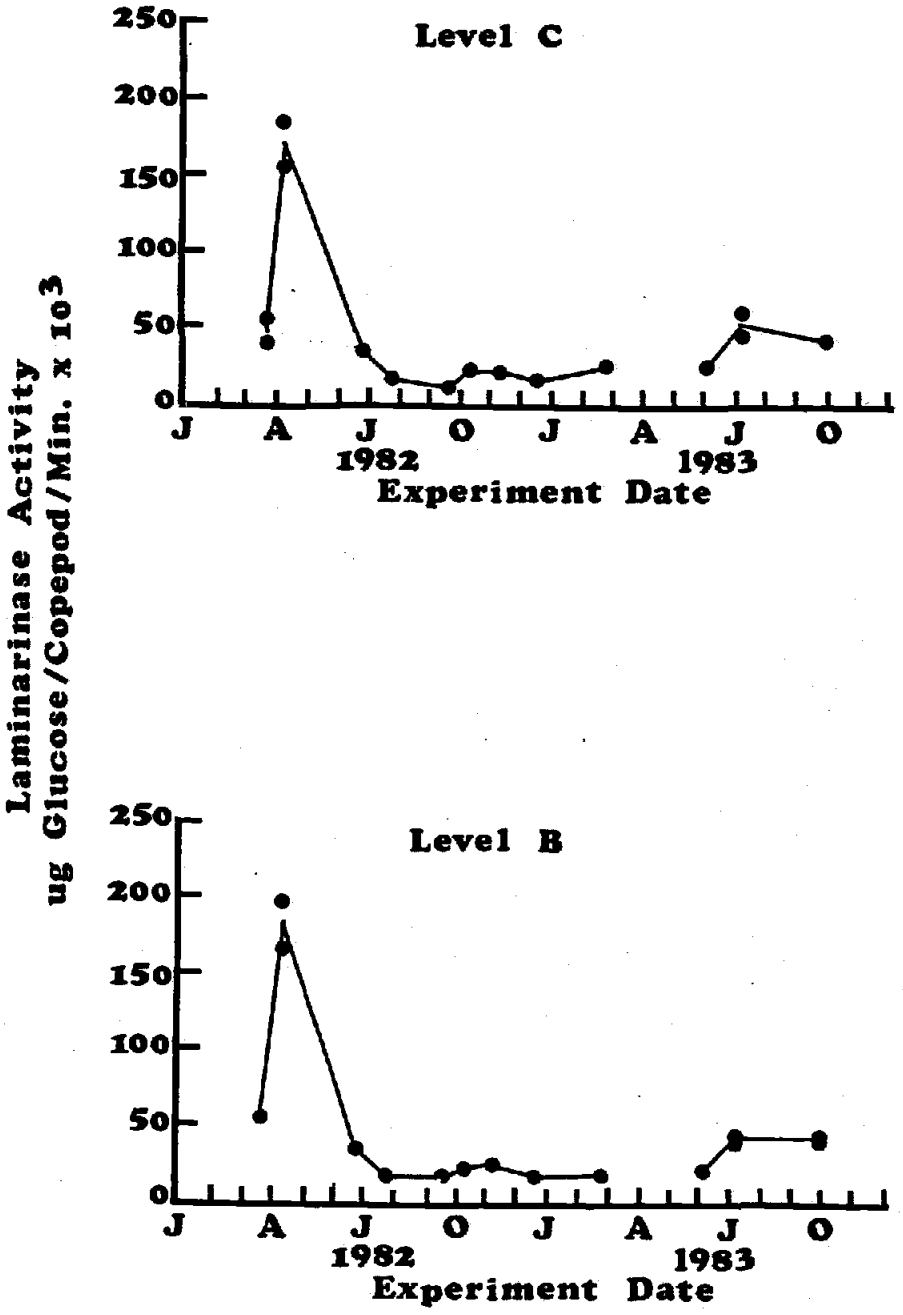
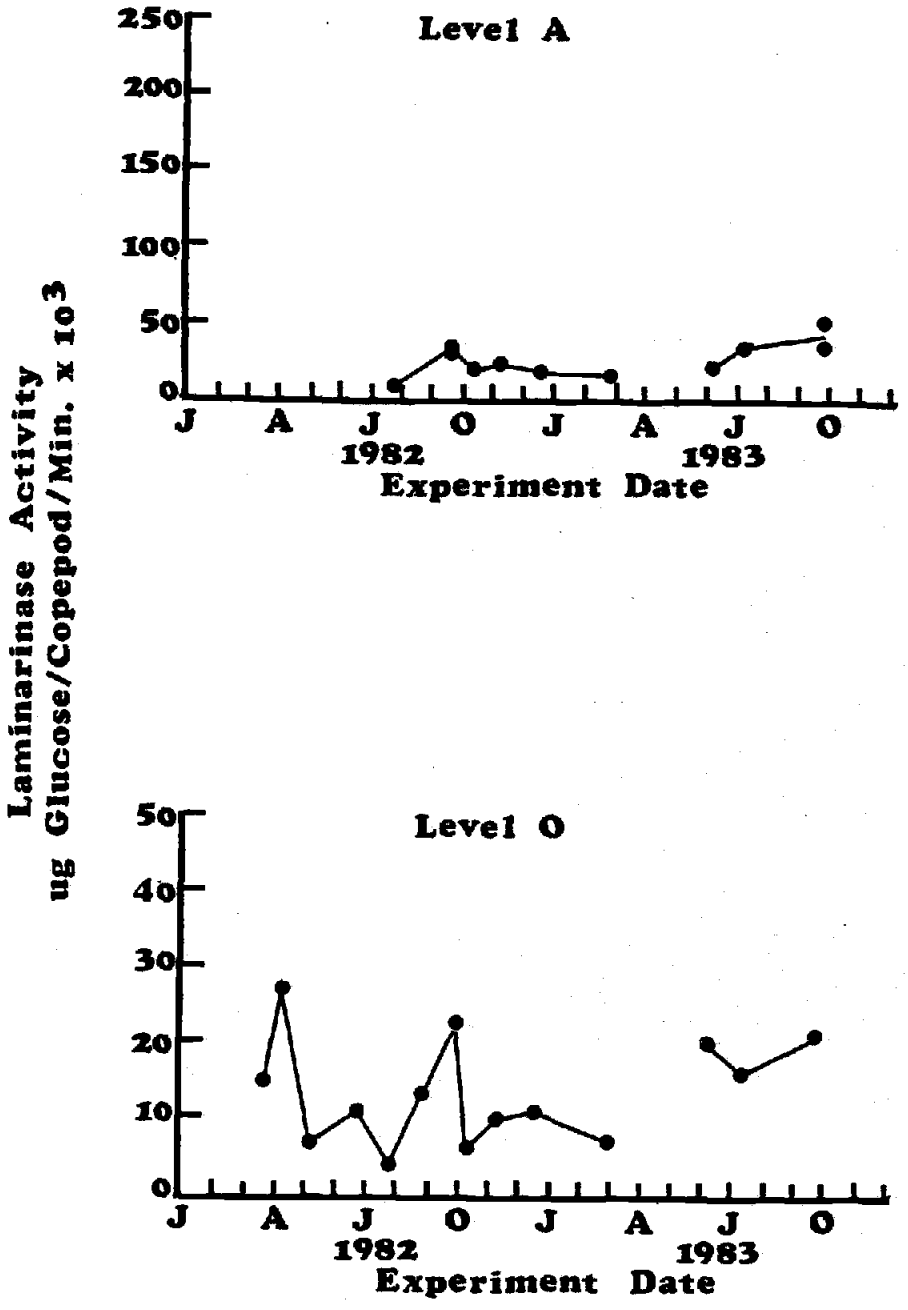

Level C
250
200
150
100
50
0
J A J O J A J O
1982
1983
Experiment Date
Level B
250
200
150
100
50
0
J A J O J A J O
1982
1983
Experiment Date
Laminarinase Activity
ug Glucose/Copepod/Min. x 10^3

Figure 27 Laminarinase activities (ug glucose/copepod/minute x 10^3) for *Acartia clausii* acclimated to food level A (approximately 0.5 x 10^6 um^3/ml) and starved in filtered seawater (level 0) for all experiments (see text for details).

Figure 27


Level A
250
200
150
100
50
0
J A J O J A J O
1982
1983
Experiment Date
Laminarinase Activity
ug Glucose/Copepod/Min. x 10³
Level O
50
40
30
20
10
0
J A J O J A J O
1982
1983
Experiment Date

maintained at low levels. This pattern is also observed for the laminarinase activities of starved copepods, though not so distinctly; for example, laminarinase activities were almost as high in September 1982 as in April 1982, in starved copepods, and both June and July 1983 activities were also relatively high. That there is any pattern at all strengthens the case for a seasonal regulation of laminarinase activity. The threshold level of enzyme activity in starved copepods presumably should be constant unless there is some seasonal regulation of enzyme levels.

The seasonal pattern of laminarinase activities for Acartia clausii was similar to that found for maximum ingestion rates (Table 8), and suggested that there was some relationship between these two parameters. This relationship was examined for all experiments except April 1982 for which no clear maximum ingestion rate was found. A significant positive correlation (t test, $p < .05$) was found between maximum ingestion rate and laminarinase activity for these experiments (Fig. 28). It should be noted that the April 1982 experiment had mean laminarinase activities of about 180 ug glucose/copepod/min x 10^6. In order for this experiment to "fit into" the relationship shown in Fig. 28, the maximum ingestion rate would have had to be 45 x 10^6 um^3/copepod/day. This value is not unlikely, as the ingestion rate found for the highest food level for this experiment was 40 x 10^6 um^3/copepod/day. It is possible that the copepods collected at this time were acclimated to high food concentrations exceeding the levels offered in the laboratory, and that if higher food concentrations had been used a maximum ingestion rate exceeding 40 x 10^6 um^3/copepod/day would have been obtained. Therefore,

it seems reasonable that Acartia clausii varies its digestive enzyme levels seasonally and that these changes are correlated with the maximum ingestion rate which can be achieved. It is concievable, though not proved, that levels of laminarinase in the digestive tract control, or help control, the rates of ingestion in this copepod. The pattern of laminarinase activity in individual experiments demonstrates that changes in digestive enzyme activities apparently require periods of time in excess of five days (Table 7), and therefore represent long-term changes in food processing capability of this copepod.

