

ENERGETICS OF THE ARCTIC SUB-ICE AMPHIPOD

Weyprechtia pinguis

by

PATRICIA NAOMI BOULTON LEWIS

A Thesis

Submitted to the Faculty of Graduate Studies
in partial fulfillment of the requirements for
the degree of Master of Science

Department of Zoology
THE UNIVERSITY OF MANITOBA

June, 1987



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ISBN 0-315-37231-1

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ABSTRACT

A partial energy budget was constructed for the Arctic sub-ice amphipod Weyprechtia pinguis during the spring season at Resolute Bay, N.W.T. Ingestion rate was measured using biogenic silica as a "tracer", and equalled 213.60 ± 32.40 (95 % confidence interval) ug dry weight algae.amphipod⁻¹.day⁻¹, or 1.056 ± 0.160 calories.amphipod⁻¹.day⁻¹. Respiration equalled 0.984 ± 0.072 calories.amphipod⁻¹.day⁻¹, while growth and molting together utilized 0.501 ± 0.125 calories.amphipod⁻¹.day⁻¹. Growth and respiration used more energy per day than was taken in through ingestion. Some of the possible reasons for this discrepancy are discussed.

ACKNOWLEDGEMENTS

I would like to express my thanks to all those who helped me with this thesis, especially Martin Curtis for his extensive assistance in both the lab and the field. Other field assistance was provided by Dan Pike, Kathy Martin-Bergmann, Peter Amaraulik, Matt Klaverkamp, and John Jorgenson. Kathy Martin-Bergmann and Martin Bergmann also provided help in the lab, and Cathy Welch made two of the nets I used for sampling. Thanks also to Tim Siferd for use of his running seawater tanks, and for gathering the January 1986 samples (along with Dan Pike and Peter Amaraulik).

The members of my committee, Drs. B.J. Hann and R.E.A. Stewart, made many suggestions which have greatly improved the thesis.

Lastly, thanks to my supervisor, Buster Welch, for his encouragement and assistance in carrying out this project, and for providing me with many unforgettable Arctic experiences.

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INTRODUCTION

The bottom surface of Arctic Ocean first-year sea ice, during the springtime, provides a unique habitat for a wide variety of organisms. The community which flourishes here is an important part of the total yearly production in these waters, in terms of both plant and animal biomass.

The base of this sub-ice food web is the algae which blooms on the under-ice surface from early spring until breakup. The algal community is heavily dominated by diatoms. Of the 196 species of sub-ice microalgae identified by Hsiao (1980), 189 were diatoms. The diatoms are largely pennate species, commonly Navicula spp. and Nitzschia spp. (Hsiao 1980). This algae has been estimated to supply from 6 to 33 % of the total annual primary production in some areas (Cross 1982). As well, it provides an important food source for a number of types of animals at a time when open water phytoplankton production has not yet begun.

The sub-ice community consists of both a meiofaunal and a macrofaunal component. The meiofauna includes nematodes, polychaetes, rotifers, and several copepod species (Carey 1985). The macrofauna consists almost entirely of gammarid amphipods, with generally one or two species dominating (Carey 1985). One such amphipod is Weyprechtia pinguis.

Weyprechtia pinguis is a circumpolar species with a wide distribution in arctic and subarctic waters (Dunbar 1954). It dominates in both numbers and biomass of amphipods on the sub-ice surface at some locations (Cross 1982, Cross and Martin 1983). Carey (1985) categorizes Weyprechtia as a member of the "shallow water fast ice community", along

with the amphipods Onisimus litoralis, Gammarus setosus and Apherusa glacialis.

To date, there have been no reports published on the diet of Weyprechtia. Bradstreet and Cross (1982) did study the diets of four sub-ice amphipods: Parathemisto sp., Gammarus wilkitzkii, Onisimus glacialis and Apherusa glacialis. All four of these species consumed ice algae, primarily the pennate diatoms Nitzschia spp. and Navicula spp. The first two amphipods also consumed crustaceans (Bradstreet and Cross 1982). Parathemisto and G. wilkitzkii are both large species, with body lengths ranging up to 35 mm (Dunbar 1957), and 33 mm (Steele and Steele 1975a) respectively. Weyprechtia is similar in size to O. glacialis, which has a mean adult body length of 9.0 mm in late summer (Griffiths and Dillinger 1981). Because of its small size, it is probable that Weyprechtia is also primarily a herbivore, at least during the sub-ice season.

Sub-ice amphipods are a major component of the diets of young ringed seals (Phoca hispida) and Arctic cod (Boreogadus saida) (Bradstreet and Cross 1982). Arctic cod, in turn, are an important source of food for several seabirds, ringed seals and narwhal (Monodon monoceros) (Bradstreet and Cross 1982). In the open water season, amphipods also serve as food for seabirds, especially thick-billed murres (Uria lomvia) and black guillemots (Cepphus grylle) in the Lancaster Sound - Barrow Strait area (Gaston and Nettleship 1980, Bradstreet 1979). Weyprechtia has also been found in the stomachs of thick-billed murres in northeast Hudson Bay (Gaston and Noble 1985).

Because of the central role amphipods such as Weyprechtia play in the sub-ice food chain, knowledge of their energy budgets can help us

understand how much energy is being obtained from the primary producers, and how much is subsequently available to higher trophic levels. The purpose of this study is to construct a partial energy budget for the amphipod Weyprechtia pinguis, focusing on the major components: feeding, growth and respiration.

According to Davis and Warren (1971) and From and Rasmussen (1984), V.S. Ivlev in 1939 was the first to subdivide the energy of food ingested by an animal into the different terms of an energy budget. Ivlev's original equation has since been modified to the form generally used today: $C = P + R + F + U$, where C = energy intake through ingestion, P = energy used in production (growth, reproductive products, exuviae), F = energy egested as feces, and U = energy lost as excretory products (Davis and Warren 1971, Hargrave 1971, Nilsson 1974, and many others). Each term in this equation can be independently measured. In this study, F and U were not quantified, but can be calculated from the measured components as $= C - (P + R)$.

METHODS

Study Area

All sampling was carried out in the vicinity of Resolute Bay, N.W.T. ($74^{\circ} 41' \text{ N}$, $94^{\circ} 51' \text{ W}$) (Figure 1). Starvation experiments were carried out at the sampling location, which was generally about 2 km offshore. Some other experiments (respiration, molting) utilized the Bedford Institute of Oceanography's ice camp, a set of Parcels located in Resolute Passage about 1 km offshore. Other procedures were done at the Fisheries and Oceans South Camp laboratory.

Collection

Animals for all types of experiments were captured from the sub-ice surface using a "sweep net" developed by Pike (1987) (Figure 2) deployed through an 18 cm (8 ") auger hole. The net was attached to a hinged arm which, when lowered into the water, would float up to the sub-ice surface. The net was turned by two people on the surface, sampling a 5.5 m^2 donut shaped area around the hole.

Feeding 1). Silica Method

Silica was chosen as a material with which to assess gut fullness and feeding rate because of the large proportion of diatoms in the sub-ice algae, and because large numbers of diatoms were found in Weyprechtia guts.

For biogenic silica analysis, a method modified from those of Paasche (1980a) and Krausse et al. (1983) was used. The amphipods were each measured for head length and placed in individual 20 mL plastic scintillation vials. Five mL of concentrated HCl plus 20 μL of H_2O_2 were

Figure 1. Location of the study area. The triangle indicates the location of Resolute Bay.

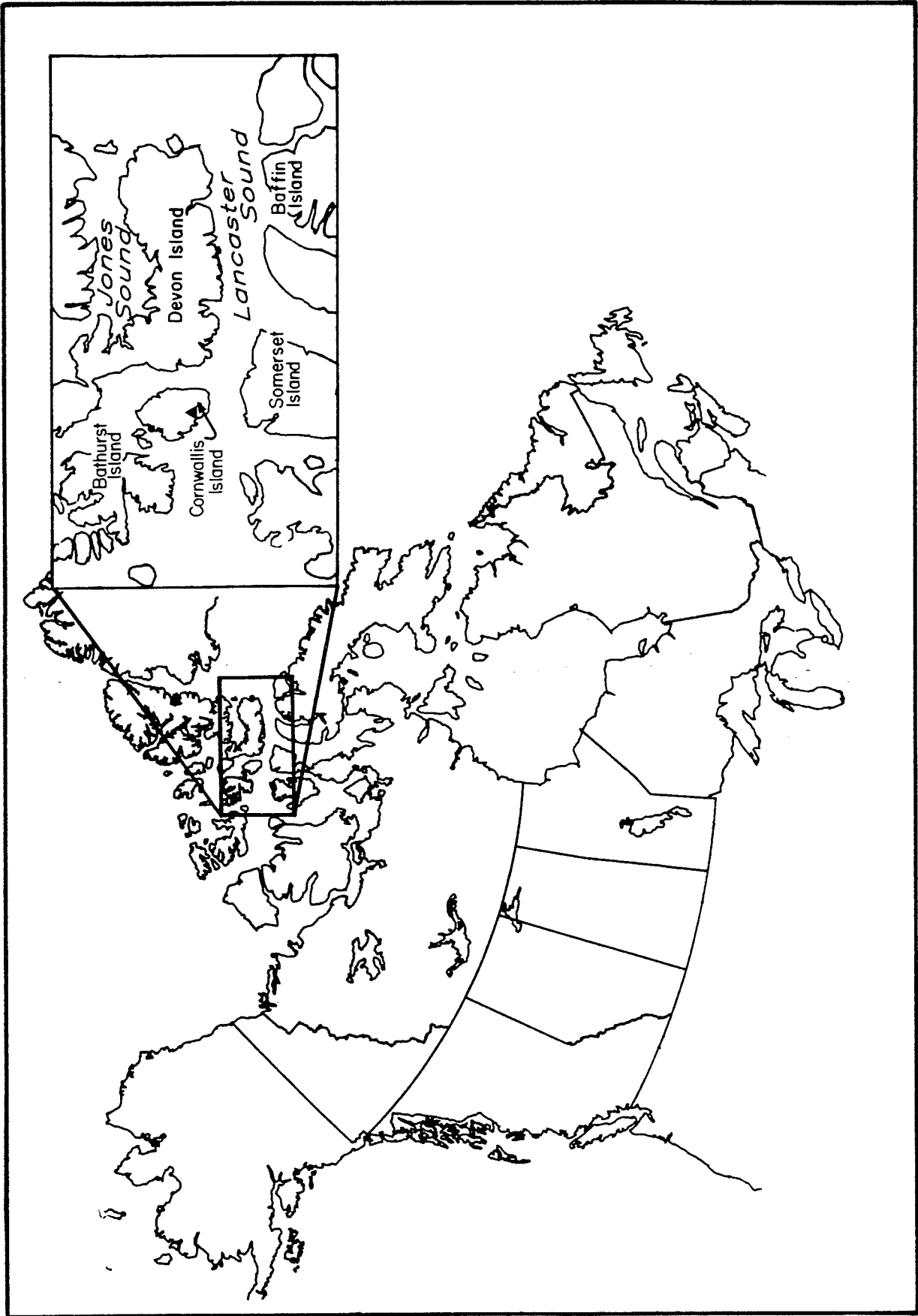
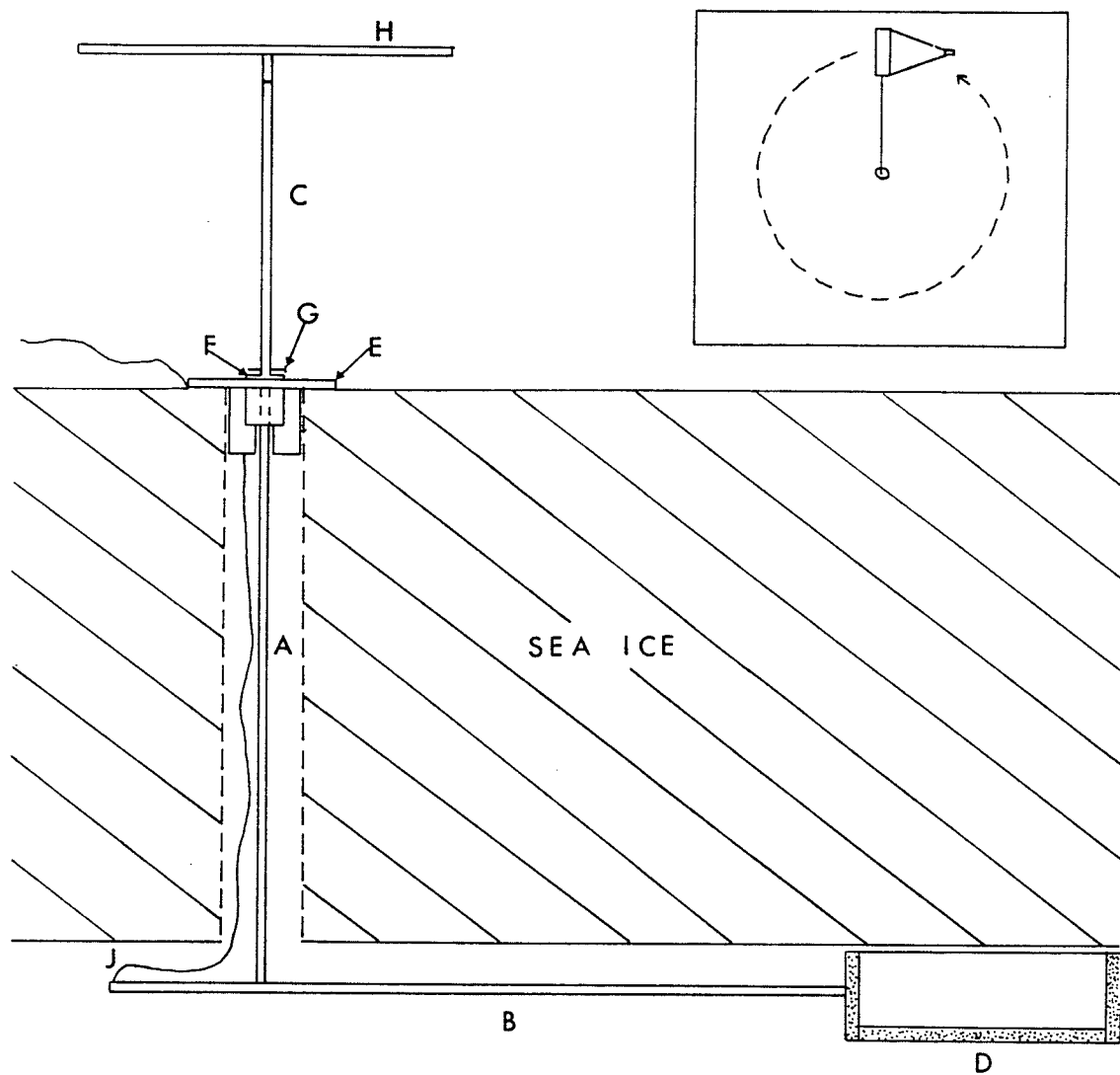


Figure 2 (from Pike 1987). The sub-ice sweep net (side view). The net is deployed through an 18 cm auger hole (A), and consists of two hinged pieces of square aluminium tubing (B & C). The net (D) floats against the sub-ice surface. A wooden insert (E) holds the system stable, while a plastic insert (F) and spike (G) suspend the net in the hole. The net is turned by the handle (H) and is retrieved by pulling on the rope (J). The inset shows a view of the net from below, and the path it would travel around a hole. Scale is roughly 1:25.



added, and the samples allowed to sit for a minimum of thirteen hours to digest all organic material. The samples were then neutralized with 10 mL of 6 M NaOH. A 5 mL subsample was transferred to a second set of plastic vials and 10 mL of 0.1 M NaOH added. These samples were then boiled for one hour, cooled, and 2 mL of 1 N HCl was added to lower the pH to 3 - 4. They were then analyzed for dissolved silica on a Technicon Auto-analyzer system, using the methods described in Stainton et al. (1977). The concentration of dissolved silica present in the known volume of sample was converted to a mass of silica for each animal.

2). Twenty-four Hour Series

To determine whether Weyprechtia fed continuously throughout the day, three 24 hour series of samples were taken: on May 20, 1985, May 9, 1986 and June 6, 1986. Amphipods were collected from the sub-ice surface at four hour intervals for a 24 hour period. The animals were killed immediately by either rapid heating or freezing, then frozen for later silica analysis. Neither heating nor freezing appeared to cause regurgitation of gut contents.

3). Feeding Rate

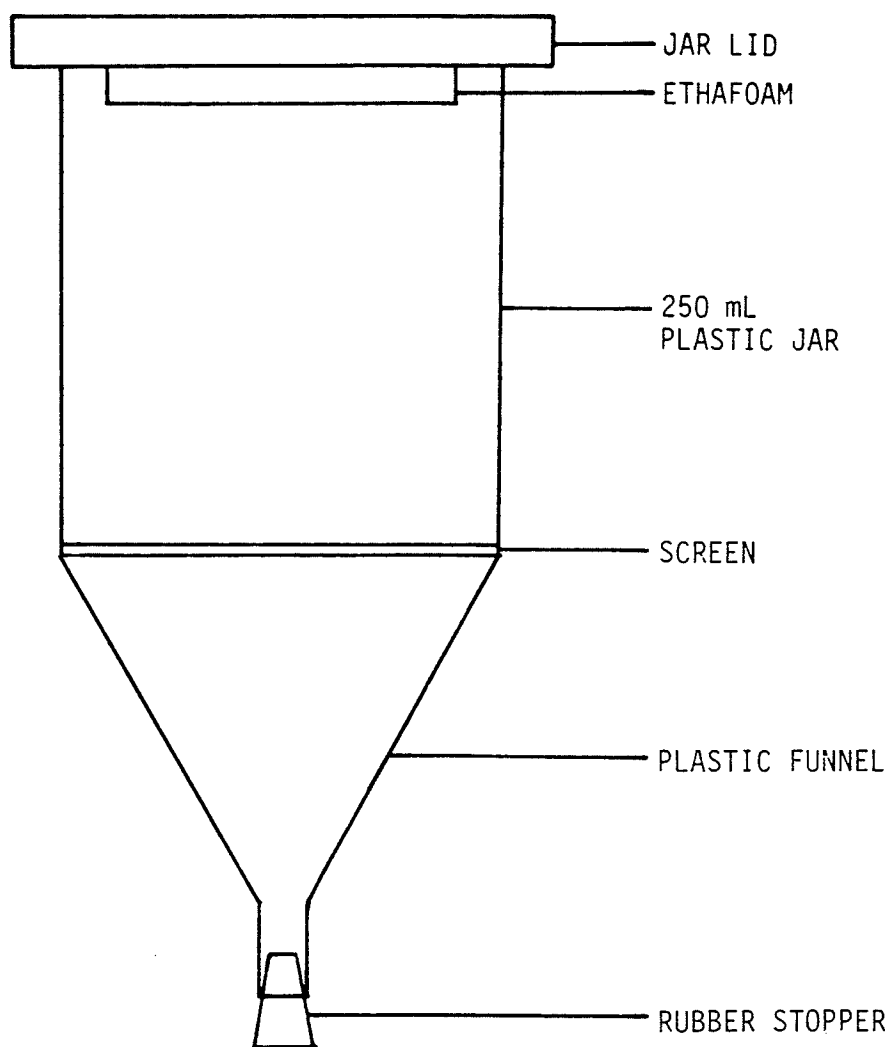
Biogenic silica was also chosen as a marker with which to assess Weyprechtia's feeding rate. By following the loss of silica from amphipod guts under short term starvation, a gut evacuation rate can be found. If the silica loss follows a negative exponential curve over time, as has been found for several zooplankton species, the slope of

that curve will represent a gut evacuation constant. This constant equals the fraction of the gut content that is lost over time, and should be the same regardless of the animal's gut fullness. Negative exponential gut evacuation curves were first found to hold for fish (Elliot and Persson 1978), and have since been observed in a number of species of marine copepods (Dagg and Wyman 1983, Tande and Bamstedt 1985, Wang and Conover 1986, Head 1986, Kiorboe and Tiselius 1987).

