ECOLOGICAL ENERGETICS OF THE DOBSON FLY, *CORYDALUS CORNUTUS*

DISSERTATION

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By

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Rates and energies of consumption (C), egestion (F), assimilation (A), respiration (R), growth (P_g), production of exuviae (P_{ev}), and production of egg masses (P_r) and associated efficiencies, and the effects of seasonal temperature, weight and metamorphic stage upon these factors were examined for a typical individual and cohort of *Corydalus cornutus* (L.) from a stream in North-Central Texas (33°23'N, 97°5'W). Dobson flies are apparently univoltine in the study area, with 11 larval instars. Emergence, oviposition and hatching occur from late May to August. The typical dobson fly hatches in mid-June, grows rapidly until November, and resumes rapid growth in March, reaching full adult size prior to leaving the stream to pupate in early June. Adult females must feed to provide energy to yolk eggs, produce egg-mass coverings and continue somatic maintenance during their week of reproductive endeavors.

Metabolic compensation enables larval dobson flies to maintain preferred and fairly constant rates of R during winter (201-451 $\mu l\ g^{-1}\ h^{-1}$; 5-15 C) and summer (985-1173 $\mu l\ g^{-1}\ h^{-1}$; 20-30 C); with a seasonal acclimatization change

point between 15-20 C. Reduction of rates of R through undercompensation during the winter when food is scarce and through partial compensation at high temperatures during the summer conserves energy which is allocated to P, resulting in high ratios of P/R (1.94) and P/A (66%) for the individual larva and, to a lesser degree, for the cohort (P/R = 1.07, P/A = 52.3%, $P/\overline{B}$ = 9.96). Rates of C, F, A and R, but not assimilation efficiency, were influenced by temperature and size.

The energy budget for a typical dobson fly during the 47 wk as a larva was: C = 4167, A = 3442, F = 725, P_g = 2075, P_{ev} = 198, and R = 1169. Ova respired 0.107 cal wk^{-1}, prepupae 357 cal wk^{-1}, male pupae 509 cal wk^{-1}, female pupae 454 cal wk^{-1}, male adults 625 cal wk^{-1} and female adults 735 cal wk^{-1}. The prepupa and pupa shed exuviae of 144 cal and 120 cal respectively. The average female produced 667 cal of eggs and 185 cal of egg-case material, which totaled 54% of adult female A.

The annual energetics of the cohort of larvae was: C = 39,150, A = 32,642, F = 6876, P_g = 13,052, P_{ev} = 3608, P_r = 359-409 and R = 15,982 cal m^{-2}.

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CHAPTER I

INTRODUCTION

Ecological energetics have been emphasized in recent biome studies conducted by the International Biological Program. Comprehensive data on the energetics of individuals and populations of animals representing different physiologies (e.g., homeotherms vs. poikilotherms), trophic levels (e.g., carnivores vs. herbivores) and ecosystems (e.g., aquatic vs. terrestrial) are central to these studies, and are necessary to develop realistic energy flow models for the various biomes. To be of maximal value to these studies and contribute significantly to ecological theory, data on energetics should be taken over appropriate time intervals (i.e., time-series data) and minimally contain the following parameters: the rates, energies and efficiencies of consumption (C), egestion (F), excretion (U), assimilation (A), respiration (R), exuviation (P_{ev}), growth (P_g) and reproduction (P_r); the relationship of these rates, energies and efficiencies to temperature and season, activity and acclimatization patterns of individuals, size and stage in the life cycle, and sex and reproductive condition; seasonal variations in densities and age composition of populations; food and feeding habits; and basic life history data.

Insects, with their high densities and turnover rates, should be important agents of energy flow in many ecosystems. Although the literature is repleat with studies of energetics of terrestrial insects (e.g., Odum and Smalley 1959, Smalley 1960, Engelmann 1961, Odum, Connell and Davenport 1962, Wiegert 1964, 1965, Qasrawi 1966, Burlacu et al. 1967, Woodland et al. 1968, Dutton 1969, Gyllenberg 1969, 1970, Mukerji and LeRoux 1969, Hinton 1971, McNeill 1971, Van Hook 1971, Schroeder 1971, 1972, Hofsvang 1972, Manga 1972, Bailey and Riegert 1973), there are few comprehensive studies dealing with aquatic insects (e.g., Trama 1957, Fischer 1966, McDiffett 1970, Lawton 1971a). This is especially true for carnivorous insects in lotic ecosystems. Lawton's (1971a) study of a lentic damselfly in England is the only complete study of energetics of an aquatic carnivorous insect that I am aware of. Thus, a comprehensive study of energetics of a lotic carnivorous insect is timely and should significantly contribute to the knowledge of ecological energetics.

The present study concerns the energetics of the dobson fly, *Corydalus cornutus*, which spends most of its life as a predaceous lotic larva known as the hellgrammite. The specific objectives of the study are: to examine the rates, energies and efficiencies of C, F, A, R, P_{ev}, P_g and P_r, and the effects of season and temperature, weight and metamorphic stage on them; to examine possible seasonal variations in metabolic rates and patterns of metabolic compensation (acclimatization) to

seasonal ambient field temperatures; to determine the life cycle of *C. cornutus* in north-central Texas and calculate the life-cycle energy budget including apportionment of assimilated energy among growth, maintenance and reproduction for a typical female dobson fly; and to estimate the annual energy flow (P + R) of a population of hellgrammites in a riffle community.

The Species Studied

Corydalus cornutus Linne (Megaloptera, Corydalidae) ranges over most of North America from Canada to Mexico east of the Continental Divide. Hellgrammites are common under larger rocks in stream riffles, where they feed opportunistically on numerous species of aquatic insects. Hellgrammites are easily distinguished from other megalopteran larvae by their eight pairs of abdominal tracheal gill tufts. Most information concerning the life history of dobson flies is from studies conducted on northern populations (Haldeman 1848, Leidy 1848, Riley 1876, Parfin 1952, Baker and Neunzig 1968). In northern regions dobson flies may have a two- or three-year life cycle (Chandler 1956), whereas evidence reported here indicates a one-year cycle in north-central Texas. Typically, the final instar larvae leave the stream and pupate in the soil, under rocks or in rotting logs several meters from the stream. The first pupal stage, the prepupa, retains the appearance of the larva, but soon molts to a cream-colored, exarate pupa. After a week or so, depending upon latitude, the nocturnal adult

emerges. Mating occurs almost immediately and females deposit egg masses several days after copulation on objects hanging directly over streams near suitable riffle habitats. Eggs hatch within about 2 weeks and the first instar larvae fall into the stream.

The Study Area

The site used for density and production estimates was a 230 m section of Elm Fork of the Trinity River located approximately 200 m downstream from the FM 455 bridge in Denton County, Texas (33°23'N, 97°5'W). It was bounded by large relatively deep pools, and averaged 6.3 m wide and 0.5 m deep during most of the year. The total study site area of 1450 m^2 contained 363 m^2 of riffle habitat suitable for hellgrammites. The riffle substrate mainly consists of large gravel aggregate with flat rocks, averaging 0.1 m^2, scattered over it. The flow rate over the riffles was 20-25 cm sec^{-1} during normal water level (i.e., non-flooding period). The riffles supported high densities of Trichoptera ($n > 3000\ m^{-2}$) and substantial numbers of Simuliidae, Stenelmidae, Ephemeroptera and Plecoptera from late November through early March. The deeper non-riffle areas have slower currents, silt bottoms and produced few insects. Hellgrammites used in laboratory studies were taken from similar sites 5-10 km downstream, known as the Green Valley area, to avoid depletion of the population being used for production measurements. Both areas are located in sections of Elm Fork which are bordered by dense

streamside vegetation common to north-central Texas. A more extensive description of the stream and surrounding area is given by Fitzpatrick (1972).

CHAPTER II

METHODS AND MATERIALS

Weights, Measures and Caloric Determinations

Dry weights of all materials used in the study were measured to the nearest 0.1 mg with an electronic analytical balance after drying materials to a constant weight in a vacuum oven (-25 psi) at 60 C. A drying time of about 24 h was sufficient for all materials except larger larvae, prepupae, pupae and adults, which required a minimum of 36 h. The 60 C temperature *in vacuu* was used to minimize volatilization and oxidation of lipids, an important consideration when performing caloric determinations. Live weights of larvae were measured to the nearest 0.1 g on a top-loading electronic balance after blotting them on paper towels to remove excess moisture.

Eggs and larvae with head capsule widths (HCW) of 1 mm or less were measured to the nearest 0.1 mm using a microscope with an ocular micrometer which was calibrated with a stage micrometer. The HCW of larger larvae, prepupae, pupae and adults were measured to the nearest 0.1 mm with a Vernier caliper. Lengths of larvae with HCW greater than 2 mm were measured to the nearest 0.1 mm by letting them attach their tail hooks over the end of a ruler and gently but firmly

extending their bodies over the face of the ruler. Volume of larvae greater than 4 mm HCW was measured to the nearest 0.01 ml by water displacement in a 5- or 10-ml graduated cylinder, depending on size.

All caloric determinations were made on materials dried in a vacuum oven (-25 psi) at 60 C to constant weight. The dried materials were ground with a mortar and pestle, pressed into pellets of known weight and combusted in a Parr adiabatic oxygen bomb calorimeter. The techniques and procedures for combustion recommended in Parr Manual No. 130 were followed. Caloric data were expressed in cal g^{-1} and cal ash-free g^{-1}. Ash weight was considered to be the dry weight of material not combusted in the bomb. Organisms were not bombed individually, but pooled to produce pellets between 0.3 and 1.0 g.

Temperature of the stream was measured from 24 May 1972 to 30 August 1973 with a minimun of one measurement each week (n = 83) by immersing a 30 cm glass-mercury thermometer in flowing water away from the bank. The mean air temperature during June and July used as the experimental temperature for respiration measurements of eggs, prepupae, pupae and adults, was calculated from daily maximum and minimum temperatures reported for Pilot Point, Texas during June and July, 1972 by the US Department of Commerce Environmental Data Service. Pilot Point was the nearest recording station, about 10 km east of the study area.

Life History

A fairly accurate census of the egg masses produced by the 1971-1972 cohort was possible because the conspicuous white egg masses were laid in specific sites over the stream. Most (90-95%) of the egg masses counted in the vicinity of the study area were laid on the exposed undersurfaces of several logs in a log jam near the center of the study area. Remnants of egg masses after the eggs have hatched are easily detected unless covered by newly-deposited egg masses. The number of unhatched and hatched egg masses around the study area was recorded monthly from May through September, 1972 and used to estimate peak oviposition and hatching dates.

Egg masses ($n > 200$) collected from the Green Valley site were used to determine: number of eggs per mass; weight and dimensions of the egg masses and individual eggs; weight and caloric content of the material covering the eggs; and incubation time. Incubation time was estimated by holding freshly-laid egg masses ($n = 29$), at 28 C ($\bar{X}$ air temperature of the study area during egg-laying and incubation period) in an environmental chamber until they hatched. Freshly-laid egg masses can be distinguished by their lightly-colored eggs. One set of three egg masses collected immediately after a female laid them later hatched in the laboratory and yielded an accurate determination of incubation time. Hatching of eggs per mass, weight of the material covering egg masses and

weight of the embryos were determined from 33 egg masses hatched in the laboratory.

First instar larvae were obtained by hatching eggs on a screen over an aerated aquarium. They were maintained at 28 C in either aged, aerated tap water or in filtered, aerated river water with no apparent differential effect. However, rearing was unsuccessful; they would eat several zooplankters soon after hatching and remain alive for 1-2 wk, but would not molt to the second instar under laboratory conditions.

Quantitative samples (n = 9) of larvae were taken approximately monthly from 24 May 1972 until 5 May 1973. (The methods are described with production methods.) Data from the samples were used to help estimate the peak hatching period, seasonal rates and patterns of growth, and the peak emergence period. Growth rates were also measured for larvae maintained in the stream in two cages constructed from 16-l cylindrical teflon containers. The inside area of the lid and bottom of each container was cut out, leaving a 2 cm rim. Holes were punched in the rims at 1 cm intervals, and the openings were covered with standard aluminum screening (ca. 0.7 mm mesh large enough to let food organisms drift in), and hardware cloth (6 mm mesh) was laced to the rims with wire. Four sheet metal screws were used to fasten the lid, and an eye bolt was attached through the side near the end with the lid to anchor it in the stream. The chambers were partially filled with

washed rocks and gravel. On 1 August 1973 one chamber containing 25 larvae was placed in a riffle in the study area. The chamber was removed to count and measure the larvae on 2 September (four first instar larvae had entered the chamber and grew) and 1 October 1973. During October a flood washed the chamber away. The second chamber was placed in a riffle near the Green Valley bridge on 2 September 1973 with 16 larvae (1.7-3.9 mm HCW). It was opened and the larvae were measured on 4 October 1973. It was swept away by the same flood.

The number of instars was estimated by using a frequency histogram of HCW, prepared from all larvae (n = 1295) measured during the quantitative sampling period and a plot of HCW before molt against increase in HCW during molt. Since separation of peaks on the HCW frequency histogram was difficult, the approximate increase in HCW at each molt was used to obtain better resolution and separation of peaks on the HCW frequency histogram.

Prepupae and pupae were obtained for study by rearing them from final instar larvae in the laboratory and by collecting them from the stream banks. They were primarily used for determinations of weight, size, caloric content, duration of each stage and respiration rates. Larvae presumed to be in the final instar were collected from the margin of the stream just prior to leaving the stream to pupate and placed in a "pupating chamber" made from a 200-1 aquarium. The

aquarium was covered with cardboard to exclude light, and photoperiod and temperature were controlled by a high intensity lamp and timer fitted to the top of the aquarium. The aquarium contained washed river gravel and rocks, sloped from near the top at one end to the bottom at the other end, and was one-third filled with continuously filtered and aerated water. Two plastic pans (20 x 30 x 15 cm), filled with sand and perforated so moisture could penetrate from beneath, were imbedded in the top of the slope to provide suitable substrate for pupation. An abundance of live chironomid larvae (*Glyptotendipes* sp.) were kept in the water for the hellgrammites to eat. Temperature during the light phase was 25-27 C in the water and 26-28 C in the sand, which was close to the mean ambient temperature (28 C) where pupation occurred near the study site. Every few days the prepupae in the plastic containers were removed to individual pint jars filled with moist sand. An artificial puparium was prepared by forming a hole in the sand, placing the prepupa in it and covering the hole with a small flat stone. The stone was removed periodically to determine the duration of the prepupal stage and to observe development of the pupa. The prepupal exuviae were removed, dried, weighed and combusted for caloric content. In retrospect, sand was a poor substrate; the grains adhered to the cast exoskeleton, which made it virtually impossible to obtain accurate weights for them or to separate them from the sand for bombing in the calorimeter.

I discovered in June of 1973 that pupating *C. cornutus* can be located in the field by diligently searching clay banks in the vicinity of the riffles. The larvae leave small mounds of earth, similar to earthworms' casts, when they dig into the banks and can be easily dug out of their shallow burrows when found.

I was unable to determine the sex of larvae or prepupae. Sex of the pupae is determined easily by the presence of the claspers on the tip of the abdomen of the males, which they retain as adults.

Virgin adult females (n = 9) and males (n = 13) were raised in the laboratory from pupae and were used to observe feeding and mating behavior, which probably occurs at night in the field. Five laboratory-raised pairs and seven other pairs collected from the field were placed in individual cages, supplied with a dish of water, various types of fresh fruit, and sugar water. These were observed intermittently for 7 days. Four freshly-emerged females and eight males were dissected to determine gonadal development, weight, HCW and caloric content at emergence.

Adult females (n = 121) and males (n = 38) were collected by attracting them to florescent lights operated from the Green Valley bridge for 1 or 2 h immediately after sunset. The number captured at the lights per hour on each date was used to determine the date of peak emergence. The adults collected were weighed, measured and used for observations of

feeding and mating behavior, determination of longevity, caloric determinations, and respiration studies.

Oviposition was observed in the field at night and spent females with their egg masses were collected immediately. The post-oviposition females were examined to determine if they retained any eggs or egg covering material, and to measure their caloric content for comparison with virgin females.

Metabolic Heat Loss

Energy lost as metabolic heat was calculated by indirect calorimetry using rates of O_2 consumption and the oxycaloric coefficient (4.825 cal ml^{-1} O_2) determined by Brody (1945) for animals on a mixed diet and a respiratory quotient of 0.83. Respiration rates of larvae were measured in closed 300-ml BOD bottles using the Winkler method (Standard Methods 1971).

Numerous factors may affect the metabolic rates of poikilotherms such as temperature, oxygen tension, previous thermal history (acclimatization), weight, activity, age, metamorphic stage, digestive activity, diurnal periodicity, sex and reproductive condition. Besides activity, temperature, previous thermal history and body weight probably have the greatest effects on metabolic rates of poikilotherms and thus were given primary consideration. The effects of other factors were either evaluated directly or the respiration experiments were designed to minimize them. To evaluate possible diurnal periodicity, metabolic rates of 12 larvae acclimated at 25 C

were measured at 25 C at 6-h intervals for 1 day and the resulting mean rates compared. Although no significant differences ($t_{0.05}$ = 0.21-1.77) among the four measurements were noted in this brief experiment, all subsequent respiration measurements were conducted only at night in the dark to reduce the possible effects of a latent diurnal periodicity in respiration rates.

Aquatic larvae of *C. cornutus* in north-central Texas may be exposed to temperatures ranging from 0-32 C. The direct metabolic effects of these temperatures, and patterns of acclimatization to them in hellgrammites, were examined in two experiments. The first was an acclimatization study in which larvae (n = 70-92 per group) were collected at different times of the year when the mean stream temperature was approximately 5, 10, 15, 20, 25 and 30 C respectively for a minimum of 2 wk. The HCW, length, volume and live weight of each larva were measured. Larvae from 3 to 600 mg dry weight were used in each group. The larvae were held in 200 ml of water in 300-ml beakers containing a 1 x 10 cm strip of Nitex nylon bolting cloth (423 μ) for them to cling to. The water was aerated twice daily and changed once daily during the experiments. The beakers and larave were held in an environmental chamber set at one of the six temperatures (5-30 C) closest to the stream's previous 2-wk temperature (= acclimatization temperature) and the current photoperiod. After acclimation to the laboratory conditions for 2-3 days without food,

respiration measurements were made first at the acclimatization temperature and then acutely at each of the five remaining temperatures on successive nights. The 5, 15 and 20 C groups were also measured at 2 C. Rates determined at the acclimatization temperatures are acclimatization rates, and those determined at other temperatures are acute rates. Two hours prior to taking respiration measurements, the beakers containing the larvae were placed in an environmental chamber set at the experimental temperature, so the larvae could gradually stabilize to the temperature and not experience an abrupt and possible stressful change when placed in the BOD bottles. The larvae were then sequentially transferred to BOD bottles filled with O_2-saturated water at the experimental temperature by grasping the Nitex to which they were clinging and gently placing them and the Nitex into the bottle. The BOD bottles containing larvae and 10 control bottles were kept in a continuously-circulating, controlled-temperature water bath. The duration of each measurement was adjusted to temperature, so the larvae consumed only between 20 to 50% of the available O_2 to avoid possible affects of lower O_2 tensions on respiration rates (Lawton 1971a). Metabolic rates of larvae greater than 4 mm HCW were determined individually, but rates of smaller larvae were measured in groups of two to six to ensure a measurable reduction in O_2 concentration. The larvae were removed in appropriate sequence by drawing the Nitex out of the bottle with a hooked dissecting needle. As the larvae

were removed, the O_2 in the BOD bottles was immediately fixed with the Winkler reagents, and the titrations were performed within 24 h. The mean O_2 concentration of the controls was used as the initial concentration for the experimental bottles. Respiration rates were calculated and expressed as $\mu l\ O_2\ g^{-1}\ h^{-1}$ and $\mu l\ O_2\ h^{-1}$ for each larva at STP according to Standard Methods (1971).

An acclimation experiment with 72 larvae sorted into six temperature acclimation groups of equal size ($\bar{X}$ = 170-180 mg, range 50-500 mg) was conducted essentially the same as the acclimatization one. The six groups, collected at 25 C, were acclimated for 22 days (30 May-22 June 1973) at 5, 10, 15, 20, 25 and 30 C and the natural photoperiod associated with similar field temperatures at the study site(LD 9:15, 10:14, 12:12, 12:12, 14:10, and 15:9, respectively). The hellgrammites were fed chironomid larvae *ad libidum* from time of collection until 2 days prior to beginning respiration measurements.