Table 8 Maximum ingestion rates (10^6 um^3/copepod/day) of Acartia clausii obtained from Ivlev equation fits to the data and mean laminarinase activities (ug glucose/copepod/minute x 10^3) for the copeods at the food levels exhibiting these ingestion levels.

Experiment Date	Maximum Ingestion Rate	Laminarinase Activity
March 19, 1982	18.19	50.50 ± 16.94
June 23, 1982	16.77	37.25 ± 4.92
July 22, 1982	13.71	17.17 ± 4.31
September 20, 1982	3.50	13.75 ± 3.54
October 8, 1982	10.72	24.50 ± 3.66
November 9, 1982	10.28	21.87 ± 2.53
December 16, 1982	10.95	17.50 ± 1.69
February 28, 1983	11.09	22.83 ± 3.82
June 6, 1983	19.74	23.00 ± 1.41
July 5, 1983	19.78	59.83 ± 7.41
September 29, 1983	9.79	39.67 ± 3.93

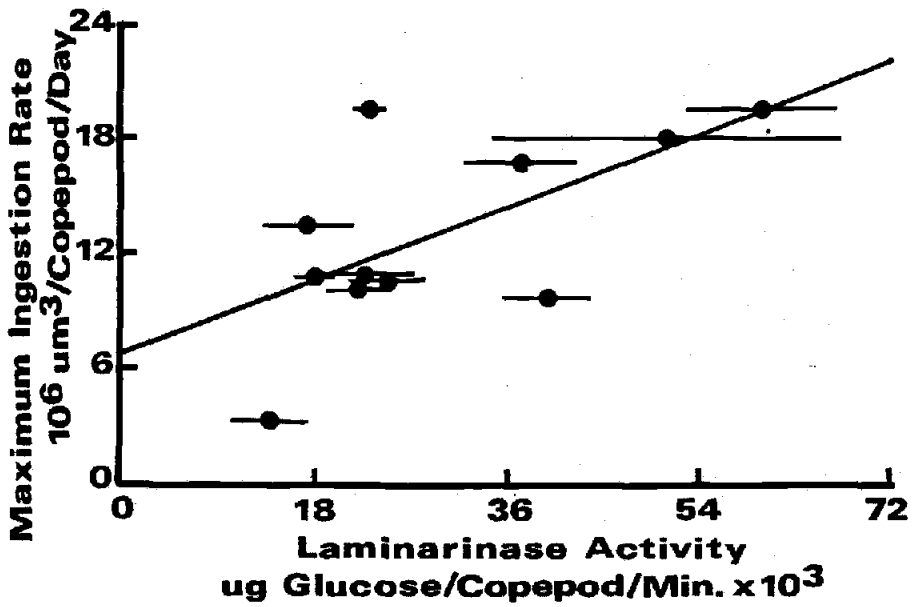


Figure 28 Maximum ingestion rates of Acartia clausii obtained from Ivlev equation fits to the data (see Table 4) versus the mean laminarinase activities for the copepods at the food levels exhibiting these ingestion levels. The linear fit shown has the form $Y = 0.21(X) + 6.78$ ($r^2 = 0.40$). The April 7, 1982 results are not included (see text for details).

Discussion

The goal of this study was to clarify the relationship between food intake (ingestion rate) and digestive enzyme activity (laminarinase) for the small neritic copepod Acartia clausii. As described earlier, the seasonal relationship between these variables is complex. Both ingestion rate and laminarinase activity were found to vary seasonally and correlations between these parameters were found to be positive, negative, or nonexistent depending on the date the experiment was conducted. In order to understand these various results it is necessary to explore in detail the physiology of food processing in copepods.

Perhaps the best known aspect of the feeding behavior of copepods is that describing the removal of particles at different food concentrations. Evidence from laboratory studies generally supports a relationship between copepod ingestion rate (biomass consumed/copepod/day) and food concentration characterized by a critical or incipient food concentration above which ingestion rates become saturated and remain constant (e.g. Mullin, 1963; Frost, 1972; 1977). Below the critical concentration there is a range of food concentration over which ingestion rate increases approximately linearly with increasing food; i.e., where volume clearance rate (filtering rate) per individual is constant (Lam and Frost, 1976). This relationship can be described mathmatically by a rectilinear model (Frost, 1972), an Ivlev curve (Parsons et al., 1967), or a Michaelis-Menton model (Mullin et al., 1975). The rectilinear and curvilinear models arise from slightly different concepts of the

ingestion process. In the rectilinear model, there is assumed to be no decrease in the rate of the food capture - ingestion process until a critical particle concentration is reached, and the rate at which water is cleared of food is constant within this range of concentrations. In the other two models the rate of ingestion decreases as the concentration of particles nears the critical food concentration, so the relationship between ingestion rate and particle concentration appears curvilinear (Mullin et al., 1975). At present, there has been no study which has included a sufficient number of data points near the critical food concentration to statistically distinguish which of these models is correct. Therefore, the choice of a model to describe the saturation response, as in this study, should be viewed as a method of summarizing ingestion rate data, rather than as an indication of the feeding behavior occurring near the critical concentration.

The rectilinear or curvilinear models of copepod feeding have been incorporated in several models of marine planktonic communities (e.g. Steele, 1974; Wroblewski and O'Brien, 1976; Steele and Frost, 1977; Steele and Mullin, 1977); however, more recently the validity of this type of model for copepod feeding in the field has been questioned. When copepods are fed natural particulates at ambient concentrations at different times of the year ingestion rates tend to be linearly related to food abundance, with no indication of a saturation plateau (e.g. Poulet, 1974; Reeve and Walter, 1977; Mayzaud and Poulet, 1978; Koeller et al., 1979; Huntley, 1981). The lack of agreement between these studies and laboratory descriptions of ingestion rate appears to result from the use of laboratory food

concentrations exceeding ambient levels found in the field, and from insufficient consideration of acclimation time and season as influential factors in the laboratory studies. For example, Mayzaud and Poulet (1978) found that copepods displayed linearly increasing ingestion rates at concentrations of natural particulates below ambient concentrations, and that ingestion rates became saturated only when copepods were allowed to graze on food concentrations artificially increased above ambient levels. These authors proposed that the saturation response observed in the laboratory is an artifact of short-term experiments in which copepods acclimated to relatively low food concentrations in nature are exposed to high food levels exceeding their digestive capability. Presumably, if copepods are given sufficient time to adjust their ingestion rates and digestive processes to the higher food levels in the laboratory, and provided the food concentrations are within the seasonal range of field concentrations, a linear relationship between ingestion rate and food concentrations would be observed.

The relationship between seasonal changes in ingestion rate, food concentration, and digestive enzyme levels is the subject of a recent hypothesis in zooplankton literature, termed the acclimation hypothesis (Hassett and Landry, 1983). According to this hypothesis zooplankton acclimate to ambient food concentrations such that higher digestive enzyme activities, and consequently higher maximum ingestion rates, are achieved at higher food levels. This hypothesis provides three predictions regarding the behavior or biochemistry of copepods acclimated to different food levels (Hassett and Landry, 1983). The first prediction is that the ingestion rate should be positively

related to food concentration after acclimation. The second prediction is that digestive enzyme activities of copepods should be positively correlated with food concentration after acclimation. The third prediction is that, at any given concentration of food to which the copepods are acclimated, ingestion rates should be positively correlated with digestive enzyme activity.

In this study the first of these predictions was not completely observed; ingestion rates were positively related to food concentrations below 2.5×10^6 um^3/ml, but became saturated at food concentrations above this level. The only exceptions to this pattern occurred for experiments conducted in March 1982, April 1982, and June 1983 where ingestion rates increased at the highest food level (Figs. 1 and 5). Since the phytoplankton concentrations used in these experiments are within the seasonal range of concentrations occurring in Yaquina Bay (Karentz, 1975; O'Connors et al., 1976), the saturation of ingestion rates at higher food concentrations may indicate the acclimation interval used was too short to allow complete adjustment to these concentrations. Mayzaud and Poulet (1978) suggested that the acclimation time required to shift from a saturation response to a linear response for ingestion rates should lie within an interval of 24 hours to six days. However, Hassett and Landry (1983) found a saturation-type ingestion response for Calanus pacificus acclimated to food concentrations in the laboratory for two weeks and a similar response was observed for Acartia clausii acclimated for five days in the present study. These results suggested that the acclimation times needed to observe a shift from saturated ingestion rates to a linear response with food concentration

in the laboratory may be on the order of weeks, and that the linear ingestion rates found in field studies are the result of long-term acclimation to food conditions.

The second prediction of the acclimation hypothesis, that digestive enzyme activities of copepods should be positively correlated with acclimation food concentration, was also not observed for Acartia clausii. Although slightly lower laminarinase activities were obtained for copepods at the lowest food levels in several experiments, enzyme activities, for the most part, remained relatively constant at each of the food concentrations. Laminarinase activities were, however, lower for copepods kept in filtered seawater without any food. This pattern was observed in all but two experiments (September 1982 and June 1983). It appears from these results that the laminarinase activity of A. clausii varied not with the concentration of food, but rather increased to some constant level in the presence of food and only decreased when food was not available. This result agrees with results obtained with Calanus pacificus collected during August 1979 and May 1982 from Puget Sound, Washington, where no significant change in laminarinase activities were found for animals acclimated to four food concentrations over a two week period (Hassett and Landry, 1983). A decrease in laminarinase activity for starved C. pacificus collected from Santa Barbara channel, California during April 1980 has also been reported by Cox and Willason (1981), although in contrast to the results obtained in the present study and by Hassett and Landry (1983), enzyme activities were found to vary with food concentration. The laminarinase activities of starved C. pacificus from the Santa

Barbara channel increased rapidly once the copepods were supplied with food, and were not significantly different at three food concentrations after feeding for 0.5 day. By 1.5 days of feeding, however, laminarinase activities were significantly different at the three food concentrations and were positively correlated with food abundance. These differences in the response of laminarinase activity to food concentration between a single species (Calanus pacificus) collected from different locations (Santa Barbara channel and Puget Sound), and between different copepod species (C. pacificus and A. clausii), may indicate that the response obtained is specific to copepods from a given location or a given time of year, possibly related to the timing of phytoplankton blooms. Hassett and Landry (1983) have questioned the validity of the Cox and Willason (1981) findings, suggesting that their results were obtained with copepods in unusually poor physiological state, perhaps due to conditions in the field prior to capture.