If ingestion and egestion are assumed to be in equilibrium, in that the animal feeds more or less continuously, then the fraction of the gut contents lost per unit time should equal the fraction gained by ingestion. The actual ingestion rate will then equal the gut evacuation constant multiplied by the silica content of a full gut. Ingestion rate will be in units of $\mu\text{g silica.amphipod}^{-1}.\text{hr}^{-1}$. This method, using other markers such as chlorophyll or dry weight, has been used to calculate feeding rates for fish (reviewed in Elliot and Persson 1978), a freshwater amphipod (Marchant and Hynes 1981), and marine copepods (Dagg and Wyman 1983, Tande and Bamstedt 1985, Wang and Conover 1986, Head 1986, Kiorboe and Tiselius 1987).

To measure feeding rate, seven short-term starvation experiments were carried out between April 14 and June 18, 1986. Freshly collected animals were sorted from other amphipods in the field, then placed in small starvation chambers (Figure 3) to a maximum of ten Weyprechtia per chamber. The number of amphipods used depended upon the number caught. The same number of amphipods (seven to ten) was killed immediately to provide the "Time 0" initial silica values. If a second sweep had to be made to obtain more amphipods, a second set of initials was taken, and a second set of starvation chambers run to fill in missing time periods.

Figure 3. A starvation chamber. The bottom of a 250 mL plastic jar was sawn off and replaced with 2 mm screening, below which was glued a plastic funnel. Amphipod feces would sink through the screen and collect in the funnel. Ethafoam glued to the jar lid allowed the chambers to float upright inside a larger container.



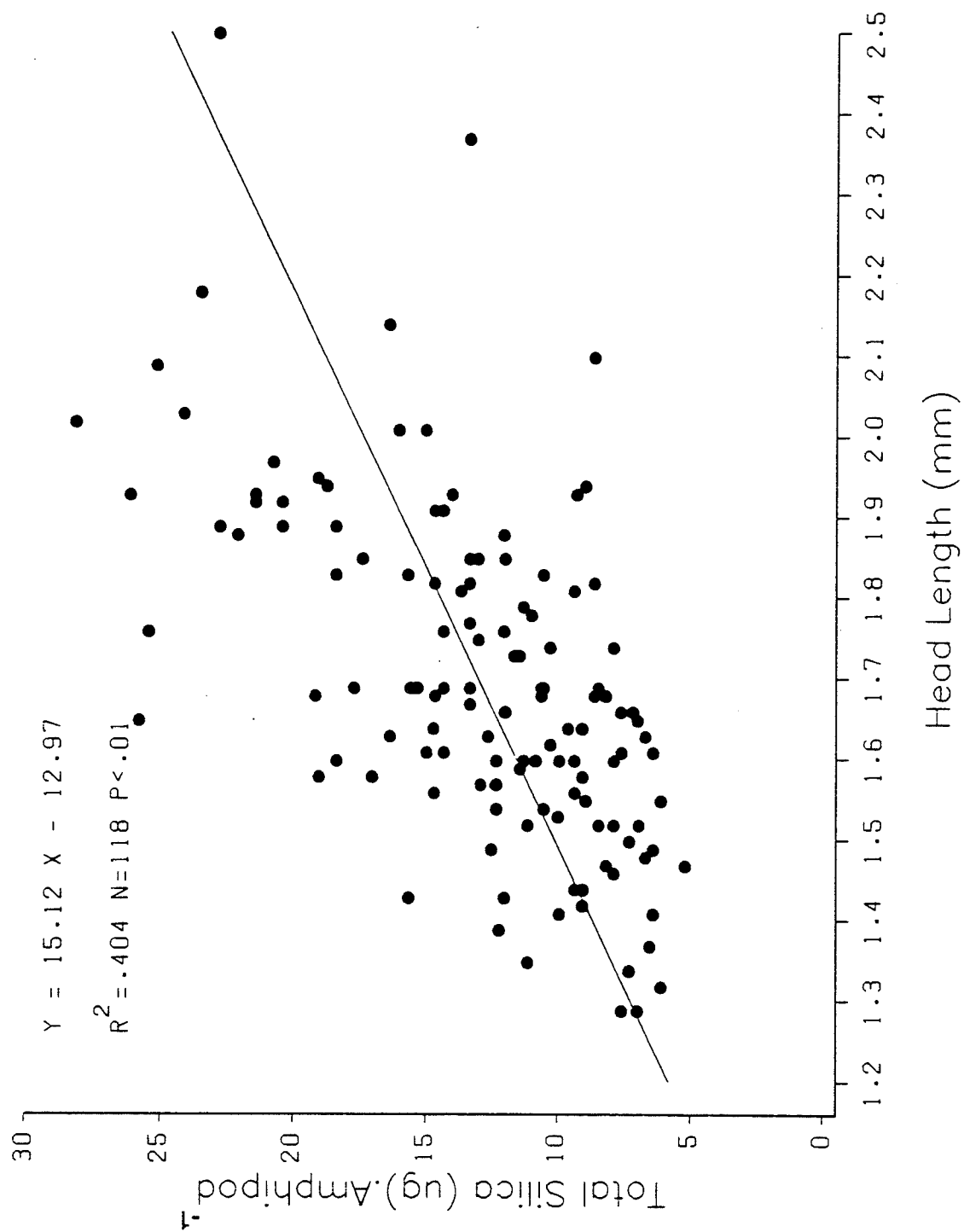
This was done for the April 24, May 8 and May 21, 1986 experiments. Three starvation chambers were placed upright in a larger plastic container filled with seawater which was then suspended beneath the ice.

All experiments lasted between 8 and 12 hours, with samples generally taken at shorter (half-hour) intervals at the beginning of the experiment, and longer intervals at the end. At each time interval, a chamber was removed from the water, the amphipods killed by rapid heating or freezing, and the samples kept at -10° or colder until subsequent analysis. In some experiments the feces were also collected at this time, by draining all the water from the starvation chamber into a plastic container. The number of intervals sampled depended on the number of amphipods initially available. All animals were analyzed for their biogenic silica content as described above.

Because a positive correlation was found between total silica content and head length for unstarved animals, differences in size among the animals in an experiment had to be taken into account. A size standardization was used, following the method of Marchant and Hynes (1981). The slope of the regression line of total body silica and head length for unstarved animals (Figure 4) was used as a conversion factor to adjust the silica content of each individual in a starvation experiment to that of an average size animal for that experiment. The difference in head length between an amphipod and the average was multiplied by the conversion factor, with the resulting number either added to or subtracted from that individual's silica content. These adjusted silica values were then regressed against time and a feeding rate was calculated.

Linear regressions, in this case and in others, were performed on a

Figure 4. The relationship between total ug Silica per individual and head length for unstarved adult Weyprechtia on May 9 and June 6, 1986.



computer using the SAS regression program (SAS Institute 1982). Analysis of variance was performed using the SAS ANOVA procedure, and analysis of covariance was performed using the SAS General Linear Models procedure (SAS Institute 1982).

4). Assimilation

a) Silica:chlorophyll:dry weight ratios

Silica:dry weight ratios were determined for sub-ice algae on three occasions, May 8, 1985 and May 3 and 19, 1986. Algae was collected from the sub-ice surface by a diver, and allowed to concentrate in a cool, darkened glass cone. On May 8, 1985 and May 3, 1986, small amounts of the concentrated algae were pipetted onto preweighed polycarbonate filters. These were dried, reweighed, and placed in small plastic vials for biogenic silica analysis. On May 19, separate filters were used for dry weight and silica analysis, so an average weight was used in calculating the silica:dry weight ratios.

For silica analysis, 15 mL of 0.1 M NaOH was added to each vial, and the samples boiled for one hour. After cooling, 2 mL of 1 N HCl was added to bring the acidity to pH 3 - 4. The samples were then analyzed for dissolved silica as before.

Chlorophyll:dry weight ratios were determined for sub-ice algae on May 3 and May 19, 1986. Known volumes of concentrated algae were pipetted onto GFC filters, and the chlorophyll extracted overnight in 90 % methanol. Fluorescence was read on a Turner model 11A fluorometer which had been previously standardized with known concentrations of chlorophyll (Stainton et al. 1977).

b) Assimilation Efficiency

Assimilation efficiency was determined by comparing the silica to dry weight ratios of amphipod feces to the sub-ice algae - an application of Conover's "ash ratios" method (Conover 1966). A similar method was described by Tande and Slagstad (1985) for copepods, using biogenic silica and ^{14}C ratios.

During the last three starvation experiments, feces produced by the amphipods were collected at each time interval. Samples were taken back to the lab and filtered onto dried and preweighed polycarbonate filters (pore size 0.6 μm). The filters were dried in a desiccator, reweighed, then placed in individual plastic scintillation vials. Some feces produced by Weyprechtia while they were being held for other experiments were also treated in this way. The feces were analyzed for their biogenic silica content as described above for algae.

Growth and Life Cycle

1). Cohort Analysis

To determine growth patterns, a large sample of amphipods was taken monthly during the field season. In 1985, samples were obtained for May, June and July, while in 1986, samples were obtained for March through August. Since it was not always possible to obtain enough animals on one day, sampling was usually repeated several times a week. Several Weyprechtia were also captured in January, 1986.

Head length was measured in 1985 with an ocular micrometer to the nearest unit (0.02 mm). In 1986, a Wild digital micrometer (Model MMS

235) was used, which measures to the nearest 0.01 mm.

To obtain a length - dry weight relationship, some measured animals were dried at 60° to constant weight, allowed to cool overnight in a desiccator, then weighed on a Mettler electrobalance (Model AE 163) to the nearest 0.01 mg. Animals were taken on March 29, May 6 and May 30 1986, to obtain a range of animal sizes.

Head length - frequency histograms were plotted for each month. Usually two cohorts were present, but in July 1985 and March 1986 there appeared to be an additional group of large adults. This group was separated from the other adults using probability paper and the method described by Cassie (1954).

Mean weights and "bootstrap" variances were calculated from the individual head lengths for each cohort using the length - dry weight equation and a computer program developed by Bird and Prairie (1985).

2). Long Term Molting

In 1986, a group of Weyprechtia were kept in the lab in order to observe molting patterns. Twenty-nine amphipods were captured on April 23, placed in individually numbered containers, and held in a large tub with running seawater (except for the period June 27 to July 14, when the containers had to be held inside a mesh bag that was suspended in the ocean). The amphipod containers consisted of large plastic vials, with the ends covered with large mesh (approx. 2 mm) screening. These vials were allowed to float freely inside the seawater tub. Temperature in the tub remained at about 0.5 to 1.0 degrees above the normal seawater temperature. Because the flow-through volume in the tub was high, oxygen concentration of the water was not monitored. Ten more

animals were added on May 14, to bring the total number to thirty-nine. Animals which died during the early stages of experiment were replaced.

The amphipods were fed an excess of ice algae on chips of ice collected from auger holes and, later in the season, a slurry of algae kept growing in the lab. Fecal pellet production indicated that the animals were feeding. Animals were fed and checked for molted exoskeletons every two to three days and their containers were cleaned periodically. Any exuviae or dead animals found were preserved in 70 % ethanol for later measurement.

Seventeen exuviae collected in May and June were not preserved, but were kept for dry weight determinations. The exuviae were rinsed in distilled water, measured for head length, dried at 60⁰, cooled, then weighed.

Respiration

Closed bottle respiration experiments were carried out in both 1985 and 1986. In 1985, experiments were run on July 11 and 26, during the open water season. In 1986, 6 experiments were run during the ice-on period, on May 7, 17, 23, 29, June 9 and 16.

In 1985, amphipods were collected from the sea floor by dragging a small net. Five or ten adult Weyprechtia were placed into 300 mL glass stoppered bottles which had been filled with filtered (500 um) seawater. Each experiment consisted of 3, 5 or 6 experimental bottles, with one or two control bottles. All the bottles were incubated in situ at a temperature of +1.0 ⁰.

In 1986, the sub-ice sweep net was used to capture amphipods from

the sub-ice surface. Animals were quickly sorted, transported to the Bedford ice camp, and placed in glass bottles as described above, except that ten animals were used each time. Incubations generally began 20 to 30 minutes after capture. In this case, the bottles were held inside a large tub with flow-through running seawater at $0^{\circ} \pm 1$.

After an incubation period of four hours, the bottles were removed, and a subsample of water was siphoned from each into a 130 mL glass stoppered bottle. A screen was used on the siphon tube to prevent feces and other material from entering the sample bottles. The amphipods were killed and preserved in 70 % ethanol for later measurement.

The subsample bottles were taken back to the laboratory the same day and titrated for oxygen concentration according to the method of Carpenter (1965) as modified by Welch (Welch and Bergmann 1985). Often two titrations would be made on the same subsample. In both 1985 and 1986, the average difference between these was $0.03 \text{ mg O}_2 \cdot \text{l}^{-1}$, close to the standard error of $0.02 \text{ mg} \cdot \text{l}^{-1}$ obtained from practice titrations.

RESULTS

Feeding

1). Twenty-four Hour Series

In the 1985 series, only three amphipods were caught at each time period, resulting in a total of only 15 points (3 samples were lost). Mean silica level on this date was $18.89 \text{ ug.amphipod}^{-1} \pm 4.66$. (Throughout the results, numbers following the $\pm$ symbol are the 95 % confidence interval). No real trend could be seen in these data (Figure 5), possibly due to the small sample size. A regression run through the 15 points did not have a significant slope ($p > 0.20$).

In May 1986, 9, 10 or 11 animals were caught each time. The resulting plot (Figure 6) shows a slight dip in average silica content in the evening and night samples, compared to the morning samples. Silica values overall seemed low on this date, averaging $10.20 \pm 0.89 \text{ ug.amphipod}^{-1}$ ($n=61$). Analysis of variance (SAS Institute 1982) indicated that there were significant differences among the mean silica values at each time period ($p < 0.01$). A Bonferroni t-test (SAS Institute 1982) showed that the 11:20 sample mean was significantly different from 4 of the 5 other means. As well, this test showed that the 7:20 mean value was significantly different from the 19:20 mean.

The pattern which occurred in May was not evident in the June twenty-four hour series. Mean silica contents did not vary much over the period (Figure 7). The overall silica content was also higher than in May, averaging $15.57 \pm 1.10 \text{ ug.amphipod}^{-1}$ ($n=67$). Analysis of variance (SAS Institue 1982) of these sample means showed no significant

Figure 5. Total ug Silica per individual adult Weyprechtia over a 24 hour period, May 20 - 21, 1985.

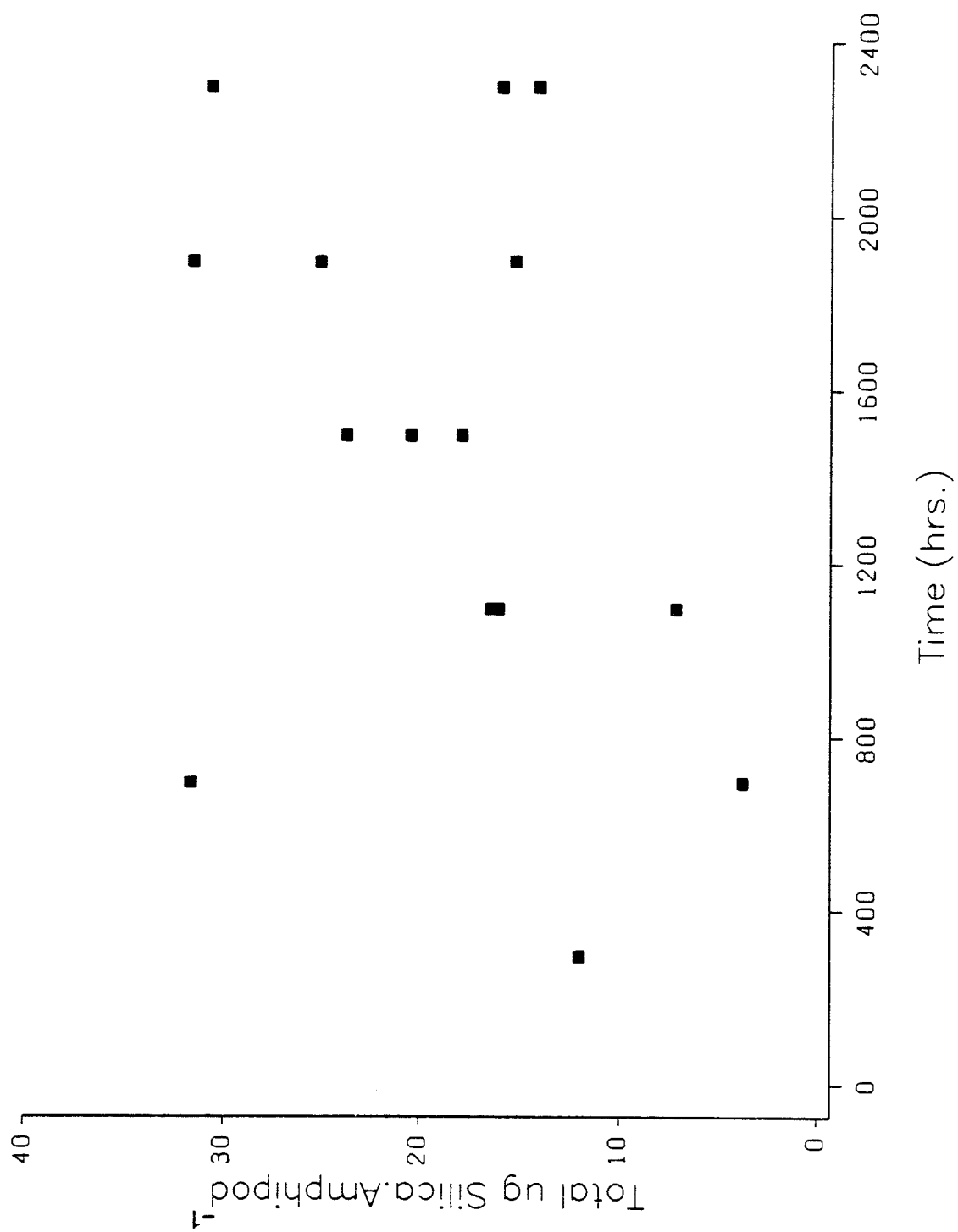


Figure 6. Mean total ug Silica per individual adult Weyprechtia over a 24 hour period, May 8 - 9, 1986. Bars are the 95 % confidence interval about the mean, and the numbers below each bar are the number of amphipods sampled at that time.