Linear regressions of log dry weight (mg) versus log $\mu l\ O_2\ h^{-1}$ per larva were prepared from the acclimatization data for each acclimatization temperature. Acute and acclimatization rate-temperature (RT) curves (Prosser 1971) were drawn to illustrate metabolic effects of previous thermal histories and experimental temperatures. Analyses of variance (ANOVA) among acclimatization temperature, experimental temperature and weight class (three-way design) and Duncan's New 5% Multiple Range Tests (NMRT) were used to statistically

evaluate the data. Three weight classes were used with the three-way ANOVA (1 $\geq$ 200 mg, 2 $\geq$ 80 mg $<$ 200 mg, and 3 $<$ 80 mg). Because of great differences in mean dry weights among acclimatization groups (5 C = 87, 10 C = 144, 15 C = 140, 20 C = 143, 25 C = 119, 30 C = 229 mg), which could mask the effects of previous thermal history, an analysis of covariance (ANCOVA; two-way design) was applied to the data for all larvae. Mean rates were compared with Duncan's NMRT. The results of the acclimation experiment were treated similarly.

First instar larvae obtained from eggs hatched in the laboratory were maintained in environmental chambers at 30 C and natural summer photoperiod (LD 15:9). Respiration rates of the larvae were measured within 3 days after hatching in a 10-station Scholander microvolumetric respirometer equipped with 25-ml respiration vessels. Groups (n = 50 or 100) of larvae were placed in the respiration vessels in 10 ml of aged, aerated tap water approximately 1 h before respiration measurements were begun. The gas phase in the vessels was atmospheric air, CO_2 was absorbed by filter paper strips saturated with 1 ml 15% KOH. The vessels were shaken moderately (1 oscillation sec^{-1}) to increase gas exchange at the air-water interface. Respiration rates were measured at 25, 28 and 30 C, which represent the range and mean of temperatures to which first instar larvae are naturally exposed. Three to six measurements were taken at 30 min intervals on each group between 1000 and 1500 h (CST). Respiration rates were converted

to STP using the method of Scholander et al. (1952) and expressed as µl O_2 g^{-1} h^{-1} and µl O_2 h^{-1} per larva. Since differences among respiration rates at the three temperatures were not significant ($t_{0.05}$ = 0.28-1.16), measurements (n = 407) were pooled.

Respiration rates of eggs in egg masses (n = 16), prepupae (n = 22), male pupae (n = 11), female pupae (n = 12), adult males (n = 16) and gravid adult females (n = 14) were also measured with the Scholander respirometer. All of these stages were maintained and measured at the mean air temperature in the vicinity of the study area during the summer (28 C). Respiration rates of the egg masses were measured in 25-ml vessels, and the other stages were measured in 45-ml vessels constructed from test tubes. The respiration vessels were wrapped in foil to exclude light when prepupae and pupae were run, because they are buried in the soil under natural conditions.

Production

Bottom samples were taken in the study area with two samplers: a modified 0.25 m^2 Hess sampler (Hess 1941) and a standard 1 ft^2 (0.09 m^2) Surber sampler. The Hess-type sampler, used to sample larger larvae (> 2 mm HCW), was covered with wire mesh (0.6 mm mesh) and hardware cloth (63 mm mesh) except for the downstream quadrant, which was fitted with a nylon collecting bag (0.6 mm mesh). The inside back half of the

sampler was covered with light canvas to direct the flow of water through the bag.

Samples were taken nine times from 24 May 1972 to 5 May 1973. Fifty samples were taken on each sampling date with the modified Hess sampler except during the period of high population density from July to November, when 25 samples were taken each time. Three Surber samples were taken on each sampling date. Samples were not taken during October, December, March and April because of high water levels.

Only the riffles in the study area were sampled quantitatively. Pilot study samples and samples at each sampling period did not yield hellgrammites in areas without rocks or gravel and flowing water. About 80% of the Hess samples included a rock larger than 20 cm; the remaining 20% were taken in gravel areas. Each Surber sample included a rock between 10 and 20 cm. An effort was made to sample in a similar manner each period by distributing the samples among the various riffle areas in the same way, and sampling the same percentage of the various habitat-types each time to produce a comparable set of annual samples.

Samples were taken by rotating the sampler slightly while firmly pressing it into the streambed and then vigorously agitating the substrate inside with a three-pronged garden fork to a depth of 10-20 cm. Since hellgrammites are reported to occur in only the upper 10 cm of riffle substrate (Poole and Stewart 1974), the sampling depth used here was assumed

adequate. After HCW, length and volume measurements of larvae were taken, they were returned to the stream. Linear regression of log HCW, length and volume, respectively, versus log dry weight (mg) were prepared from data on larvae (n = 445) collected throughout the year from the Green Valley bridge site for respiration studies. Head capsule width was the best predictor of dry weight (r^2 = 0.92) and was used for weight determination of all larvae that were sampled during the year.

The Surber sampler was used for density estimates of small (< 2 mm HCW) larvae. The substrate enclosed by the sampler was agitated thoroughly with the hand fork, and each of the larger rocks was scrubbed with a nylon brush to dislodge larvae. The larvae and debris collected by the Surber were put into a 1.5-liter container with 0.5 l of 70% isopropanol poured through the everted collection bag into the container. The invertebrates were hand-picked from the samples in a large white procelain enamel tray under a 2X macroscope. The hellgrammites were then separated from the other organisms under a variable power, zoom dissecting microscope. Head capsule width measurements of large larvae (> 2 mm HCW) were made with a Vernier caliper, and those of smaller larvae were taken with an ocular micrometer. These two instruments were compared by measuring 25 larvae between 1 and 5 mm HCW and were found to be equivalently precise. The number of larvae in each 0.1 mm HCW class were summed separately for

the Hess and Surber samples on each sampling date, and HCW-frequency histograms prepared.

The two sampling estimates were compared, based on the assumption that the two samplers collected larvae with a 2-3 mm HCW with equal effectiveness. Mesh sizes of both samplers were small enough to capture larvae in this size range, and retrieval of larvae in the debris by each method is equally effective on this size larvae. The comparison was not based on larger larvae because the Surber is not effective at capturing hellgrammites far above this size range, as they prefer rocks larger than the Surber can include. The number m^{-2} of larvae estimated in the 2-3 mm HCW range during June, July and August by the Surber (136.41) was 3.64 times that estimated by the Hess (37.44). The Surber produced higher density estimates because it is limited by its design to sampling the best habitats for small hellgrammites, the shallow fast-flowing areas. The Surber is not as tall (30.5 cm) as the Hess (70 cm) and is more dependent on a fast current because it is not enclosed on the front and sides. Each Surber sample density estimate was divided by 3.64 to equate the two sampling methods. I believe there was minimal error introduced through this conversion for additional reasons: the Hess sample data were probably more reliable due to the larger number of samples; an error produced by a false assumption concerning small larvae (0.5-1.9 mm HCW) would have a smaller effect than one applied to the larger larvae (2-11 mm HCW);

and HCW-frequency histogram of the "corrected" data displayed the expected regular type 3 survivorship curve (Deevey 1947) with no irregular inflection occurring at 2 mm.

The N m^{-2} and mean HCW of the larvae in the 1972-1973 cohort for each sampling date were calculated and mean dry weights of the larvae were obtained from the HCW-weight relationship expressed by the equation:

$$w = (-0.273)HCW^{2.87} \tag{1}$$

where: w = dry weight (mg) and HCW is in mm.

Annual production for the cohort was then calculated using the instantaneous growth method (Ricker 1946, 1971, Waters and Crawford 1973). The general equation for calculating production by this method is:

$$P = G\langle B\rangle \tag{2}$$

where G is the instantaneous growth rate during a sampling interval and $\langle B\rangle$ is the midpoint biomass. Assuming linear growth and mortality between sample dates, the equation becomes:

$$P = \sum_{i=1}^{N} [\log_n(\overline{wt}_{x+1}/\overline{wt}_x)](B_x + B_{x+1}/2) \tag{3}$$

where N = the number of sampling intervals, $\overline{wt}_x$ and $\overline{wt}_{x+1}$ are the mean weights of the animals at the beginning and end of

each interval and B_X and B_{X+1} are the biomasses at the beginning and end of each interval.

Feeding Studies

Experiments to determine rates of C, F and A of hellgrammites as functions of body weight and temperature were performed in flowing and static systems. The flowing water apparatus consisted of four sets of five 250-ml separatory funnels connected in series by Tygon tubing. Water was circulated from the small to the large end with Masterflex peristaltic pumps at 600-800 ml min^{-1}. After the water passed through the flasks, it emptied into a vigorously-aerated 20-liter aquarium; then the intake on the pump returned the aerated water from the aquarium to the flasks. Each flask was separated from the others by Nitex mesh (423 μ) that retained the hellgrammites and their chironomid prey. An additional piece of Nitex with approximately the same dimensions as the separatory funnel was placed inside for the larvae to cling to. Different currents caused by the shape of the vessel allowed the larvae to select the flow rate they preferred. The entire apparatus was kept in an environmental chamber.

Twenty larvae ($\overline{X}$ = 236 mg; range = 43-722 mg dry wt), collected when the stream was at 25 C, were held in finger bowls in an environmental chamber set at 25 C and the appropriate photoperiod (LD 14:10) for 2 days and fed chironomid larvae *ad libidum*. The water in the finger bowls was

continuously aerated. The hellgrammites were then placed in the separatory funnels between 1100 and 1200 h (CST) and 50 preweighed chironomids each and left for 24 h at 25 C and LD 14:10. The following day the remaining chironomids were removed from each chamber, counted and weighed to determine the amount eaten. Since the rates of C and regression coefficients for weight-specific and whole animal rates between the flowing and static systems were not significantly different, the static system was used because of its convenience.

One hundred fifty larvae, collected on 30 May 1973 when the stream temperature was near 25 C, were divided into six feeding groups of equivalent weight ($\overline{X}$ = 179-242 mg; range = 20-600 mg dry wt). Larvae were placed individually in finger bowls (10 cm x 4.5 cm) with 150 ml of continuously aerated water. Each larva was provided with a (1 x 10 cm) rectangle of Nitex to which they could cling. Each group was placed in an environmental chamber set at its respective experimental temperature (5, 10, 15, 20, 25 or 30 C) and the photoperiod at the time of the year when the stream would be near that temperature. During the 12-day acclimation period the hellgrammites were fed live chironomid larvae *ad libidum*. The water was changed daily using aerated, aged tap water kept in each of the environmental chambers.

Chironomid larvae (*Glyptotendipes* sp.) were used for the feeding studies for the following reasons: they are one of the natural foods of hellgrammites and are reported to be

selected for under certain conditions (Stewart et al. 1973); they are very hardy and tolerant of rapid changes in temperature; size classes are easily separated; and hellgrammites almost always consume them whole, eliminating the need to correct for incomplete consumption.

Chironomid larvae were collected from the sewage oxidation ponds at Aubrey, Texas. They were effectively separated into size classes by washing them for 2-3 h through a set of wire-screen seives. Only one size class (presumably third instar) of chironomids was used ($\bar{X}$ live wt = 8.3 mg) as prey, to avoid possible differences in caloric content between chironomid developmental stages and simplify calculations and analysis of data. Chironomids were fasted for 2-3 days and then washed again on the seives prior to use.

Measurements of C and F for hellgrammites acclimated to 20, 25 and 30 C were taken each 24 h for a period of 5 days. At the beginning of each period (between 1300-1400 h CST) each larva was offered 0.1, 0.2, 0.3 or 0.4 g of live chironomids, depending on the size of the hellgrammite and temperature of acclimation, so each was provided a small excess of prey. After 24 h the uneaten chironomids were removed from each dish and reweighed to determine the live weight eaten. Live weights were converted to dry weights by multiplying them by the dry weight/live weight ratio (1.141).

Egestion was measured by filtering the feces produced during the 24-h period. The water was poured into a clean

beaker and the hellgrammite, Nitex and finger bowl were washed into it to collect any feces adhering to them. This water was then filtered using predried, tared Millipore filters (0.45 μ). The filters were subsequently dried and weighed again to determine the weight of feces produced per day. The filtrate was checked to determine if any organic material had passed through the filter by comparing total organic carbon and inorganic carbon in samples of filtrate with water controls using a Beckman total organic carbon analyzer. Since no differences were detected, filtration was assumed to be complete.

Rates of C and F of larvae acclimated to 5, 10 and 15 C were measured in the same way, except their lower rates required a time interval longer than 24 h. The larvae acclimated to 5 and 10 C were left for the entire 5-day period of the feeding study (i.e., remaining chironomids were removed and weighed, and egesta collected only after the fifth day of the experiment). Rates of the 15 C group were measured after days one, three and five of the experiment).

The ratio of dry weight to live weight of chironomids were obtained by weighing seven 10-g groups of live chironomids, drying them in a vacuum oven (-25 psi) at 60 C for 48 h, and reweighing them. Six caloric determinations of chironomids were made, and the dry weights ingested by the hellgrammites were converted to calories. Rates of C were expressed as cal day^{-1} and cal g^{-1} day^{-1} for each larva.

The caloric content of the feces was determined from samples of feces collected from the hellgrammites used in the feeding study. On the day following completion of the feeding study the feces from each temperature group were collected on filters which were dried and combusted for total caloric content. The caloric value of the washed and dried filter paper was predetermined by bombing two samples of it, and caloric value of the feces was calculated by subtraction. Egestion values were then converted to cal day^{-1} per larva and cal g^{-1} day^{-1} per larva.

Assimilation was calculated for each larva by subtracting calories egested from the calories consumed and expressed as cal day^{-1} and cal g^{-1} day^{-1}. Assimilation efficiencies (AE = A/C x 100) were then calculated for each larva.

To determine the relationship between weight and rates of C, F, A and AE at each temperature, linear regressions of larval weight versus weight specific and whole animal rates of each of these measures were performed using arithmatic and log-transformed values. The coefficients of determination (r^2) were higher for log-transformed data indicating exponential relationships.

Two-factor ANOVA using log-transformed data were also used to determine effects of larval dry weight and acclimation temperature on weight-specific and whole animal rates of C, F, A and AE. To facilitate these analyses, each temperature group was divided into three dry weight (mg) classes [(1) >200,

(2) $\bar{<}200>100$, (3) <100]. Duncan's NMRT were used to compare means from each ANOVA. Due to the wide variation in size within each acclimation group, ANCOVA were used to adjust for weight and assess the effects of acclimation temperatures on rates of C, F and A in cal per larva. The ANCOVA were also followed by Duncan's NMRT to compare means of C, F, A and AE among temperature acclimation groups.

Energy Budgets

The equations representing the energy budget for an individual or population are based on the algebraic statement of the First Law of Thermodynamics (Wiegert 1968) and may be written:

$$C = P + R + F + U$$

$$A = C - (F + U)$$

$$P = P_g + P_{ev} + P_r \quad .$$

Each term is expressed in cal $time^{-1}$ for individuals and kcal $area^{-1}$ $time^{-1}$ for populations. This notation follows that of the IBP with the exception of P_{ev} which represents production of exuviae. Exuviae are normally considered to be the cast exoskeletons of insects and other arthropods but could also represent feathers, hair, skin, mucous, etc., for other taxa.

Excretory energy losses (U) were not calculated for *C. cornutus* larvae because they are probably ammoniotelic, losing

an insignificant amount of energy through excretion (Winberg 1956, Krueger et al. 1968). *Sialis lutaria*, another aquatic megalopteran, excretes 90% of its nitrogenous wastes in the form of ammonia (Shaw 1955, Staddon 1955).

Individual Energy Budget

Total C of the typical dobson fly during its existence as an aquatic larva (331 days) was calculated with the following equation:

$$C = \sum_{i=1}^{331} (a_t w_i^{b_t}) \qquad (4)$$

where a_t and b_t are coefficients of regression for larval weight versus C in cal day^{-1} per larva at each of the six experimental temperatures (5-30 C) used in the feeding study and w_i is the larval weight on the i^{th} day. The 331 days were divided into eleven 5 C weight-temperature intervals centered on 5, 10, 15, 20, 25 and 30 C (see Chapter III, Fig. 1). The weight w_i was incremented daily within each interval by: $w_i = w_{i-1} + \Delta w\ day^{-1}$. Assimilation was calculated by multiplying values of C for each temperature interval by AE values determined for each temperature; then F was obtained as C - A = F. Annual C was obtained by summing the interval estimates. No attempts were made to experimentally quantify adult values of C, A or F. There has been some controversy concerning whether adult Megaloptera feed in nature (Haldeman

1848, Leidy 1848, DuBois and Geigy 1935, Parfin 1952, Azam and Anderson 1969).

Larval R was calculated using a similar summation equation:

$$R = \sum_{i=1}^{331} [(a_t w_i^{b_t}/1000)](24)(4.825) \qquad (5)$$

where the regression coefficients a_t and b_t describe the relation between larval weight and µl O_2 h^{-1} per larva. The first expression enclosed by parentheses yields a rate of O_2 consumption in ml h^{-1} for a given weight and temperature interval; when multiplied by 24 h and 4.825 cal ml^{-1} O_2, this gives the cal day^{-1} of metabolic heat loss.

Respiration energy loss of eggs, prepupae, male and female pupae, adult males and adult females was calculated by multiplying the O_2 consumption rates in ml day^{-1} per individual for each stage times the estimate in days for the duration of the stages and 4.825.

Growth (P_g) for the typical hellgrammites was calculated as the difference in total caloric content of a first instar larva and a full-fed final instar larvae (i.e., larvae collected at margin of stream during emergence period). Total P_{ev} of larvae was obtained using the equation:

$$P_{ev} = \sum_{i=1}^{10} (a_{ev} HCW_i^{b_{ev}})(cal_i) \quad . \qquad (6)$$

The mean HCW at each molt, obtained from the HCW-frequency histogram used to estimate the number of instars, was entered into the equation of HCW versus exuvium dry weight (prepared from molting data on 60 larvae in the laboratory) and used to estimate the mean exuvium weight at each of the 10 molts. These weights were multiplied by their caloric values and summed. Production of prepupal and pupal exuviae were calculated from experimentally-determined mean dry weights and caloric determinations of each. Since dobson flies exhibit no parental care, reproductive effort (RE), or energy allocated to reproduction (P_r) by the typical female, was equated to the mean caloric values of eggs and egg mass coverings produced per female. Caloric contents of newly-emerged females and males, gravid females, spent females, and males were determined and compared.

Population Energy Budget

Values of each component of the population energy budget were expressed as cal m^{-2} and kcal $cohort^{-1}$. These were based on density estimates for ecological area (363 m^2) as opposed to crude area (1450 m^2) of the study site.

The total C of the 1972-1973 cohort of hellgrammites was calculated with the following equation:

$$C = \sum_{i=1}^{16} N\, m_i^{-2} (a_t \bar{w}_i^{\,b_t}) day_t \qquad (7)$$

where the parenthetical expression yields C in cal day^{-1} for larvae of mean weight $\bar{w}_i$, calculated using the regression coefficients ($a_t b_t$; from Eq. 4) for the appropriate temperature span (day_t = number of days a typical larvae spent in one of the 16 weight-temperature spans of 5, 10, 15, 20, 25 or 30 C; and w_i is the mean weight of the cohort during each sampling interval). Then, summing C in cal day^{-1} for larvae of w_i at a particular temperature (5-30 C) times the number of days spent in that temperature range (day_t) and the mean number of larvae estimated to be present during the interval gives the annual C for the cohort. Total A was estimated by multiplying C for each temperature interval by the appropriate AE value, and F was estimated by C - A.

Annual R for the cohort was estimated using an equation similar to Eq. 4:

$$R = \sum_{i=1}^{16} (a_t \bar{w}_i^{\,b_t}/1000)(N\ m_i^{-2})(24)(day_t)(4.825) \qquad (8)$$

where a_t and b_t are regression coefficients for larval weight versus ml O_2 h^{-1} per larvae.