The final prediction of the acclimation hypothesis suggests that there should be a positive correlation between ingestion rates and the activity of digestive enzymes when copepods are allowed sufficient time to acclimate to food concentrations. Once again this prediction did not appear to be valid for A. clausii. A significant positive correlation between laminarinase activity and ingestion rate was found in three experiments; however, the majority of experiments showed no correlation between these parameters. In general, it appears that the acclimation hypothesis did not apply when Acartia clausii was acclimated to food concentrations in the laboratory for five days, except for certain experiments mentioned previously. In the majority

of experiments laminarinase activities showed no relation to ingestion rates, and therefore the utilization of laminarinase activities to predict ingestion rates for this copepod in short-term experiments holds little promise.

Evidence of long-term acclimation, or seasonal adjustment, in A. clausii is demonstrated by the variability found in ingestion rates, at identical food concentrations, for copepods collected at different times of the year. Maximum ingestion rates during spring, and at times in summer, were twice those observed during other times of the year. The maximum ingestion rate for April 1982 could not be resolved, but it appears that it could have been much higher than the rates measured at other times of the year. Since the experimental conditions of these experiments remained constant, the increased ingestion rates must have arisen from long-term physiological adjustments in the copepods that were carried over from the field. Apparently these long-term adjustments were not altered by a laboratory acclimation interval of five days in the present study (and longer in other studies). There are several studies which have reported seasonal changes in the grazing rates of copepods feeding on ambient concentrations of natural particulates (e.g. Martin, 1970; Poulet, 1976; 1977; 1978; Mayzaud and Poulet, 1978; Dagg and Wyman, 1983; Nicolajsen et al., 1983). A common feature of these studies was increased grazing rates in the spring and summer months, which coincided with increases in the concentration of phytoplankton and frequently temperature. Unfortunately, changes in the quality and concentration of food particles and varying physical parameters inherent in these field studies did not allow conclusions about the

primary factors influencing the seasonal changes in grazing rates. Attempts to identify these factors in controlled laboratory experiments have also had limited success. Skiver (1980) found seasonal variation in grazing rates for Acartia when fed ambient concentrations of micronic spheres at field temperatures, indicating that changes in food quality alone is not responsible for seasonal ingestion rate variations. In addition, experiments conducted at constant temperature and food concentrations have shown seasonal variation in grazing rates (O'Connors et al., 1976; Runge, 1980), suggesting that factors other than temperature and food concentration must be involved in seasonal grazing rate fluctuations.

Some of the factors which have been proposed to explain seasonal changes in grazing rates include changes in water temperature, size of the copepods, food quality, the reproductive state of the animals, food availability, and the level of digestive enzymes. The effects of changing temperature on copepod grazing rates appears to depend on the time scale over which such changes occur. When copepods are collected at one temperature and subjected to various temperatures below their upper limits of thermal tolerance, a linear increase in ingestion rates with increasing temperatures is usually observed (e.g., Anraku, 1964; Heinle, 1969; Fernandez, 1978; Deason, 1980). However, when the ingestion rates of neritic copepods at ambient temperatures are compared over an annual cycle there is often no change in ingestion rates (Conover and Huntley, 1980; Conover, 1980). The temperature short-term effect was apparently negated in the long-term studies by temperature acclimation of the copepods, variations in food concentration, and changes in the size of the copepods occurring

throughout the annual cycle. In Yaquina Bay, where the copepods were collected for the present study, the offshore upwelling of cold water generally balances the greater solar heating of water during the summer period, so that there is only a very damped annual cycle of temperature in the coastal ocean and in the lower reaches of the bay (Miller, 1983). These small temperature changes (4 °C) were unlikely to have caused the variations in grazing rates observed for A. clausii, especially because ingestion rates varied for experiments conducted at the same temperature with copepods collected at different times of the year. Seasonal changes in the body size of Acartia also did not appear to account for the observed changes in ingestion rate. Sufficient numbers of animals were available for determinations of dry weight in four of the experiments conducted in this study. The dry weights of Acartia ranged between 6.3 and 9.8 ug/copepod, but ingestion rates calculated on a dry weight basis for these experiments still varied by a factor of 2.5.

Changes in the biochemical composition or quality of food particles which can occur seasonally due to the succession of different phytoplankton species and changing physical conditions also may modify copepod grazing rates. Copepods appear to be able to select food particles on the basis of their nutritional characteristics. For example, Acartia clausii was able to preferentially ingest microcapsules containing phytoplankton extract over non-enriched microcapsules (Poulet and Marsot, 1978). In addition, A. clausii did not ingest plastic spheres intermediate in size between two sizes of diatoms, while it did ingest the diatoms (Donaghay and Small, 1979). Copepods also exhibited higher grazing rates on log-phase

cultures than on senescent cultures of diatoms in the laboratory (Conover, 1956; Mullin, 1963), and in mixtures of food particles ingestion rates apparently increased in proportion to the amount of 'high quality' food in the animals' diet (Richman and Dodson, 1983). The work by Samain et al. (1981) indicated that these changes in grazing rate were all probably due to the biochemical characteristics of the food particles. In the study by Samain et al. (1981), the ingestion rates of Artemia on the same species of phytoplankton varied depending on the chemical composition of the cells; cells that were rich in proteins and poor in carbohydrates were ingested at lower rates than cells with a high carbohydrate-to-protein ratio. The changes in ingestion rates observed in these studies occurred in short-term experiments ($\leqslant$24 hours), and thus appeared to represent short-term adaptations in feeding behavior. Therefore, although food quality apparently is an important parameter regulating ingestion rates, it is unlikely that it would explain the long-term seasonal variation in grazing rates obtained with a single food source in the present study.

The co-occurrence of increased ingestion rates and increased fecundity of copepods suggests that seasonal variation in grazing rates may be influenced by the reproductive state of the animals. The seasonal pattern of fecundity for A. clausii was not examined in this study; however, the many factors affecting egg-laying rates of copepods do not allow conclusions as to whether fecundity influences ingestion rate or is just one effect of the overall seasonal adjustment in these animals. It is just as plausible that ingestion rate influences fecundity. The number of eggs produced per female has

been shown to increase with increasing ingestion rate, food quality, and food concentration, as well as with increasing temperature and female body size (e.g. Gaudy, 1971; Checkley, 1980; Uye, 1981). All of these factors can vary seasonally. In one seasonal study Gaudy (1971) found that the fecundity of A. clausii fed seven different species of phytoplankton varied depending on the food source, but that there were large changes in egg-laying rates with season despite constant conditions of food concentration and temperature. It appears, therefore, that although copepod ingestion rates are affected by changes in temperature, body size, food quality, and possibly reproductive state, these parameters do not account for all of the seasonal change in ingestion rates of Acartia clausii.

The results of the present study suggest that seasonal changes in the activity of digestive enzymes may help explain seasonal changes in ingestion rates of Acartia clausii. Although the predictions of the acclimation hypothesis were not observed in the individual experiments conducted in the present study, this concept, if extended somewhat, may explain the long-term changes found for laminarinase activity and ingestion rates. Laminarinase activities within any one experiment remained relatively constant at all food levels, and decreased only for copepods kept in filtered seawater. However, the levels of laminarinase activity were different among these experiments. Enzyme activities at each of the food concentrations and filtered seawater were highest during April 1982, then decreased to low values during the summer, fall and winter of 1982, and increased slightly during July and September 1983. This variation in enzyme activities suggested a seasonal pattern of high activities in the

spring, low activities during the fall and winter and moderately high, but somewhat variable, enzyme activities during the summer months. This pattern was similar to that observed for maximum ingestion rates. This seasonal pattern of laminarinase activities was similar to the results found for other enzymes in marine zooplankton, and may be a general feature in temperate zooplankton. For example, the digestive enzymes amylase and trypsin in adult and copepodid stages of Calanus finmarchicus and C. helgolandicus were low in the winter, associated with reduced metabolism and a discontinuation of feeding, and then increased during the spring and summer (Hallberg and Hirche, 1980; Hirche, 1981; 1983). The enzyme activity of succinic dehydrogenase, which has been used as an index of respiratory activity, also showed a marked seasonal variation in the mysid Neomysis integer, with highest activities observed in May (Raymont et al., 1967). Livingstone (1981) also reported that the induction of enzymes appears to regulate seasonal changes of metabolism in the common mussel Mytilus edulis. The specific activity of glucose-6-phosphate dehydrogenase from the hepatopancreas of this animal was positively correlated with the level of metabolism and exhibited high activities in the summer and declined during the autumn and winter.