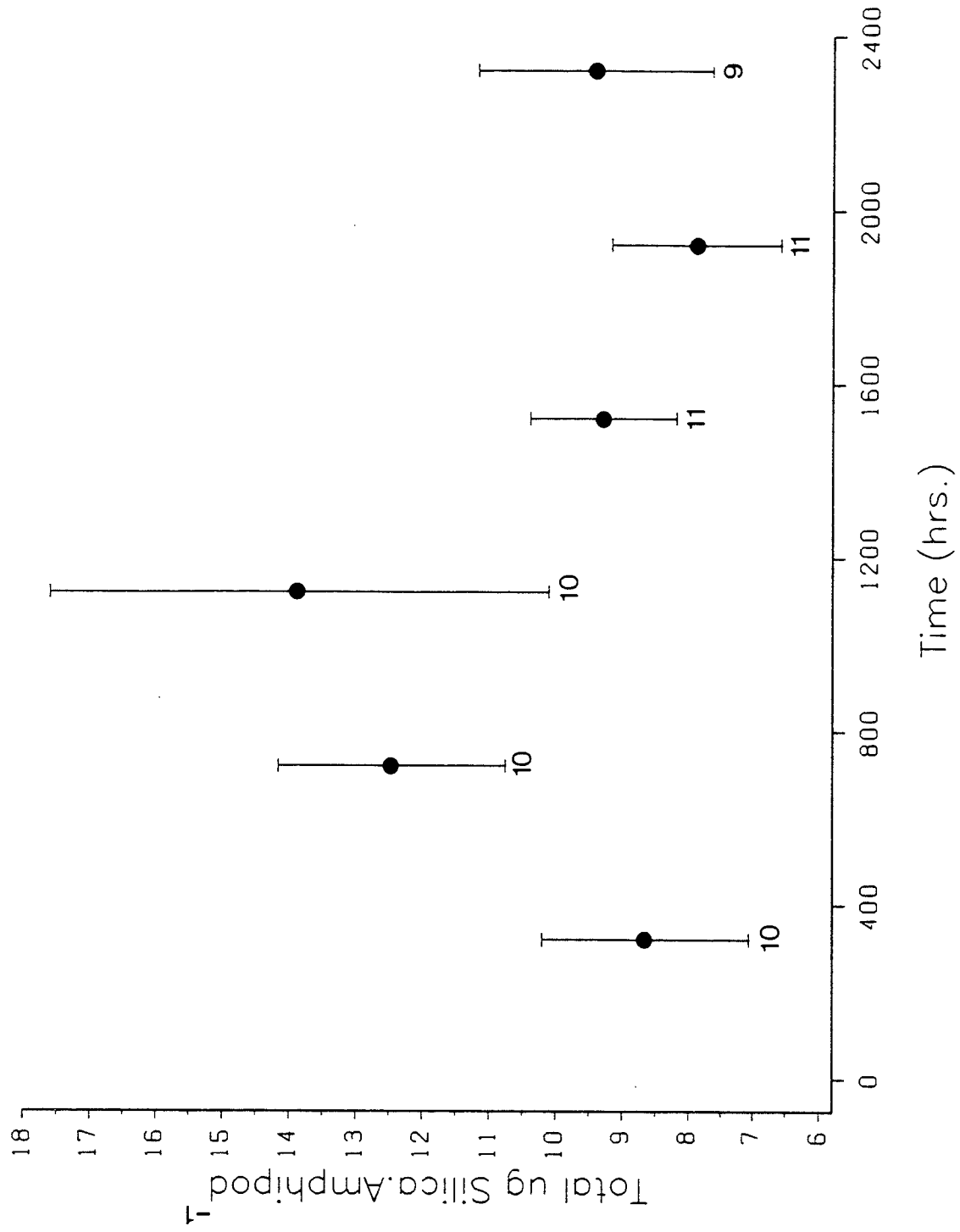
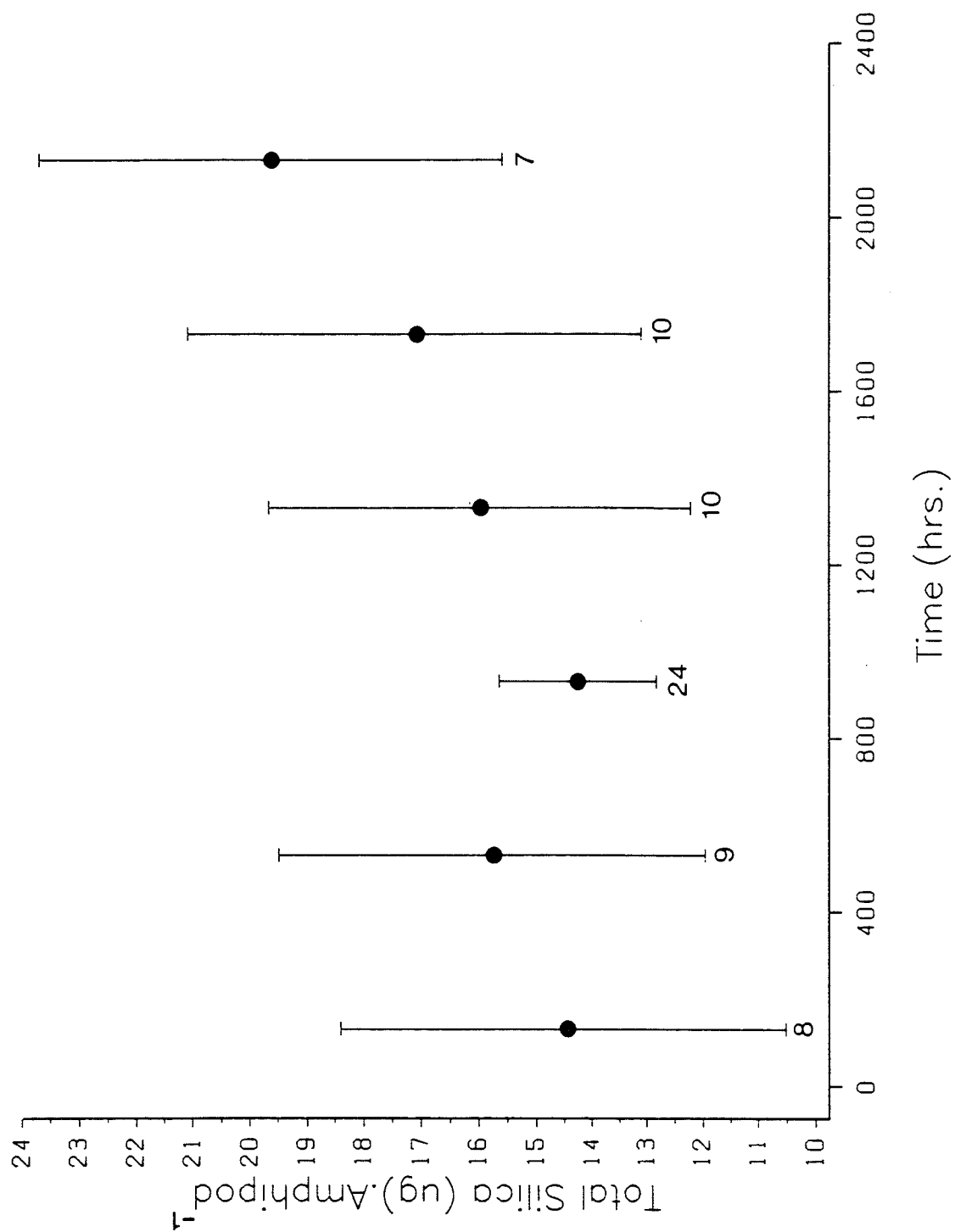


Figure 7. Mean total ug Silica per individual adult Weyprechtia over a 24 hour period, June 6 - 7, 1986. Bars are the 95 % confidence interval about the mean, and the numbers below each bar are the number of amphipods sampled at that time.



differences among them ($p > 0.26$).

In all of these cases, no strong patterns of total silica content were observed over the 24-hour period, suggesting that there may be no strong daily feeding patterns in these amphipods.

2). Feeding Rate

The loss of silica over time was initially plotted separately for each of the seven starvation experiments. The slopes of these lines (which equal the gut evacuation constants) were used to calculate feeding rates (Table 1). Analysis of covariance, using a model to test heterogeneity of slopes (SAS Institute 1982), indicated no significant difference among these slopes ($p > 0.24$). As well, feeding rates for each experiment were not significantly correlated with the average size of the animals in that experiment ($p > 0.05$). Because of this, the data were pooled and one line was plotted (Figure 8). The coefficient of determination for this line was 0.238 ($n=507$, $p < 0.001$). The slope of this line (0.079 ± 0.012) was used to calculate an overall feeding rate (Table 1). The rate obtained this way, $0.935 \pm 0.142 \text{ ug silica.amphipod}^{-1}.\text{hr}^{-1}$, is close to the average obtained from the seven separate experiments, $0.944 \pm 0.234 \text{ ug silica.amphipod}^{-1}.\text{hr}^{-1}$ (Table 1).

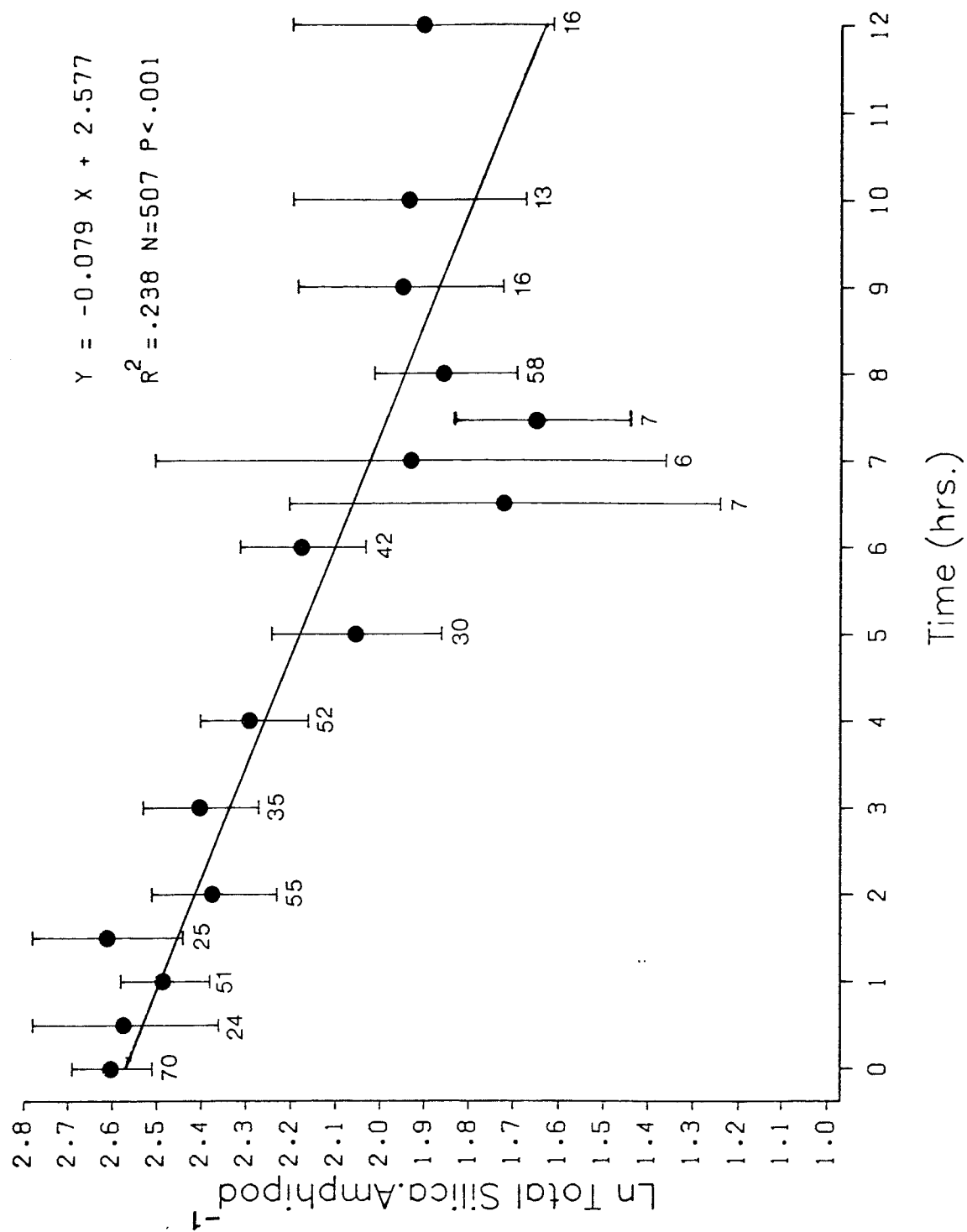
For comparison, a linear regression was run on the untransformed data. The coefficient of determination was slightly lower than that for the exponential line, equalling 0.228 ($n=507$, $p < 0.001$). There is no statistical evidence for choosing one model over the other.

There is no further evidence given from the rate of feces production. If gut evacuation is linear, then a constant amount of material should be egested per unit time until the gut is empty (Dagg

Table 1. Calculation of feeding rates for Weyprechtia from the seven starvation experiments. Feeding rate is equal to the gut evacuation constant multiplied by the full gut silica value for an average size animal (mean head length) for each experiment. Full gut Si values for each size were obtained from the plot shown in Figure 4.

Experiment Date	Gut. Evac. Constant	Mean Head Length (mm)	Full Gut Si (μg)	Feeding Rate $\mu\text{g Si Amphipod}^{-1}\text{hr}$
April 14	0.064	1.47	9.26	0.593
April 24	0.101	1.54	10.31	1.041
May 8	0.061	1.61	11.37	0.694
May 21	0.085	1.71	12.89	1.096
May 31	0.092	1.80	14.25	1.311
June 10	0.077	1.77	13.79	1.062
June 18	0.059	1.77	13.79	0.814
	$\bar{x} = 0.077$ ± 0.015			$\bar{x} = 0.944$ ± 0.234
All dates	0.079 ± 0.012	1.64 ± 0.02	11.83	0.935 ± 0.142

Figure 8. Decrease in mean $\ln$ Silica per individual Weyprechtia over time for all the 1986 starvation experiments combined. Dots are the means at each time period, the bars are the 95 % confidence interval, and the numbers below each bar are the number of amphipods sampled at that time.



and Wyman 1983). If the gut empties exponentially, then there should be a levelling off in the amount of fecal material produced over time. In two of the three starvation experiments in which feces were collected at each time, there is a significant linear correlation between the amount of feces produced with time, rather than a clear levelling off. The coefficients of determination for the two lines equal 0.783 ($n=11$, $p < 0.05$) and 0.710 ($n=7$, $p < 0.05$).

3). Assimilation

a) Silica:chlorophyll:dry weight ratios

The relationship between silica and dry weight for sub-ice algae was determined on May 8, 1985 and May 3 and 19, 1986. The 1985 samples gave a silica:dry weight ratio of 0.094 ± 0.005 ($n=4$) (Table 2). On May 3, 1986 the average ratio of silica:dry weight was 0.110 ± 0.006 ($n=7$). The results for May 19 were similar (Table 2), with an average silica:dry weight ratio of 0.107 ± 0.004 ($n=8$).

Using both the 1985 and 1986 results gave an overall silica:dry weight ratio of 0.105 ± 0.004 . This corresponds well to the ratio of elemental silica to dry weight of between 0.1 to 0.3 determined for "typical plankton diatoms" by Paasche (1980b).

The dry weight:chlorophyll ratio was 156.70 ± 22.50 on May 3, 1986, and 111.77 ± 8.18 on May 19 (Table 3). These two means are significantly different from each other (t -test $p < 0.05$) (Sokal and Rohlf 1969), perhaps indicating that the amount of chlorophyll per unit weight increases as the season progresses.

Table 2. Silica to dry weight ratios for sub-ice algae, May 5, 1985 (A), May 3, 1986 (B) and May 19, 1986 (C). The mean is given for each date $\pm$ the 95% confidence interval.

	No.	Algae Dry Wt. (mg)	Total mg Silica	Si:Dry Wt.
A	1	4.19	0.409	0.098
	2	8.62	0.788	0.091
	3	8.26	0.779	0.094
	4	8.12	0.749	0.091
				$\bar{x} = 0.094$ ± 0.005
B	1	24.66	2.558	0.104
	2	52.01	5.571	0.107
	3	39.46	4.046	0.103
	4	41.16	4.366	0.106
	5	31.08	3.667	0.118
	6	29.70	3.291	0.111
	7	31.28	3.729	0.119
				$\bar{x} = 0.110$ ± 0.006
C	1	3.00	0.312	0.104
	2	3.00	0.328	0.109
	3	3.00	0.342	0.114
	4	3.00	0.325	0.108
	5	3.00	0.325	0.108
	6	3.00	0.319	0.106
	7	3.00	0.293	0.098
	8	3.00	0.332	0.111
				$\bar{x} = 0.107$ ± 0.004
			All dates	$\bar{x} = 0.105$ ± 0.004

Table 3. Dry weight: chlorophyll relationship for sub-ice algae determined on May 3 (A) and May 19, 1986 (B).

	No.	Dry Weight (μg)	μg Chl	Dry Wt.:Chl
A	1	5820	41.10	141.61
	2	5820	44.55	130.64
	3	5820	43.00	135.35
	4	5820	36.07	161.35
	5	5820	31.22	186.42
	6	5820	38.70	150.39
	7	5820	30.30	191.08
				$\bar{x} = 156.70$ ± 22.35
B	1	3000	32.25	93.02
	2	3000	26.28	114.16
	3	3000	28.65	104.71
	4	3000	27.05	110.91
	5	3000	24.68	121.56
	6	3000	28.65	104.71
	7	3000	27.05	110.91
	8	3000	23.08	129.98
	9	3000	25.88	115.92
				$\bar{x} = 111.77$ ± 8.18

b) Assimilation Efficiency

Attempts to measure assimilation efficiency for Weyprechtia were not successful (Table 4). Of the 33 measurements made, only three gave a silica to dry weight ratio greater than that found for the algae. Assimilation efficiencies for those three values are: 45.9, 37.1 and 45.0 %

Growth and Life Cycle

1). Cohort Analysis

The length-frequency histograms (Figures 9 and 10) for each month show two distinct cohorts of Weyprechtia, juveniles and adults. The exceptions are July 1985 and March 1986, in which a third group of large animals appeared. These groups were separated from the other adults using "Cassie curves" (Figures 11 and 12). Many of the large Weyprechtia in March 1986 were females with oostegites, modified appendages which form the brood pouch, indicating that they are sexually mature and able to carry young (Steele 1967). This cohort was not present after March, as they probably died. Weyprechtia's lifespan therefore appears to be a maximum of 24 to 26 months.

Two females caught in mid January, 1986 were carrying unhatched young. One (head length 2.32 mm), was carrying 135 young. The other, (head length 2.09 mm), had 58 young in the brood pouch. The young were all still enclosed in a membrane but appeared well developed with a distinct head, appendages, and large eyes. Because free-living young were caught under the ice in March, they must be released sometime between mid January and March.