Total energy available for P (= P_g + P_{ev}) of the hellgrammite population was estimated as the difference between annual A and R and compared with the results obtained with the production estimate described earlier for P_g plus the estimate for larval P_{ev}. The cohort's larval P_{ev} was estimated with the equation:

$$P_{ev} = \sum_{i=1}^{10} N\, m_i^{-2} (ev_i) \qquad (9)$$

where $N\, m_i^{-2}$ is the estimated number of larvae present in the study site during each of 10 moltings; and ev_i is the caloric equivalent of the mean exuvium of each molt.

The energy allocated to P_r by the 1972-1973 cohort was estimated indirectly by two methods: first, the number of adult females that emerged and reproduced was set equal to one-half the total estimate of full-fed final instar larvae based on the 5 May 1973 density estimate (assumptions: sex ratio of final instar larvae is 1:1; all larvae present on 5 May successfully pupate without mortality until all egg masses are deposited; all females reproduce) and each female was estimated to lay 2.3 egg masses. The density estimate for 5 May was used because some larvae begin pupation in early May. Thus, P_r was estimated as the product of the number of females and the caloric equivalent of their eggs and egg mass coverings. Since this is obviously an overestimate, the second method was based on the census of egg masses produced by the 1971-1972 cohort. Unfortunately no census was made of egg masses produced by the 1972-1973 cohort because the log bridge oviposition site was washed away by a flood.

CHAPTER III

RESULTS

Life History

Female dobson flies deposit egg masses on objects overhanging the stream or projecting above its surface (e.g., live vegetation, logs, bridges, large rocks). The egg masses are usually concentrated directly over the main channel of the stream in areas where they will not be exposed to direct sunlight. Riffles without upstream sites suitable for oviposition are depauperate of hellgrammites, whereas those riffles in the same stream with suitable upstream sites support large populations. The eggs are encased in a bright white protective material which is secreted from a gland in the tip of the female's abdomen. The egg masses are oval in shape with a mean length of 18 mm and width of 15 mm (n = 30). The eggs are arranged in these masses in semicircular rows usually three layers deep in the center and tapering to one layer on the edges. Observation of oviposition in the field indicated females usually lay two egg masses but occasionally produce a third smaller mass. Dissection of eight gravid females to determine the number of eggs per female ($\bar{X}$ = 2976; SD = 380; n = 8 eggs per female) and a count of eggs per egg mass ($\bar{X}$ = 1309; SD = 432; n = 33)

support estimates based on field observations of the number of egg masses laid per female (2976/1309 = 2.3).

Table 1 gives the number of unhatched, hatched and total egg masses counted in the study area from May through September 1973 that apparently were produced by the 1971-1972 cohort. Oviposition began in late May and continued until late August with slightly more than one-half of the eggs being deposited by 24 June. Approximately two-thirds of all the egg masses had hatched by 25 July. Incubation time for 28 field-collected egg masses of uncertain age was 12.9±5 days in the laboratory at 28 C. Of three egg masses collected immediately after oviposition one hatched after 14 days and the other two after 15 days. Thus, dobson fly eggs probably hatch within 2 wk in north-central Texas. Completion of hatching before September is adaptive because flooding generally begins in late September. The flood which occurred during the third week of September 1973 had little effect on egg production by the cohort, although it did obliterate the remains of the hatched egg masses, indicating a significant mortality factor on late-hatching egg masses.

Total egg mass production by the cohort probably exceeded the total (304) observed during the last month of oviposition (August), because new masses are frequently deposited over and sometimes obscure previously hatched egg masses. At least 48 (312-264) appear to have been obscured in this manner between 25 July and 22 August. Therefore, minimal production

Table 1. The number of egg masses laid by the 1971-1972 cohort of *C. cornutus*.

Sample Date	Number Unhatched	Number Hatched	Total
24 May	9	0	9
24 Jun	157	22	179
25 Jul	70	242	312
22 Aug	40	264	304
28 Sep	0	(flood)	(flood)

of egg masses by the cohort was estimated at 352 by adding these 48 egg masses to the August count.

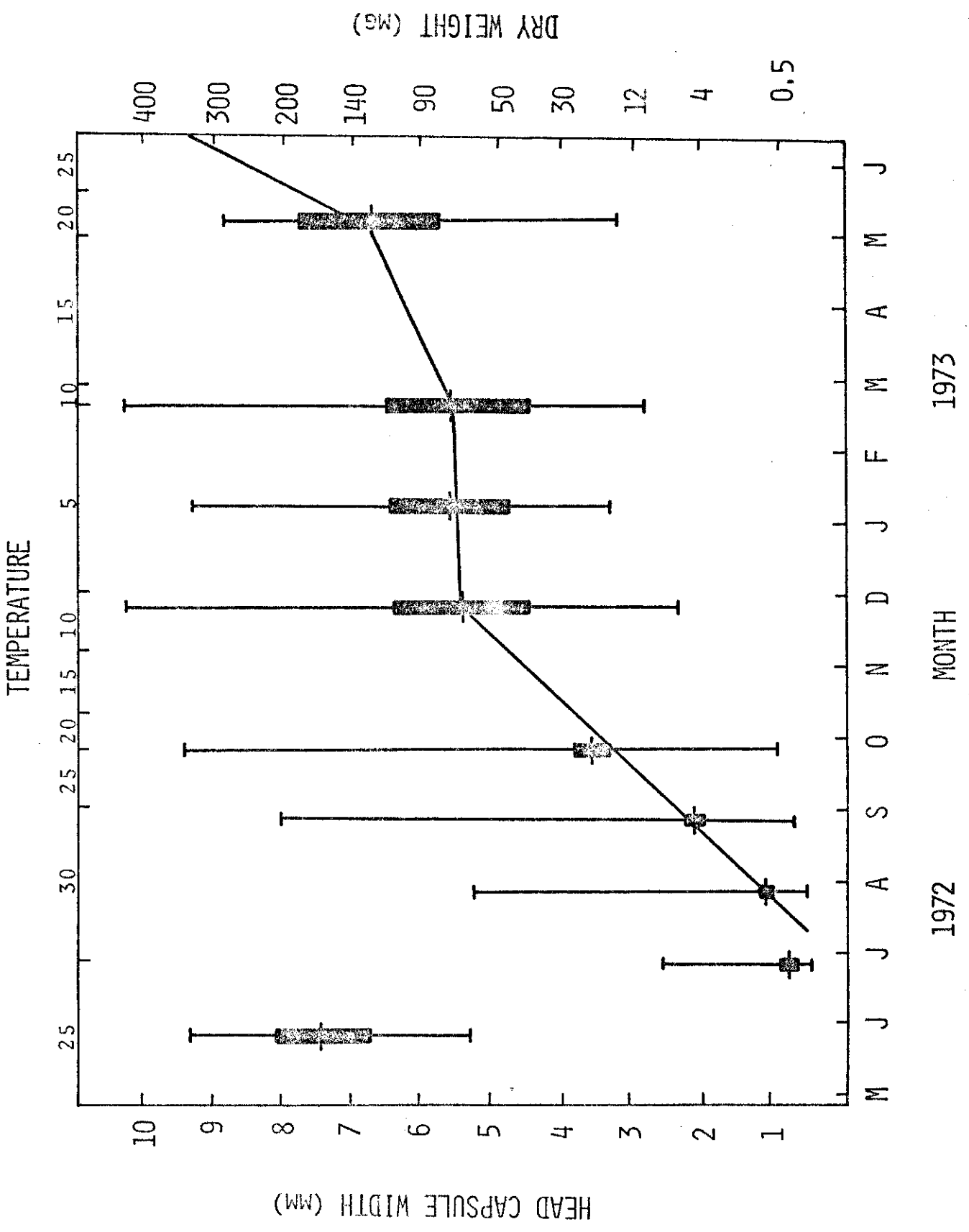
The eggs hatch at night and first instar larvae (HCW = 0.5±0.05 mm, dry wt = 0.04±0.015 mg; Table 2) scramble out of the covering, fall in large groups to the water below. All first instar larvae have one or more gas bubbles in their gut, perhaps for buoyancy; many eggs are laid over pools and the young larvae have to reach the riffles to survive. They are positively phototaxic when in still water, but in flowing (or circulating) water they cling to the undersurfaces of objects and avoid light.

The growth pattern of hellgrammites in the 1972-1973 cohort (Fig. 1) indicated that the typical dobson fly which began as a first instar larva in July grew to a HCW of 5.6 mm and a weight of about 75 mg by late November. Growth virtually ceased during the winter from November through February, when the stream temperature was below 10 C. Growth resumed in the spring with pupation occurring in June, when the typical larva had reached a HCW of 9.5 mm and a dry weight of 341.2 mg. Although there was a large size range of hellgrammites present in the riffle throughout the year due to the extended period of oviposition and hatching, and different growth rates of larvae, dobson flies in north-central Texas apparently have a one-year life cycle. Presence of a few larvae of emergent size throughout the year indicates that larvae hatched late in the year may have a two-year development

Table 2. The head capsule width, dry weight and duration in days of the stages in the life cycle of *C. cornutus* except instars 2-11.

Stage of Development	HCW (mm) $\bar{X}$±SD	N	Dry Weight (mg) $\bar{X}$±SD	N	Duration (days) $\bar{X}$±SD	N	Range
Egg	0.3±0.02	10			12.9±5	28	7-21
First Instar	0.5±0.05	37	0.04±0.02	33			
Prepupae	9.5±0.8	23	372.5 ±109	15	7.1±2	16	4-11
Pupae					6.9±1	11	5- 8
Male	10.7±0.9	10	435.1 ±83	8			
Female	9.7±1.0	11	382.9 ±87	9			
Adults, male	10.2±1.3	19	280.2 ±78	16	4.8±2	12	2- 8
Adults, femlae	8.9±0.8	36			4.7±2	12	2- 7
Newly-emerged	9.0±0.5	4	259.5 ±40	4			
Gravid			371.8 ±81	32			
Spent			228.3 ±56	12			

Fig. 1. The growth pattern of the 1972-1973 cohort of *Corydalus cornutus* in relation to temperature. The rectangles represent ±2 Standard Error and the vertical lines the range of larvae measured at each sampling date.


DRY WEIGHT (MG)
400
300
200
140
90
50
30
12
4
0.5
TEMPERATURE
25
20
15
10
5
10
15
20
25
30
25
HEAD CAPSULE WIDTH (MM)
10
9
8
7
6
5
4
3
2
1
M J J A S O N D J F M A M J
1972
MONTH
1973

time or there may be an overlap of cohorts resulting from extended periods of emergence and fast growth rates of young larvae, or both.

Actual growth rates of larvae maintained in growth chambers in the stream compared with the growth rates determined from field data are shown in Fig. 2. Larvae at the FM 455 study site had mean growth rates of 0.65 and 2.00 mg day^{-1} respectively for the months of August and September. Larvae at the Green Valley site had a growth rate of 0.91 mg day^{-1} during September. These growth rates compare well with the growth rates shown in Fig. 1 over the same time periods (August = 0.54, September = 1.71 mg day^{-1}). The growth chamber study was ended in October, when a flood washed the chambers away.

The HCW-frequency histogram (Fig. 3) suggests there are approximately 11 instars during the larval development of *C. cornutus*, because the peaks representing instars are not clearly separated. The regression of HCW before molting versus the increase in HCW at each molt (Fig. 4) helps to resolve the peaks. For example, the seventh instar, centered at 3.5 mm HCW on Fig. 3, increases its HCW 1.0 mm when it molts (Fig. 4), thus centering the peak for the eighth instar at 4.5 in Fig. 3. The location of the 11^{th} instar at 9.5 mm HCW was verified by comparison with the mean HCW of prepupa (9.5 mm, Table 2).

Full-fed larvae or prepupae congregate at the stream margin during spring months and finally leave the stream at

Fig. 2. Growth of hellgrammites in two cages placed in two riffle areas of the study stream. The rectangles represent ±2 Standard Error and the vertical lines the range.

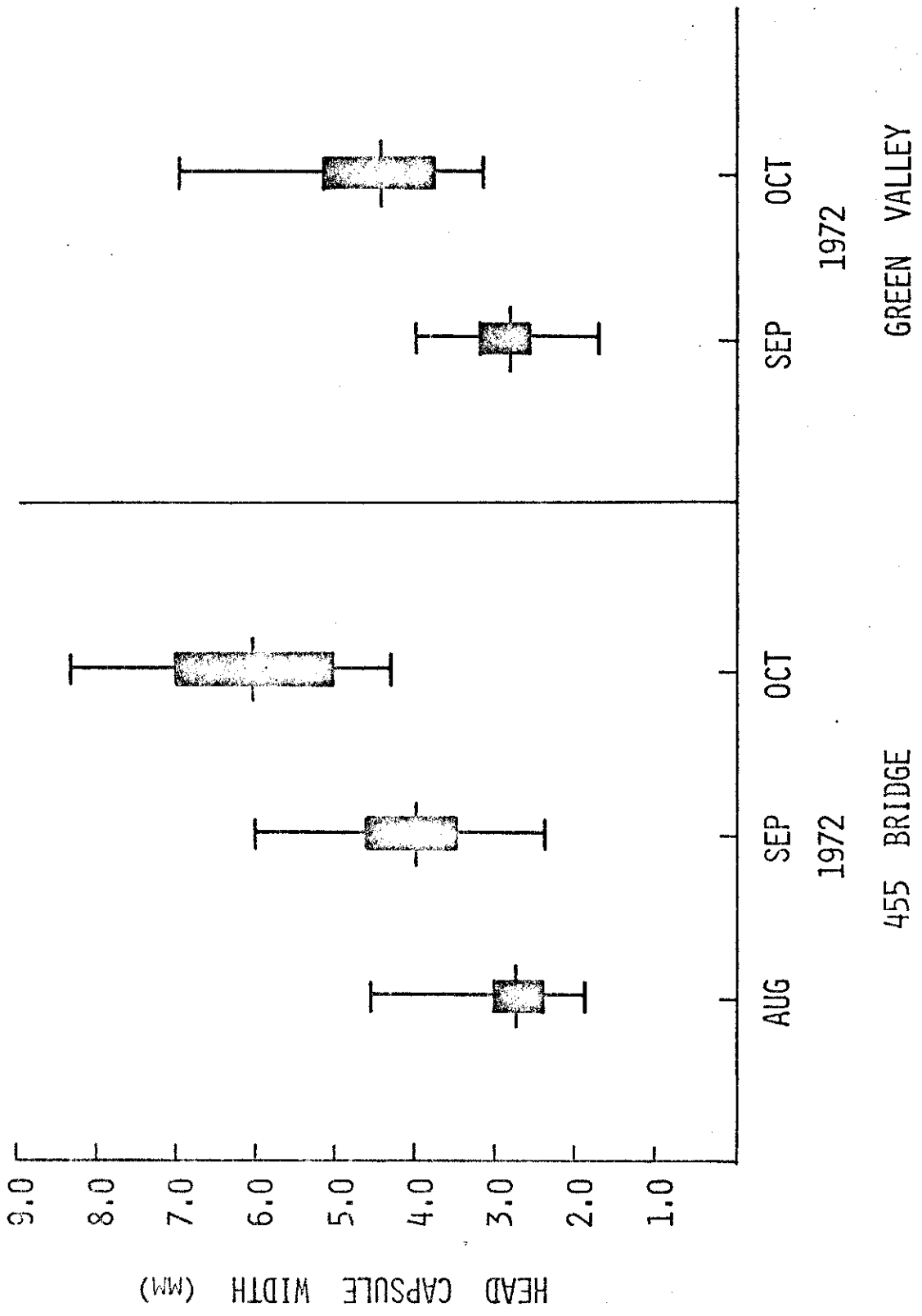

HEAD CAPSULE WIDTH (MM)
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
AUG
SEP
OCT
1972
455 BRIDGE
SEP
OCT
1972
GREEN VALLEY

Fig. 3. Head capsule width frequency histogram for *Corydalus cornutus* larvae with the probable instar numbers indicated.

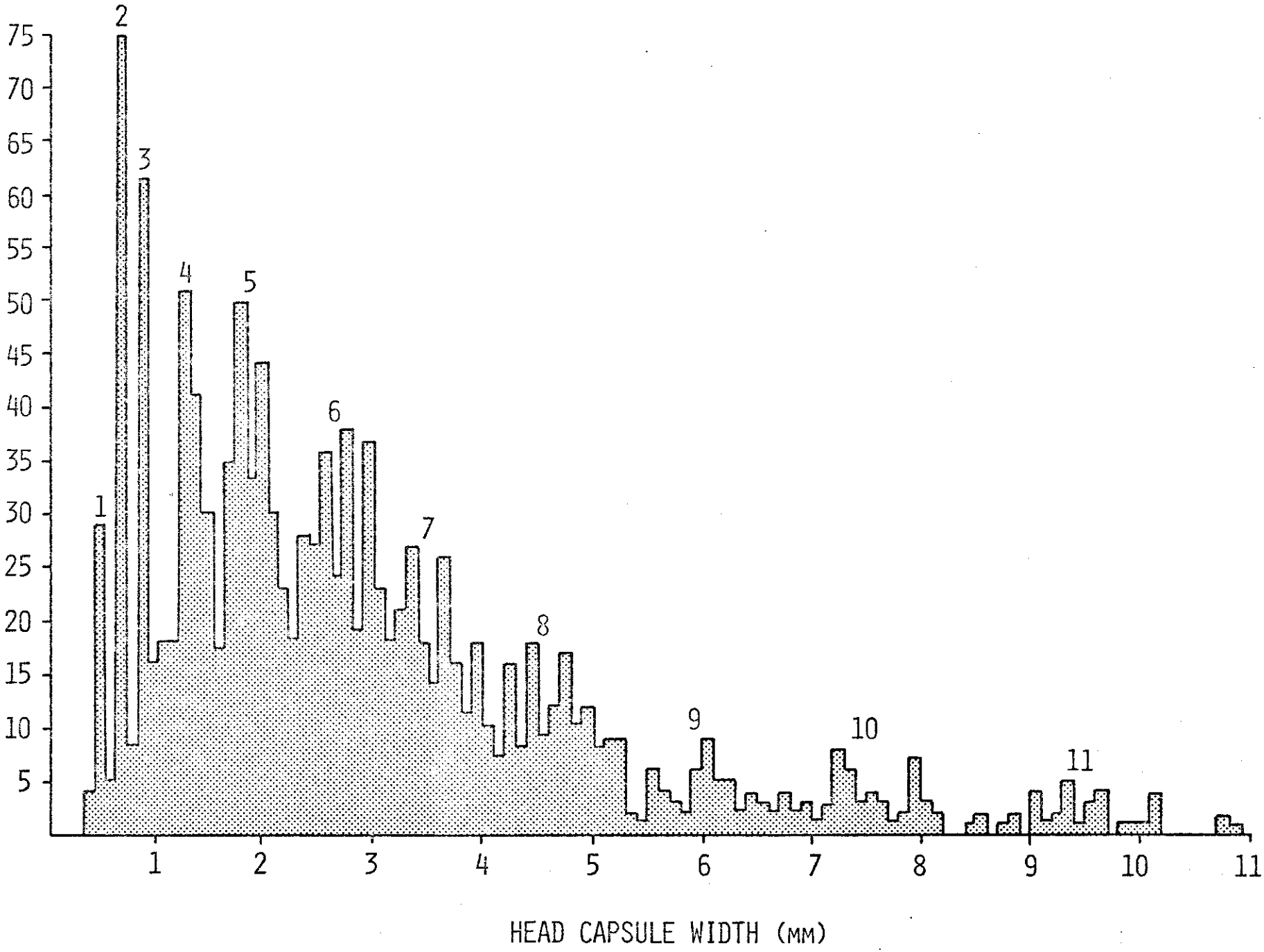
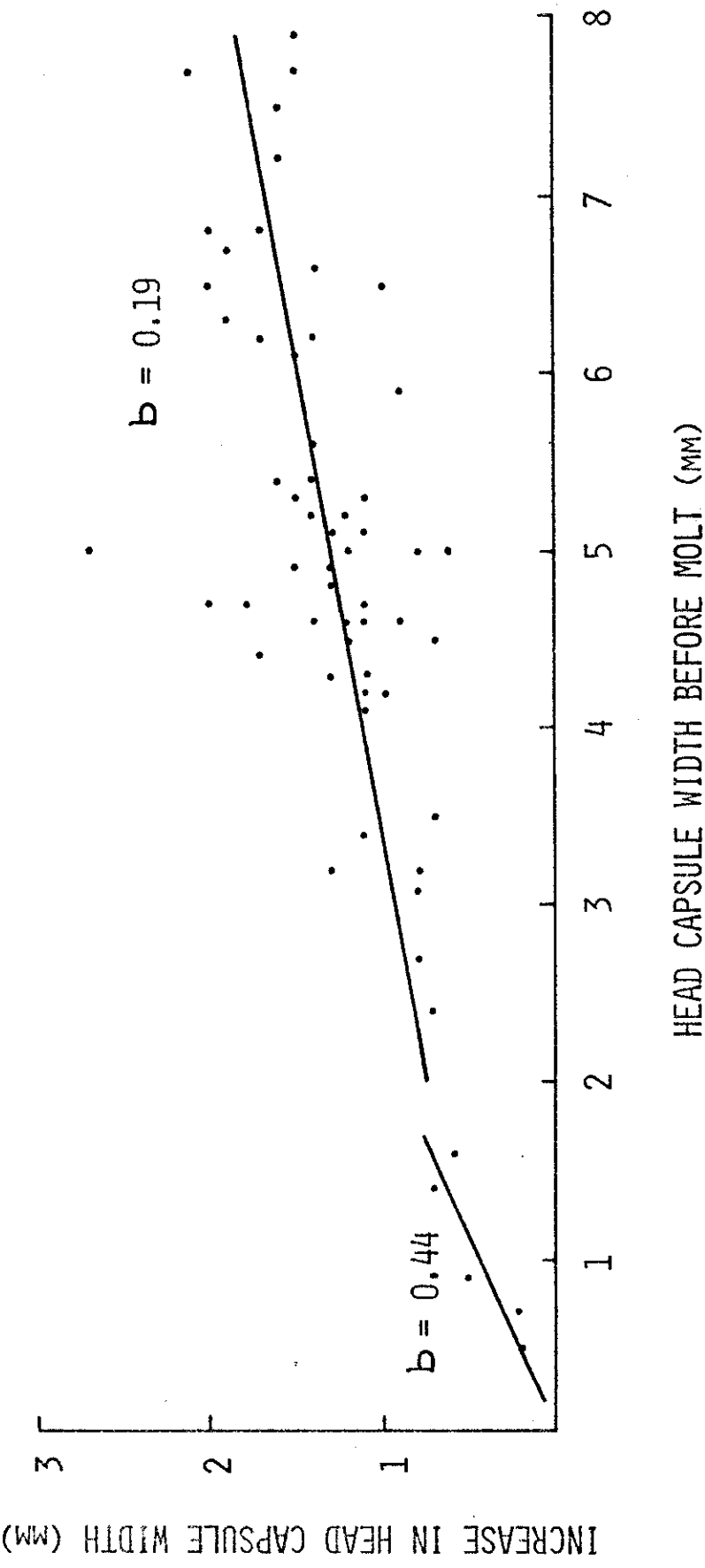