Food particle concentrations in Yaquina Bay followed a seasonal pattern similar to the pattern of digestive enzyme activity in A. clausii; therefore, it was possible that the predictions of the acclimation hypothesis were still valid, but that both the measured ingestion rates and laminarinase activities reflected long-term adjustment of A. clausii to field concentrations rather than any short-term acclimation to the food concentrations provided in the

laboratory. Evidence supporting this proposition can be seen from the relationship between maximum ingestion rates and laminarinase activities for this copepod. A positive correlation between these parameters was found, as predicted by the acclimation hypothesis (Fig. 28). This result implies that laminarinase activities may allow prediction of the maximum ingestion rates attainable by copepods collected at a given time of the year. In other words, measurements of digestive enzyme activity may provide an indication of the grazing potential or capacity which copepods can achieve, given a sufficient concentration of food particles of the appropriate nutritional characteristics, at a given time of the year. According to this "capacity hypothesis" the actual ingestion rate measured may be lower than the theoretical maximum calculated from measurements of laminarinase activity; however, given optimal food concentrations, ingestion rates would increase until the maximum rate was attained. This hypothesis is consistent with the results of the present study, where laminarinase activities remained constant despite decreased ingestion rates at the lowest food levels. The copepods at these low food levels presumably had the capacity to achieve higher ingestion rates; however, due to insufficient food concentration at these levels, they were unable to achieve their maximum ingestion rates.

The factors responsible for seasonal changes in laminarinase activity could not be identified from the data accumulated in this study. Although the level of laminarinase activity in A. clausii appeared to be associated with the general pattern of phytoplankton abundance with season found in Yaquina bay (Karentz, 1975), there may be several other factors which contribute to the observed changes in

enzyme activity. Marine copepods often exhibit seasonal changes in respiration (e.g. Marshall and Orr, 1958; Conover, 1959; 1962; Cowey and Corner, 1963; Bamstedt, 1979; Hirche, 1983) and in other physiological attributes associated with diapause. The cues which appear to trigger the production of resting eggs and the onset of diapause include changes in temperature and photoperiod (Johnson, 1979; Marcus, 1980; 1982a; 1982b), similar to the situation found in terrestial insects (Elgmork, 1967; Elgmork and Nilssen, 1978). These physiological changes may also result from some form of internal timing mechanism (Miller, in press), or from changes in the seasonal production of hormones from neurosecretory cells (Carlisle and Pitman, 1961). Therefore, it was possible that any of the above factors or a combination of the physical and biological parameters affecting ingestion rates, in addition to food concentration, could have led to altered levels of digestive enzymes in Acartia clausii. More work on the factors affecting physiological changes in this copepod are required before this issue can be resolved.

It appears that whatever cues trigger changes in laminarinase activity these processes require periods of time greater than five days, because laminarinase activities remained constant during this time interval in individual experiments. The Belehradek temperature function predicts that the maximum lifetime of adult female A. clausii for the temperatures found in Yaquina Bay is 38 to 50 days (Uye, 1981). Therefore, unless levels of digestive enzyme activities have a genetic basis and vary seasonally because of differences among successive generations, changes in enzyme activities should occur on a time scale less than about 38 days. Again, digestive enzyme levels in

Acartia clausii apparently represent a long-term response which sets maximum food processing capability at different times of the year. Head and Conover (1983) also found that changes in laminarinase activity for stage V Calanus hyperboreus require periods of time in excess of five days. In their study significant enzyme induction, in the laboratory, did not occur until after about one week at 8-9 °C or about two weeks at 1-2 °C. It appears that copepods must utilize other mechanisms for regulating the actual amount of material ingested at different food concentrations over short periods of time. A variable gut clearance rate might be one mechanism to explain varying ingestion rates in the face of constant digestive enzyme activities.

It is often assumed that the feeding behavior of copepods can be viewed as an energy optimization process; i.e., that these animals seek to maximize their assimilation of essential nutrients from the food material consumed (Lam and Frost, 1976; Lehman, 1976). The important parameters regulating the amount of material assimilated by copepods are ingestion rate, the digestive rate and the length of time food remains in the gut. From a recent model which examined interactions between these processes it appears there are two ways that copepods can adjust their maximum ingestion rate (Slagstad and Tande, 1981). One way is to adjust the gut passage time, and the other is to alter the rate of digestion. Because the gut volume is presumably constant, higher ingestion rates can be attained only by decreasing the gut passage time or by increasing the digestive rate so that food is processed more rapidly. The positive correlation found for maximum ingestion rates and laminarinase activities of A. clausii suggests that variations in digestion rate are more important

in determining the maximum amount of food that can be processed. However, in individual experiments laminarinase activity remained constant despite decreases in ingestion rates at the lowest food concentrations. As suggested earlier, the digestive enzyme levels appear to indicate that the copepods had the capacity to achieve higher ingestion rates at these food levels, but were unable to attain these rates because of low food concentrations. Therefore, at low food concentrations, Acartia may increase the retention time of food in the gut to allow more complete processing of the material consumed, and thereby partially compensate for their inability to attain maximum ingestion rates. Evidence supporting this mechanism has been found for Acartia tonsa and Eucalanus attenuatus (Arashkevich, 1977). Both of these species showed an inverse relationship between food concentration and the duration of digestion. Thus, by decreasing gut clearance rate these copepods could assimilate a larger amount of material at low food concentrations and therefore optimize food assimilation for ingestion rates below their maximum rate, which is set by the level of digestive enzyme activity.

The lack of rapid changes in laminarinase activity in response to altered ingestion rates or food concentrations in short-term experiments probably is related to the rate of production of the types of cells responsible for enzyme production. Studies of the morphology of the mid-gut of copepods have shown that several cell types are present. In Calanus there are four distinct types of cells, called R-, B-, D-, and E-cells (Hirche, 1980). It has been suggested that the B-cells are responsible for producing digestive enzymes (Arnaud et al., 1978), and Hirche (1980) found a positive correlation between

the abundance of these cells and the level of enzyme activity. The R-cells are thought to have an absorptive and transporting function (Arnaud et al., 1978; Ong and Lake, 1969). E-cells are probably undifferentiated cells giving rise to other cell types and D-cells have been interpreted by Arnaud et al. (1978) as R-cells that have been suppressed owing to development of the B-cells in the glandular part of the mid-gut. Thus, the lack of rapid changes in laminarinase activity in Acartia may be due to the time required for production of B-cells from E-cells and redistribution of these cell types within the mid-gut region.

Conclusions

1) Ingestion rates for Acartia clausii increased approximately linearly with food concentrations below 2.5 x 10^6 um^3/ml and reached a maximum rate at concentrations above this level. Ivlev fits to the data were statistically the same for experiments conducted during fall and winter months. Maximum ingestion rates were greatest during spring and summer and lowest during fall and winter.

2) Copepod laminarinase activity in individual experiments remained relatively constant at all food concentrations for five days, and decreased only for starved individuals. There was no significant correlation between laminarinase activity and ingestion rate in the majority of experiments. Therefore, this enzyme does not appear to be a useful index of ingestion rate in short-term experiments.

3) The level of copepod laminarinase activity apparently varied seasonally. The highest activities were found during spring months and decreased to low levels during the fall and winter.

4) The maximum ingestion rate for A. clausii was positively correlated with the level of laminarinase activity. Therefore this enzyme appears to be an index of the maximum ingestive capacity of this copepod. Measured short-term ingestion may or may not reach the maximum capacity to ingest, at any given time or place in the sea. Presumably the level of digestive enzyme activity represents a physiological adjustment in the rate of food processing in response to

biological or physical factors operating over time intervals in excess of five days. The time required for changes in enzyme levels may be related to the time required for production and rearrangement of specific-enzyme producing cells in the mid-gut.

References

Alcaraz, M., G.-A. Paffenhofer, and J.R. Strickler. 1980. Catching the algae: a first account of visual observations on filter-feeding calanoids. In: Ecology and Evolution of Zooplankton Communities, pg. 241-248. W.C. Kerfoot (Ed.). University Press of New England.

Allan, G. G., J. Lewin, and P.G. Johnson. 1972. Marine Polymers. IV. Diatom polysaccharides. Botanica mar. 15: 102-108.

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

Anraku, M. 1964. Some technical problems encountered in quantitative studies of grazing and predation by marine planktonic copepods. J. Oceanogr. Soc. Japan. 20: 221-231.

Arashkevich, E.G. 1977. Duration of food digestion in marine copepods. Pol. Arch. Hydrobiol. 21: 431-438.

Arnaud, J., M. Brunet and J. Mazza. 1978. Studies on the midgut of Centropages typicus (copepod, calanoid). I. Structural and ultrastructural data. Cell Tissue Res. 187: 333-353.

Bamstedt, Ulf. 1979. Seasonal variation in the resperatory rate and ETS activity of deep-water zooplankton from the Swedish west coast. In: Thirteenth European Marine Biology Symposium, pg. 267-274. E. Naylor and R.G. Hartnoll (Eds.). Pergamon Press, New York.

Beattie, A., E.L. Hirst and E. Percival. 1961. Studies on the metabolism of the Chrysophyceae. Comparitive structural investigations on leucosin (chrysolaminarin) from diatoms and laminarin from the brown algae. Biochem. J. 79: 531-537.

Bond, R.M. 1934. Digestive enzymes of the pelagic copepod, Calanus finmarchicus. Biol. Bull. Woods Hole 67: 461-465.

Boyd, C.M., S.L. Smith and T.J. Cowles. 1980. Grazing patterns of copepods in the upwelling system off Peru. Limnol. Oceanogr. 25: 583-596.

Bull, A.T. and C.G.C. Chesters. 1966. The biochemistry of laminarin and the nature of laminarinase. In: Advances In Enzymology. Vol. 28. F.F. Nord (Ed.) pg. 325-364. InterScience Publishers, New York.

Carlisle, D.B. and W.J. Pitman. 1961. Diapause, neurosecretion and hormones in Copepoda. Nature 190: 827-828.

Checkley, D.M., Jr. 1980. The egg production of a marine planktonic copepod in relation to its food supply: Laboratory studies. Limnol. Oceanogr. 25: 430-446.

Chesters, C.G.C. and A.T. Bull. 1963a. The enzymatic degradation of laminarin. I. The distribution of laminarinase among micro-organisms. Biochem. J. 28: 28-31.

Chesters, C.G.C. and A.T. Bull. 1963b. The enzymatic degradation of laminarin. II. The multicomponent nature of fungal laminarinases. Biochem. J. 28: 31-38.