Table 4. Calculation of assimilation efficiencies for adult *Weyprechtia*, 1986. For the first six dates listed, designated with a P, feces were collected from animals held for other purposes (e.g. respiration), and were pooled together. For May 31, June 10 and June 18, feces were collected over the course of the starvation experiments. The silica:dry weight ratio for algae is 0.105.

Date	Time of Collection	Feces Dry Wt. (mg)	Total $\mu\text{g Si}$	Feces Si:Dry Wt.	Assim. Efficiency
May 14 (P)		4.23	127.04	0.030	---
May 19 (P)		2.11	408.64	0.194	45.9%
		1.26	210.24	0.167	37.1%
May 20 (P)		7.37	328.64	0.045	---
		9.99	448.32	0.045	---
May 21 (P)		3.05	583.36	0.191	45.0%
		3.97	282.40	0.071	---
May 23 (P)		5.02	485.44	0.097	---
June 9 (P)		2.07	162.68	0.079	---
May 31	1 hr.	1.56	19.84	0.013	---
	2 hr.	5.64	25.76	0.005	---
	3 hr.	3.07	37.76	0.012	---
	4 hr.	2.01	59.52	0.030	---
	6 hr.	2.24	41.60	0.019	---
	8 hr.	1.68	47.68	0.028	---
June 10	1 hr.	2.34	39.84	0.017	---
	1.5 hr.	2.75	34.86	0.013	---
	2 hr.	2.07	68.06	0.033	---
	3 hr.	4.10	92.96	0.023	---
	4 hr.	4.44	89.64	0.020	---
	5 hr.	3.40	111.22	0.033	---
	6 hr.	5.01	132.80	0.027	---
	7 hr.	5.68	167.66	0.030	---
	8 hr.	3.55	94.62	0.027	---
	10 hr.	7.20	86.32	0.012	---
	12 hr.	7.62	147.74	0.019	---
June 18	1 hr.	1.30	33.08	0.025	---
	1.5 hr.	1.72	35.99	0.021	---
	2 hr.	2.75	59.54	0.022	---
	4 hr.	2.22	87.26	0.039	---
	6 hr.	3.54	146.79	0.041	---
	10 hr.	3.60	125.37	0.035	---

Figure 9. Head length frequency histograms for Weyprechtia: May 4, 5 and 7, June 5 & 6, and July 3 & 10, 1985.

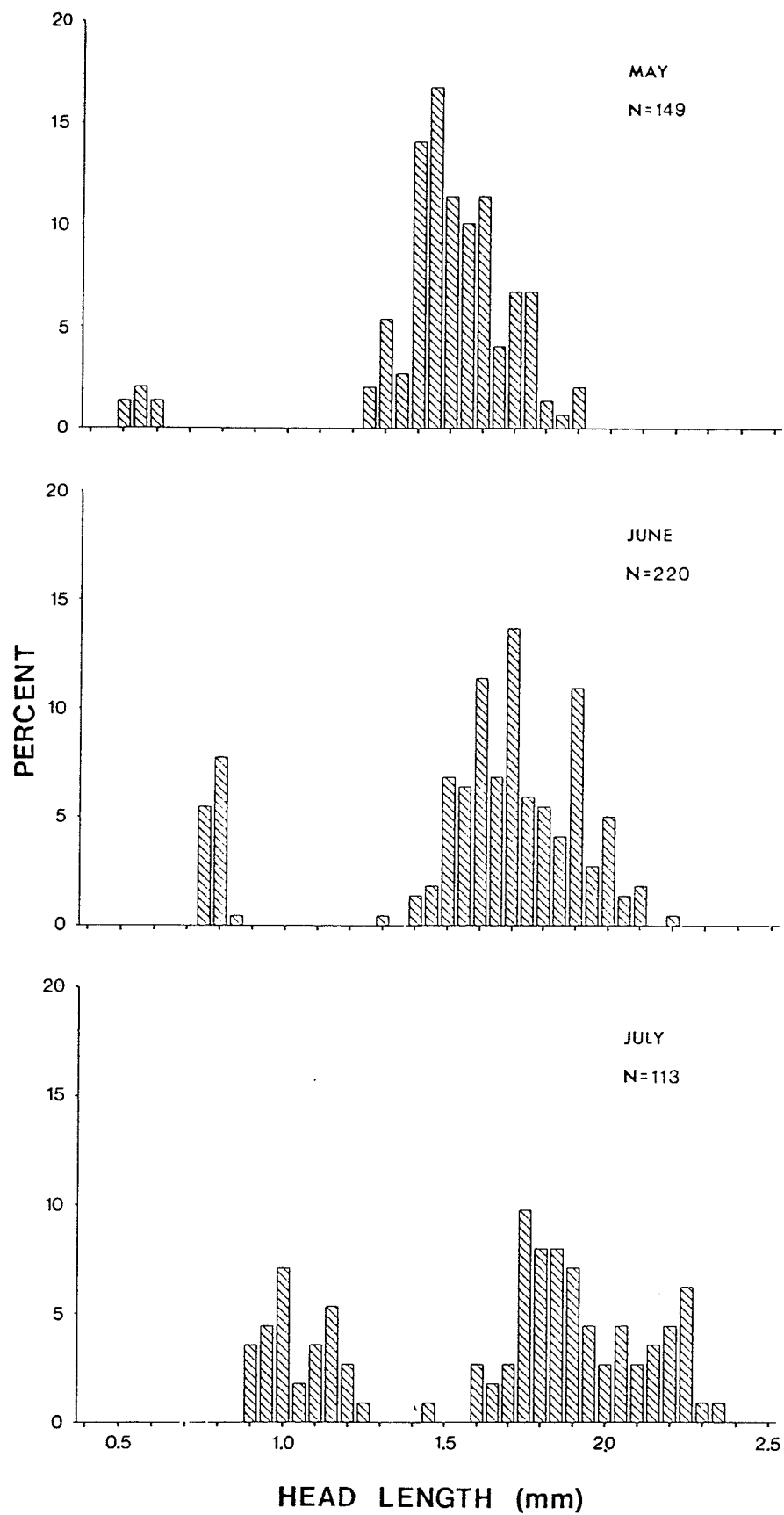


Figure 10. Head length - frequency histograms for Weyprechtia: March 28 & 29, April 24, May 26, 27, 29, & 31, June 25 & 28, July 26 & 30, and August 22 & 25, 1986.

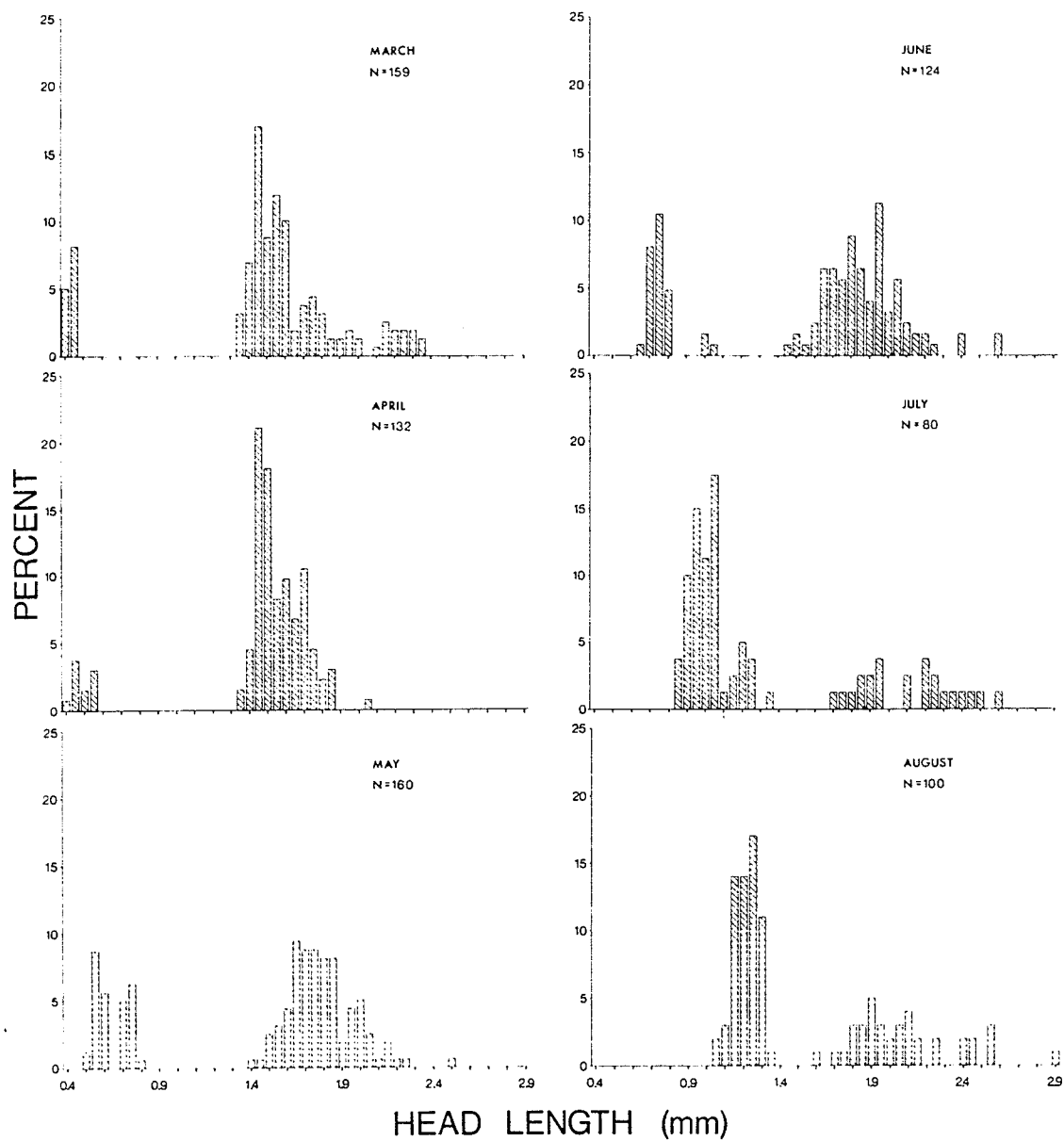


Figure 11. The Cassie curve for adult and juvenile Weyprechtia, July, 1985 (originally plotted on probability paper). Points of inflection in the curve, taken at 30 and 77 %, are used to separate cohorts or groups. The average head length for each group is read at the intersection of the plotted lines (open circles) and the 50 % vertical line.

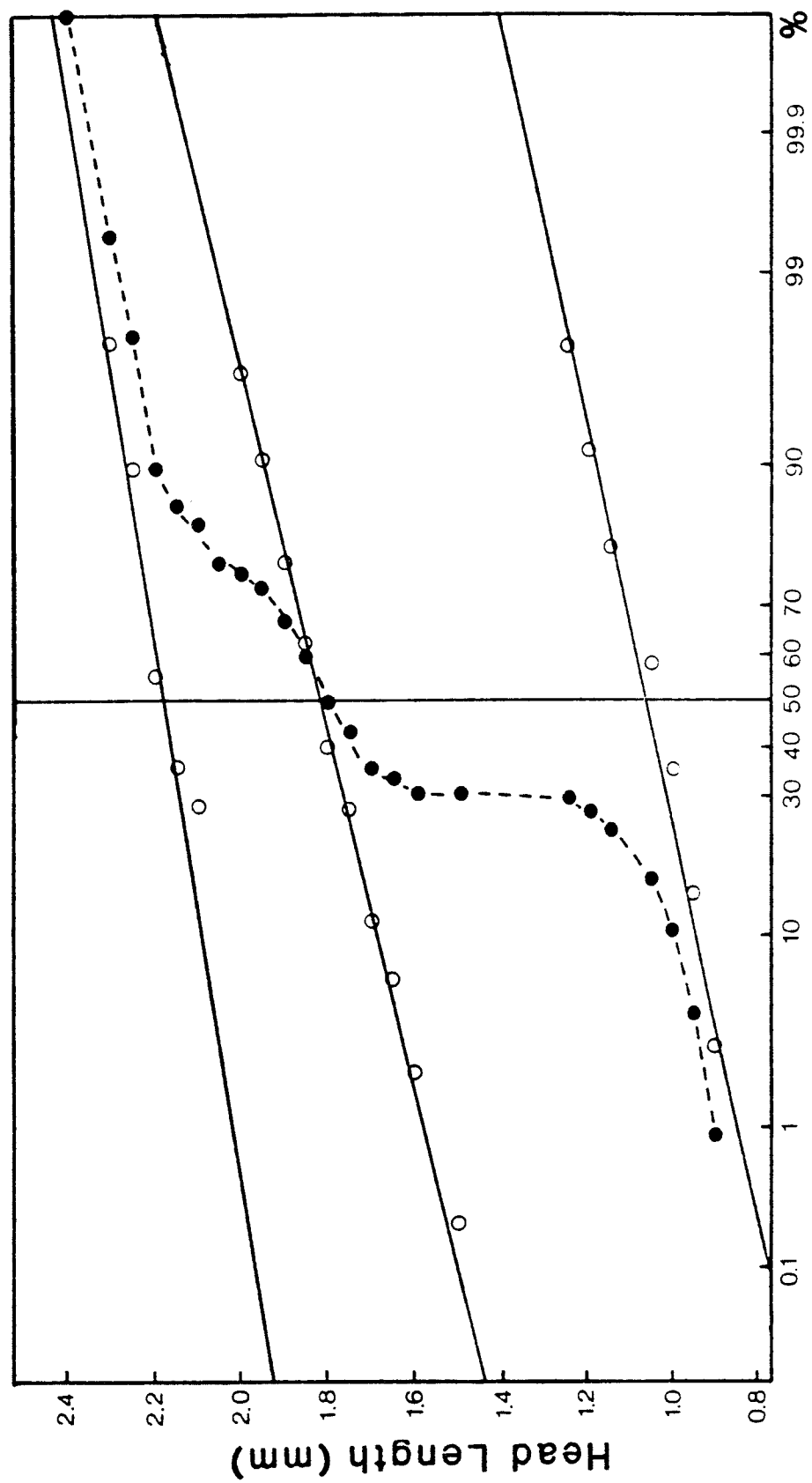
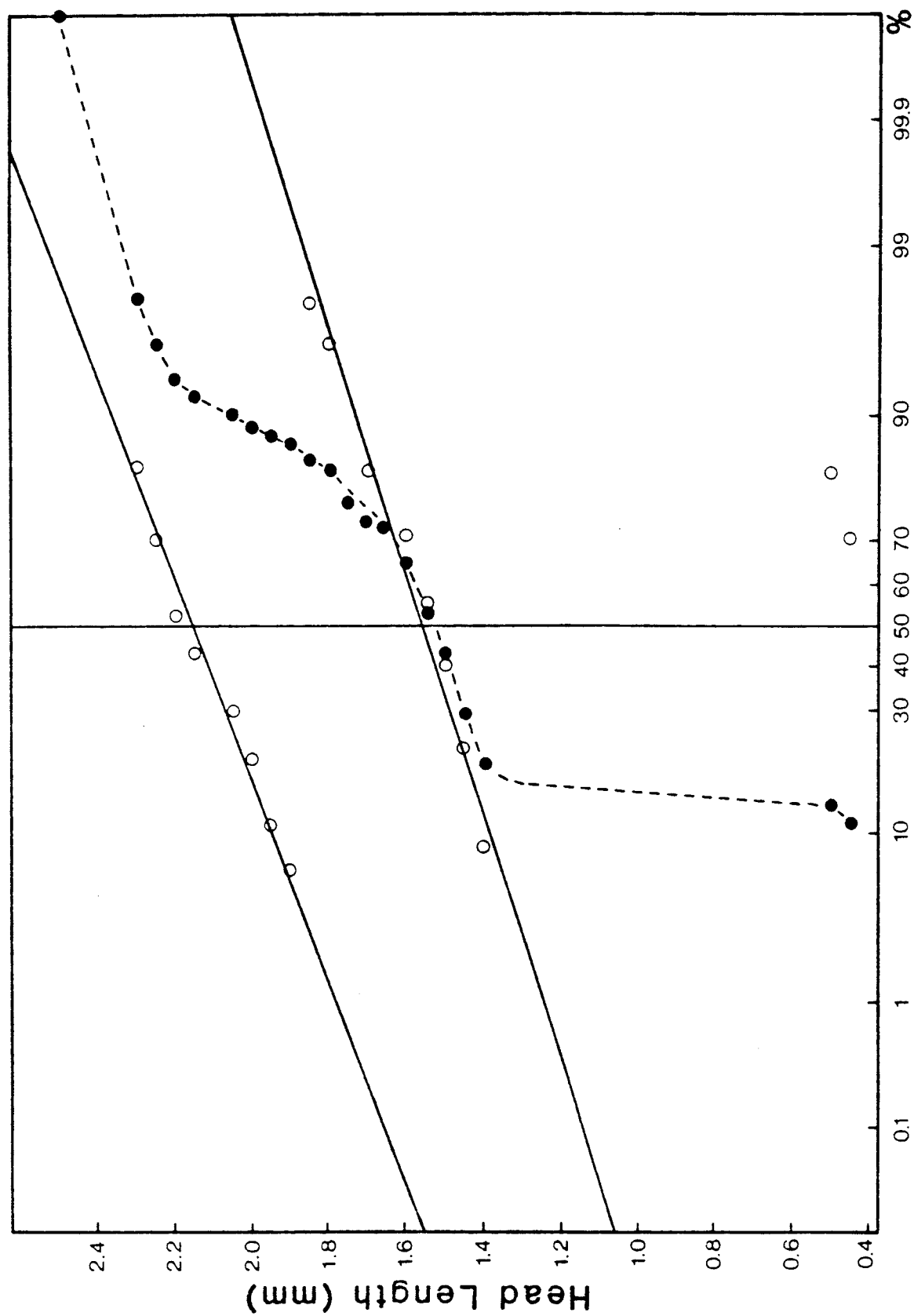


Figure 12. The Cassie curve for adult and juvenile Weyprechtia, March, 1986 (originally plotted on probability paper). Points of inflection in the curve, taken at 14 and 86 %, are used to separate cohorts or groups. The average head length for each group is read at the intersection of the plotted lines (open circles) and the 50 % vertical line.



For each month, a mean head length was calculated for both the adult and juvenile cohorts of Weyprechtia (Table 5). When these means are plotted for 1985 and 1986, the overall pattern of growth can be seen (Figure 13). Growth proceeds rapidly in the spring and summer season for both juveniles and adults and levels off in the fall and winter.

Head lengths for each month were converted to dry weights using the length - dry weight relationship (Figure 14). The means for each month are given in Table 6. A plot of these mean weights over time for both 1985 and 1986 (Figure 15) shows a similar pattern of increase to that of head length.