75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
1
2
3
4
5
6
7
8
9
10
11
1
2
3
4
5
6
7
8
9
10
11
HEAD CAPSULE WIDTH (MM)

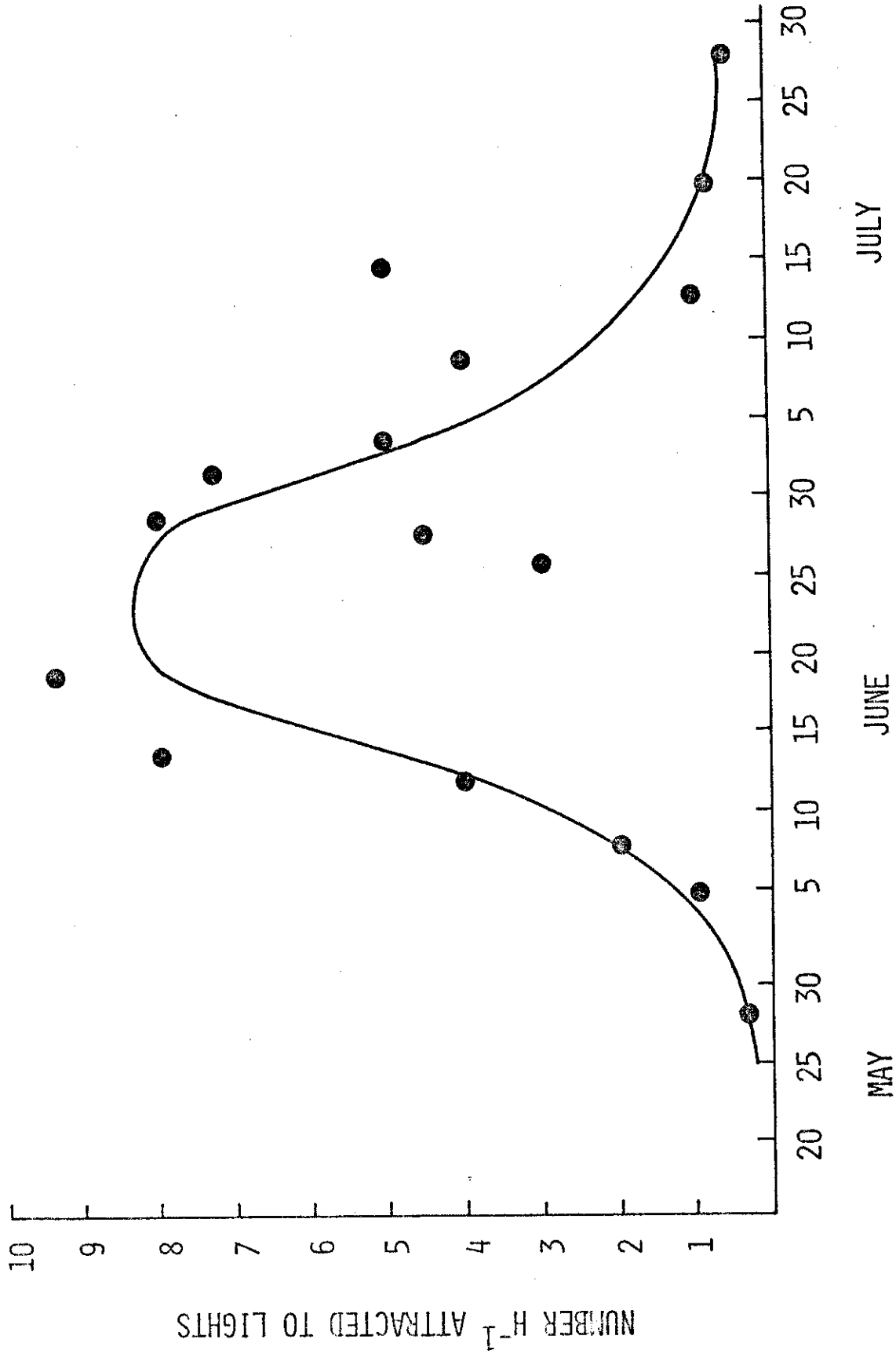
Fig. 4. Increase in head capsule width with molting in *Corydalus cornutus* larvae.


b = 0,19
b = 0,44
1
2
3
4
5
6
7
8
INCREASE IN HEAD CAPSULE WIDTH (MM)
HEAD CAPSULE WIDTH BEFORE MOLT (MM)

night and burrow into the soil. They are wary during the first day and hastily return to the water if disturbed; but they gradually become quiescent as they approach the transition to the pupal stage. The prepupae molt into cream-colored exarate pupae in approximately 7 days, leaving their exuviae in the burrows. The pupae gradually become active, darken in color and dig an exit from the puparium just prior to emergence. The final molt occurs at night and the adults emerge from the burrows. Male pupae and adults, are slightly larger than females (Table 2).

The pattern of adult emergence of the 1972-1973 cohort is shown in Fig. 5. The data represent the number of adults collected per hour at lights on the Green Valley bridge. Presence of egg masses indicates that adults were in the area from the middle of May until late September. However, the frequency of adults collected at the lights from 28 May until 28 July indicates that peak emergence occurred between mid-June to early July. Although the total of 121 females and 39 males collected at the lights suggests an inbalanced sex ratio, the sex ratio of pupae collected in the field was 1:1 (12 females and 13 males). The preponderance of females attracted to the lights may not reflect the true sex ratio of adults in the area because (1) lights may be more attractive to females; (2) males' flight may be hindered by their large mandibles; and (3) the bridge where the lights were operated was a favorite oviposition site of the females.

Fig. 5. The pattern of emergence of adult *Corydalus cornutus* during 1973.


NUMBER H-1 ATTRACTED TO LIGHTS
10
9
8
7
6
5
4
3
2
1
20
25
30
5
10
15
20
25
30
5
10
15
20
25
30
MAY
JUNE
JULY

Five pairs of adults reared from pupae in the laboratory and seven pair that appeared to be newly-emerged when collected in the field had a mean life span of about 5 days with ranges of 2-7 days (females) and 2-8 days (males). Parfin (1952) reported a mean longevity of 8 days for each sex with a range from 4-13 days for males and 6-10 days for females; Davis (1903) reported 3 days for males and 3-10 days for females. Both sexes drank water and sugar water, and females licked juices of fruits in their cages. Although they were active and appeared to be healthy, copulation was not observed and eggs were not laid. The maximum observed longevity (7 days) was used as an estimate of adult life span for calculations involving preparation of the energy budget.

Dissection of newly-emerged females (n = 4) revealed that their eggs are very small at emergence and require considerable yolking, presumably after fertilization. The egg mass covering material, always present in a gland in the tip of the abdomen of gravid females, is not present in newly-emerged females. The testes of males are large and appear to be fully-developed immediately after emergence. Dissection of post-oviposition females (n = 12) indicates that they lay all of their eggs and use all of the egg case covering material. Females die within a few hours after oviposition.

Calorimetry

Caloric values of the major stages in the life cycle, except specific instars 2-11, and additional materials

necessary for constructing the energy budget are given in Table 3. Ova had the highest caloric values of any stage in the life cycle. The exuviae were relatively low in caloric content. Total caloric value of newly-emerged females was lower than that of gravid females that had completed yolking their eggs ($t = 8.84$; $P > 0.05$); however, no real differences were detected among carcasses of newly-emerged, spent and gravid females ($t_{0.05} = 0.34\text{-}1.76$).

The caloric values for all the larvae used in the respiration experiments divided into three weight classes (Table 4) indicate that large larvae have higher caloric content per gram than smaller larvae, especially during the month of May just prior to pupation. When the size classes within collection periods are pooled, a pattern of seasonality of caloric values emerges (Fig. 6), which indicates that larvae decrease slightly in cal g^{-1} during the winter but gradually store calories (probably as lipids) through the spring prior to emergence. The caloric values of the 15 August collection, composed primarily of animals belonging to the 1973-1974 cohort, does not indicate that the larvae decrease in cal g^{-1} from May to August.

Respiration

The annual pattern of stream temperature in the study site during 1972-1973 is shown in Fig. 7. Temperature ranged from 0 C in the winter to 32 C in the summer and was relatively

Table 3. Caloric values of the major stages in the life cycle of *C. cornutus* except instars 2-11 and additional materials necessary for constructing an energy budget.

Material	$\bar{X}$ cal g^{-1} Ash-free	Range	N*	$\bar{X}$ wt (dry mg)	N*	Biocontent (cal)
Eggs dissected from females (total)	6599	6583-6615	2	101.1	10	667
Egg covering material dissected from females	6238	6107-6369	2	29.6	10	185
Egg covering material after hatching	6464	6437-6491	3	7.4	33	48
Egg masses, just laid	6631	6453-6809	2	62.7	22	416
Egg masses, mature	6461	6452-6470	2	65.2	33	421
First instar larvae	6171	6151-6190	3	0.044	33	0.272
Exuviae of larvae	4290	4074-4408	3	**		
Prepupae	5570	5502-5645	3	372.5	15	2075
Exuviae of Prepupae	4171	4078-4263	2	34.4	**	144
Pupae, female	5500	5449-5550	2	382.9	9	2106
Pupae, male	5108	5020-5184	3	435.1	8	2222
Exuviae of pupae	4655	4555-4756	2	25.8	1	120
Male adults, newly-emerged	5071	5039-5119	3	280.2	16	1420
Female, newly-emerged	5062	5030-5095	2	259.6	4	1314
Female, gravid	5498	5461-5535	2	371.8	32	2044
Carcass of gravid female	5195	5105-5279	3	234.8	10	1220
Female, spent	5181	5047-5243	4	228.3	12	1183

*N = number of determinations.

**Estimated using regression Eq. 6.

Table 4. Caloric values of *C. cornutus* larvae in relation to time of year, temperature and size class.

Collection Date	°C	$\overline{wt}$±SD (mg)	N_1	Cal g^{-1}±SD	Range	N_2*
27 Sep 1972	25	347±113	10	5010±89	4902-5102	4
		115±58	29	4943±75	4800-5007	5
		17±12	21	4799±92	4707-4891	2
28 Nov 1972	10	357±71	12	5118±166	4941-5296	4
		172±86	16	5172±144	5028-5315	2
		44±27	30	4967±40	4927-5007	2
12 Jan 1973	5	277±83	8	5061±13	5048-5074	2
		97±29	20	5004±43	4961-5047	2
		33±15	32	5016±93	4923-5109	2
23 Mar 1973	15	403±100	8	5344±32	5302-5378	3
		143±73	29	5461±72	5370-5533	2
		45±19	23	5220±4	5216-5223	3
8 May 1973	20	315±158	20	5752±97	5672-5918	4
		91±24	16	5424±11	5413-5435	2
		36±18	24	5233±32	5201-5265	2
15 Aug 1973	30	453±133	27	5303±63	5229-5379	4
		86±34	11	5262±29	5233-5291	2
		15±10	21	4976±56	4920-5032	2

*N_2 is the number of caloric determinations made on N_1 larvae.

Fig. 6. Seasonal changes in cal g^{-1} of *Corydalus cornutus*. The rectangles represent ±2 Standard Error and the vertical lines the ranges.

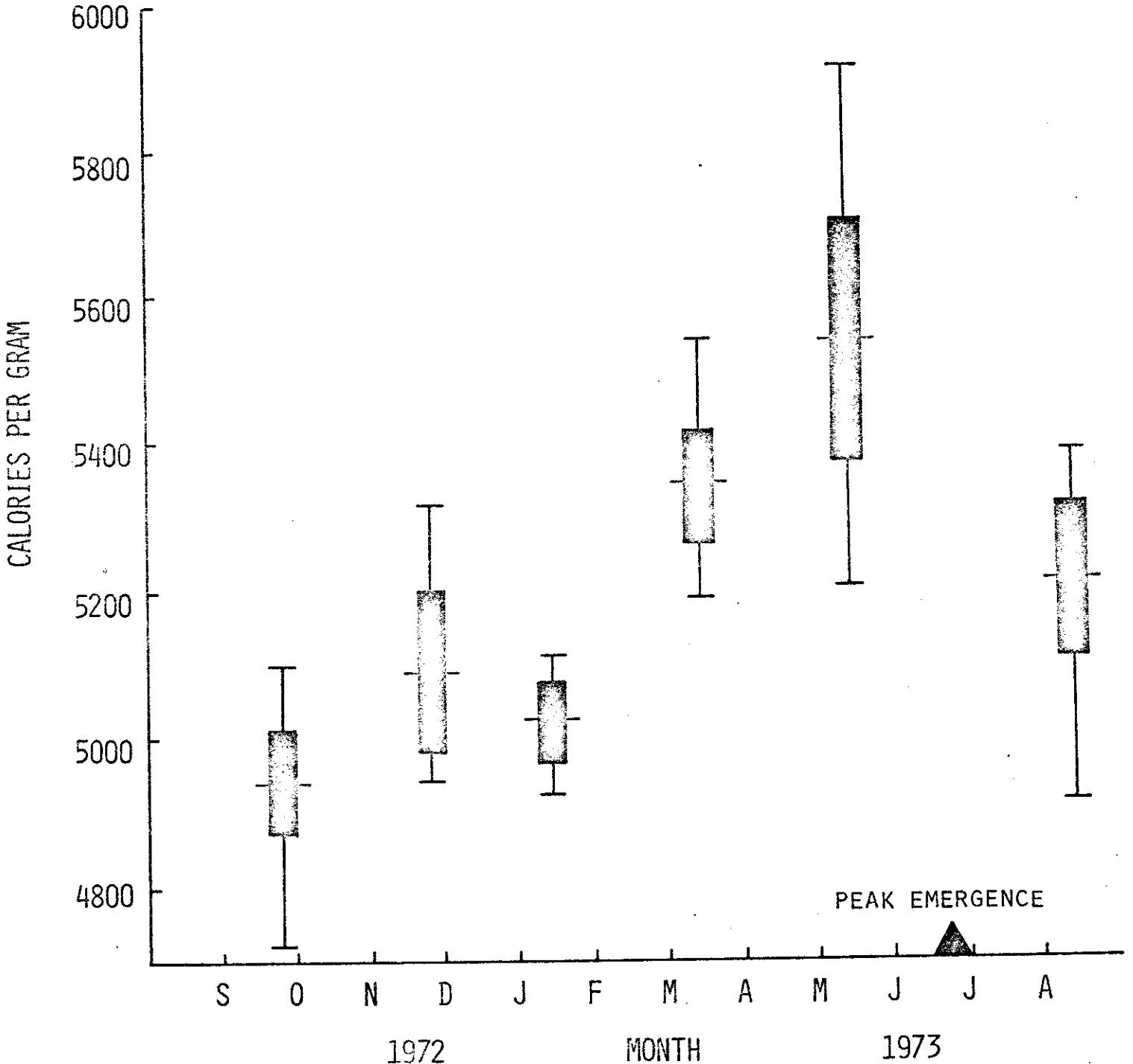
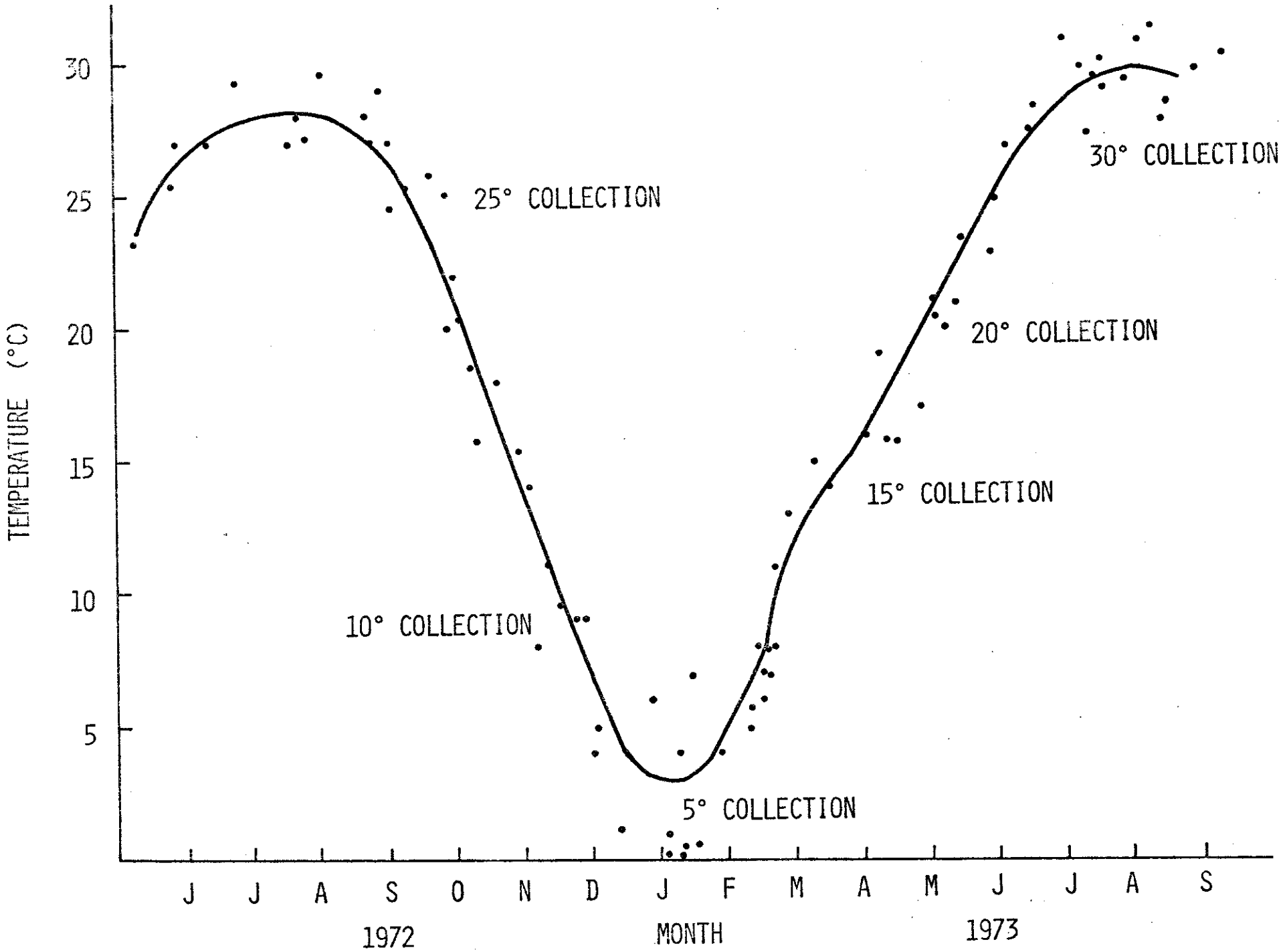

6000
5800
5600
5400
5200
5000
4800
CALORIES PER GRAM
PEAK EMERGENCE
S
O
N
D
J
F
M
A
M
J
J
A
1972
MONTH
1973

Fig. 7. Seasonal changes in water temperatures in the study site during 1972-1973.