Chesters, C.G.C. and A.T. Bull. 1963c. The enzymatic degradation of laminarin. III. Some effects of temperature, pH and various chemical reagents on fungal Laminarinases. Biochem. J. 28: 38-46.

Conover, R.J. 1956. Oceanography of Long Island Sound 1952-1954. I. Biology of Acartia clausii and A. tonsa. Bull. Bingham. Oceanogr. Coll. 15: 156-233.

Conover, R.J. 1959. Regional and seasonal variation in the respiratory rate of marine copepods. Limnol. Oceanogr. 4: 259-268.

Conover, R.J. 1962. Metabolism and growth in Calanus hyperboreus in relation to its life cycle. Rapp. P. v. Reun. Cons. perm. int. Explor. Mer. 153: 190-197.

Conover, R.J. 1980. General rules of grazing in pelagic ecosystems. In: Primary Productivity In The Sea. pg. 461-485. P. Falkowski (Ed.), Plenum Press, New York.

Conover, R.J. 1981. Nutritional strategies for feeding on small suspended particles. In: Analysis Of Marine Ecosystems. pg. 363-395. A.R. Longhurst (Ed.).

Cowey, C.B. and E.D.S. Corner. 1963. On the nutrition and metabolism of zooplankton. II. The relationship between the marine copepod Calanus Helgolandicus and particulate material in Plymouth sea water, in terms of amino acid composition. J. Mar. Biol. Ass. U.K. 43: 495-511.

Cox, J.L. 1981. Laminarinase induction in marine zooplankton and its variability in zooplankton samples. J. Plankton Res. 3: 345-356.

Cox, J.L. and S.W. Willason. !981. Laminarinase induction in Calanus pacificus. Mar. Biol. Lett. 2: 307-311.

Cox, J.L., L.R. Haury and J.J. Simpson. 1982. Spatial patterns of grazing-related parameters in California surface waters, July 1979. J. Mar. Res. 40: 1127-1153.

Cox, J.L., S. Willason and L. Harding. 1983. Consequences of distributional heterogeneity of Calanus pacificus grazing. Bull. Mar. Sci. 33: 213-226.

Dagg, M., T. Cowles, T. Whitledge, S. Smith, S. Howe and D. Judkins. 1980. Grazing and excretion by zooplankton in the Peru upwelling system during April 1977. Deep-Sea Research. 27A: 43-59.

Dagg, M.T. and K.D. Wyman. 1983. Natural ingestion rates of the copepods Neocalanus plumchrus and N. cristatus calculated from gut contents. Mar. Ecol. Prog. Ser. 13: 37-46.

Deason, E.E. 1980. Grazing of Acartia hudsonica (A. clausii) on Skeletonema costatum in Narragansett Bay (USA): Influence of food concentration and temperature. Mar. Biol. 60: 101-113.

Dexter, B.L. 1983. Developmental grazing capabilities of Pseudocalanus sp. and Acartia clausii (CI to adult). Oregon State Universtiy Ph.D. Dissertation. 166 pp.

Donaghay, P.L. and L.F. Small. 1979. Food selection capabilities of the estuarine copepod Acartia clausii. Mar. Biol. 52: 137-146.

Donaghay, P.L. 1980. Experimental and conceptual approaches to understanding algal-grazer interactions. Oregon State University Ph.D. Dissertation. 214 pp.

Elgmork, K. 1967. Ecological aspects of diapause in copepods. Proc. Symp. Crust. Part III. pp. 947-954.

Elgmork, K. and J.P. Nilssen. 1978. Equivalence of copepod and insect diapause. Verh. Internat. Verein. Limnol. 20: 2511-2517.

Fernandez, F. 1978. Metabolisms y alimentacion en copepodes planctonicos del Mediterraneo: Respuesta a la temperatura. Inv. Pesq. 42: 97-139.

Ford, C.W. and E. Percival. 1965. The carbohydrate of Phaeodactylum tricornutm. I. Preliminary examination of the organism, and characterization of low molecular weight material of a glucan. J. Chem. Soc. 7035-7042.

Frolander, H.F., C.B. Miller, M.J. Flynn, S.C. Myers, and S.T. Zimmerman. 1973. Seasonal cycles of abundance in zooplankton populations of Yaquina Bay, Oregon. Mar. Biol. 21: 277-288.

Frost, B. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod Calanus pacificus. Limnol. Oceanogr. 17: 805-815.

Frost, B. 1977. Feeding behavior of Calanus pacificus in mixtures of food particles. Limnol. Oceanogr. 22: 472-491.

Frost, B. 1980. The inadequacy of body size as an indicator of niches in the zooplankton. In: Ecology and Evolution of Zooplankton Communities. pg. 742-753. W.C. Kerfoot (Ed.). University Press of New England.

Gaudy, R. 1971. Etude experimentale de la ponte chez trois especes de copepodes pelagiques (Centropages typicus, Acartia clausii et Temora stylifera). Mar. Biol. 9: 65-70.

Gaudy, R. and J. Boucher. 1983. Relation between respiration, excretion (ammonia and inorganic phosphorous) and activity of amylase and trypsin in different species of pelagic copepods from an Indian Ocean equatorial area. Mar. Biol. 75: 37-45.

Hallberg, E. and H.-J. Hirche. 1980. Differentiation of mid-gut in adults and over-wintering copepodids of Calanus finmarchicus (Gunnerus) and C. helgolandicus Claus. J. exp. mar. Biol. Ecol. 48: 283-295.

Handa, N. 1969. Carbohydrate metabolism in the marine diatom Skeletonema costatum. Mar. Biol. 4: 208-214.

Handa, N. and H. Tominaga 1969. A detailed analysis of carbohydrates in marine particulate matter. Mar. Biol. 2: 228-235.

Handa, N. and K. Yanagi. 1969. Studies on water-extractable carbohydrates of the particulate matter from northwest Pacific Ocean. Mar. Biol. 4: 197-207.

Handa, N. 1970. Dissolved and particulate carbohydrates. In: Symp. Organic Matter in Natural Waters. pp. 129-152. D.W. Hood (Ed.). University of Alaska.

Hartley, H.O. 1961. The modified Gauss-Newton method for fitting of non-linear regression functions by least squares. Technometrics 3: 269-280.

Hassett, R.P. and M.R. Landry. 1983. Effects of food-level acclimation on digestive enzyme activities and feeding behavior of Calanus pacificus. Mar. Biol. 75: 47-55.

Haug, A. and S. Myklestad. 1973. Studies on the phytoplankton ecology of the Trondheimsfjord. I. The chemical composition of phytoplankton populations. J. Exp. Mar. Biol. Ecol. 11: 15-26.

Head, E.J.H. and R.J. Conover. 1983. Induction of digestive enzymes in Calanus hyperboreus. Mar. Biol. Lett. 4: 219-231.

Heinle, D.R. 1969. Temperature and zooplankton. Chesapeake Sci. 10: 186-209.

Hirche, H.-J. 1981. Digestive enzymes of copepodids and adults of Calanus finmarchicus and C. helgolandicus in relation to particulate matter. Kieler Meeresforsch., Sonderh. 5: 174-185.

Hirche, H.-J. 1983. Overwintering of Calanus finmarchicus and Calanus helgolandicus. Mar. Ecol. Prog. Ser. 11: 281-290.

Huntley, M. 1981. Nonselective, nonsaturated feeding by three calanoid copepod species in the Labrador Sea. Limnol. Oceanogr. 26: 831-842.

Itoh, K. 1970. A consideration of feeding habits of planktonic copepods in relation to the structure of their oral parts. Bull. Plankton Soc. Japan. 17: 1-10.

Ivlev, V.S. 1955. Experimental ecology of the feeding of fishes. Yale Univ. 1961.

Johnson, J.K. 1979. Effects of temperature and salinity on production and hatching of dormant eggs of Acartia californiensis (Copepoda) in an Oregon estuary. Fishery Bull. 77: 567-584.

Karentz, D. 1975. The distribution of planktonic diatoms in Yaquina estuary, Oregon. Oregon State University M.S. Dissertation. 137 pp.

Kerfoot, W.C. 1980. Evolution and Ecology of Zooplankton Communities. Univ. Press of New England.

Koehl, M. and J.R. Strickler. 1981. Copepod feeding currents: food capture at low reynolds numbers. Limnol. Oceanogr. 26: 1062-1073.

Koeller, P.A., J.E. Barnwell-Clarke, F. Whitney, M. Takahashi. 1979. Winter conditions of marine plankton populations in Saanich Inlet, B.C., Canada. III. Mesozooplankton. J. exp. mar. Biol. Ecol. 37: 161-174.

Kremer, J.N. and S.W. Nixon. 1978. A Coastal Marine Ecosystem Similation and Analysis. Springer-Verlag, Berlin.

Lam, R.K. and B. Frost. 1976. Model of copepod filtering response to changes in size and concentration of food. Limnol. Oceanogr. 21: 490-500.

Landry, M.R. 1976. The structure of marine ecosystems: an alternative. Mar. Biol. 35: 1-7.

Lehman, J.T. 1976. The filter-feeder as an optimal forager, and the predicted shapes of feeding curves. Limnol. Oceanogr. 21: 501-516.

Livingston, D.R. 1981. Induction of enzymes as a mechanism for the seasonal control of metabolism in marine invertebrates: Glucose-6-phosphate dehydrogenases from the mantle and hepatopancreas of the common mussel Mytilus edulis L. Comp. Biochem. Physiol. 69B: 147-156.

Lowry, O.H., N.J. Rosebrough, A. Lewis Farr, and R.J. Randall. 1951. Protein measurement with the Folin Phenol reagent. J. Biochem. 193: 265-275.

Marcus, N.H. 1980. Photoperiodic control of diapause in the marine calanoid copepod Labidocera aestiva. Biol. Bull. 159: 311-318.