The increase in head length over time for the 1986 adults appears to be linear (Figure 16). The coefficient of determination for the regression equals 0.945. The three means obtained in 1985 for adult head length fall well within the 95 % confidence limits about this line. As well, analysis of covariance, using a model to test the heterogeneity of slopes (SAS Institute 1982), showed no significant difference between the slopes of the 1985 and 1986 lines, if each was plotted separately ($p > 0.16$). Combining the two years data gives the line: $y = 0.005x + 1.064$ ($r^2 = .903$, $n=9$, $p < 0.001$). The increase in adult dry weight appeared curvilinear in initial plots, so a semi-log line was used to model growth. Again, the 1985 data falls within the confidence limits of the semi-log regression (Figure 17), and analysis of covariance showed no significant difference between the slopes of the 1985 and 1986 lines ($p > 0.46$). Combining the 1985 and 1986 data produces the line: $\log y = 0.004x + 0.442$ ($r^2 = .913$, $n=9$, $p < 0.001$).

For juveniles, the increase in head length over time for 1986 also appears linear (Figure 18). The coefficient of determination for this

Table 5. Mean monthly head lengths $\pm$ the 95% confidence interval for juvenile (A) and adult (B) Weyprechtia, 1985 and 1986.

Month	1985	n	1986	n
A				
March	--		0.43 $\pm$ 0.01	21
April	--		0.49 $\pm$ 0.03	12
May	0.55 $\pm$ 0.03	7	0.64 $\pm$ 0.03	44
June	0.78 $\pm$ 0.01	30	0.76 $\pm$ 0.03	33
July	1.05 $\pm$ 0.04	33	1.02 $\pm$ 0.03	57
August	--		1.22 $\pm$ 0.02	62
B				
March	--		1.53 $\pm$ 0.03 2.15 $\pm$ 0.07	115 23*
April	--		1.56 $\pm$ 0.02	121
May	1.52 $\pm$ 0.02	142	1.79 $\pm$ 0.03	116
June	1.73 $\pm$ 0.02	190	1.88 $\pm$ 0.05	91
July	1.93 $\pm$ 0.04	80	2.11 $\pm$ 0.11	23
August	--		2.07 $\pm$ 0.09	38

* represents the two-year old cohort

Figure 13. Mean monthly head lengths for adult and juvenile Weyprechita, 1985 and 1986. The circles represent a cohort born in the spring of 1984, the squares represent a cohort born in the spring of 1985, and the triangles represent the 1986 cohort. Lines are fitted by eye.

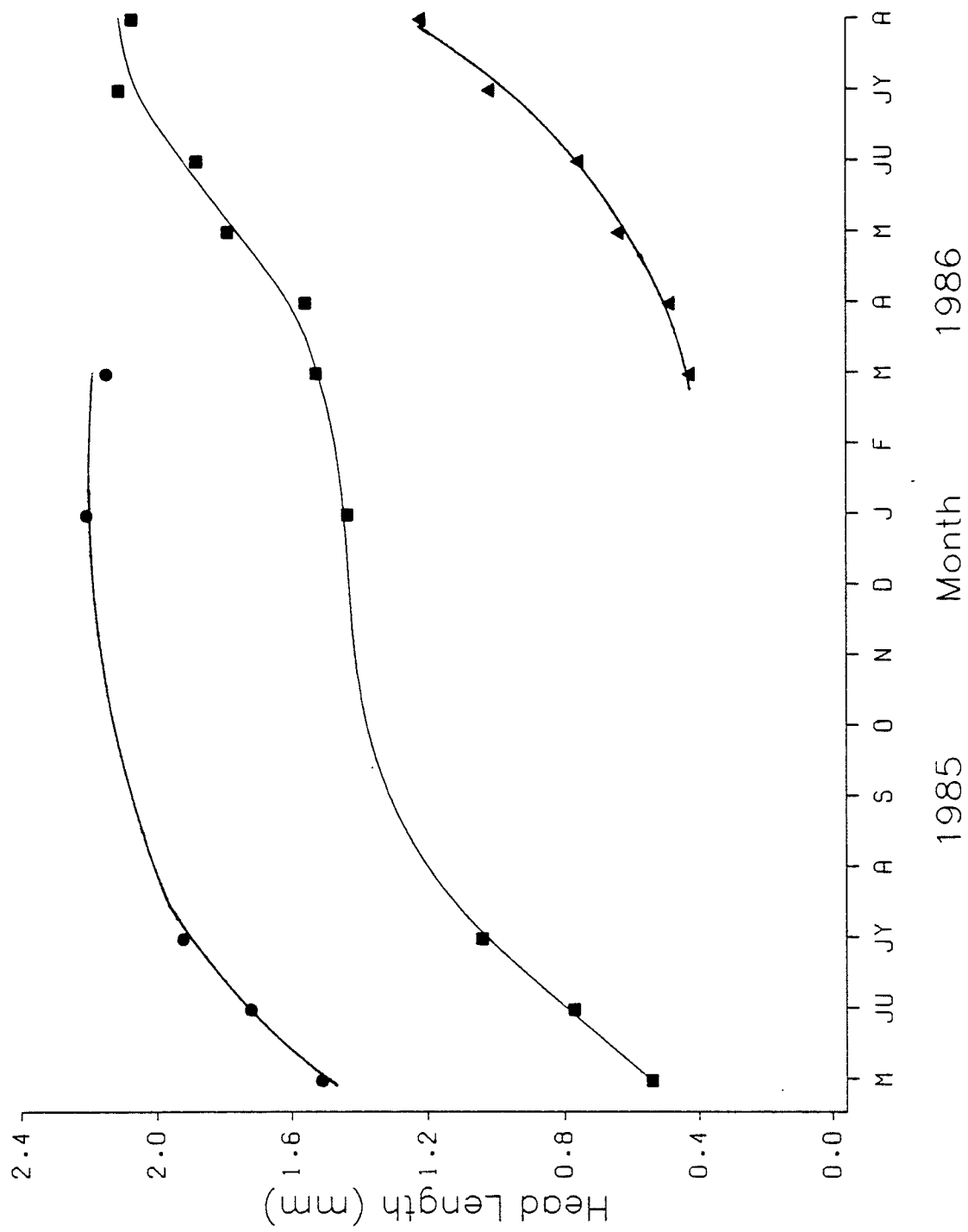


Figure 14. The head length - dry weight relationship for adult and juvenile Weyprechtia.

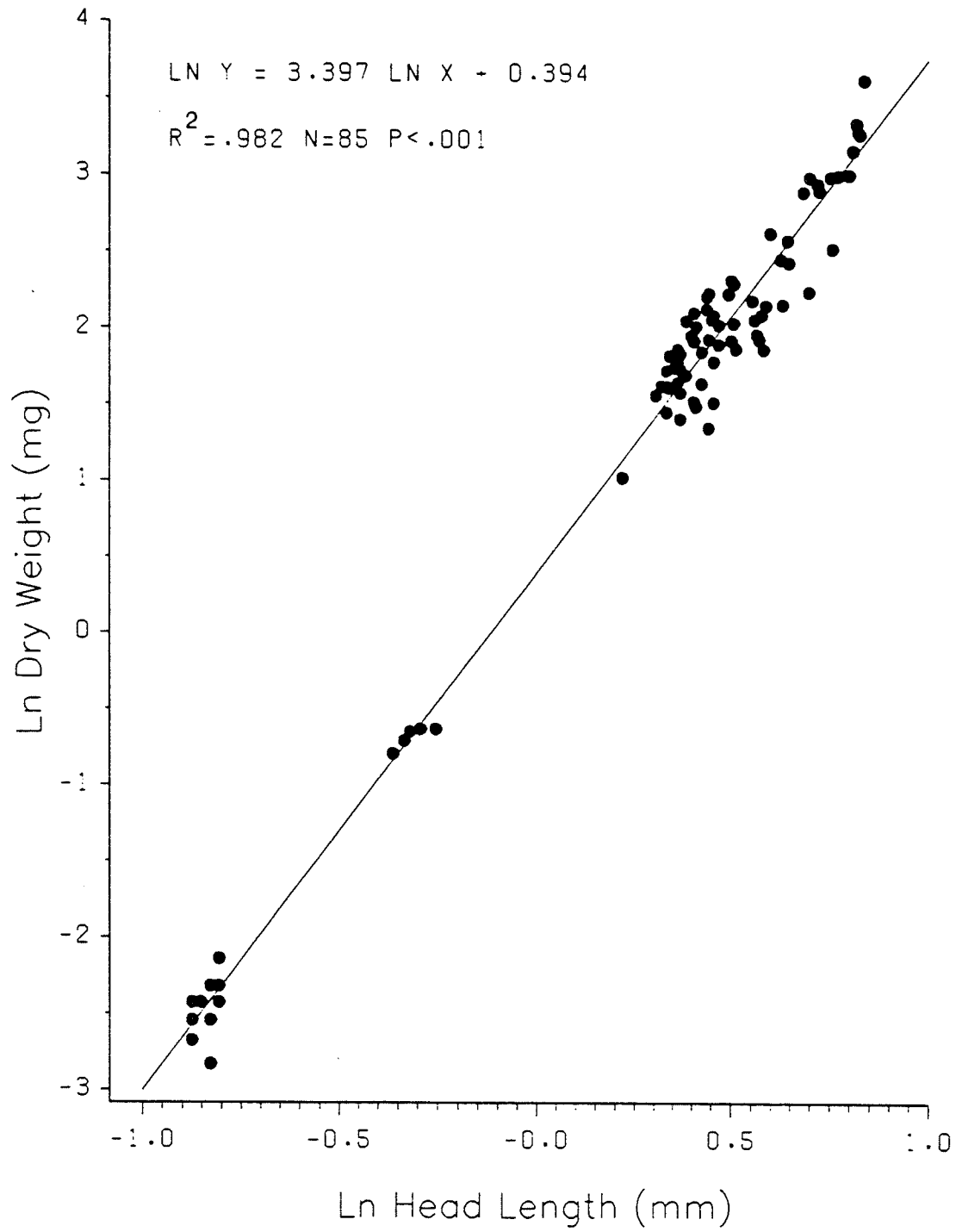


Table 6. Mean monthly dry weights $\pm$ the 95% confidence interval for juvenile (A) and adult (B) Weyprechtia, 1985 and 1986.

Month	1985	n	1986	n
A				
March	--		0.09 $\pm$ 0.01	21
April	--		0.14 $\pm$ 0.04	12
May	0.20 $\pm$ 0.04	7	0.35 $\pm$ 0.05	44
June	0.67 $\pm$ 0.06	30	0.64 $\pm$ 0.13	33
July	1.84 $\pm$ 0.26	33	1.70 $\pm$ 0.21	57
August	--		2.97 $\pm$ 0.21	62
B				
March	--		6.80 $\pm$ 0.47 20.61 $\pm$ 2.67	115 23*
April	--		7.15 $\pm$ 0.50	121
May	6.60 $\pm$ 0.45	142	11.43 $\pm$ 0.92	116
June	10.15 $\pm$ 0.57	190	13.66 $\pm$ 1.42	91
July	14.70 $\pm$ 1.23	80	20.29 $\pm$ 3.97	23
August	--		19.47 $\pm$ 3.50	38

* represents the two-year old cohort

Figure 15. Mean monthly dry weights for adult and juvenile Weyprechtia, 1985 and 1986. The circles represent a cohort born in the spring of 1984, the squares represent a cohort born in the spring of 1985, and the triangles represent the 1986 cohort. Lines are fitted by eye.

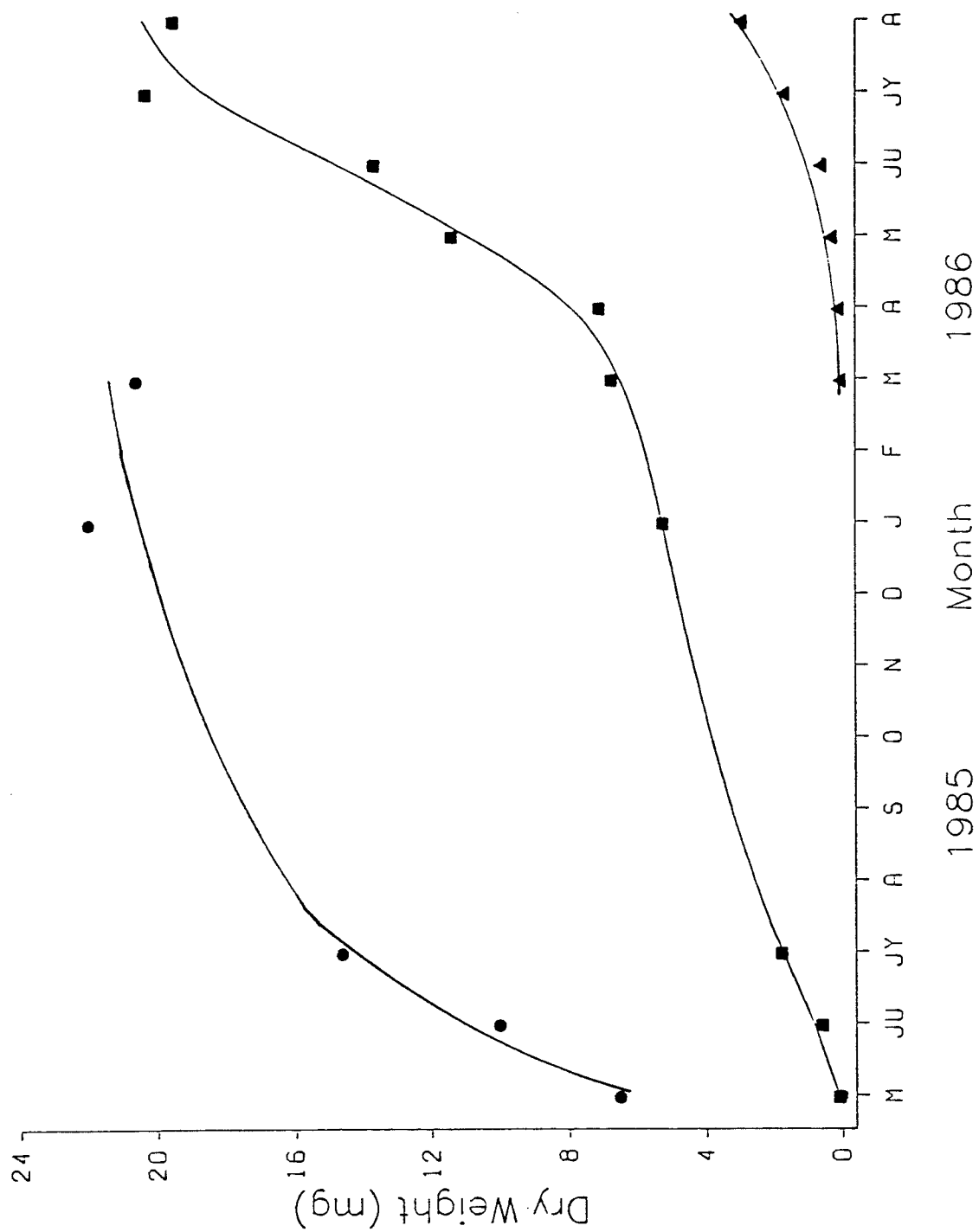


Figure 16. The relationship between head length and Julian date for adult Weyprechtia, 1986. The dashed lines are the 95 % confidence interval about the line. The squares are the means obtained in 1985. The lines were fitted by computer regression (SAS Institute 1982).

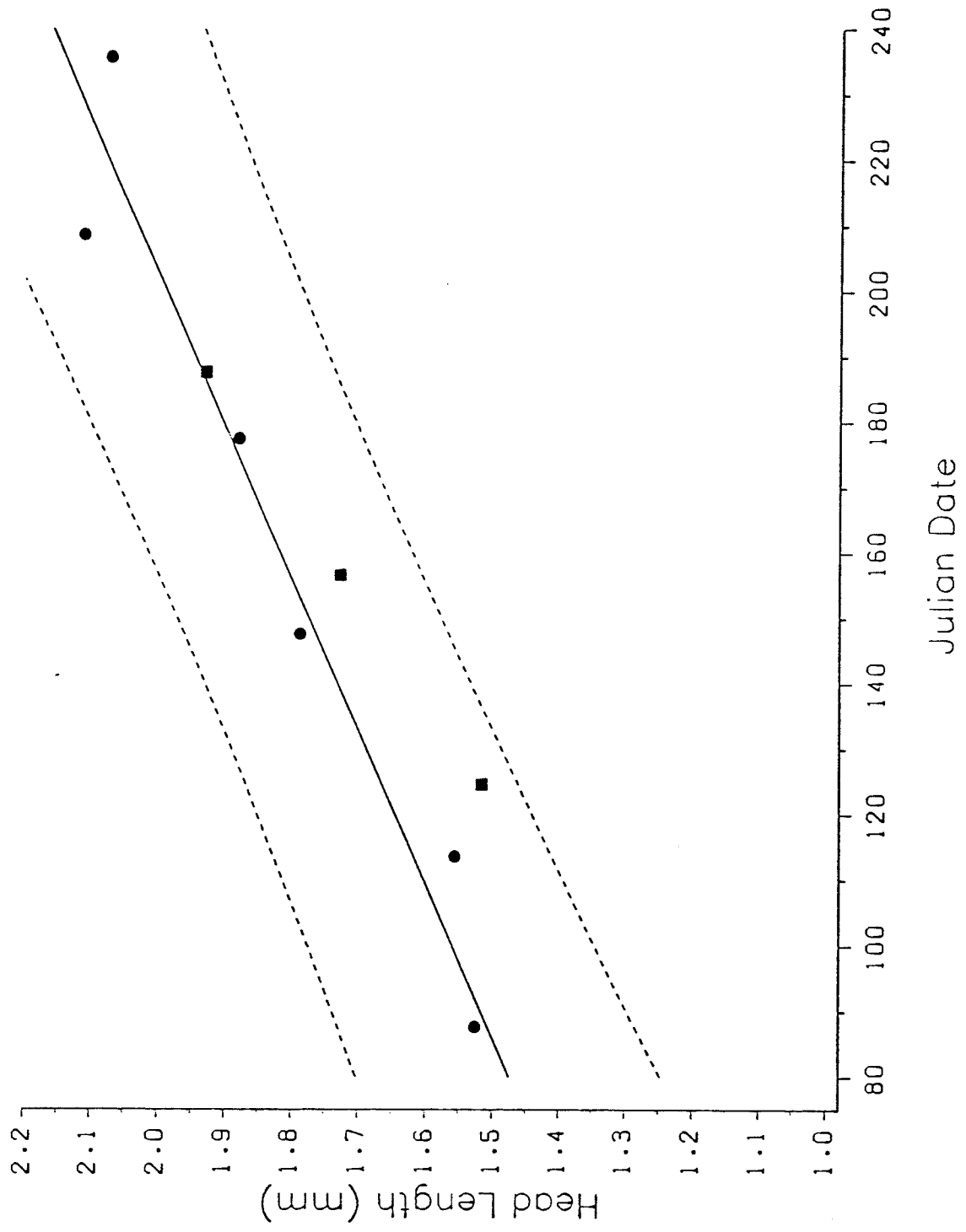


Figure 17. The relationship between dry weight and Julian date for adult Weyprechtia, 1986. The dashed lines are the 95 % confidence interval about the line. The squares are the means obtained in 1985. The lines were fitted by computer regression (SAS Institute 1982).