TEMPERATURE (°C)
30
25
20
15
10
5
25° COLLECTION
30° COLLECTION
20° COLLECTION
15° COLLECTION
10° COLLECTION
5° COLLECTION
J J A S O N D J F M A M J J A S
1972
MONTH
1973

stable between 25 and 30 C from June to September and around 5 C from December to February. During the fall and spring, temperature was less predictable, changing from 5 to 25 C rather quickly.

Effects of seasonal temperatures on respiration rates and patterns of metabolic compensation to them in larval dobson flies are shown in Figs. 8-10 and Tables 5-8. Table 5 gives the mean O_2 consumption rates of each acclimatization group at each experimental temperature. Tables 6 and 7 give the results for two three-factor ANOVA using acclimatization temperature, experimental temperature and weight as variables. The resultant F-tests show highly significant effects for each factor and their interactions. Since there were incomplete cells (i.e., all acclimatization groups were not measured at all experimental temperatures—see Table 5), two analyses were necessary to include all of the determinations made from 5-30 C and to obtain the block design necessary for the analysis.

Results of the two-factor ANCOVA used to adjust for the extensive size range of larvae within each acclimatization group and the considerable variations in mean weight are shown in Table 8. The F-tests indicate highly-significant effects for each factor and their interaction. The adjusted means (after ANCOVA) are statistically compared among acclimatization groups at each experimental temperature with Duncan's 5% NMRT in Table 9 and within acclimatization groups

Fig. 8. Acclimatization and acclimation O_2 consumption rate-temperature curves of *Corydalus cornutus* larvae.

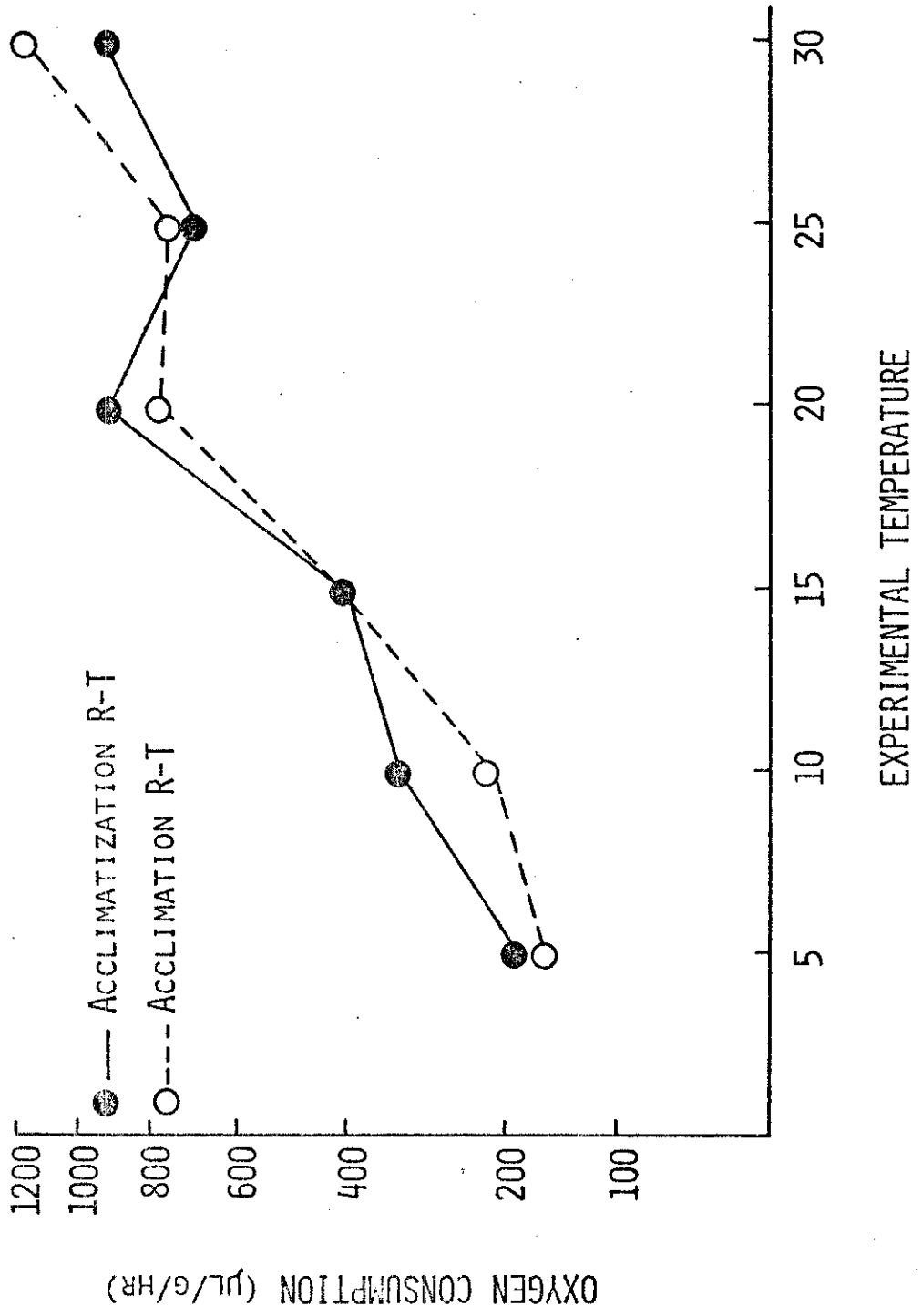

OXYGEN CONSUMPTION (µL/G/HR)
1200
1000
800
600
400
200
100
5
10
15
20
25
30
EXPERIMENTAL TEMPERATURE
ACCLIMATIZATION R-T
ACCLIMATION R-T

Fig. 9. Acutely determined O_2 consumption rate-temperature curves of six acclimatization groups of *Corydalus cornutus* larvae.

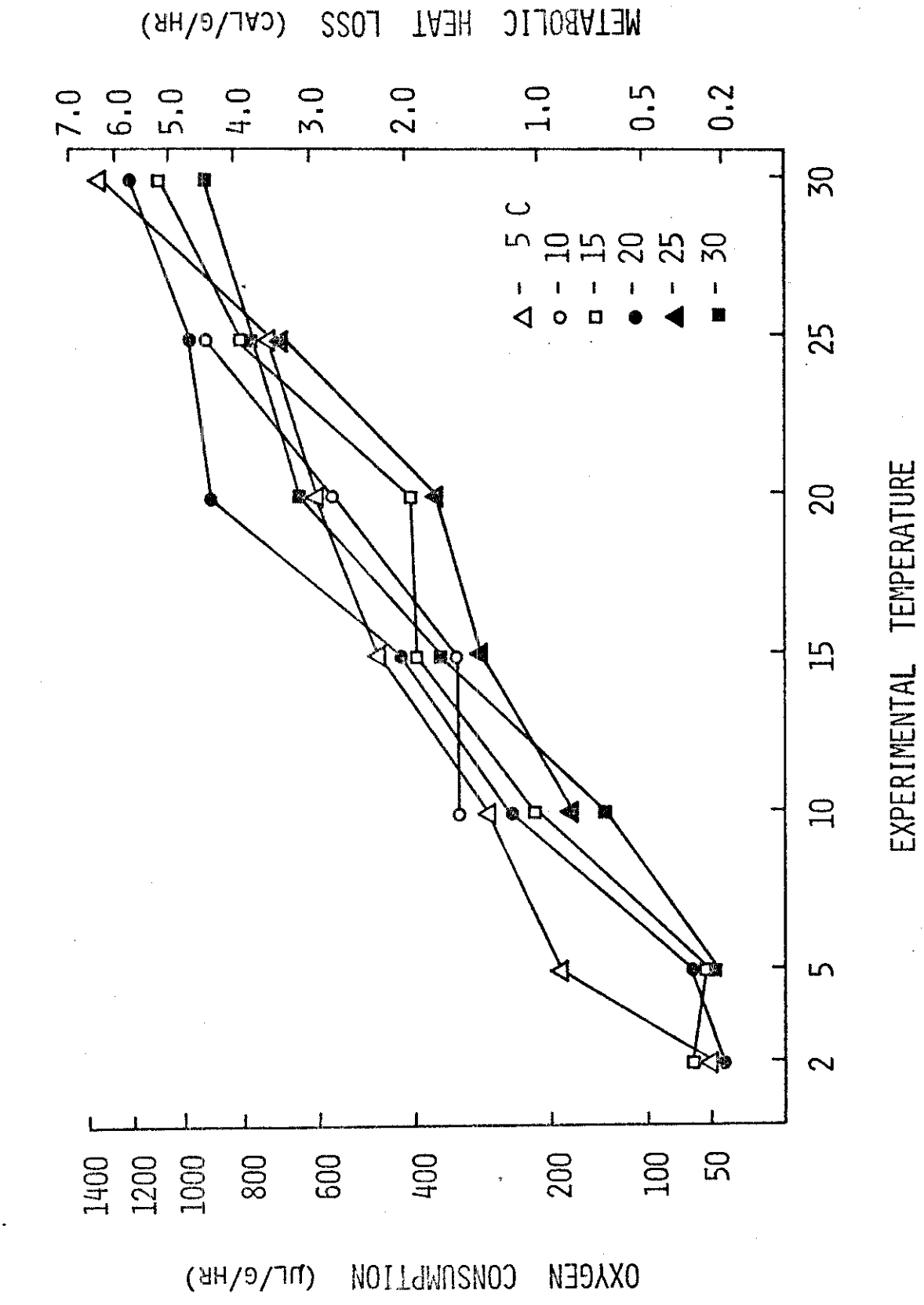

METABOLIC HEAT LOSS (CAL/G/HR)
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.5
0.2
5 C
10
15
20
25
30
OXYGEN CONSUMPTION (µL/G/HR)
1400
1200
1000
800
600
400
200
100
50
2
5
10
15
20
25
30
EXPERIMENTAL TEMPERATURE

Fig. 10. Abbreviated acutely determined O_2 consumption rate-temperature curves of six acclimatization groups of *Corydalus cornutus* larvae.

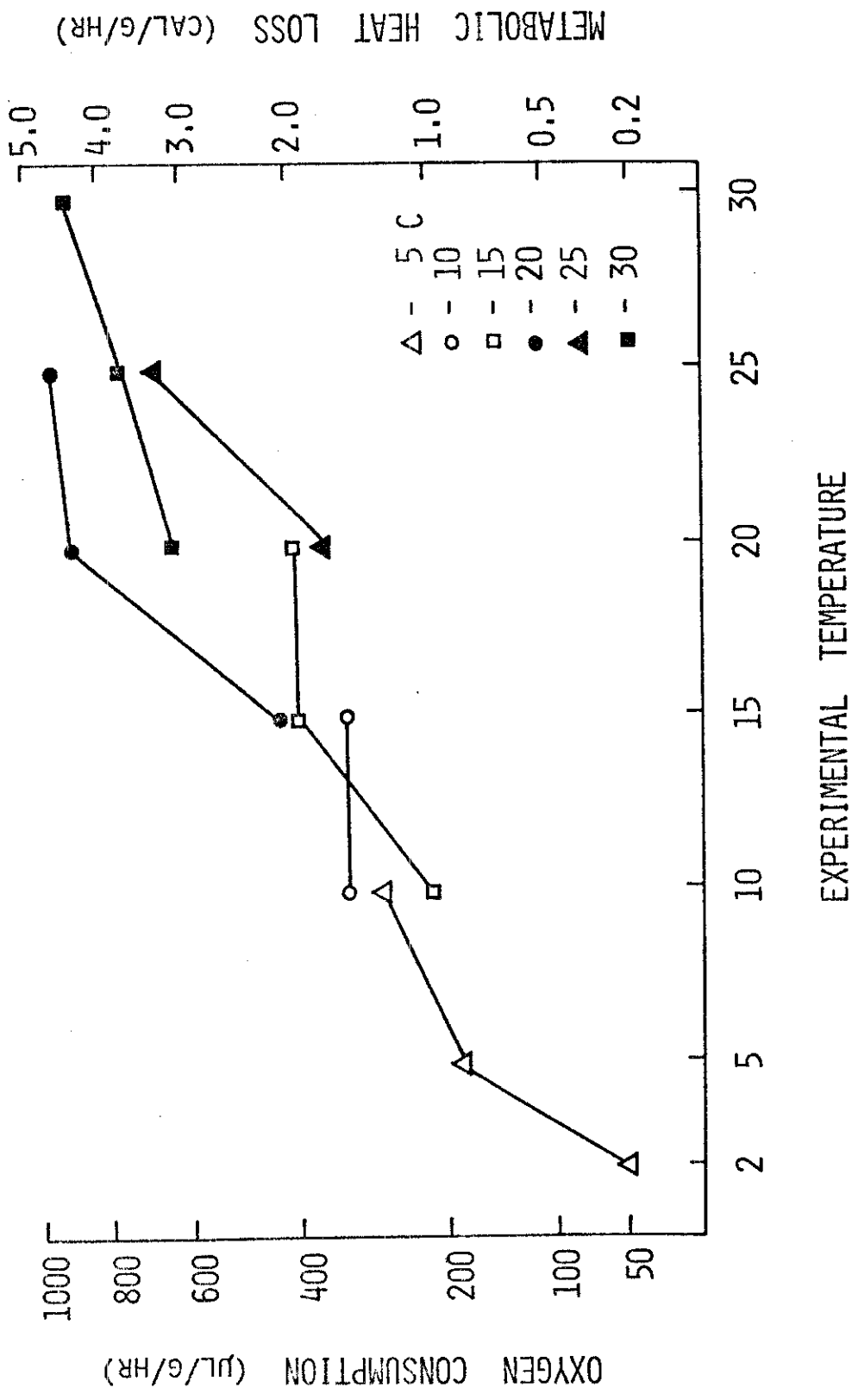

METABOLIC HEAT LOSS (CAL/G/HR)
5.0
4.0
3.0
2.0
1.0
0.5
0.2
5 C
10
15
20
25
30
OXYGEN CONSUMPTION (µL/G/HR)
1000
800
600
400
200
100
50
2
5
10
15
20
25
30
EXPERIMENTAL TEMPERATURE

Table 5. Mean acutely determined O_2 consumption rates in $\mu l\ O_2\ g^{-1}\ h^{-1}$ of *C. cornutus* larvae acclimatized to and determined at 5, 10, 15, 20, 25 and 30 C.*

Determination Temperature °C	Acclimatization Temperatures °C					
	5	10	15	20	25	30
2	56	-	69	48	-	-
5	201	-	48	56	-	54
10	335	347	222	257	197	148
15	553	354	451	458	354	479
20	721	603	411	985	465	810
25	906	980	820	1031	865	1003
30	1599	-	1098	1239	-	1173

*N = 44-60 measurements per cell.

Table 6. Results of three-factor ANOVA of acutely determined standard metabolic rates of *C. cornutus* larvae acclimatized to 5, 10, 15, 20, 25 and 30 C and each measured at 10, 15,20 and 25 C.

Source of Variance	MS X 10^4	DF	F-ratio	Probability
1 Acclimatization temperature	141	5	26.4	<0.001
2 Determination temperature	2607	3	488.1	<0.001
3 Weight class	1966	3	368.2	<0.001
Interaction of 1 and 2	70	15	13.1	<0.001
Interaction of 1 and 3	25	15	4.7	<0.001
Interaction of 2 and 3	205	9	38.4	<0.001
Interaction of 1, 2 and 3	19	45	3.6	<0.001
Error	5	1304		

Table 7. Results of three-factor ANOVA of acutely determined standard metabolic rates of *C. cornutus* larvae acclimatized to 5, 15, 20 and 30 C and measured at 5, 10, 15, 20, 25 and 30 C.

Source of Variance	MS X 10^4	DF	F-ratio	Probability
1 Acclimatization temperature	97	3	13.2	<0.001
2 Determination temperature	3659	5	501.9	<0.001
3 Weight class	2026	3	277.8	<0.001
Interaction of 1 and 2	72	15	9.9	<0.001
Interaction of 1 and 3	29	9	3.9	<0.001
Interaction of 2 and 3	203	15	27.8	<0.001
Interaction of 1, 2 and 3	19	45	2.6	<0.001
Error	7	1292		

Table 8. Results of three two-way design ANCOVA of acutely-determined standard metabolic rates of *C. cornutus* larvae.

Acclimatized to 5, 10, 15, 20, 25 and 30 C and each measured at 10, 15, 20 and 25 C.

Source of Variance	MS	DF	F-ratio	Probability
Acclimatization temperature	0.99	5	52	<0.001
Determination temperature	15.18	3	803	<0.001
Interaction	0.33	15	17	<0.001
Error	0.02	1031		

Acclimatized to 5, 15, 20 and 30 C and each measured at 5, 10 15, 20, 25 and 30 C.

Source of Variance	MS	DF	F-ratio	Probability
Acclimatization temperature	2.09	3	92	<0.001
Determination temperature	34.56	5	1521	<0.001
Interaction	0.67	15	30	<0.001
Error	0.02	1031		

Acclimatized to 5, 15 and 20 C and each measured at 2, 5, 10, 15, 20, 25 and 30 C.

Source of Variance	MS	DF	F-ratio	Probability
Acclimatization temperature	1.38	2	66	<0.001
Determination temperature	35.30	6	1688	<0.001
Interaction	0.82	12	39	<0.001
Error	0.02	902		

Table 9. Mean O_2 consumption rates in µl O_2 g^{-1} h^{-1} following ANCOVA among 5, 10, 15, 20, 25 and 30 C acclimatization groups acutely determined at 2, 5, 10, 15, 20, 25 and 30 C indicating the results of Duncan's 5% NMRT.*

Determination Temperature °C	Mean Acutely Determined O_2 Consumption Rates of Six Acclimatization Groups					
2	43(20)	52(5)	60(15)			
5	47(30)	51(15)	54(20)	178(5)		
10	141(30)	178(25)	219(15)	251(20)	288(5)	324(10)
15	302(25)	331(10)	347(30)	398(15)	417(20)	468(5)
20	380(25)	398(15)	575(10)	617(30)	617(5)	912(20)
25	708(25)	759(5)	776(30)	794(15)	912(10)	954(20)
30	933(30)	1096(15)	1202(20)	1349(5)		

*The rank-ordered means are followed by the acclimatization temperatures in parentheses. Means not underscored by a common line are significantly different ($P < 0.05$).

in Table 10. Although the respiration rates of the three acclimatization groups measured at 2 C covered a narrow range of values (Table 9), they were significantly different due to the low variability of the rates at that temperature. The 5, 10 and 20 C acclimatization groups had significantly higher rates at their respective acclimatization temperatures and the 25 and 30 C had the lowest rates of any of the groups measured at their respective acclimatization temperatures. The mean O_2 consumption rates compared within acclimatization groups (Table 10) shows significant differences between determination temperatures, except for the 10, 15 and 20 C acclimatization groups measured at their acclimatization temperatures compared with the 5 C higher determination temperatures.