Marcus, N.H. 1982a. The reversibility of subitaneous and diapause egg production by individual females of Labidocera aestiva (Copepoda:Calanoida). Biol. Bull. 162: 39-44.

Marcus, N.H. 1982b. Photoperiodic and temperature regulation of diapause in Labidocera aestiva (Copepoda:Calanoida). Biol. Bull. 162: 45-52.

Marshall, S.M. and A.P. Orr. 1958. On the biology of Calanus finmarchicus X. Seasonal changes in oxygen consumption. J. mar. Biol. Ass. U.K. 37: 459-472.

Martin, J.H. 1970. Phytoplankton-zooplankton relationships in Narragansett bay. IV. The seasonal importance of grazing. Limnol. Oceanogr. 15: 413-418.

Mayzaud, P. and R.J. Conover. 1976. Influence of potential food supply on the digestive enzyme activity of neritic copepods. In: Proceedings of the 10th Europ. Mar. Biol. Symp. Astond, Belgium. 2: 415-427.

Mayzaud, P. and S.A. Poulet. 1978. The importance of the time factor in the response of zooplankton to varying concentrations of naturally occurring particulate matter. Limnol. Oceanogr. 23: 1133-1154.

Mayzaud, P. and O. Mayzaud. 1981. Kinetic properties of digestive carbohydrases and proteases of zooplankton. Can. J. Fish. Aquatic Sci. 38: 535-543.

Miller, C.B. 1983. Zooplankton of estuaries. In: B.H. Ketchum (Ed.). The Ecology of Estuaries and Inland Seas; Encyclopedia of World Ecosystems. North Holland, Amsterdam.

Miller, C.B. in press. Ontogenetic migrations and diapause phases in large, grazing copepods of the oceanic subarctic Pacific.

Muchmore, A.V., D. Epel, A.M. Weaver and R.T. Schimke. 1969. Purification and properties of an exo-B-D-1,3-glucanase from sea urchin eggs. Biochim. Biophys. Acta. 178: 551-560.

Mullin, M.M. 1963. Some factors affecting the feeding of marine copepods of the genus Calanus. Limnol. Oceanogr. 8: 239-250.

Mullin, M.M. 1967. On the feeding behavior of planktonic copepods and the separation of their ecological niches. Proc. Symp. Crust. Part III. pp. 955-964.

Mullin, M.M., E.F. Stewart and F.J. Fuglister. 1975. Ingestion by planktonic grazers as a function of concentration of food. Limnol. Oceanogr. 20: 259-262.

Myklestad, S. 1974. Production of carbohydrates by marine

planktonic diatoms. I. Comparison of nine different species in culture. J. exp. mar. Biol. Ecol. 15: 261-274.

Nelson, T.E., J.V. Scaletti, F. Smith and S. Kirkwood. 1963. The use of enzymes in structural studies on polysaccharides I. The mode of attack of a B-D-(1,3)-glucanase on laminarin. Can. J. Chem. 41: 1671-1678.

Neter, J. and W. Wasserman. 1974. Applied Linear Statistical Models. R.D. Irwin, Inc. Georgetown, Ontario.

Nicolajsen, H., F. Mohlenberg and T. Kiorboe. 1983. Algal grazing by the planktonic copepods Centropages hamatus and Pseudocalanus sp.: Diurnal and seasonal variation during the spring phytoplankton bloom in the Oresund. Ophelia 22: 15-31.

Nival, P. and S. Nival. 1976. Particle retention efficiencies of an herbivorous copepod, Acartia clausii (adult to copepodite stages): Effects on grazing. Limnol. Oceanogr. 21: 24-38.

O'Connors, H.B., L.F. Small and P.L. Donaghay. 1976. Particle-size modification by two size classes of the estuarine copepod Acartia clausii. Limnol. Oceanogr. 21: 300-308.

O'Connors, H.B., D.C. Biggs, and D.V. Ninivaggi. 1980. Particle-size-dependent maximum grazing rates for Temora longicornis fed natural particle assemblages. Mar. Biol. 56: 65-70.

Ong, J.E. and P.S. Lake. 1970. The ultrastructural morphology of the midgut diverticulum of the calanoid copepod Calanus helgolandicus (Claus) (Crustacea). Aust. J. Zool. 18: 9-20.

Paffehnofer, G-A., J.R. Strickler, and M. Alcarez. 1982. Suspension-feeding by herbivorous calanoid copepods: A cinematographic study. Mar. Biol. 67: 193-199.

Parsons, T.R., R.J. LeBrasseur, and J.D. Fulton. 1967. Some observations on the dependence of zooplankton grazing on the cell size and concentration of phytoplankton blooms. J. Oceanogr. Soc. Japan. 23: 10-17.

Parsons, T.R., M. Takahashi, and B. Hargrave. 1977. Biological Oceanographic Processes. Pergamon Press, New York.

Percival, E. and R.H. McDowell. 1967. Chemistry and Enzymology of Marine Algal Polysaccharides. Academic Press, New York.

Poulet, S.A. 1973. Grazing of Pseudocalanus minutus on naturally occurring particulate matter. Limnol. Oceanogr. 18: 564-573.

Poulet, S.A. 1974. Seasonal grazing of Pseudocalanus minutus on particles. Mar. Biol. 25: 109-123.

Poulet, S.A. 1976. Feeding of Pseudocalanus minutus on living and non-living particles. Mar. Biol. 34: 117-125.

Poulet, S.A. 1977. Grazing of marine copepod develomental stages on naturally occurring particles. J. Fish. Res. Bd. Can. 34: 2381-2387.

Poulet, S.A. 1978. Comparison between five coexisting species of marine copepods feeding on naturally occurring particulate matter. Limnol. Oceanogr. 23: 1126-1143.

Poulet, S.A. and P. Marsot. 1978. Chemosensory grazing by marine calanoid copepods (Arthropoda:Crustacea). Science 200: 403-405.

Raymont, J.E.G., S. Krishnaswamy, and J. Tundisi. 1967. Biochemical studies on marine zooplankton. IV. Investigations on succinic dehydrogenase activity in zooplankton with special reference to Neomysis integer. J. Cons. perm. int. Explor. Mer. 31: 164-169.

Reeve, M.R. and M.A. Walter. 1977. Observations on the existence of lower threshold and upper critical food concentrations for the copepod Acartia tonsa Dana. J. exp. mar. Biol. Ecol. 29: 211-221.

Richman, S. and S.I. Dodson. 1983. The effect of food quality on feeding and respiration by Daphnia and Diaptomus. Limnol. Oceanogr. 28: 948-956.

Riley, G.A. 1963. Organic aggregates in sea water and the dynamics of their formation and utilization. Limnol. Oceanogr. 8: 372-381.

Rosenburg, G.G. 1980. Filmed observations of filter feeding in the marine planktonic copepod Acartia clausii. Limnol. Oceanogr. 25: 738-742.

Runge, J.A. 1980. Effects of hunger and season on the feeding behavior of Calanus pacificus. Limnol. Oceanogr. 25: 134-145.

Samain, J.F., J. Moal, J.Y. Daniel, and J.R. Le Coz. 1981. Possible processes of nutritive adaptations for zooplankton: a demonstration on Artemia. Kieler Meeresforch., Sonderh. 5: 218-228.

Schnack, S. 1981. The structure of the mouthparts of copepods in Kiel Bay. Meers. Sond. aus. Bd. 29: 89-101.

Skiver, J. 1980. Seasonal resource partitioning patterns of marine calanoid copepods: Species interactions. J. exp. mar. Biol. Ecol. 44: 229-245.

Slagstad, D. and K.S. Tande. 1981. A mathmatical model of the assimilation process in the copepod Calanus finmarchicus (Gunnerus): computer simulations discussed in relation to experimental results. Kieler Meers., Sond. 5: 229-239.

Steel, R.G.D. and J.H. Torrie. 1980. Principles and Procedures of Statistics A Biometrical Approach. McGraw-Hill Book Co., New York.

Steele, J.H. 1974. The Structure of Marine Ecosystems. Harvard University Press, Cambridge. 128 pp.

Steele, J.H. and B. Frost. 1977. The structure of planktonic communities. Phil. Trans. Royal Soc. Lond. 280: 485-534.

Steele, J.H. and M.M. Mullin. 1977. Zooplankton dynamics. In: The Sea. Vol. 6. E.D. Goldberg, I.N. McCave, J.J. O'Brien, and J.H. Steele (Eds.). John Wiley, New York. pp. 857-890.

Stewart, W.D.P. 1974. Algal Physiology and Biochemistry. Blackwell Scient. Publ. Oxford. 989 pp.

Strickland, J.D.H. and T.R. Parsons. 1972. A Practical Handbook of Seawater Analysis. Fish. Res. Bd. Canada, Bull. 167: 331 pp.

Uye, S.-I. 1981. Fecundity studies of neritic calanoid copepods Acartia clausii Giesbrecht and A. steueri Smirnov: A simple empirical model of daily egg production. J. exp. mar. Biol. Ecol. 50: 255-271.

Vacquier, V.D. 1971. The appearance of B-1,3-glucanohydrolase activity during differentiation of the gut of sand dollar plutei. Dev. Biol. 26: 1-10.

Vanderploeg, H.A. and R.L. Ondricek-Fallscheer. 1982. Intersetule distances are a poor predictor of particle-retention efficiency in Diaptomus sicilis. J. Plankton Res. 4: 237-244.

Wroblewski, J.S. and J.J. O'Brien. 1981. On modelling the turbulent transport of passive biological variables in aquatic ecosystems. Ecol. Modelling 12: 29-44.

Yule, A.B. and D.J. Crisp. 1983. A study of feeding behavior in Temora longicornis (Muller) (Crustacea:Copepoda). J. exp. mar. Biol. Ecol. 71: 271-282.