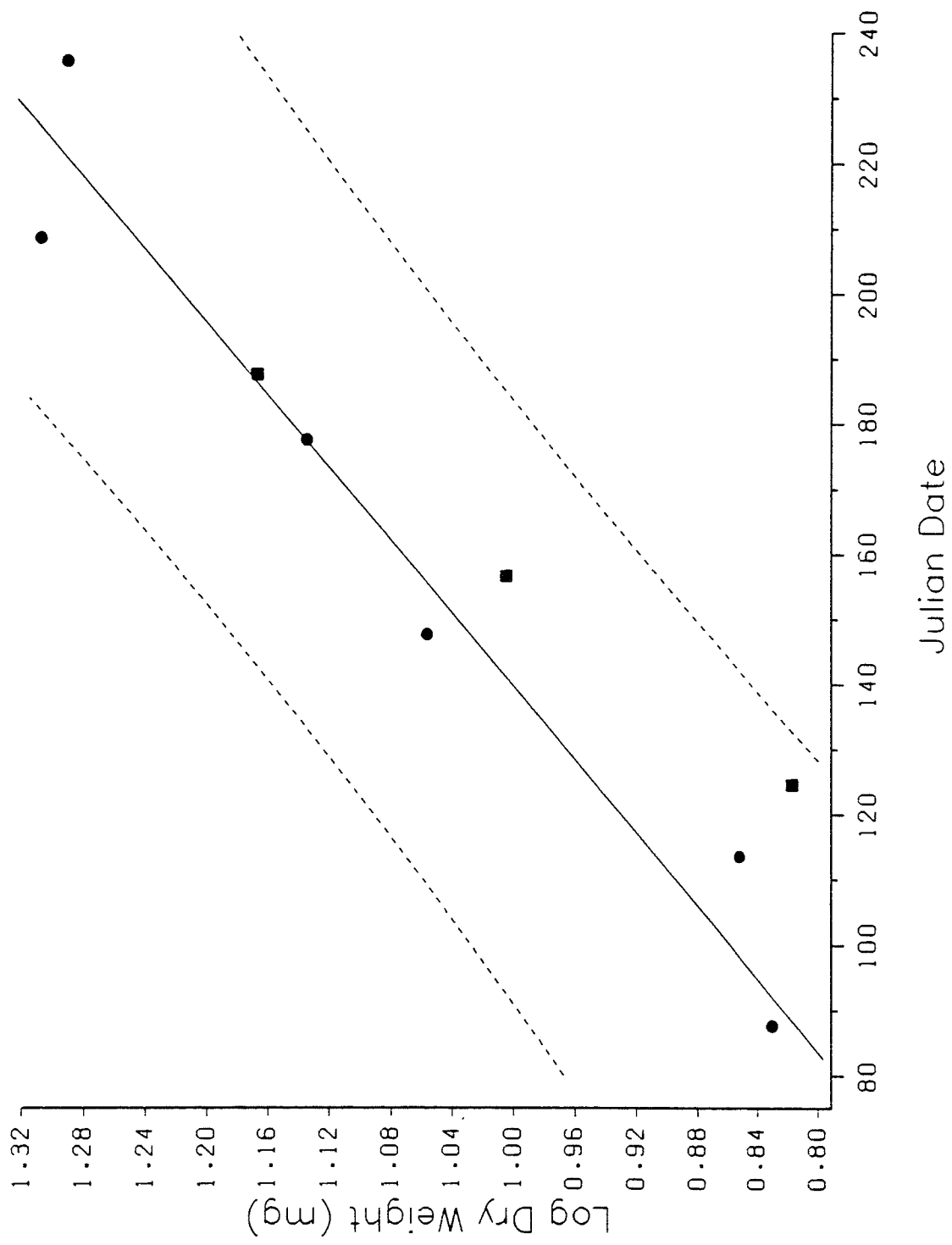
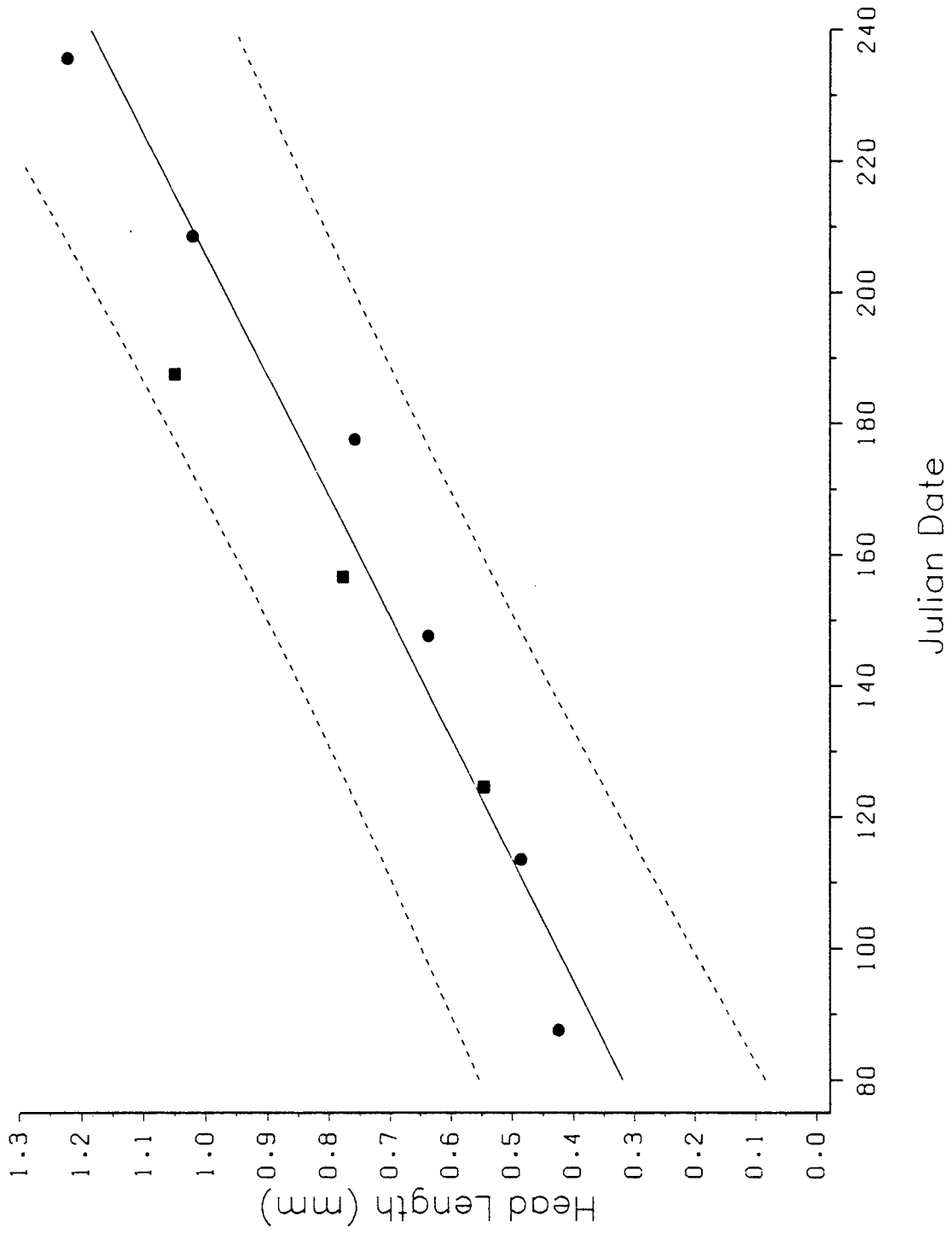


Figure 18. The relationship between head length and Julian date for juvenile Weyprechtia, 1986. The dashed lines are the 95 % confidence interval about the line. Squares are the means obtained in 1985. The lines were fitted by computer regression (SAS Institute 1982).



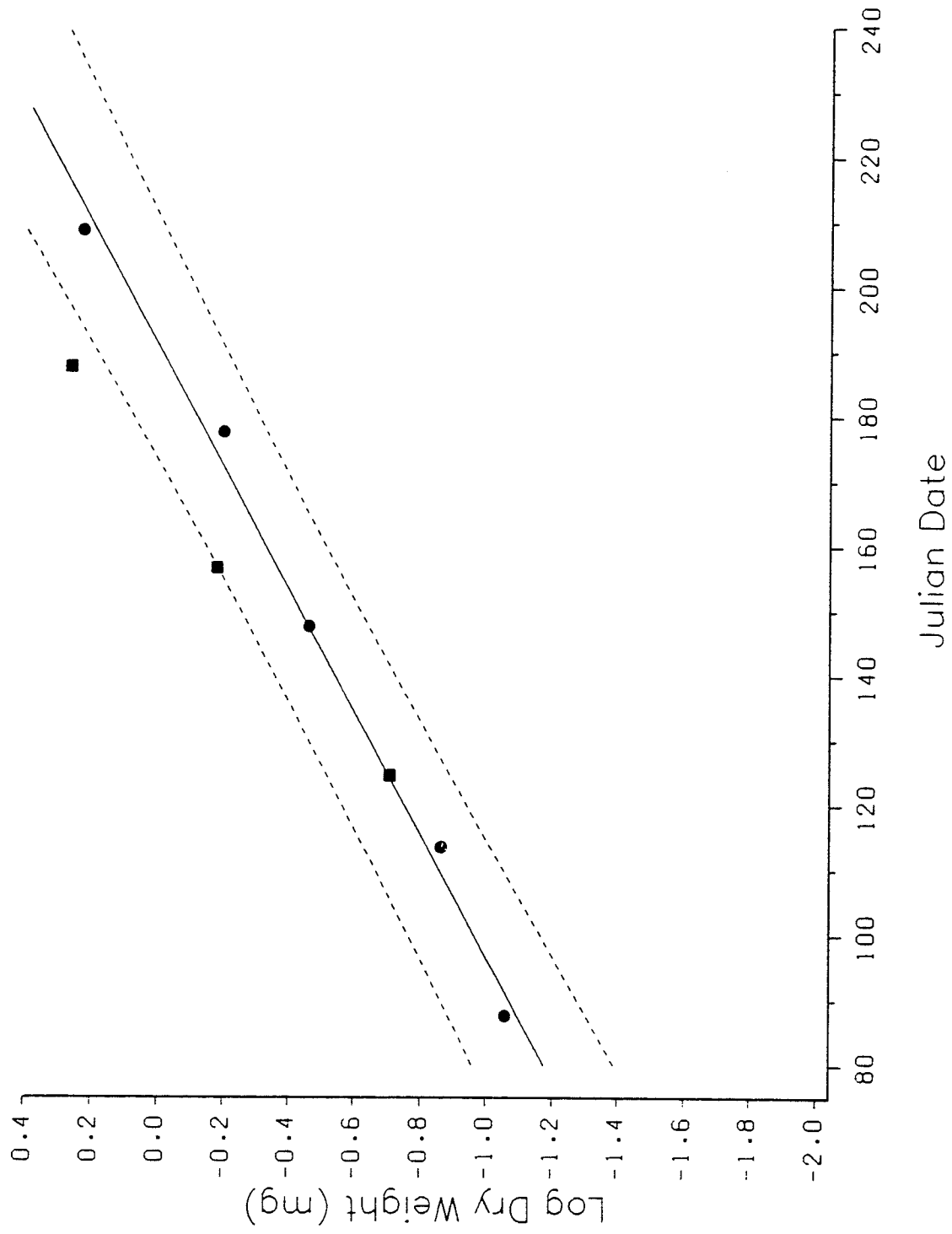
line equals 0.962. The means for 1985 fall well within the 95 % confidence interval around this line (Figure 18). As well, analysis of covariance indicated no significant difference between the slopes of the 1985 and 1986 lines ($p > 0.13$). Combining the two years data gives a straight line regression of $y = 0.006x - 0.128$ ($r^2=.936$, $n=9$, $p < 0.001$). The increase in juvenile dry weight over time did not appear to be linear in initial plots, so, as with the adults, a semi-log line was used to model this growth. When the 1985 data was plotted on this line (Figure 19), two of the three points fell outside of the 95 % confidence interval. Analysis of covariance indicates that there is a significant difference between the slopes of the 1985 and 1986 lines ($p < 0.05$). For 1985, the regression is: $\log y = 0.015x - 2.600$ ($r^2=.998$, $n=3$, $p < 0.05$), while for 1986, the line is: $\log y = 0.011x - 2.017$ ($r^2=.995$, $n=6$, $p < 0.001$).

For adult and juvenile head lengths, the slopes of the lines equal the rate of increase per day over the spring season. For adults, this rate equals 0.005 ± 0.002 mm per day, while for juveniles, it equals 0.006 ± 0.002 mm per day. For both adult and juvenile dry weight, the slopes of the semi-log lines represent the instantaneous coefficient of growth (Chapman 1971). For adults, this slope equals 0.004 ± 0.001 , or an increase of 0.4 % of body dry weight per day. For juveniles in 1985, the slope equals 0.015 ± 0.001 , for an increase of 1.5 % of body dry weight per day. In 1986 the slope is slightly lower, equalling 0.011 ± 0.001 , giving an increase in body dry weight of 1.1 % per day.

2). Molting

Of the total of 51 Weyprechtia kept for the long term molting

Figure 19. The relationship between dry weight and Julian date for juvenile Weyprechtia, 1986. The dashed lines are the 95 % confidence interval about the line. Squares are the means obtained in 1985. The lines were fitted by computer regression (SAS Institute 1982).



study, only 7 survived for the entire 125 day period (April 23 to Aug. 25). Due to replacement, 25 animals were alive at the end of the experiment - 17 adults and 8 juveniles. Observations on the ten extra adults were all begun prior to May 15 so these animals spent at least 103 days in captivity. The 8 juveniles were all captured on June 11 and so were held for 76 days.

Of the Weyprechtia adults in captivity after May 15, 15 molted twice, 11 molted once and 11 did not molt at all. Of the 11 which did not molt, 9 had died before the end of the experiment.

For both adults and juveniles, molting took place at roughly two times, at the end of May and early June, and at the end of July and early August (Figure 20). Almost all of the animals which molted twice did so within these two periods. A chi-square test indicates that molts were significantly clumped in time, not evenly distributed over the period of captivity ($p < 0.005$) (Sokal and Rohlf 1969).

The average length of time between molts for the animals which molted twice was $57.3 \text{ days} \pm 2.4 \text{ days}$ (Table 7). The range of the intermolt interval was 38 to 66 days. The average head length of the first molt (for the two molt animals only) was $1.62 \pm 0.09 \text{ mm}$, while the average head length of their second molt was $1.78 \pm 0.09 \text{ mm}$ (Table 7). Growth rate calculated from the increase in molt head length over the intermolt period equals $0.003 \pm 0.001 \text{ mm.day}^{-1}$.

Of the 8 juvenile Weyprechtia kept, 6 molted within the two week period between July 28 and Aug. 11 (Table 8). The average head length of the juvenile exuviae was $0.95 \pm 0.08 \text{ mm}$. This is close to the average head length for juveniles of $1.02 \pm 0.03 \text{ mm}$ found at the end of July 1986.

Figure 20. Number of molts over time for adult and juvenile Weyprechtia in the long-term molting experiment.
▲ represents the start of the experiment, ▼ indicates the end point.

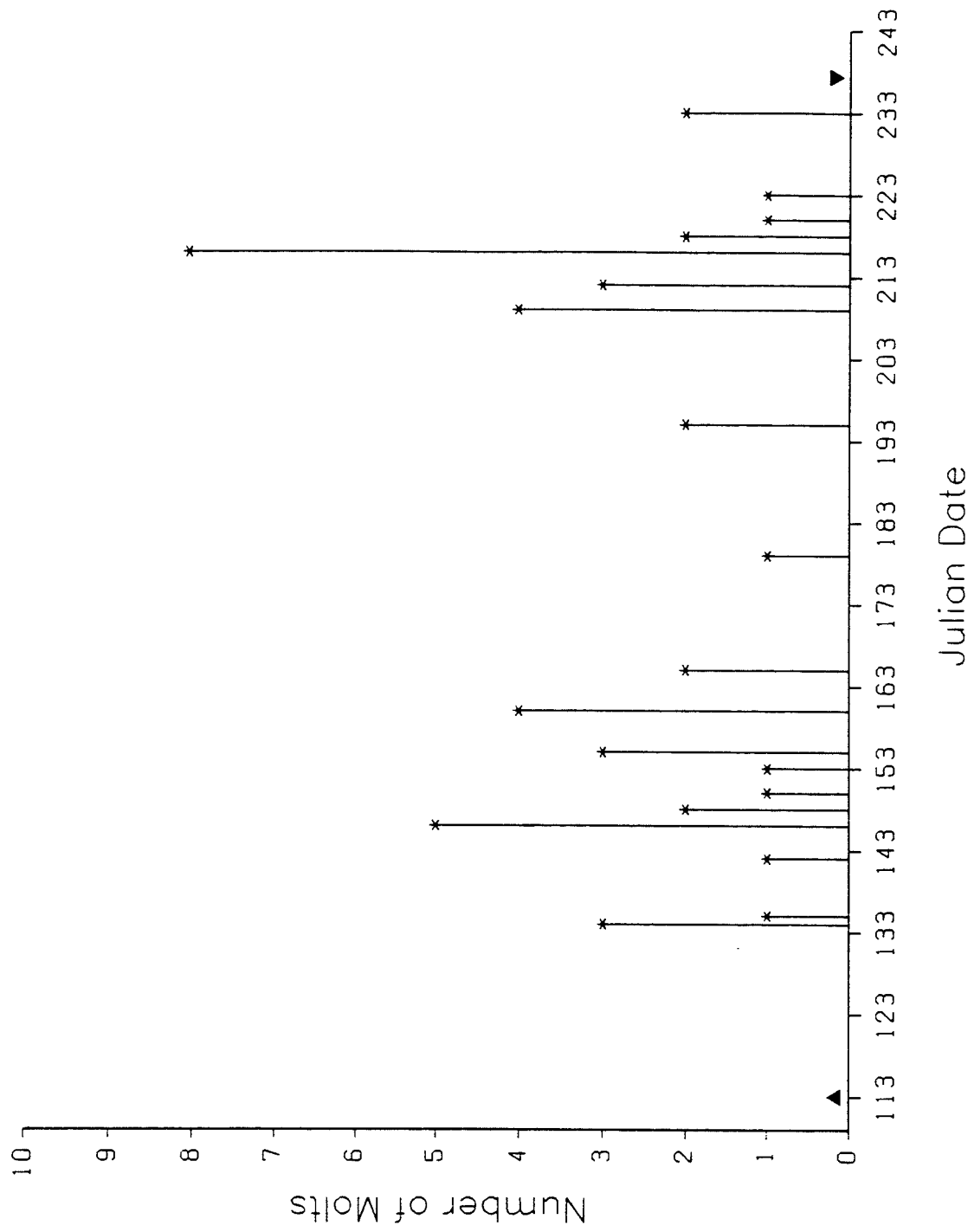


Table 7. Molt interval, dates of molting, and exuvia head length for 15 adult Weyprechtia which molted twice while in captivity.