The acclimatization and acclimation RT curves (Fig. 8) show that hellgrammites can partially metabolically compensate (Precht Type 3; Precht et al. 1955, Precht 1958) in the field and laboratory to temperatures normally encountered during the year in north-central Texas streams. The low Q_{10}'s (< 2) between 20 and 30 C and between 5 and 15 C separated by a high Q_{10} ($\simeq 4$) between 15 and 20 C, suggest that hellgrammites can maintain "preferred" winter and summer levels of metabolism with partial independence from short-term changes in stream temperature. The RT curves of the acutely-determined metabolic rates of seasonally-collected hellgrammites are shown in Fig. 9. Although there is considerable translation

Table 10. Mean O_2 consumption rates in µl O_2 g^{-1} h^{-1} following ANCOVA within 5, 10, 15, 20, 25 and 30 C acclimatization groups acutely determined at 2, 5, 10, 15, 20, 25 and 30 C indicating the results of Duncan's 5% NMRT.*

Acclimatization Temperature °C	Determination Temperatures (°C)						
	2	5	10	15	20	25	30
5	52	178	288	468	617	759	1349
10	-	-	324	331	575	912	-
15	60	51	219	398	398	794	1096
20	43	54	251	417	912	954	1202
25	-	-	178	302	380	708	-
30	-	47	141	347	617	776	993

*Means not underscored by a common line are significantly different ($P < 0.05$).

(Prosser 1974) among the RT curves and similarity in Q_{10}'s (Table 11), adaptive patterns of short-term (acute metabolic compensation) are obscure. Since hellgrammites seldom experience acute changes in ambient temperatures much greater than ±5 C, it is more realistic and informative to plot acute rates for each acclimatization group at ±5 C from their respective acclimatization temperatures (Fig. 10). These plots reveal two adaptive patterns of metabolic homeostasis to short-term changes in ambient temperatures; one in the "preferred" winter and one in the "preferred" summer range.

Metabolic acclimatization and acute insensitivity below 20 C in the 5, 10 and 15 C groups suggests that hellgrammites with a previous thermal history below 20 C maintain a "preferred" winter rate around 300 µl g^{-1} h^{-1} in the 5 to 15 C range. Since the stream temperatures fluctuate rapidly in the 5 and 20 C range during the fall and spring, acute metabolic insensitivity is adaptive. The rate of the 15 C group was much lower than that of the 20 C group when both were measured at 20 C, indicating metabolic insensitivity in cold-acclimatized larvae to temporary increases in temperatures from 15 to 20 C. The higher rate of the 20 C group at 20 C indicates that hellgrammites are capable of acclimatizing at 20 C to produce higher rates when the temperature is stable around or above 20 C. Thus, it appears that the winter-summer acclimatization "change-point" is somewhere between 15 and 20 C. Hellgrammites collected at temperatures below 20 C were

Table 11. Q_{10} values for acutely determined standard metabolic rates in six thermal acclimatization groups of *C. cornutus* larvae between seven experimental temperatures.

Acclimatization Temperature °C	Q_{10} Values for Changes in Experimental Temperatures					
	2-5	5-10	10-15	15-20	20-25	25-30
5	60.2	2.6	2.6	1.7	1.5	3.2
10			1.0	3.0	2.5	
15	0.6	18.4	3.3	1.0	4.0	1.9
20	2.1	21.6	2.8	4.8	1.1	1.6
25			2.9	1.6	3.5	
30		9.0	6.1	3.2	1.6	1.5

lethargic and inactive. Since preferred food organisms (Trichoptera, Simulidae and other aquatic insect larvae) were scarce during the winter, lowered metabolism should be adaptive in energy conservation. Results from laboratory feeding studies (see section on Feeding Studies, Chapter III) agree with energy conservation at low temperatures: larvae have low ingestion rates below 20 C; only 44% of the 10 C-acclimated animals ate anything during a 5-day feeding experiment, and 5 C-acclimated animals did not feed at all.

Since respiration rates of all groups measured at 2 C were close to 50 µl O_2 g^{-1} h^{-1}, hellgrammites either cannot compensate to very cold temperature or they shut down metabolically (i.e., Precht Type 5 undercompensation; Precht et al. 1955, Precht 1958). The high Q_{10} (60.2) between 2 and 5 C in the 5 C group (Table 11) tends to support this. All other acclimatization groups had considerably lower acute rates at 5 C than the 5 C-collected group's rate (50 vs. 178 µl O_2 g^{-1} h^{-1}).

The warm-acclimatized 20, 25 and 30 C groups showed a similar pattern of controlled metabolic rates with a "preferred" summer rate around 800 µl O_2 g^{-1} h^{-1}. The 25 and 30 C acclimatization groups had lower metabolic rates when measured at their respective acclimatization temperatures than the other groups at 25 and 30 C (Fig. 9 and Table 9). This indicates that larvae exposed to stream temperatures around and above 25 C can depress their metabolism through

long-term acclimatization. The lower metabolic rates could be adaptive because they result in less metabolic heat loss, leaving more energy available for production. The acclimatization rates of the 20, 25 and 30 C-collected groups combined with the metabolic insensitivity to acute changes in temperature shown by the 20 and 30 C acclimatization groups between 20 and 30 C resulted in the fairly constant metabolic rates around 800 µl O_2 g^{-1} h^{-1} of larvae during the summer months from May through September.

Table 12 gives mean respiration rates for each major stage in the life cycle of *C. cornutus* acclimatized to 28 C, except for the specific larval instars (2-11), and the estimated metabolic heat loss during each stage. First instar larvae had respiration rates slightly over three times as high as eggs. There were no significant differences detected among first instar larvae measured at 25, 28 and 30 C ($t = 0.28$ to -1.16; $P < 0.05$), and there were no differences among prepupae, female pupae and male pupae ($t = 0.12$ to 1.6; $P < 0.05$) or between male adults and female adults ($t = 1.27$; $P < 0.05$). Adult respiration rates were nearly twice as high as the rates of pupating stages.

Production

The estimated N m^{-2} of larvae in each 0.5 mm HCW size class measured at each sampling date are given in Table 13. These estimates (ecological density), for the 363 m^2 of

Table 12. Mean respiration rates and total metabolic heat loss of the stages in the life cycle of *C. cornutus* acclimatized at 28 C except specific instars 2-11.

Development Stage	Temp °C	N*	Respiration µl O_2 h^{-1}±SD	$\bar{X}$ wt (mg)	Respiration µl O_2 g^{-1} h^{-1}±SD	Time (h)	R (cal)
Egg	28	16	0.13±0.04	0.044	3,009±910	336	0.214
First Instar	25	29	0.46±0.19	0.044	10,482±4,325		
	28	10	0.44±0.06	0.044	10,092±1,377		
	30	18	0.60±0.13	0.044	13,751±2,887		
Prepupa	28	22	440.67±168	372.5	1,564±657	168	357.12
Pupa, female	28	12	560.57±141	382.9	1,464±367	168	454.39
Pupa, male	28	11	627.85±175	435.1	1,443±402	168	508.94
Adult, female	28	26	906.45±316	371.8	2,438±850	168	734.77
Adult, male	29	16	768.59±155	280.2	2,743±554	168	623.02

*N represents a mean of 3-6 measurements; 50 or 100 first instar were used in each respirometer vessel.

**Metabolic heat loss of first instar larvae was obtained using a regression equation prepared from 30 C acclimatization data of larger larvae (estimate = 0.50 µl O_2 h^{-1} = 0.0058 cal day^{-1}).

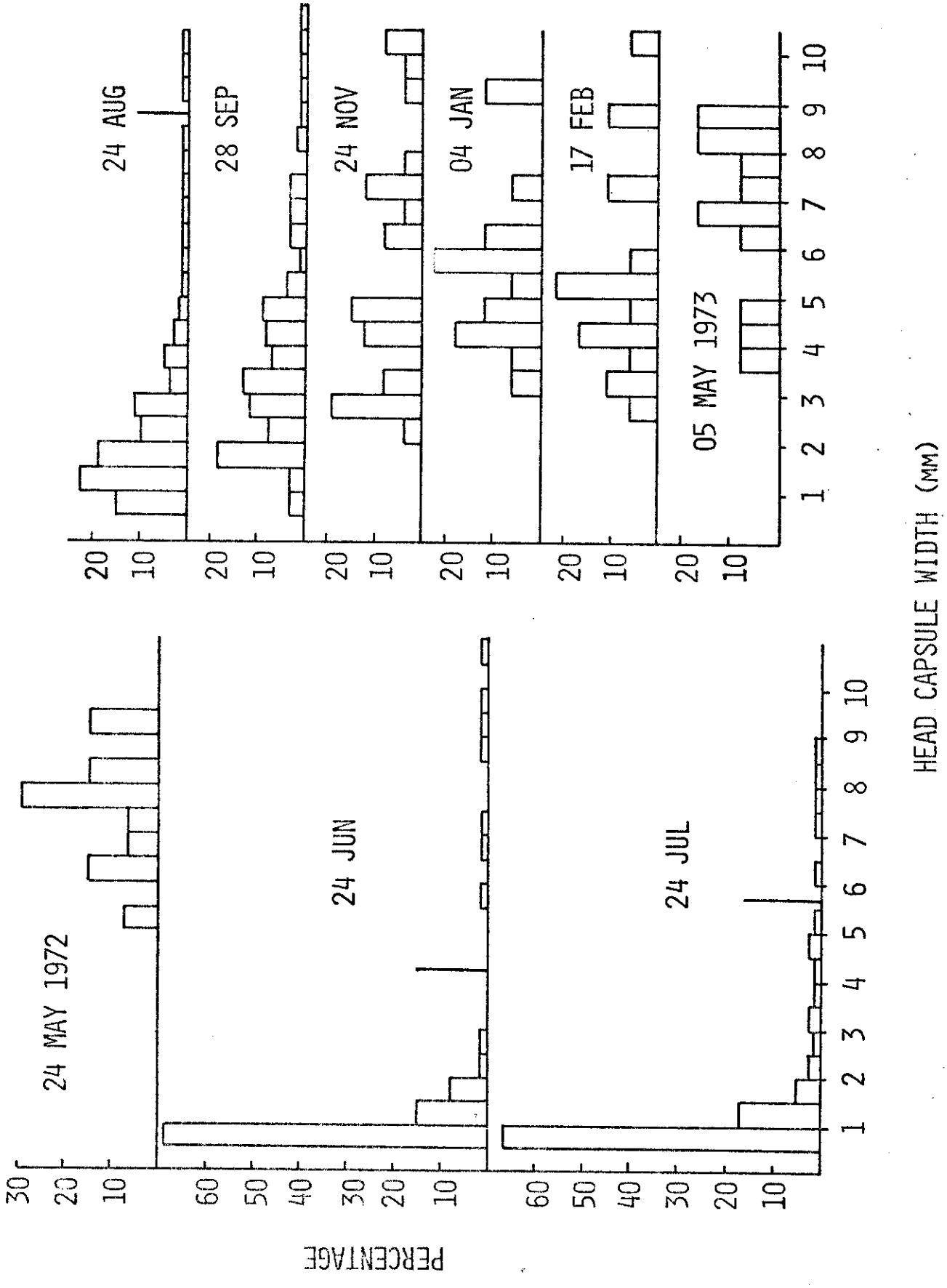
Table 13. The number of *Corydalus cornutus* larvae per square meter, by 0.5 mm HCW size class at each sampling date, 1972-1973.

HCW Size Class (mm)	24 May	24 Jun	24 Jul	24 Aug	28 Sep	24 Nov	04 Jan	17 Feb	05 May	Cohort Totals
0.5- 0.9		26.61	150.89	17.75	.99					196.24
1.0- 1.4		5.91	38.46	26.63	.99					71.99
1.5- 1.9		2.96	11.83	22.68	6.90					44.37
2.0- 2.4		.16	4.64	12.64	2.88	.16				20.48
2.5- 2.9		.24	2.24	12.80	4.16	.80		.08		20.32
3.0- 3.4			5.12	5.60	4.64	.32	.08	.16		15.92
3.5- 3.9			2.24	6.08	2.56		.08	.08	.08	11.12
4.0- 4.4			1.44	3.04	2.88	.48	.24	.24	.08	8.40
4.5- 4.9			3.68	1.76	3.04		.16	.08	.08	8.80
5.0- 5.4	.08		1.60	1.44	1.44	.64	.08	.32		5.52
5.5- 5.9		.08		.80	.16		.32	.08		1.36
6.0- 6.4	.16		.32	1.28	1.12	.32	.16		.08	2.96
6.5- 6.9	.08	.08		.64	.96	.16			.16	1.92
7.0- 7.4	.08	.16	.32	.48	.96	.48	.08	.16	.08	2.24
7.5- 7.9	.32		.64	.48		.16			.08	.72
8.0- 8.4	.16		.16	.48	.64				.16	1.28
8.5- 8.9		.08	.16		.16			.16	.16	.48
9.0- 9.4	.16	.24		.48	.16	.16	.16			.48
9.5- 9.9		.40		.16	.16	.16				.32
10.0-10.4				.16	.32	.32		.08		.72
10.5-10.9		.16			.16					.16
COHORT TOTALS	1.04	35.88	222.14	114.58	35.28	4.16	1.36	1.44	.96	315.80

riffles in the total 1450 m^2 of stream bottom in the study area, must be multiplied by 0.25 to express density in terms of the entire stream bottom (crude density). Figure 11 gives the percentage of larvae in each size class on each sampling date. Examination of Figs. 1 and 11, and Table 13 shows that larvae hatched from early June until late September and exhibited a wide size range during most of the year. The first instar larvae appeared in greatest numbers in the 24 July sample (Table 13). This accords with estimates of peak emergence of adults (24 June), oviposition (1 July) and hatching (15 July). The relative numbers of larvae present on 24 May 1972 (1.04 m^{-2}) and 5 May 1973 (0.96 m^{-2}) support the assumption that the population was in steady state.

Division of the 1971-1972 and the 1972-1973 cohorts, indicated on Fig. 11 and Table 13, was based on the estimated growth rates of larvae. The maximum growth rate observed in the rearing cages placed in the riffles (Fig. 2) was 3 mm HCW during the month of September. The larvae may grow faster during the spring than in the fall, but it is doubtful they grew from 2.9 mm HCW to 8.5 mm HCW (5.6 mm) from 24 June to 24 July or from 5.4 mm HCW to 10.4 mm HCW between 24 July and 24 August. Thus, the cohorts were divided on 24 July at the gap between 5.4 mm HCW and 6.0 mm HCW and on 24 August at the gap between 8.4 mm HCW and 9.0 mm HCW. The few (0.8 m^{-2}) large larvae present on 24 August, assumed to be part of the 1971-1972 cohort, could have emerged during the summer of

Fig. 11. Head capsule width frequencies by percentage of larvae of *Corydalus cornutus* in the 1972-1973 cohort. The cohorts is indicated by a vertical line.


24 MAY 1972
24 JUN
24 JUL
24 AUG
28 SEP
24 NOV
04 JAN
17 FEB
05 MAY 1973
PERCENTAGE
HEAD CAPSULE WIDTH (MM)

1972 (one adult was collected as late as 22 September of that year); or some of them may have taken 2 years to complete their life cycle. Even if there is an error in cohort separation and all larvae from the 1971-1972 cohort emerged prior to 24 July 1972, the N m^{-2} for July and August would be underestimated by only 0.7% each.

Production was calculated by Eq. 10 and the results are given in Table 14. Algebraic-summation of the sampling interval production estimates shows an annual cohort production estimate of 2.51 g m^{-2}. The mean annual standing crop (0.252 g m^{-2}) divided by the total annual production gives an annual turnover ratio (Waters 1969, Waters and Crawford 1973) of 9.96. This is 10% higher than the life cycle, (= annual) instantaneous growth rate (8.96) for hellgrammites calculated by:

$$\log_n \left(\frac{\text{final instar } \overline{wt}}{\text{first instar } \overline{wt}} \right) \quad . \qquad (10)$$

Feeding Study

Table 15 gives the rates of C, F and A and the AE values for hellgrammites acclimated to 10, 15, 20, 25 and 30 C. Larvae acclimated to 5 C did not feed during the 5-day feeding experiment and only 44% (n = 11) of the 10 C-acclimated larvae fed. Mean rates for the 10 C group were calculated for only the 11 larvae that fed during the 5-day period. The

Table 14. Calculation of annual production of *Corydalus cornutus* larvae by the instantaneous growth method.

Sample Date	$N m^{-2}$	$\overline{wt}$ (mg)	B $g m^{-2}$	G	<B> $(g m^{-2})$	P $(g m^{-2})$
24 Jun	35.88	0.29	0.011			
				0.936	0.087	0.081
24 Jul	222.14	0.74	0.164			
				1.829	0.346	0.632
24 Aug	114.58	4.61	0.528			
				1.503	0.629	0.945
28 Sep	35.28	20.73	0.731			
				1.195	0.508	0.607
24 Nov	4.16	68.53	0.285			
				0.083	0.193	0.016
04 Jan	1.36	74.44	0.101			
				-0.046	0.101	-0.004
17 Feb	1.44	71.10	0.102			
				0.596	0.113	0.067
05 May	0.96	129.06	0.124			
				0.972	0.171	0.166
24 Jun*	0.64	341.2	0.218			
			$\overline{X}$ = 0.252			Total = 2.510

*No sample was taken 24 June 1973; the $N m^{-2}$ (0.64) was calculated by assuming that the mortality rate between 5 May and 24 June was equal to the previous interval; the weight (341.2 mg) is based on the mean HCW of final instar larvae (9.5 mm).

Table 15. Mean rates of consumption, egestion and assimilation, and assimilation efficiencies of *C. cornutus* larvae acclimated to 10, 15, 20, 25 and 30 C. Larvae acclimated to 5 C did not feed or defecate.

Acclimation Temp (°C)	Number	dry $\overline{wt}$ (mg)±SD	C		F		A		AE
			cal day^{-1}±SD	cal g^{-1} day^{-1}±SD	cal day^{-1}±SD	cal g^{-1} day^{-1}±SD	cal day^{-1}±SD	cal g^{-1} day^{-1}±SD	%±SD
10	25	242±184	7±3	56±75	1±1	8±8	6±3	48±68	85±6
15	23	220±180	15±9	100±61	3±2	14±7	12±8	85±54	81±11
20	25	238±157	64±43	357±205	6±3	41±34	58±42	316±190	85±13
25	25	217±139	73±39	435±297	10±5	63±34	63±36	382±302	82±10
30	22	179±122	100±49	680±248	15±6	124±76	85±46	556±206	82±8

weight of chironomids consumed by each larva and the weight of feces produced were converted to calories using empirically-determined values (chironomids = 5155±97 cal g^{-1}, n = 6; feces = 4023±39, n = 3).

Table 16 gives the statistical comparison of mean weight-specific rates of C, F and A and the AE values among acclimation groups. Rates of C and A were not significantly different between 20 and 25 C. The rates of the 20 and 25 C groups were generally four-five times higher than those of the 15 C group. This supports the observation for respiration rates that there is a metabolic rate change-point between 15 and 20 C in this population of hellgrammites. Assimilation efficiencies were not significantly different among the acclimation temperatures. Linear regressions of larval weight versus consumption in cal day^{-1} per larva (Fig. 12) illustrate the metabolic change-point between 15 and 20 C in whole-animal consumption rates.

Results of two-factor ANOVA on weight-specific rates of C, F and A and AE (Table 17) show that both acclimation temperature and weight significantly affected the rates of C, F and A, but there were no significant interaction effects between weight and temperature. Neither temperature nor weight effected AE values.

Analyses of covariance were used because of variations in larval weight within and among acclimation groups to determine the effects of temperature on the rates (Table 18). The

Table 16. Comparisons among mean rates of consumption, defecation and assimilation expressed as cal g^{-1} day^{-1} and assimilation efficiencies for *C. cornutus* larvae acclimated to 10, 15, 20, 25 and 30 C using Students' t-tests.*

	Acclimation Temperature				
Variable	10	15	20	25	30
C	56	100	357	435	680
F	8	13	41	63	124
A	48	85	316	382	556
AE	85	81	85	82	82

*Means not underscored by a common line are significantly different ($P < 0.05$).