Appendix

Table 9 Data obtained for the experiment conducted with adult Acartia clausii females collected on March 19, 1982. The acclimation food concentration refers to the mean cell concentration of Thalassiosira weissflogii (10^6 um^3/ml) to which the copepods were kept at during the three day acclimation period (see text for details). The ingestion rates (10^6 um^3/copepod/day) shown were obtained from 24 hour grazing experiments following the acclimation interval. LA refers to laminarinase activities expressed as ug glucose/copepod/minute x 10^3 for copepods from each grazing flask. LP refers to laminarinase activities expressed as ug glucose/mg protein/hour. The standard deviations for the enzyme measurements were calculated from the laminarinase activities of two samples of 20 copepods removed from each grazing flask. The 0 food level data refers to copepods which were starved in filtered seawater throughout the experiment.

Food Level	Flask #	Acclimation Food Concentration	Ingestion Rate	LA	LA Std Dev	LP	LP Std Dev
F	1	9.87	30.73	88.0	65.9	2256.9	873.2
F	2	9.95	22.62	50.0	5.3	1683.7	88.9
E	1	7.46	14.63	45.0	7.9	2010.1	175.1
E	2	7.45	11.18	32.0	1.3	1537.0	65.9
D	1	4.91	13.81	47.0	25.0	2598.9	1699.4
D	2	4.80	12.20	45.0	0.0	1796.5	169.4
C	1	2.28	14.45	57.0	1.3	2203.0	151.5
C	2	2.16	13.83	39.0	2.6	1576.9	254.1
B	1	0.83	10.45	54.0	2.6	2515.0	395.2
B	2	0.82	8.99	55.0	11.8	2747.9	592.8
0	1	0.00	-	15.0	5.3	1117.8	395.2

Table 10 Data obtained for the experiment conducted with adult Acartia clausii females collected on April 7, 1982. The acclimation food concentration refers to the mean cell concentration of Thalassiosira weissflogii (10^6 um^3/ml) to which the copepods were kept at during the three day acclimation period (see text for details). The ingestion rates (10^6 um^3/copepod/day) shown were obtained from 24 hour grazing experiments following the acclimation interval. LA refers to laminarinase activities expressed as ug glucose/copepod/minute x 10^3 for copepods from each grazing flask. LP refers to laminarinase activities expressed as ug glucose/mg protein/hour. The standard deviations for the enzyme measurements were calculated from the laminarinase activities of two samples of 20 copepods removed from each grazing flask. The 0 food level data refers to copepods which were starved in filtered seawater throughout the experiment.

Food Level	Flask #	Acclimation Food Concentration	Ingestion Rate	LA	LA Std Dev	LP	LP Std Dev
F	1	8.00	39.29	132.0	15.8	2560.1	306.0
F	2	8.53	38.93	151.0	26.3	3621.7	632.4
E	1	6.29	19.75	183.0	0.0	4381.8	0.0
E	2	6.45	19.91	201.0	13.2	4828.9	316.2
D	1	3.99	17.70	204.0	19.8	5321.7	515.5
D	2	4.05	15.49	147.0	28.9	3396.4	668.8
C	1	1.61	12.48	184.0	23.7	4426.5	569.1
C	2	1.69	14.87	153.0	15.8	3666.4	379.4
B	1	1.02	12.07	198.0	48.7	5952.3	1462.2
B	2	1.02	11.86	166.0	2.6	4974.2	79.0
0	1	0.00	-	26.0	2.6	1304.1	131.7

Table 11 Data obtained for the experiment conducted with adult Acartia clausii females collected on June 23, 1982. The acclimation food concentration refers to the mean cell concentration of Thalassiosira weissflogii (10^6 um^3/ml) to which the copepods were kept at during the three day acclimation period (see text for details). The ingestion rates (10^6 um^3/copepod/day) shown were obtained from 24 hour grazing experiments following the acclimation interval. LA refers to laminarinase activities expressed as ug glucose/copepod/minute x 10^3 for copepods from each grazing flask. LP refers to laminarinase activities expressed as ug glucose/mg protein/hour. The standard deviations for the enzyme measurements were calculated from the laminarinase activities of two samples of 20 copepods removed from each grazing flask. The 0 food level data refers to copepods which were starved in filtered seawater throughout the experiment.

Food Level	Flask #	Acclimation Food Concentration	Ingestion Rate	LA	LA Std Dev	LP	LP Std Dev
F	1	10.31	15.74	48.0	10.4	683.0	295.3
F	2	10.20	18.82	39.0	2.8	595.0	62.4
E	1	7.35	15.77	36.0	1.1	520.5	47.2
E	2	7.29	15.43	32.0	11.8	455.3	179.9
D	1	4.86	18.17	36.0	2.8	575.7	47.6
D	2	4.78	16.71	40.0	9.4	567.8	178.6
C	1	2.26	14.60	36.0	2.1	561.9	66.1
C	2	2.24	18.47	35.0	4.9	552.6	58.1
B	1	0.75	12.76	33.0	5.4	665.5	90.0
B	2	0.76	12.65	28.0	3.7	540.3	104.1
0	1	0.00	-	11.0	6.4	493.3	251.0

Table 12 Data obtained for the experiment conducted with adult Acartia clausii females collected on July 22, 1982. The acclimation food concentration refers to the mean cell concentration of Thalassiosira weissflogii (10^6 um^3/ml) to which the copepods were kept at during the three day acclimation period (see text for details). The ingestion rates (10^6 um^3/copepod/day) shown were obtained from 24 hour grazing esperiments following the acclimation interval. LA refers to laminarinase activities expressed as ug glucose/copepod/minute x 10^3 for copepods from each grazing flask. LP refers to laminarinase activities expressed as ug glucose/mg protein/hour. The standard deviations for the enzyme measurements were calculated from the laminarinase activities of two samples of 20 copepods removed from each grazing flask. The 0 food level data refers to copepods which were starved in filtered seawater throughout the experiment.

Food Level	Flask #	Acclimation Food Concentration	Ingestion Rate	LA	LA Std Dev	LP	LP Std Dev
E	1	7.14	12.66	15.0	6.7	311.9	102.2
E	2	6.90	18.12	16.0	7.0	344.2	155.0
D	1	4.42	13.85	12.0	3.9	237.2	55.1
D	2	4.35	14.05	24.0	2.8	472.0	93.8
C	1	2.07	12.39	19.0	5.7	357.0	105.7
C	2	2.16	9.65	17.0	1.1	365.9	45.1
B	1	0.69	11.50	15.0	3.7	317.7	83.4
B	2	0.71	11.08	17.0	2.1	367.3	21.3
A	1	0.41	5.46	9.0	4.9	251.4	122.8
A	2	0.40	4.67	7.0	3.2	194.8	47.1
0	1	0.00	-	4.0	1.9	138.5	67.8

Table 13 Data obtained for the experiment conducted with adult Acartia clausii females collected on September 20, 1982. The acclimation food concentration refers to the mean cell concentration of Thalassiosira weissflogii (10^6 um^3/ml) to which the copepods were kept at during the three day acclimation period (see text for details). The ingestion rates (10^6 um^3/copepod/day) shown were obtained from 24 hour grazing experiments following the acclimation interval. LA refers to laminarinase activities expressed as ug glucose/copepod/minute x 10^3 for copepods from each grazing flask. LP refers to laminarinase activities expressed as ug glucose/mg protein/hour. The standard deviations for the enzyme measurements were calculated from the laminarinase activities of two samples of 20 copepods removed from each grazing flask. The 0 food level data refers to copepods which were starved in filtered seawater throughout the experiment.

Food Level	Flask #	Acclimation Food Concentration	Ingestion Rate	LA	LA Std Dev	LP	LP Std Dev
E	1	7.35	5.67	12.0	1.3	315.9	34.4
E	2	7.38	3.97	14.0	6.6	364.5	171.9
D	1	4.85	2.89	9.0	0.0	251.5	39.5
D	2	4.86	3.23	12.0	3.9	327.5	86.7
C	1	2.32	1.91	9.0	2.6	266.1	75.2
C	2	2.29	2.18	14.0	3.9	355.4	90.2
B	1	0.77	2.48	17.0	0.0	422.1	49.7
B	2	0.81	2.54	18.0	1.3	472.4	9.3
A	1	0.38	2.02	36.0	9.2	929.8	16.3
A	2	0.38	1.83	24.0	10.5	519.0	225.8
0	1	0.00	-	23.0	3.9	735.4	124.7

Table 14 Data obtained for the experiment conducted with adult Acartia clausii females collected on October 8, 1982. The acclimation food concentration refers to the mean cell concentration of Thalassiosira weissflogii (10^6 um^3/ml) to which the copepods were kept at during the three day acclimation period (see text for details). The ingestion rates (10^6 um^3/copepod/day) shown were obtained from 24 hour grazing experiments following the acclimation interval. LA refers to laminarinase activities expressed as ug glucose/copepod/minute x 10^3 for copepods from each grazing flask. LP refers to laminarinase activities expressed as ug glucose/mg protein/hour. The standard deviations for the enzyme measurements were calculated from the laminarinase activities of two samples of 20 copepods removed from each grazing flask. The 0 food level data refers to copepods which were starved in filtered seawater throughout the experiment.

Food Level	Flask #	Acclimation Food Concentration	Ingestion Rate	LA	LA Std Dev	LP	LP Std Dev
E	1	7.43	10.12	29.0	6.6	464.6	156.0
E	2	7.46	10.76	22.0	2.6	372.0	29.2
D	1	4.74	9.79	29.0	1.3	483.9	106.0
D	2	4.77	9.95	21.0	1.3	334.3	10.1
C	1	2.15	11.09	22.0	2.6	344.2	100.2
C	2	2.15	11.63	25.0	6.6	301.8	19.0
B	1	0.75	10.17	22.0	5.3	346.7	63.0
B	2	0.73	9.74	22.0	0.0	357.8	6.7
A	1	0.38	3.96	17.0	2.6	295.3	9.7
A	2	0.42	3.97	18.0	1.3	336.9	17.5
0	1	0.00	-	6.0	1.3	176.3	51.8

Table 15 Data obtained for the experiment conducted with adult Acartia clausii females collected on November 9, 1982. The acclimation food concentration refers to the mean cell concentration of Thalassiosira weissflogii (10^6 um^3/ml) to which the copepods were kept at during the three day acclimation period (see text for details). The ingestion rates (10^6 um^3/copepod/day) shown were obtained from 24 hour grazing experiments following the acclimation interval. LA refers to laminarinase activities expressed as ug glucose/copepod/minute x 10^3 for copepods from each grazing flask. LP refers to laminarinase activities expressed as ug glucose/mg protein/hour. The standard deviations for the enzyme measurements were calculated from the laminarinase activities of two samples of 20 copepods removed from each grazing flask. The 0 food level data refers to copepods which were starved in filtered seawater throughout the experiment.