No.	Days Between Molts	Date of First Molt	Exuvia Head (mm)	Date of Second Molt	Exuvia Head (mm)
1	58	June 9	1.49	August 6	1.66
2	63	May 26	m.v.	July 28	1.73
3	64	May 28	1.41	July 31	1.55
12	61	May 28	1.67	July 28	1.91
13	58	June 9	1.66	August 6	1.74
14	54	June 28	1.47	August 21	1.50
18	51	June 14	1.68	August 4	1.70
21	61	June 4	1.93	August 4	2.14
24	38	July 14	1.47	August 21	1.76
27	63	June 2	1.66	August 4	1.75
34	49	June 9	1.71	July 28	1.85
36	66	May 26	m.v.	July 31	1.91
37	56	June 9	1.53	August 4	1.75
38	51	June 14	1.71	August 4	1.90
39	66	May 30	1.80	August 4	1.96
$\bar{x} = 57.3$			$\bar{x} = 1.62$	$\bar{x} = 1.79$	
± 2.4			± 0.09	± 0.09	
$n = 15$			$n = 13$	$n = 15$	

m.v. = missing value

Table 8. Molt dates and head lengths for 6 juvenile Weyprechtia which molted while in captivity.

Animal No.	Date Molted	Exuvia Head Length (mm)
29	July 28	0.96
33	July 31	0.94
35	August 4	0.82
16	August 4	1.01
32	August 8	1.04
11	August 11	0.94
		$\bar{x} = 0.95$
		± 0.08

A total of 17 adult exuviae were dried and weighed. The average exuvia weight was 1.74 ± 0.31 mg (Table 9). This corresponds to an average of 21.8 % of the body dry weight.

Respiration

Average drop in the O_2 concentrations of the experimental bottles in 1986 was 15.6 % relative to the control bottles, in which concentrations ranged from 10.56 to 12.13 mg $O_2.l^{-1}$. These are normal concentrations for sea surface waters in this area. For example, the control O_2 concentration on May 26, 1986 was 10.56 mg. l^{-1} . A vertical series done that day had an average O_2 concentration of 10.47 mg. l^{-1} over 2, 3, and 5 m. (B. Welch, unpublished data).

In 1985, respiration rate averaged 1.038 ± 0.057 mg $O_2.g$ dry wt. $^{-1}.hr^{-1}$ for the July 11 experiment, and 0.758 ± 0.140 mg $O_2.g$ dry wt. $^{-1}.hr^{-1}$ on July 26 (Table 10). The July 26 values may be unreliable, as there were only 5 Weyprechtia per bottle, while in all other experiments, 10 were used. Over the four hour period, O_2 concentration in the July 26 bottles dropped by only 0.98 mg. l^{-1} , a drop of 9.4 %. On all other occasions, O_2 concentrations dropped by between 1.5 to 2.0 mg. l^{-1} .

Respiration rate for adult Weyprechtia in 1986 ranged from a low of 0.787 mg $O_2.g$ dry wt. $^{-1}.hr^{-1}$ to 1.060 mg $O_2.g$ dry wt. $^{-1}.hr^{-1}$ (Table 10). The low value, which was the average of three replicates on May 17, is well outside the 95 % confidence intervals of the other five experiments. The next lowest value is 0.952 mg $O_2.g$ dry wt. $^{-1}.hr^{-1}$. Excluding this low value, the average respiration rate for the 1986

Table 9. Exuviae head lengths and dry weights for 17 adult Weyprechtia. Animal dry weights are calculated from the length-weight relationship for an animal having the same head length as the exuvia.

Exuvia Head (mm)	Exuvia Dry Weight (mg)	Animal Dry Weight (mg)	Exuvia as % of Animal Dry Weight
1.66	2.41	8.30	29.0
1.71	1.55	9.17	16.9
1.65	1.30	8.13	16.0
1.53	1.23	6.29	19.6
1.56	1.25	6.72	18.6
1.64	2.08	7.96	26.1
1.46	1.25	5.36	23.3
1.59	1.48	7.17	20.6
1.72	2.12	9.36	22.6
1.57	0.92	6.86	13.4
1.69	1.88	8.82	21.3
1.65	1.67	8.13	20.5
1.41	1.07	4.76	22.5
1.93	3.41	13.84	24.6
1.66	2.01	8.35	24.1
1.71	2.21	9.24	23.9
1.53	1.80	6.33	28.4
	$\bar{x} = 1.74$		$\bar{x} = 21.8$
	± 0.31		± 2.2

Table 10. Average respiration rates $\pm$ the 95% confidence interval for adult Weyprechtia, 1985 and 1986.

Experiment Date	No. of Bottles	No. of Amphipods Per Bottle	Respiration Rate	
			mg O ₂ ·g dry wt ⁻¹ · hr ⁻¹	mg O ₂ ·Amphipod ⁻¹ · hr ⁻¹
July 11, 1985	5	10	1.038 $\pm$ 0.057	0.015 $\pm$ 0.002
July 26 "	5	5	0.758 $\pm$ 0.140	0.013 $\pm$ 0.005
May 7, 1986	6	10	1.060 $\pm$ 0.081	0.010 $\pm$ 0.002
May 17 "	3	10	0.787 $\pm$ 0.040	0.008 $\pm$ 0.000
May 23 "	6	10	1.011 $\pm$ 0.070	0.012 $\pm$ 0.001
May 29 "	5	10	0.952 $\pm$ 0.077	0.011 $\pm$ 0.001
June 9 "	5	10	0.990 $\pm$ 0.072	0.013 $\pm$ 0.001
June 16 "	5	10	1.021 $\pm$ 0.101	0.013 $\pm$ 0.001
			$\bar{x}$ = 0.964 $\pm$ 0.039 n = 40	$\bar{x}$ = 0.012 $\pm$ 0.001 n = 40

experiments is $1.007 \pm 0.050 \text{ mg O}_2 \cdot \text{g dry wt.}^{-1} \cdot \text{hr}^{-1}$.

Respiration rates on a per individual basis are less variable than those on a per gram dry weight basis (Table 10), and ranged from 0.008 to $0.013 \text{ mg O}_2 \cdot \text{amphipod.}^{-1} \cdot \text{hr}^{-1}$ in 1986, and from 0.010 to $0.020 \text{ mg O}_2 \cdot \text{amphipod.}^{-1} \cdot \text{hr}^{-1}$ in 1985. The overall average in 1986 was $0.011 \text{ mg O}_2 \cdot \text{amphipod.}^{-1} \cdot \text{hr}^{-1}$ (± 0.001 , $n=30$), and in 1985 was $0.015 \text{ mg O}_2 \cdot \text{amphipod.}^{-1} \cdot \text{hr}^{-1}$ (± 0.002 , $n=10$).

Respiration rates for both years combined were positively correlated with amphipod size. The relationship between respiration rate and animal size is often expressed in the form: $\text{rate} = a \cdot \text{weight}^b$, or $\log \text{rate} = \log a + b \log \text{weight}$, where $b = 0.75$ (Kleiber 1975, Grodzinski et al. 1975, Lavigne 1982). This relationship for Weyprechtia is: $\log \text{rate} (\text{mg O}_2 \cdot \text{Amphipod}^{-1} \cdot \text{hr}^{-1}) = -2.741 + 0.752 \log \text{dry weight (mg)}$ ($r^2 = .569$, $p < 0.001$) (Figure 21).

As found for other animals such as copepods (e.g. Bamstedt and Tande 1985), the weight-specific respiration rate declined relative to increasing body weight (Figure 22). The slope is significantly different from 0 ($p < 0.05$), although the coefficient of determination is weak ($r^2 = .125$).

Figure 21. The relationship between respiration rate and mean individual dry weight for adult Weyprechtia, 1985 and 1986 combined.

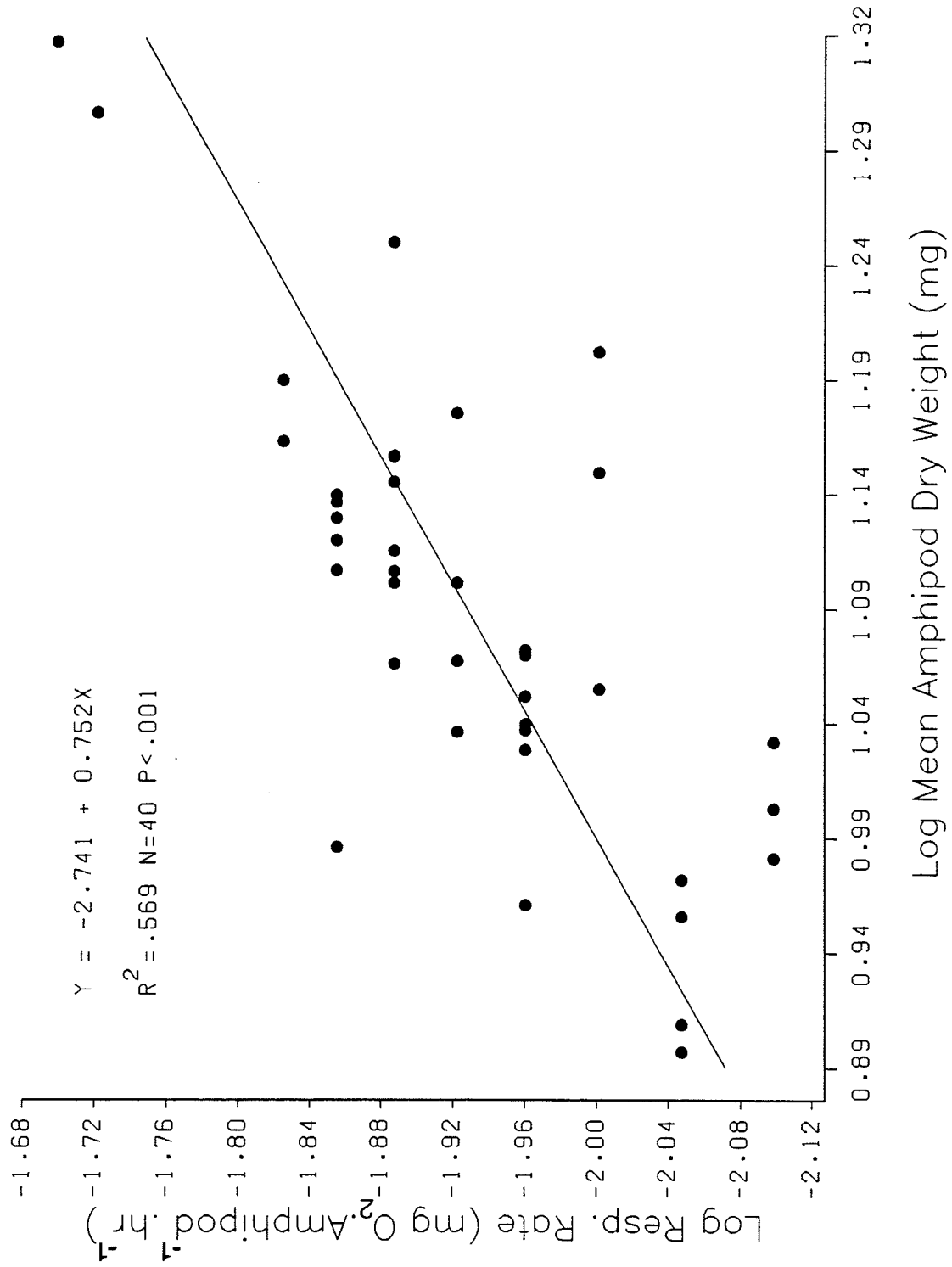
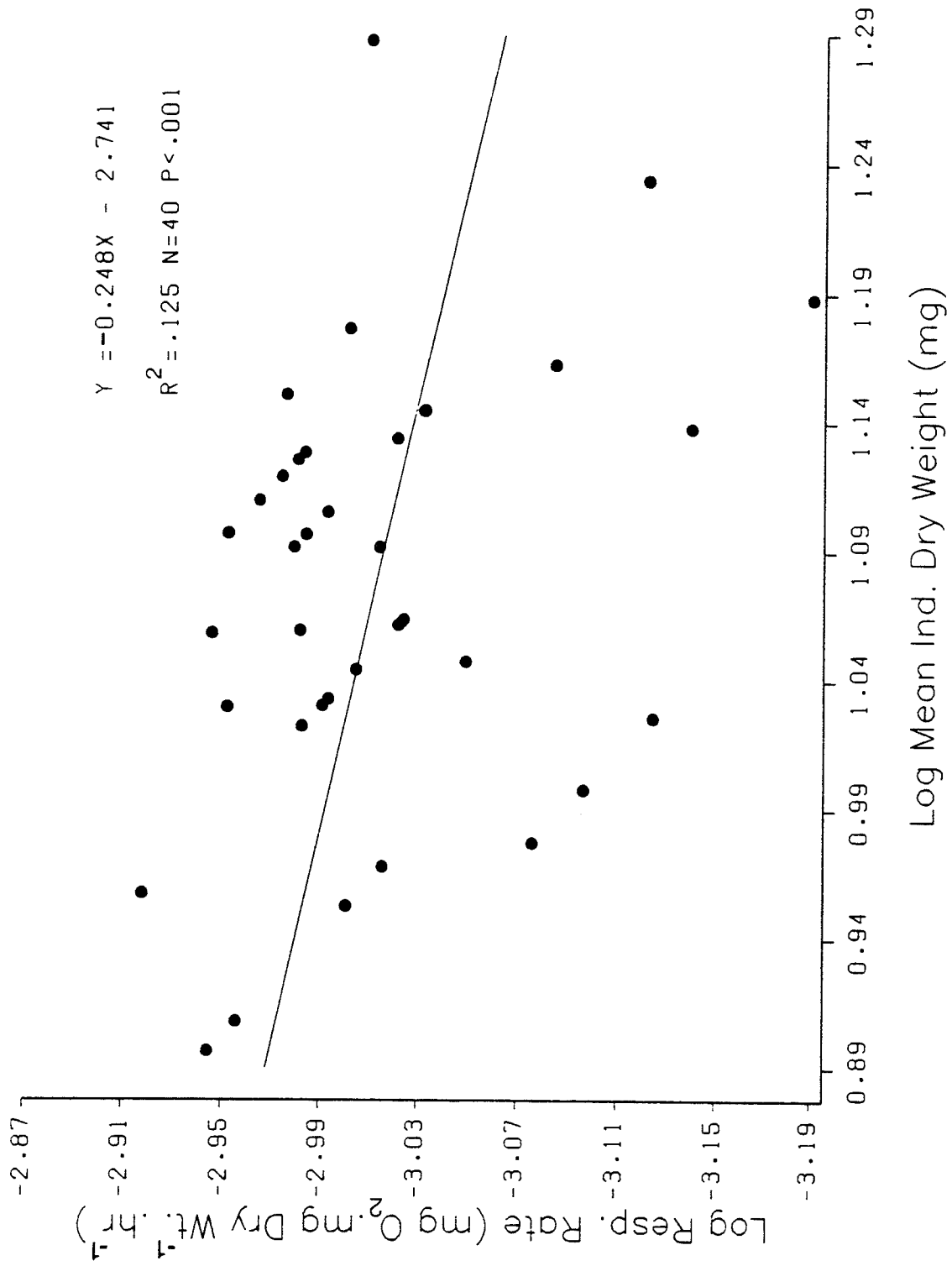


Figure 22. The relationship between weight - specific respiration rate and mean individual dry weight for adult Weyprechtia, 1985 and 1986 combined.



DISCUSSION

Feeding and Assimilation

As indicated in the results, there is little difference between a straight line and a negative exponential curve for the estimates of silica clearance in the starvation experiments. This was also found for the only other amphipod (Gammarus pseudolimnaeus) for which the starvation method has been used (Marchant and Hynes 1981). In that study, as in this one, the exponential was used to simplify the calculation of ingestion rate.

The negative exponential curve has been found to hold for a number of copepod species (Dagg and Wyman 1983, Tande and Bamstedt 1985, Wang and Conover 1986, Head 1986, Kiorboe and Tiselius 1987), but more experiments should be done to see if it holds equally as well for amphipods. As well, more work is needed to determine the effects of starvation on gut passage. For example, Dagg and Walser (1987) found that gut passage in copepods was constant at or above a certain food concentration, but that it slowed dramatically at lower food concentrations. Kiorboe and Tiselius (1987) also found gut clearance rates for the copepod Acartia tonsa were reduced in the absence of food. This may also be true for amphipods. Hargrave (1972) found that starvation in the amphipod Hyaella azteca resulted in reduced rates of gut clearance. Bärlocher and Kendrick (1975) found a large difference in gut passage time for the amphipod Gammarus pseudolimnaeus when given food and when not. During starvation the gut still contained food after many weeks. Given a negative exponential evacuation curve, the gut

should never completely empty.

It is difficult to assess the significance of the feeding rate obtained for Weyprechtia of $22.44 \pm 3.41 \text{ ug Si.amphipod}^{-1}.\text{day}^{-1}$, as there are no similar results for any arctic amphipods with which to compare this value. Using the silica:dry weight ratio calculated in this study, this ingestion rate corresponds to an average of $213.60 \pm 32.40 \text{ ug dry weight algae.amphipod}^{-1}.\text{day}^{-1}$, or an average of 2.7 % of the body dry weight per day for the average size amphipod used in the starvation experiments. This rate seems low, as the smaller marine amphipod Anisogammarus pugettensis consumed 21.2 % of its body weight per day at a temperature of 10° (Chang and Parsons 1975). An adult male Gammarus pseudolimnaeus consumed 10.7 mg dry weight of natural food per day at 0° , or 80 % of its body dry weight per day (Marchant and Hynes 1981). However, this stream-dwelling amphipod ingests sand as well as detritus, and sand made up over half of the gut content dry weight (Marchant and Hynes 1981).

In some experiments with copepods, results have been compared with those obtained from direct feeding experiments. Kiorboe et al. (1982) found that the two methods gave the same results for Centropages hamatus. However, in their experiments with the copepod Temora longicornis, Wang and Conover (1986) found ingestion rates determined from starvation experiments to be lower than those determined from grazing experiments. This difference was thought to be caused by undetected loss of their marker (chlorophyll) in the gut. They later determined that chlorophyll can be destroyed or absorbed during gut passage (Conover et al. 1986). The use of silica as a marker in my experiments should have avoided this problem.

However, the use of silica as a marker to measure feeding rate assumes that the amphipods are ingesting the entire diatom frustule. This may or may not be the case. Frustules appeared in the gut contents examined, but these could have been only the upper or lower half of the complete frustule. If the entire frustule is not eaten, then ingestion will be underestimated by this method. Ingestion will also be underestimated if the amphipods selectively feed on the non-diatoms in the sub-ice algae. In most cases, though, the diatom community "overwhelmingly exceeds" the non-diatoms (Hsiao 1980), so Weyprechtia would have to be extremely selective in order to make non-diatoms a large part of its diet.

Selective feeding, if it occurs, will also affect the assimilation results, leading to an underestimate of assimilation efficiency (Conover 1966). Even if feeding is not selective, some silica could be lost as parts of frustules during the feeding process. This again would lead to an underestimate of assimilation.

One assumption of the ratios method of measuring assimilation is that all fecal material is derived from the food (Johannes and Satomi 1967). Amphipods, however, enclose their feces in a peritrophic membrane, which is derived from assimilated material, and not from food in the gut (Lautenschlager et al. 1978). This membrane adds a small amount of weight to the feces, and so will contribute to an underestimate of assimilation.