Fig. 12. Consumption rates for *C. cornutus* larvae acclimated to 10, 15, 20, 25 and 30 C as a function of their dry weight.

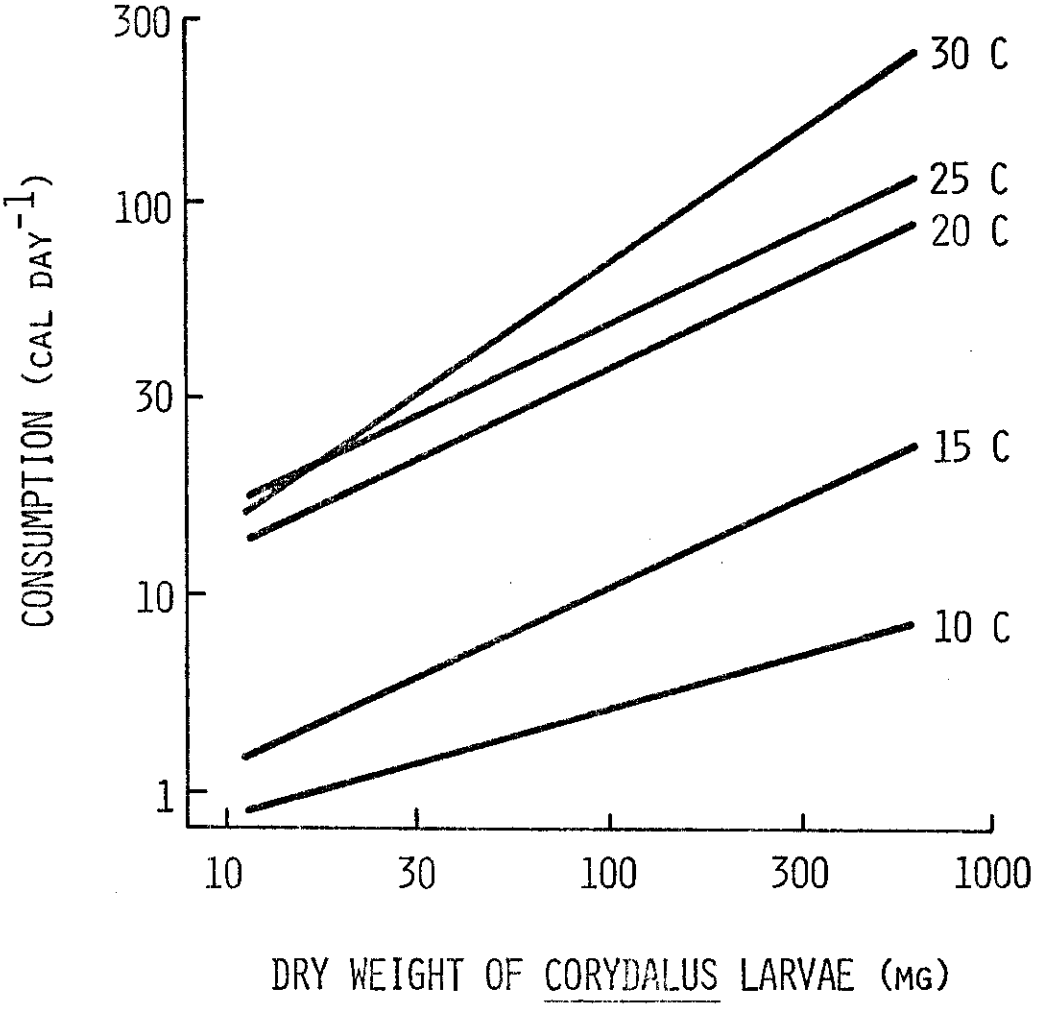

300
100
30
10
1
CONSUMPTION (CAL DAY^{-1})
30 C
25 C
20 C
15 C
10 C
10
30
100
300
1000
DRY WEIGHT OF CORYDALUS LARVAE (MG)

Table 17. Results of four two-factor ANOVA to assess the effects of acclimation temperature and weight on the rates of consumption, egestion and assimilation and assimilation efficiencies of *C. cornutus* larvae.

	Source of Variance	MS	DF	F-ratio	Probability
C	Temperature	1,212,802	3	34	<0.01
	Weight	604,249	2	18	<0.01
	Interaction	47,923	6	3	<0.21
	Error	33,404	83		
F	Temperature	38,567	3	49	<0.01
	Weight	52,967	2	13	<0.01
	Interaction	8,024	6	1	<0.02
	Error	2,909	83		
A	Temperature	849,575	3	26	<0.01
	Weight	343,626	2	16	<0.01
	Interaction	54,423	6	3	<0.16
	Error	33,939	83		
AE	Temperature	55	3	0.45	<0.72
	Weight	56	2	0.46	<0.64
	Interaction	127	6	1.04	<0.41
	Error	123	83		

Table 18. Results of four one-factor ANCOVA to assess the effects of temperature on the rates of consumption, egestion and assimilation and assimilation efficiencies of *C. cornutus* larvae.

Variable	Source of Variance	MS	DF	F-ratio	Probability
C	Temp	1,134,176	3	31.8	<0.001
	Error	35,634	90		
F	Temp	38,946	3	10.5	<0.001
	Error	3,714	90		
A	Temp	771,310	3	21.7	<0.001
	Error	35,503	90		
AE	Temp	84	3	0.7	<0.561
	Error	123	90		

F-tests show that acclimation temperature had a significant effect ($P < 0.001$) on rates on C, F and A but no apparent effect on AE ($P = 0.56$).

Individual Energy Budget

The energy budget was constructed for the typical dobson fly in the 1972-1973 cohort that began life as an egg on 1 July 1972, took 2 wk to incubate, and hatched on 14 July. After about 47 wk (14 July 1972 to 10 June 1973) of development, the larva left the stream, spent 1 wk as a prepupa (10 June-17 June), another week as a pupa (17 June-24 June), and then emerged as an adult. The average adult female died on approximately 1 July after depositing her eggs and completing her life cycle.

Energy lost as metabolic heat (R) by a typical larva during development was calculated according to Eq. 5 and is given in Table 19. The values of R for the typical egg, prepupa, male pupa, female pupa, adult male and adult female are given in Table 12.

Growth (P_g) for the typical larva was calculated as the difference between the biocontent of the average prepupa and a first instar larva (2074.83 - 0.27 = 2074.56 cal). Total P_{ev} (Table 20) was calculated according to Eq. 6 using the biocontent for larval exuviae given in Table 3 (4171 cal g^{-1}) and the weight of the exuvium at each molt. Weight of the

Table 19. Summation of energy lost as metabolic heat for a typical hellgrammite integrating the effects of weight and temperature.*

Temp °C	Time (days)	$\overline{wt}_1$ (mg)	$\overline{wt}_2$ (mg)	Δwt/day (mg)	Regression Coeff a	Regression Coeff b	R (ml O_2)	R (cal)
30	49	0.4	6.6	0.13	0.62	0.66	10.2	49.2
25	27	6.6	16.4	0.36	0.51	0.65	10.0	48.3
20	11	16.4	24.6	0.75	0.67	0.61	7.7	37.2
15	27	24.6	48.1	0.87	0.24	0.65	11.7	56.5
10	25	48.1	74.9	1.07	-0.12	0.81	12.7	61.3
5	79	74.9	74.9	0	-0.40	0.82	26.1	125.9
10	6	74.9	76.0	0.18	-0.12	0.81	3.6	17.4
15	65	76.0	121.0	0.69	0.24	0.65	55.2	266.3
20	6	121.0	129.1	1.35	0.67	0.61	12.8	61.8
20	12	129.1	154.0	2.08	0.67	0.61	27.6	133.2
25	24	154.0	341.2	7.80	0.51	0.65	64.7	312.1
						Total	242.3	1169.2

*The 47-wk larval development period was divided into 11 segments of temperature, each with specific growth rates. An iterative summation program based on Eq. 5 was used to linearly increment weight daily and calculate the values of R.

Table 20. Production of exuviae by a typical *C. cornutus* larva during its aquatic development.

Molt No.	HCW of Larva Before Molt	Weight of Exuvium (mg)	Biocontent (cal)
1	0.5	0.044	0.19
2	0.7	0.095	0.41
3	0.9	0.168	0.72
4	1.3	0.386	1.66
5	1.9	0.909	3.90
6	2.7	2.008	8.62
7	3.5	3.606	15.47
8	4.6	6.681	28.66
9	6.0	12.166	52.19
10	7.5	20.126	86.34
		Total	198.16

exuvium at each molt was obtained from the HCW-exuvial weight relationship (Fig. 13).

The total energies of C, F and A for a typical hellgrammite using regression coefficients to calculate C, according to Eq. 4, are given in Table 21. Assimilation was calculated as C x AE and F as C - A. Since empirical data for C were obtained for larvae from 19.4 mg to 610.7 mg among the five temperature groups, rates of the larva from 0.044 mg (1st instar) to 19.4 mg had to be obtained by extrapolation from the regression equations. Alternatively, C can be estimated by the equation:

$$C = (P_g + P_{ev} + R)/(AE) \qquad (11)$$

for the three intervals when the larva was below 19.4 mg, or for each of the intervals, in Table 22. All three estimates of C and the resulting energy budgets are given in Table 22.

The estimate of C derived from Eq. 11 is probably the best estimate because: (1) the laboratory feeding rates of *Pyrrhosoma nymphula* fed *ad libidum* have been reported to overestimate feeding rates in the field by 20-70%, whereas C estimates based on $P + R + E_V + F$ compared well with estimates of field feeding rates calculated from gut clearance times (Lawton 1971b); (2) Stewart et al. (1973) reported that stomachs of only 121 (25.9%) of the 468 *C. cornutus* collected from the Brazos River, Texas contained food during February to May when temperatures were probably between 10-20 C, whereas 44-100% of

Fig. 13. Production of exuviae in *Corydalus cornutus* in relation to larval head capsule width before molting.

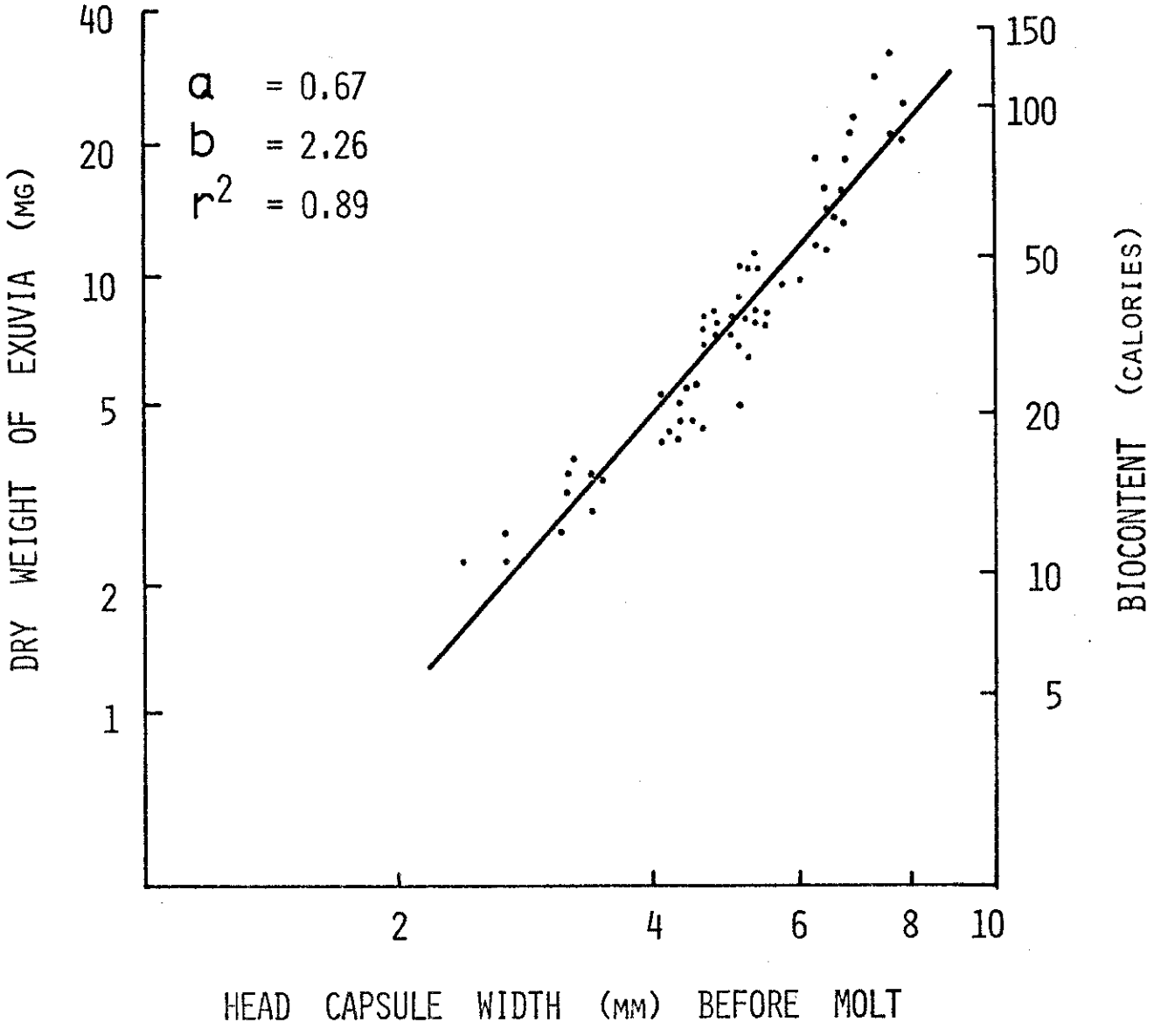

a = 0.67
b = 2.26
r2 = 0.89
DRY WEIGHT OF EXUVIA (MG)
BIOCONTENT (CALORIES)
HEAD CAPSULE WIDTH (MM) BEFORE MOLT
40
20
10
5
2
1
150
100
50
20
10
5
2
4
6
8
10

Table 21. Summation of energies of consumption, egestion and assimilation for a typical hellgrammite integrating the effects of weight and temperature.*

Temp °C	Time* (days)	$\overline{wt}_1$ (mg)	$\overline{wt}_2$ (mg)	Δwt/day (mg)	Regression Coeff a	Regression Coeff b	C (cal)	F (cal)	A (cal)	AE
30	49	0.04	6.6	0.13	0.50	0.67	336.2	60.5	275.7	0.82
25	27	6.6	16.4	0.36	0.74	0.47	473.4	95.2	388.2	0.82
20	11	16.4	24.6	0.75	0.65	0.46	201.7	30.3	171.4	0.85
15	27	24.6	48.1	0.87	0.12	0.45	196.3	37.3	159.0	0.81
10	25	48.1	74.9	1.07	0.16	0.27	53.5	8.0	45.5	0.85
5	79	74.9	74.9	0	-	-	0	0	0	-
10	6	74.9	76.0	0.18	0.16	0.27	13.6	2.0	11.6	0.85
15	65	76.0	121.0	0.69	0.12	0.45	731.6	139.0	592.6	0.81
20	6	121.0	129.9	1.35	0.65	0.46	252.2	37.8	214.4	0.85
20	12	129.0	154.0	2.08	0.65	0.46	534.4	80.1	454.3	0.85
25	24	154.0	341.2	7.80	0.74	0.47	1761.8	317.1	1444.7	0.82
						Total	4554.7	797.3	3757.4	

*The 47-wk larval development period was divided into 11 segments of temperature, each with specific growth rates. An iterative summation program based on Eq. 4 was used to linearly increment weight daily and calculate the values of C.

Table 22. A comparison of three energy budgets calculated for a typical individual *C. cornutus* larvae based on three methods of estimating consumption.

A. Based on regression coefficients (Table 19).

	calories	% of C	% of A
C	4,555	-	-
A	3,757	82.5	-
F	798	17.5	-
P_g	2,075	45.6	55.2
P_{ev}	198	4.3	5.3
R	1,169	25.7	31.1

B. Based on Eq. 11 while larva was small ($\bar{<}$ 24.6 mg) and regression coefficients (Table 19) when larger.

	calories	% of C	% of A
C	3,899	-	-
A	3,217	82.5	-
F	682	17.5	-
P_g	2,075	53.2	64.5
P_{ev}	198	5.1	6.2
R	1,169	30.0	36.3

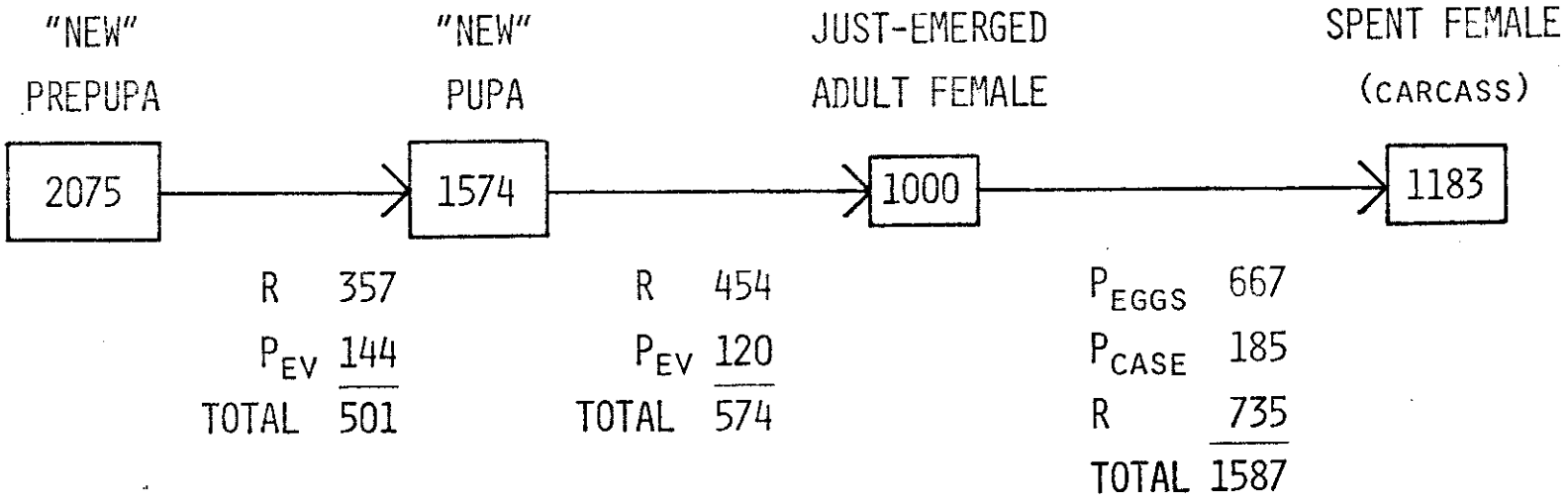
C. Based entirely on Eq. 11.

	calories	% of C	% of A
C	4,167	-	-
A	3,442	82.6	-
F	725	17.4	-
P_g	2,075	49.8	60.3
P_{ev}	198	4.8	5.8
R	1,169	28.1	34.0

the larvae in this study fed at similar temperatures; and (3) there was greater variability in the laboratory-determined rates of C than for the other components of the energy budget (P_g, P_{ev}, R, AE). Therefore, although the three methods yield similar results, further calculations concerning the individual energy budget were based on the energy budget derived from Eq. 11 given in Table 22C. The P_r (851.8 cal) for the typical female dobson fly was calculated by adding the average total biocontent of eggs (667.2 cal) and egg covering materials (184.6 cal) dissected from gravid females (Table 3).

The energetics of a female dobson fly from the time she left the water to pupate until her death is summarized in Fig. 14 using the data from Tables 3 and 12. The typical prepupa (sex undetermined) left the stream with an approximate biocontent of 2075 cal (Table 3). The prepupa expended about 357 cal as R and shed an exuvium of 144 cal. Thus, the new pupa should have begun with a total biocontent of 1574 cal. This is 532 cal lower than the value given in Table 3 for female pupae because of a difference in estimated mean weights of prepupa and female pupae. During the pupal stage, 454 cal were lost as R and 120 cal were shed in the pupal exuvium leaving approximately 1000 cal for the emergent female. This accords with the actual bioconetnt of four newly-emerged females (1314 cal; Table 3). Since the newly-emerged female did not contain yolked eggs or egg covering material, she must

Fig. 14. The estimated biocontent and energy allocation of each metamorphic stage and the adult of the typical *Corydalus cornutus* female from beginning pupation until death. Biocontent of the "new" prepupa and spent female were taken from Table 3; biocontent of the "new" pupa and just-emerged female are estimates based on R and P_{ev} losses.