Food Level	Flask #	Acclimation Food Concentration	Ingestion Rate	LA	LA Std Dev	LP	LP Std Dev
E	1	7.31	8.19	21.0	2.1	423.5	23.3
E	2	7.34	9.75	19.0	0.0	368.1	16.8
D	1	4.70	10.16	25.0	2.1	451.9	29.3
D	2	4.72	10.95	20.0	0.0	387.1	0.0
C	1	2.17	10.87	22.0	2.8	414.0	71.3
C	2	2.17	11.26	19.0	6.4	367.4	110.0
B	1	0.74	9.20	24.0	1.4	464.3	6.1
B	2	0.73	9.19	25.0	4.2	482.5	60.1
A	1	0.41	5.35	25.0	0.7	576.4	0.6
A	2	0.34	5.07	25.0	3.5	556.0	94.9
0	1	0.00	-	10.0	0.7	346.6	18.9

Table 16 Data obtained for the experiment conducted with adult Acartia clausii females collected on December 16, 1982. The acclimation food concentration refers to the mean cell concentration of Thalassiosira weissflogii (10^6 um^3/ml) to which the copepods were kept at during the three day acclimation period (see text for details). The ingestion rates (10^6 um^3/copepod/day) shown were obtained from 24 hour grazing experiments following the acclimation interval. LA refers to laminarinase activities expressed as ug glucose/copepod/minute x 10^3 for copepods from each grazing flask. LP refers to laminarinase activities expressed as ug glucose/mg protein/hour. The standard deviations for the enzyme measurements were calculated from the laminarinase activities of two samples of 20 copepods removed from each grazing flask. The 0 food level data refers to copepods which were starved in filtered seawater throughout the experiment.

Food Level	Flask #	Acclimation Food Concentration	Ingestion Rate	LA	LA Std Dev	LP	LP Std Dev
E	1	7.42	13.63	16.0	2.8	275.4	59.6
E	2	7.42	14.46	18.0	2.1	304.0	30.7
D	1	4.79	11.02	18.0	2.1	291.7	35.3
D	2	4.79	11.57	21.0	0.7	346.6	18.9
C	1	2.34	8.23	16.0	7.1	328.7	59.2
C	2	2.33	8.55	16.0	1.4	282.3	25.0
B	1	0.74	6.99	17.0	1.4	304.3	18.1
B	2	0.75	7.10	18.0	1.4	317.4	11.7
A	1	0.33	7.57	17.0	0.0	323.8	7.3
A	2	0.36	7.18	18.0	2.8	331.8	45.0
0	1	0.00	-	11.0	0.0	348.3	25.9

Table 17 Data obtained for the experiment conducted with adult Acartia clausii females collected on February 28, 1983. The acclimation food concentration refers to the mean cell concentration of Thalassiosira weissflogii (10^6 um^3/ml) to which the copepods were kept at during the three day acclimation period (see text for details). The ingestion rates (10^6 um^3/copepod/day) shown were obtained from 24 hour grazing experiments following the acclimation interval. LA refers to laminarinase activities expressed as ug glucose/copepod/minute x 10^3 for copepods from each grazing flask. LP refers to laminarinase activities expressed as ug glucose/mg protein/hour. The standard deviations for the enzyme measurements were calculated from the laminarinase activities of two samples of 20 copepods removed from each grazing flask. The 0 food level data refers to copepods which were starved in filtered seawater throughout the experiment.

Food Level	Flask #	Acclimation Food Concentration	Ingestion Rate	LA	LA Std Dev	LP	LP Std Dev
E	1	7.33	9.98	22.0	2.8	455.2	58.5
E	2	7.43	10.47	20.0	0.7	396.5	4.9
D	1	4.87	11.59	17.0	2.8	350.7	41.4
D	2	4.84	11.25	26.0	1.4	487.4	4.9
C	1	2.33	11.63	26.0	7.1	523.9	166.2
C	2	2.34	11.12	26.0	2.1	495.0	63.6
B	1	0.86	7.55	16.0	2.8	398.6	47.2
B	2	0.89	7.67	20.0	0.7	441.8	27.8
A	1	0.46	4.63	15.0	2.8	381.2	37.8
A	2	0.47	4.69	14.0	3.5	383.2	75.2
0	1	0.00	-	7.0	0.7	259.8	3.8

Table 18 Data obtained for the experiment conducted with adult Acartia clausii females collected on June 6, 1983. The acclimation food concentration refers to the mean cell concentration of Thalassiosira weissflogii (10^6 um^3/ml) to which the copepods were kept at during the three day acclimation period (see text for details). The ingestion rates (10^6 um^3/copepod/day) shown were obtained from 24 hour grazing experiments following the acclimation interval. LA refers to laminarinase activities expressed as ug glucose/copepod/minute x 10^3 for copepods from each grazing flask. LP refers to laminarinase activities expressed as ug glucose/mg protein/hour. The standard deviations for the enzyme measurements were calculated from the laminarinase activities of two samples of 20 copepods removed from each grazing flask. The 0 food level data refers to copepods which were starved in filtered seawater throughout the experiment.

Food Level	Flask #	Acclimation Food Concentration	Ingestion Rate	LA	LA Std Dev	LP	LP Std Dev
E	1	6.47	21.18	22.0	0.7	386.2	37.1
E	2	6.55	17.53	21.0	2.1	364.6	67.7
D	1	4.12	11.61	23.0	1.4	413.6	51.5
D	2	4.19	12.86	23.0	6.4	399.4	38.1
C	1	2.05	9.33	25.0	6.4	502.6	58.1
C	2	2.07	10.29	24.0	4.2	486.4	27.9
B	1	0.86	7.14	22.0	0.7	600.0	0.0
B	2	0.85	7.21	20.0	0.7	521.4	30.3
A	1	0.43	3.83	22.0	3.5	480.5	103.7
A	2	0.41	3.42	21.0	4.9	555.9	99.2
0	1	0.00	-	20.0	0.0	444.4	0.0

Table 19 Data obtained for the experiment conducted with adult Acartia clausii females collected on July 5, 1983. The acclimation food concentration refers to the mean cell concentration of Thalassiosira weissflogii (10^6 um^3/ml) to which the copepods were kept at during the three day acclimation period (see text for details). The ingestion rates (10^6 um^3/copepod/day) shown were obtained from 24 hour grazing experiments following the acclimation interval. LA refers to laminarinase activities expressed as ug glucose/copepod/minute x 10^3 for copepods from each grazing flask. LP refers to laminarinase activities expressed as ug glucose/mg protein/hour. The standard deviations for the enzyme measurements were calculated from the laminarinase activities of two samples of 20 copepods removed from each grazing flask. The 0 food level data refers to copepods which were starved in filtered seawater throughout the experiment.

Food Level	Flask #	Acclimation Food Concentration	Ingestion Rate	LA	LA Std Dev	LP	LP Std Dev
E	1	7.30	20.82	62.0	7.8	1220.4	101.6
E	2	7.39	21.21	64.0	2.8	1066.6	5.2
D	1	4.64	18.51	65.0	2.1	1173.0	11.7
D	2	4.67	21.98	61.0	2.8	1294.6	345.9
C	1	2.17	17.10	62.0	2.1	1040.0	56.6
C	2	2.19	17.31	45.0	0.0	818.2	0.0
B	1	0.70	14.64	46.0	6.4	864.5	63.0
B	2	0.72	13.72	42.0	5.6	763.6	102.8
A	1	0.37	8.36	36.0	6.4	738.6	167.7
A	2	0.38	7.45	38.0	0.7	805.4	55.8
0	1	0.00	-	16.0	2.1	488.3	30.6

Table 20 Data obtained for the experiment conducted with adult Acartia clausii females collected on September 29, 1983. The acclimation food concentration refers to the mean cell concentration of Thalassiosira weissflogii (10^6 um^3/ml) to which the copepods were kept at during the three day acclimation period (see text for details). The ingestion rates (10^6 um^3/copepod/day) shown were obtained from 24 hour grazing experiments following the acclimation interval. LA refers to laminarinase activities expressed as ug glucose/copepod/minute x 10^3 for copepods from each grazing flask. LP refers to laminarinase activities expressed as ug glucose/mg protein/hour. The standard deviations for the enzyme measurements were calculated from the laminarinase activities of two samples of 20 copepods removed from each grazing flask. The 0 food level data refers to copepods which were starved in filtered seawater throughout the experiment.

Food Level	Flask #	Acclimation Food Concentration	Ingestion Rate	LA	LA Std Dev	LP	LP Std Dev
E	1	7.33	10.45	33.0	2.8	760.9	23.9
E	2	7.36	9.91	38.0	7.1	810.8	69.6
D	1	4.80	11.62	40.0	0.0	888.9	0.0
D	2	4.82	10.62	43.0	2.1	881.4	86.9
C	1	2.38	7.85	44.0	0.7	916.2	37.6
C	2	2.39	8.06	40.0	9.2	943.3	167.2
B	1	0.94	6.67	47.0	9.2	941.5	119.3
B	2	0.96	-	42.0	0.7	874.1	36.6
A	1	0.49	5.35	52.0	2.8	1134.1	32.5
A	2	0.47	5.51	36.0	1.4	832.9	77.9
0	1	0.00	-	21.0	7.1	710.5	156.3