In the attempts to measure assimilation in this study, it is clear that at least one of the above factors may have occurred, as the silica:dry weight ratios found for the feces were generally smaller than the ratio determined for the algae. However, I believe that there was

also an error made in the method which resulted in lower amounts of silica being extracted from the feces than should have been possible.

The peritrophic membrane of amphipod feces is composed primarily of chitin (Lautenschlager et al. 1978), within which fecal material is tightly compacted. Fecal pellets, therefore, should have been ground up or digested before the silica analysis to allow all the silica present to be released into solution during the hydrolysis. In some experiments fecal material appeared somewhat intact after the analysis.

Some evidence that silica was left in the pellets can be seen in a comparison between the silica analysis of the pooled samples and those from the starvation experiments (Table 4). In the pooled feces, an average of 337.42 ug silica was found per sample. These samples sat in the NaOH solution for an average of 12.7 days prior to analysis. The samples from the starvation experiments soaked on average for only 5 days and contained a mean of only 79.86 ug silica. The longer waiting period appears to have allowed more silica to be released from the pellets.

Loss of silica from the pellets to the seawater during the course of an experiment does not seem likely. Tande and Slagstad (1985) found no evidence of silica "leaking" from copepod feces even after the pellets had been suspended in seawater for 34 hours. Concentrations of silica in the water taken from the starvation chambers at the end of the experiments were no higher than surface seawater concentrations taken on or about the same day.

Due to the failure of this method of measuring assimilation and the probable underestimate of ingestion rate by the starvation method, the true rate of feeding by Weyprechtia remains unknown.

Growth and Life Cycle

Weyprechtia's growth and life cycle patterns are similar to those reported for some other arctic amphipods which also have two year life cycles. Weyprechtia continues to grow during the winter months, as does the Arctic amphipod Onisimus glacialis (Griffiths and Dillinger 1981), but at a slower rate than during the spring and summer (Figure 13). Embryonic growth and development also takes place during the winter, since females with fairly well developed young were caught in January.

Although no animals were caught during the fall months, breeding must occur at this time. Breeding probably takes place over a fairly short period, so that the release of young can be more precisely timed to coincide with increasing food abundance in spring. This has been a suggested strategy for arctic organisms in general (Dunbar 1957), and arctic amphipods in particular (Steele 1967, Steele and Steele 1975b).

Embryonic development times have been determined for two species of arctic amphipods. Gammarus wilkitzkii was calculated to require 123 days at 0° while G. setosus would require 117 days at 0° (Steele and Steele 1975b). If a similar time period is needed by Weyprechtia, then breeding would have to take place in late October or early November to have young released by late January or early February. Gravid females of the amphipod Onisimus glacialis were found in November in the waters off Alaska, and were thought to breed between September and November (Griffiths and Dillinger 1981).

To compensate for producing a single brood, some amphipods produce larger eggs and may also produce more embryos per female than amphipods

which produce multiple broods (Steele and Steele 1975b). The arctic gammarids Gammarus wilkitzkii and G. setosus, for example, produce from 90 to 250 young, and from 40 to 150 young respectively, while more southerly species of Gammarus produce from 5 to 110 young per brood (Steele and Steele 1975b). The two gravid Weyprechtia seen in January were carrying 58 and 135 young each, which is very close to the range for Gammarus setosus, even though Weyprechtia is a smaller animal.

To produce and carry such large broods, female Weyprechtia may grow to a larger size than males. Some of the larger animals caught were found in late March, and were females with oostegites. These animals had probably recently released young.

It is not possible to sex younger Weyprechtia, so it could not be determined whether males and females grew at different rates. There is some evidence for differential growth rates. The length-frequency histogram for July 1985 shows a bimodal peak for the adult animals, confirmed by a Cassie curve (Figure 11) which could represent males and females. No bimodal peaks were seen in the 1986 graphs, probably due to the low numbers of adults caught in July and August. However, the absolute size range of the animals did increase over 1986. In March and April 1986, the difference in head length between the largest and the smallest adult was 0.52 and 0.54 mm respectively. By August of that year, that difference had increased to 1.26 mm.

Because a differential growth rate for Weyprechtia could not be determined, the energy required for growth must be assumed to be equal for the two sexes. If females are growing faster than males, they will be putting more energy into growth and require more calories than males. Further energy is also required by the females for reproductive effort

in the form of eggs.

However, it should not be assumed that female Weyprechtia will grow to be larger than males. In some amphipod species, males grow faster and attain a larger final size than females. This occurs in some gammarid species: Gammarus oceanicus and G. salinus from the Oslofjord (Skadsheim 1984) and Chaetogammarus marinus in Denmark (Leinweber 1985).

Molting

Very little information is available on molting patterns of arctic amphipods. The only other species that has been studied is Gammarus setosus. Steele and Steele (1975b) found that it took 13 molts for this animal to reach maturity and that this required, on average, 317 days for males and 346 days for females. This produces an average intermolt period of 24 days for males and 27 days for females, much shorter than the 57 day interval observed for Weyprechtia in this study. If Weyprechtia continues to molt at a roughly two month interval all year, it would take 10 or 11 molts before they became mature, assuming their first molt is in March of the year they are born, and that they mature in September or October the following year.

Molting in the captive Weyprechtia in this study appeared to be somewhat synchronous. This is probably the result of the short breeding time postulated above, which would lead to a short period in which all young are released. Since they all appeared to grow at similar rates, molting should be fairly synchronous, if it is dependent on body size.

It is also possible, however, that the conditions of captivity disrupted molting patterns. The animals held for the long term

experiment were subjected to some stress in the feeding and cleaning activities. Of the 51 animals started in captivity, (at various times - the maximum number ever held at one time was 39) 26 died and 2 were lost during feeding or cleaning. Of the 26 that died, 6 died while attempting to molt, which may indicate that molting itself is a stressful activity. The animals which died spent, on average, 35 days in captivity before they died.

Each exuvia represents a loss of assimilated energy to the animal. In this case, the dry weight of each exuvia averaged 21.8 % of the dry weight of the amphipod that produced it (Table 9). This percentage is higher than the average of 10 % of body dry weight found for exuviae of Euphausia pacifica (Lasker 1966), and the average of 13 % of body dry weight for the mysid Metamysidopsis elongata (Clutter and Theilacker 1971). No similar values have yet been reported for amphipods.

Respiration

Respiration rates obtained for Weyprechtia were lower than those found by Opalinski (1979) for Antarctic amphipods. Respiration rates for 6 Antarctic species ranged from 0.018 to 0.141 mg O₂.individual⁻¹.hr⁻¹. However, three of those six species were much larger than Weyprechtia, one averaging 162.8 mg dry weight. Adult Weyprechtia average between 15 and 20 mg dry weight. The respiration rates determined for the three species closer in size to Weyprechtia were 0.018, 0.026 and 0.027 mg O₂.amphipod⁻¹.hr⁻¹ (Opalinski 1979). These values are closer to the range of 0.008 to 0.020 mg O₂.amphipod⁻¹.hr⁻¹ found for Weyprechtia (Table 10). Respiration rates determined for the Arctic amphipod

Onisinus affinis averaged $0.004 \text{ mg O}_2 \cdot \text{amphipod}^{-1} \cdot \text{hr}^{-1}$, for a slightly smaller animal (10 mg dry weight) (Percy 1980). The weight specific respiration rate for O. affinis was also lower, at $0.469 \text{ mg O}_2 \cdot \text{g dry weight}^{-1} \cdot \text{hr}^{-1}$ (Percy 1980), than the average of $0.964 \text{ mg O}_2 \cdot \text{g dry weight}^{-1} \cdot \text{hr}^{-1}$ found for Weyprechtia in this study.

The relationship between respiration rate and amphipod dry weight for Weyprechtia (Figure 21) had a slope, 0.752, very close to the value found in a wide variety of animals (0.75) (Kleiber 1975, Grodzinski et al. 1975, Lavigne 1982). Ivleva (1980) found this slope ranged from 0.60 to 0.79 for a number of types of crustaceans, and that it generally increased with decreasing temperature. The value of 0.75 has been determined empirically from studies such as these, and has so far no theoretical basis (Lavigne 1982).

Because it was not possible to separate male and female Weyprechtia, differences in respiration rate between the sexes could not be measured. If the females are not carrying young, there may not be a difference, as Opalinski and Jazdzewski (1978) found for six species of Antarctic amphipods. However, Klekowski et al. (1973) found that, on an individual basis, female amphipods (Paramoera walkeri) with eggs used about five times as much oxygen as did juveniles and adolescents. Female Weyprechtia with broods may also respire faster than males, due to the effort of carrying the extra weight of eggs or young.

In any measurement of respiration, the effects of the experimental conditions must be considered. The actual method of oxygen measurement should not affect the results. Four methods compared by Lawton and Richards (1970), including the Winkler method, were all found "equally suitable" for respiration measurements. It is in the handling and

treatment of the experimental animals that differences will arise.

In several studies, it has been observed that respiration rate decreases during the early stages of an experiment (Bamstedt and Tande 1985). There are two possible explanations for this. One is that starvation may be lowering respiration rates. Ikeda (1977) compared fed and starved animals of a number of zooplankton species, and found that respiration rate decreased with starvation. However, in another experiment, the effects of short-term starvation (less than 24 hours) were unclear (Ikeda and Dixon 1984). Ikeda and Dixon (1984) also observed a positive correlation between oxygen uptake rates and ingestion rate in the krill Euphausia superba. They suggested that specific dynamic action, or the energy released through deamination and other processes, was the main cause of increased respiration rate in these animals. If starvation is the main cause of lowered respiration rates, then rates obtained near the beginning of an experiment will most closely reflect natural rates. The decline in respiration rate over an experiment could also result from a recovery from abnormally high rates generated by the stress of capture or the experimental conditions (Bamstedt and Tande 1985).

Because the effects of stress are difficult to assess, and to avoid starvation effects, respiration measurements on Weyprechtia were made as soon as possible after capture.

Amphipods may have been less active inside the containers than they would be outside, although they were observed to move about fairly constantly. As well, amphipods continually move their pleopods, presumably to aerate their gills, which should result in only a small difference between a swimming and a non-swimming animal.

ENERGY BUDGET - SUMMARY

An energy budget can now be constructed for an individual adult Weyprechtia, for the period from April to June, and a temperature within $\pm 1^{\circ}$ of 0° C.

Ingestion

Adult Weyprechtia were found to ingest 0.935 ± 0.142 ug Si.amphipod $^{-1}$.hr $^{-1}$ (numbers following the $\pm$ symbol are the 95 % confidence interval). Using the silica to dry weight ratio of 0.105, this corresponds to 8.90 ± 1.35 ug dry weight algae.amphipod $^{-1}$.hr $^{-1}$, or 213.60 ± 32.40 ug dry weight algae.amphipod $^{-1}$.day $^{-1}$. Using a caloric value for diatoms of 4943 cal.gm dry weight $^{-1}$, obtained by Cummins and Wuycheck (1971) for Navicula sp., 1.056 ± 0.160 cal.amphipod $^{-1}$.day $^{-1}$ is ingested.

Growth

Although adult growth was best modeled by a semi-log regression ($r^2=.913$, $p < 0.001$), a linear regression can be used equally as well to obtain an average growth rate for the spring season ($r^2=.902$, $p < 0.001$). Using this regression, adult Weyprechtia increase in body weight at a rate of 0.105 ± 0.030 mg per day. Two species of amphipods from Frobisher Bay (Onisimus littoralis and Gammarus setosus) contained an average of 4.17 calories.mg dry weight $^{-1}$ (Percy and Fife 1981). Using this as an approximate value for Weyprechtia, 0.438 ± 0.125 cal.amphipod $^{-1}$.day $^{-1}$ is being put into growth.

Molting

The exuviae of two freshwater amphipods measured by Mathias (1971) averaged 2.052 calories.mg dry weight⁻¹. In this study, Weyprechtia exuviae averaged 1.74 mg in dry weight. Using Mathias' value, each Weyprechtia exuvia contained 3.57 calories. Since the average intermolt period found for Weyprechtia was 57 days, 0.063 cal.day⁻¹. are used by adults in molting.

Respiration

The average respiration rate calculated in this study was 0.012 ± 0.001 mg O₂.amphipod⁻¹.hr⁻¹. An average value for converting the rate of oxygen consumption to rate of heat production is 3.38 calories. mg⁻¹ for herbivorous animals (Elliott and Davison 1975). Using this value, a respiration rate of 0.041 ± 0.003 cal.amphipod⁻¹.hr⁻¹ is obtained, or 0.984 ± 0.072 cal.amphipod⁻¹.day⁻¹.

Adding the costs of growth and molting gives a value of 0.501 ± 0.125 cal.amphipod⁻¹.day⁻¹ for Weyprechtia's total production. Adding the value calculated for respiration gives a total of 1.474 ± 0.197 cal.amphipod⁻¹.day⁻¹. This is a minimum value for the total assimilated energy needed per day by an adult Weyprechtia during the spring season. It may be higher for females, for example, as they also have to allocate some energy for reproduction. It also does not take into account the energetic costs of the activities of molting and locomotion, and the energy lost as soluble excretory products.

The ratio of production to assimilated energy is termed the production efficiency or growth efficiency (Grodzinski et al. 1975). For

Weyprechtia this ratio equals 0.34, indicating that 34 % of the assimilated energy is put into production of new tissue. This is close to the average of 40.5 % found for other short-live poikilotherms (Grodzinski et al. 1975). In general, poikilotherms will have higher production efficiencies than homeotherms, due to their lower metabolic costs (Lavigne 1982).

The measured ingestion rate, at $1.056 \pm 0.160 \text{ cal.amphipod}^{-1}.\text{day}^{-1}$, is actually lower than the value found for total assimilated energy. Because the respiration and growth results correspond fairly well to those found in other amphipods, it is probable that ingestion has been underestimated, rather than that production and or respiration have been overestimated.

Because the ingestion rate measured here is lower than the value for assimilated energy, an assimilation efficiency cannot be determined. As well, a value for egestion and excretion cannot be calculated. Knowing the true assimilation efficiency, assuming the production and respiration values are correct, would indicate by how much ingestion has been underestimated. For example, if the true assimilation efficiency equalled 40 %, ingestion would have to equal $3.69 \text{ cal.amphipod}^{-1}.\text{day}^{-1}$, or approximately 3.5 times the measured rate. If assimilation efficiency was 60 %, then ingestion rate would be $2.46 \text{ cal.amphipod}^{-1}.\text{day}^{-1}$, or 2.4 times the measured rate, and if assimilation efficiency was 80 %, ingestion would be 1.8 times the measured rate.

The actual assimilation efficiency likely falls somewhere within this range of values. Efficiencies found for other diatom-eating marine crustaceans range from 50 % for the decapod Palaemonetes pugio feeding on Nitzschia closterium (Johannes and Satomi 1967), to 86.4 % for adult

Calanus hyperboreus feeding on Thalassiosira anguste-lineata (Tande and Slagstad 1985). Some assimilation efficiencies have been determined for amphipods feeding on various other types of food. Gammarus pulex, for example, had an assimilation efficiency of between 30 and 40 % when feeding on alder leaves. This low value probably results from the inability of the amphipods to utilize the leaf directly (Bärlocher and Kendrick 1975). A much higher efficiency of from 67.9 to 83.2 % was observed when G. pseudolimnaeus was fed leaf fungi (Bärlocher and Kendrick 1975).

A mid-range value for Weyprechtia assimilation efficiency would be 70 %. Using this value, ingestion rate would be $2.121 \text{ cal.amphipod}^{-1}.\text{day}^{-1}$, or about twice the measured rate. This discrepancy raises questions about the accuracy of the method used to measure ingestion rate. The most likely explanation for the underestimate of ingestion is that the rate of egestion changes dramatically under starvation conditions. It may be that amphipods such as Weyprechtia require a constant amount of incoming food to push material through the intestine, as suggested by Hargrave (1972) for the deposit-feeding amphipod Hyaella azteca. If the difference in egestion rate between feeding and starved amphipods could be measured, then perhaps a correction factor could be calculated which would compensate for the lower egestion rate under starvation. Alternately, other methods should perhaps be developed which could measure ingestion directly.

Utilizing the ingestion rate obtained in this study, a minimum estimate can be made of the impact Weyprechtia has on the standing stock of sub-ice algae. In early May, 1985, Weyprechtia occurred at an average density of $6.7 \text{ amphipods.m}^{-2}$ (Pike 1987). This is a minimum number, as

it is based on sweep net catches which are known to be not 100 % efficient. In early June, 1985, an average of $3.6 \text{ amphipods.m}^{-2}$ were found. Numbers in 1986 were lower, ranging from $0.7 \text{ amphipods.m}^{-2}$ in mid-May to $0.1 \text{ amphipods.m}^{-2}$ in late June (Pike 1987). These densities all occurred between water depths of 0 to 50 m, where most of the amphipod biomass was found (Pike 1987), and are similar to sub-ice densities of 0.8 to $6.7 \text{ Weyprechtia.m}^{-2}$ reported by Cross (1982) at Cape Hatt, Baffin Island.

Using the ingestion rate of $213.60 \text{ ug dry weight algae.amphipod}^{-1}.\text{day}^{-1}$, Weyprechtia consumed $1.43 \text{ mg dry weight algae.m}^{-2}.\text{day}^{-1}$ in May, 1985, and $0.77 \text{ mg dry weight algae.m}^{-2}.\text{day}^{-1}$ in June. In 1986, Weyprechtia consumption ranged from $21.36 \text{ ug dry weight algae.m}^{-2}.\text{day}^{-1}$ in late June to $149.52 \text{ ug dry weight algae.m}^{-2}.\text{day}^{-1}$ in May.

In the spring period, standing stocks of sub-ice algae range from 50 to $100 \text{ mg chlorophyll.m}^{-2}$ at low snow sites (M. Bergmann, pers. com.). Using the overall average of the dry weight:chlorophyll ratios in Table 3 (131.42), the standing stock of sub-ice algae ranges from 6.57 to $13.14 \text{ g dry weight.m}^{-2}$.

Even at their highest density in 1985, Weyprechtia would be consuming only 0.02 % of the algal standing crop per day at the lower end of the biomass range, or 0.01 % per day at the higher end. These estimates will, however, be low due to the problems discussed earlier with the method of measuring ingestion. However, even if ingestion is wrong by an order of magnitude, these amphipods would still not appear to have much impact upon the sub-ice algae crop.

Other amphipod species will also be grazing the sub-ice algae,

although usually only one or two species would be present in densities as high as Weyprechtia in 1985 (Carey 1985). The total impact of all amphipods on the sub-ice algae will therefore probably still be low, and so most of the primary production will not be utilized by the pelagic food web, but will sink to the bottom. This is similar to what is observed to happen to most of the open water primary production (Longhurst et al. 1984). The algal production then becomes available to benthic animals such as bivalves, polychaetes, and some amphipods on a year-round basis (Thomson et al. 1986). It is possible that amphipods such as Weyprechtia also utilize the algal detritus in the late summer, fall and winter months, and so consume much more of the sub-ice algae crop at those times than is possible during the short spring sub-ice bloom.

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