"NEW"
PREPUPA
"NEW"
PUPA
JUST-EMERGED
ADULT FEMALE
SPENT FEMALE
(CARCASS)
2075
1574
1000
1183
R 357
P_{EV} 144
TOTAL 501
R 454
P_{EV} 120
TOTAL 574
P_{EGGS} 667
P_{CASE} 185
R 735
TOTAL 1587

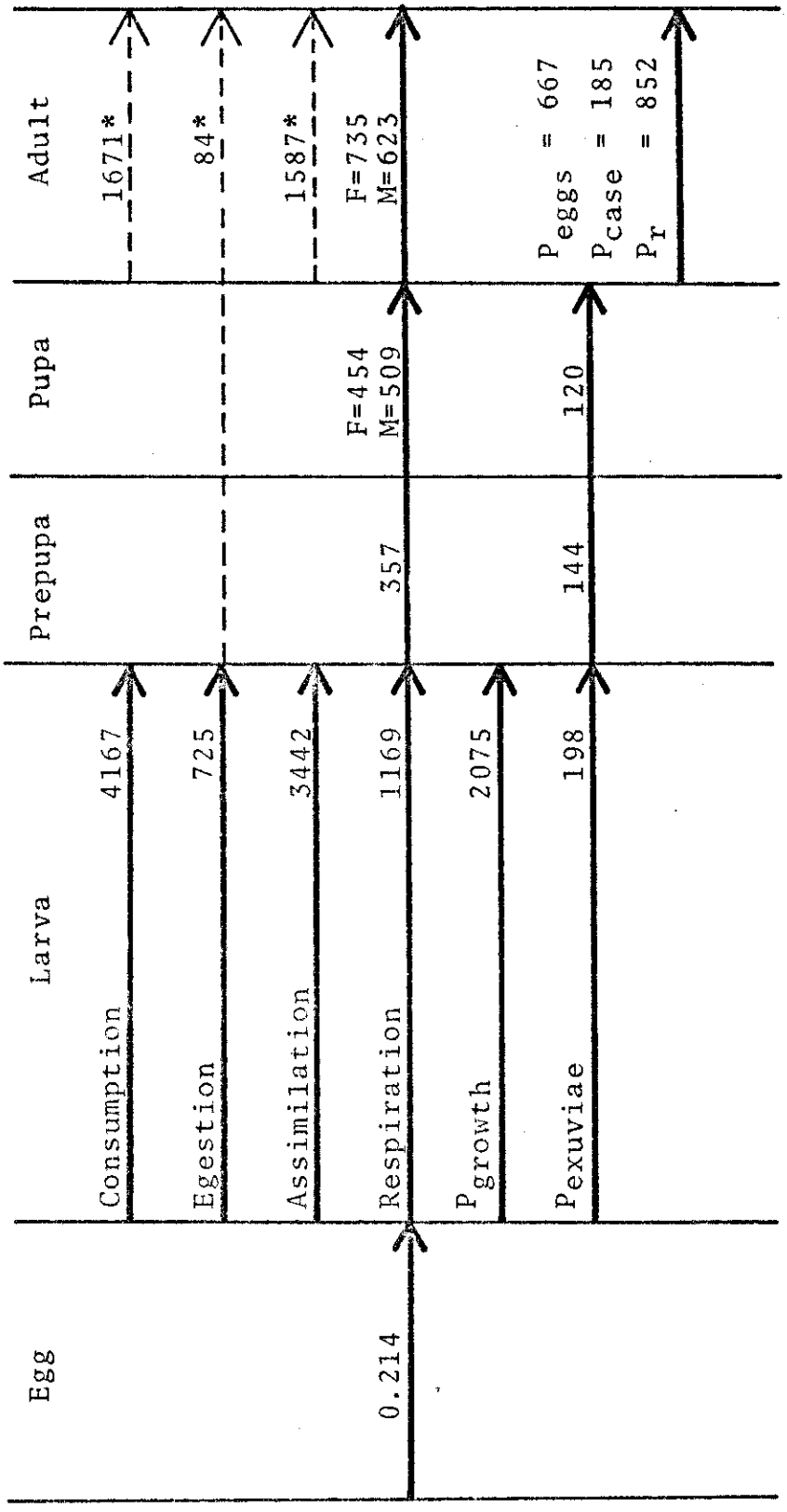
have produced 667 and 185 cal respectively between emergence and oviposition (ca. 7 days). During this period her minimal energy lost as R was 735 cal. Thus, the minimal total energy expended by the adult female ($R + P_r$) was 1587 cal, which is slightly more than her total biocontent at emergence. Since the biocontent of the typical spent female (1183 cal) is not significantly different ($t = 1.67$; $P > 0.05$) from recently-emerged females, a minimum of 1587 cal must have been consumed. This energy could be obtained from less than 0.5 ml of fruit juice (ca. 4000 cal g^{-1}).

If the AE for readily-absorbed fruit juices is at least 95%, a female must consume 1671 cal to supply the 1587 cal needed for P_r and R. Male dobson flies probably do not feed. Their large mandibles ($\bar{X}$ = 24.4 mm) probably preclude feeding, and they do not require the energy for producing egg masses that females do. Males were observed to drink only water in the laboratory and not fruit juices.

Although quantitative feeding studies were not run on adults, qualitative feeding studies in the laboratory support the contention that they must feed in the field. Ripe hackberry (*Celtis laevigatus*) fruit are abundant around the stream and are a potential source of nutrition for the adults.

The energy budget for the typical female dobson fly from egg through adult is summarized in Fig. 15. Since there is no parental care, a female dobson fly's total RE is equivalent to the biocontent of her egg masses (852 cal), which is 50.1

Fig. 15. Summary of the life cycle energy budget of a dobson fly, *Corydalus cornutus*, from egg through adult with all values expressed in cal per individual.



*Estimated values—see text for explanation.

and 53.7% of her adult C and A, respectively. In a steady state or equilibrium population, the minimal cost to a female to replace herself is equivalent to the percentage of her lifetime A which is allocated to P_r (852/4029 cal = 17%).

An instantaneous measure of RE is the ratio of P_r to some quantitative measurement of the female's carcass (e.g., ova cal/carcass cal, $\overline{wt}$ of ova/$\overline{wt}$ of carcass and $\overline{N}$ of eggs/female). This instantaneous method applied to *C. cornutus* yields RE estimates of 852 cal/1220 cal = 70%, 130.7 mg/234.8 mg = 56% and 2976 ova per female respectively (based on values in Table 3).

Population Energy Budget

The annual energy budget for the 1972-1973 cohort was calculated based on the assumptions that the cohort began on 24 June 1972 and left the stream by 24 June 1973. The annual energy lost as metabolic heat was calculated with Eq. 8, and the results are given in Table 23. The caloric equivalent of P_g (13,052 cal m^{-2}) was determined by multiplying the production estimate (2.51 g m^{-2}; Table 14) by the mean caloric value of larvae (5200±254 cal g^{-1}). The energy lost as P_{ev} was calculated with Eq. 9 after assigning each of the 10 molts to the appropriate sampling interval (Table 24) and using the caloric value of each exuvium in Table 20. Consumption was calculated in three ways: (1) according to Eq. 7 as shown in Table 25; (2) with Eq. 11 for small (< 20.7

Table 23. Summation of energy lost as metabolic heat by the 1972-1973 cohort of *C. cornutus* larvae integrating the effects of weight and temperature.

Sample Date	N m^{-2}	$\overline{wt}$ (mg)	$\langle N\ m^{-2} \rangle$	$\langle wt \rangle$ (mg)	°C	R µl O_2 $larva^{-1}$ h^{-1}	R µl O_2 h^{-1}	Time (h)	R ml O_2	R cal
24 Jun	35.88	0.3								
			129.0	0.5	30	2.7	343	720	247	1192
24 Jul	222.14	0.7								
			168.4	2.7	30	8.1	1361	744	1018	4887
24 Aug	114.58	4.6								
			74.9	12.7	30	22.5	1683	168	283	1365
					25	16.7	1252	672	841	4058
28 Sep	35.28	20.7								
					20	47.5	938	264	247	1193
			19.7	44.6	15	20.8	411	648	266	1284
					10	16.4	324	456	148	713
24 Nov	4.16	68.5								
					10	24.1	66	120	8	39
			2.8	71.5	5	13.3	32	864	32	153
04 Jan	1.36	74.5								
			1.4	72.8	5	13.5	19	1056	20	96
17 Feb	1.44	71.1								
					10	31.6	38	168	6	31
			1.2	100.1	15	35.3	42	1536	65	314
					20	77.8	93	120	11	54
05 May	0.96	129.1								
					20	131.1	105	312	33	158
			0.8	235.2	25	110.4	88	576	51	245
					30	154.2	123	336	42	200
24 Jun	0.64	341.2								
								Total	3312	15,982

Table 24. Production of exuviae by the 1972-1973 cohort of *C. cornutus* larvae during their aquatic development.

Sample Date	N m^{-2}	$\langle N\ m^{-2} \rangle$	Molt No.	cal ev^{-1}	P_{ev} cal m^{-2}
24 Jun	35.88				
			1	0.19	24.51
		129.01	2	0.41	52.89
			3	0.72	92.89
24 Jul	222.14				
			4	1.66	279.48
		168.36	5	3.90	656.60
24 Aug	114.58				
			6	8.62	645.90
		74.93	7	15.47	1,159.17
28 Sep	35.28				
		19.72	8	28.66	565.18
24 Nov	4.15				
		2.76	-		
24 Jan	1.36				
		1.40	-		
17 Feb	1.44				
		1.20	9	52.19	62.63
05 May	0.96				
		0.80	10	86.34	69.07
24 Jun	0.64				
				TOTAL	3,608.32

Table 25. The annual consumption of the 1972-1973 cohort of *Corydalus cornutus* larvae.*

Date	N m^{-2}	$\overline{wt}$ (mg)	<N m^{-2}>	<wt> (mg)	Temp °C	C cal $larva^{-1}$ day^{-1}
24 Jun	35.88	0.3				
			129.01	0.5	30	1.4
24 Jul	222.14	0.7				
			168.36	2.7	30	6.2
24 Aug	114.58	4.6				
					30	17.4
			74.93	12.7	25	18.1
28 Sep	35.28	20.7				
					20	25.6
			19.72	44.6	15	7.3
					10	4.0
24 Nov	4.16	68.5				
					10	4.6
			2.76	71.5	5	0
04 Jan	1.36	74.5				
			1.40	72.8	5	0
17 Feb	1.44	71.1				
					10	5.0
			1.20	100.1	15	10.5
					20	37.2
05 May	0.96	129.1				
					20	55.1
			0.80	235.2	25	71.5
					30	122.7
24 Jun	0.64**	341.2				

*Each sampling interval was divided into appropriate temperature intervals and C was calculated according to Eq. 7.

**No sample was taken 24 June 1973; the N m^{-2} (0.64) was calculated by assuming that the mortality rate between 5 May and 24 June was equal to the previous interval; the weight (341.2 mg) is based on the mean HCW of final instar larvae (9.5 mm).

Table 25--Continued

Interval (days)	C cal Interval^{-1}	C cal day^{-1}	F cal	A cal	AE
30	5,457	181.9	982	4,475	0.82
31	32,098	1,035.4	5,778	26,320	0.82
7	9,105	1,300.8	1,639	7,466	0.82
28	38,072	1,359.7	6,853	31,219	0.82
11	5,559	505.4	834	4,725	0.85
27	3,876	143.6	736	3,140	0.81
19	665	35.0	100	565	0.85
5	28	5.5	4	24	0.85
36	0	0	0	0	-
44	0	0	0	0	-
7	19	2.6	3	16	0.85
64	805	12.6	153	652	0.81
5	223	44.6	33	190	0.85
13	573	44.1	86	487	0.85
24	1,374	57.2	247	1,127	0.82
14	1,374	98.2	247	1,127	0.82

larvae and Eq. 7 for larger larvae; and (3) with Eq. 11 for all larvae. The resultant energy budgets are given in Table 26. The first method (Table 26A) using Eq. 7 apparently seriously overestimates for the small larvae. The third form of the energy budget using Eq. 11 (Table 26C) probably represents the cohort energy budget most accurately.

The allocation of energy to P_r by the cohort was estimated by two methods. The first was calculated by

$$P_r = (0.96 \text{ larvae } m^{-2}) \times (852 \text{ cal } P_r/\text{female}) = 409 \text{ cal} \quad (12)$$

where 0.96 equals one-half the density of full-fed final instar larvae on 5 May (assumptions: 1:1 sex ratio and zero mortality until oviposition), and the second was calculated by

$$P_r = [(352 \text{ egg masses}/363 \text{ } m^2)/(2.3 \text{ egg masses/female})] \times (852 \text{ cal}) = 359 \text{ cal} \quad . \quad (13)$$

The estimates are 1.3% and 1.1% of cohort assimilation respectively.

Table 26. A comparison of three larval population energy budgets for *C. cornutus* based on three methods of estimating consumption.

A. Based on regression coefficients (Table 25).

	calories	% of C	% of A
C	99,228	-	-
A	81,533	82.2	-
F	17,695	18.8	-
P_g	13,052	13.2	16.0
P_{ev}	3,608	3.6	4.4
R	15,982	16.1	19.6

B. Based on Eq. 11 for small larvae ($\leq$ 20.7 mg) and on regression coefficients when larger (Table 25).

	calories	% of C	% of A
C	42,355	-	-
A	35,282	83.3	-
F	7.073	16.7	-
P_g	13,052	30.8	37.0
P_{ev}	3,608	8.5	10.2
R	15,982	37.7	45.3

C. Based entirely on Eq. 11.

	calories	% of C	% of A
C	39,518	-	-
A	32,642	82.6	-
F	6,876	17.4	-
P_g	13,052	33.0	40.0
P_{ev}	3,608	9.1	11.1
R	15,982	40.4	49.0

CHAPTER IV

DISCUSSION

Life History

Although emergence of adult *C. cornutus* with subsequent mating, oviposition and hatching is somewhat concentrated (Fig. 1), synchrony in these events is considerably less than in many other aquatic insects (e.g., mayflies; Lawton 1971a). Synchronous emergence must increase individual fitness by maximizing probability of finding mates, producing young at optimal times of the year, etc. Dobson flies of both sexes release a fetid liquid excrement that may be a pheromone for locating each other for mating. As long as hatching is completed before fall floods occur in north-central Texas, the only obvious disadvantage to a late-laying female dobson fly is that her offspring may require 2 yr to reach maximal emergence size. Since the probability of surviving 2 yr must be considerably less than for 1 yr, these late hatchlings (small, HCW < 3 mm, larvae that were present in fall and winter samples) may pupate and emerge at significantly smaller sizes than early hatchlings after only 1 yr. Collection of small (HCW < 7 mm) adults supports this hypothesis.

The univoltine life cycle and growth pattern (Fig. 1) exhibited by *C. cornutus* in north-central Texas are similar

to those of two other Megaloptera, *Sialis rotunda* and *S. californica*, in Oregon (Azam and Anderson 1969). The growth pattern suggests that larval growth is food or temperature dependent or both. Growth ceases during periods of low temperature ($\leq$ 10 C) and food scarcity (November-March). Rapid growth immediately after hatching (June-November) enables larval dobson flies to pass rapidly through periods of high mortality and take advantage of the abundant benthic insect fauna present during the late summer and fall. The number of instars reported here for *C. cornutus* accords with those in *S. rotunda* and *S. californica* (Azam and Anderson 1969). The duration of prepupal, pupal and adult stages of dobson flies in north-central Texas is similar to those of dobson flies in Minnesota (Parfin 1952) and Missouri (Davis 1903).

Although there are no definitive reports on feeding by adult dobson flies, there is some indirect evidence supporting my contention that females must feed. Parfin (1952) reported successfully feeding adults of both sexes honey-water solution for several days. Several workers have shown that adult megalopterans, including *C. cornutus*, are attracted to fermented molasses, fermented bananas, brown sugar and beer painted on stream-side trees (Brimley 1908, Champlain and Kirk 1926, Parfin 1952). DuBois and Geigy (1935) reported collecting *Sialis lutaria* with pollen on the head and thorax. Azam and Anderson (1969) found the same species with their "mouth parts

appressed to flowers"; but reported actual feeding was doubtful because their digestive tracts were not well-developed.

Most megalopterans do not produce egg cases. Instead they secrete an adhesive material which merely bonds the eggs to whatever substrate they are deposited on (Baker and Neunzig 1968). The adaptive value of the hard egg case produced by *C. cornutus* is undoubtedly protection afforded to the eggs. The color probably prevents excessive heating by reflecting light. The egg cases appear to virtually eliminate predation and parasitism, since only three egg masses in the thousand or so observed during the course of this study appeared to have been attacked. Azam and Anderson (1969) reported that about 14% of *S. rotunda* and 37-65% of *S. californica* eggs, which are not protected by egg cases, are destroyed by a hymenopteran parasitoid.

The number of ova in female dobson flies and in their egg masses in north-central Texas are approximately equal to reports by other workers. Riley (1879) reported that females from Missouri carried about 3000 ova. Baker and Neunzig (1968) reported that egg masses (n = 3) of *C. cornutus* in North Carolina contained a mean of 1080 ova.

Calorimetry

The pattern of variation in cal g^{-1} is definitely correlated to stages of development in the life cycle of *C. cornutus* (Tables 3 and 4, Fig. 6) and the season of the year.

The larvae store energy in autumn for use during brumation. During spring growth they continually increase in cal g^{-1} with a very rapid increase just prior to pupation, then decrease to approximately 500 cal g^{-1} during metamorphosis. The range and pattern of cal g^{-1} in *C. cornutus* are very similar to most values reported for other insects (Trama 1957, Woodland et al. 1958, Smalley 1960, Wiegert 1965b, Gyllenberg 1967, Mukerji and LeRoux 1969, McDiffett 1970, Schaefer and Washinko 1970, Hinton 1971, Lawton 1971a, McNeill 1971, Wissing and Hassler 1971, Bailey and Riegert 1973). Changes in caloric values of insects associated with the development of the larvae, metamorphosis and vitellogenesis are accompanied by changes in lipid content (Laughlin 1956, Moran 1959, Lambremont and Blum 1963, Strong 1963, Gilby 1965).

Respiration

The patterns of metabolic compensation exhibited by larval dobson flies (Figs. 8-10) enable them to maintain relatively constant "preferred" winter and summer rates, which conserve energy during periods when food is scarce and when temperatures are relatively high in the summer. The generally low metabolic rates and metabolic consistency result in energy savings which are allocated to production. The comparatively low metabolic rates in *C. cornutus* below 10 C suggest undercompensation (Precht et al. 1955, Precht 1958, Prosser 1974). The obvious selective value of undercompensation is

reduction in maintenance costs during periods of low food availability or reduced O_2 tensions or both. The former is the more likely cause for *C. cornutus*, which lives in flowing, highly-oxygenated water. Undercompensation or metabolic "shut-down" has been observed in numerous aquatic and semi-aquatic vertebrate poikilotherms (e.g., Pocrnjić 1965, Roberts 1966, Dunlap 1969, 1971, Fitzpatrick et al. 1971, 1972, Fitzpatrick 1973a), and several invertebrates (e.g., Berg 1953, Korg 1954, Bert et al. 1958, Burky 1971). Similarly, adaptive patterns of partial metabolic compensation (Precht et al. 1955, Precht 1958, Prosser 1974) have been observed in numerous vertebrates and invertebrates (e.g., Edwards and Irving 1943a, b, Bishop and Gordon 1967, Roberts 1967, Dunlap 1969, 1971, Vernberg 1969, Newell and Pye 1970, Dame 1972, Fitzpatrick 1972a, b, Miller and Mann 1973). However, there are only a few reports of metabolic compensation in insects. Pattée (1955) reported partial acclimatization to temperature by *Libellula* and possible acclimatization by *Pyrrhosoma* (two odonates). Lawton (1971a) studied *P. nymphula* and reported that it if acclimatized it was immediate (Bullock 1955), occurring within 1 h. Bullock (1955) discussed studies by Parhon (1909) and Sayle (1928) which reported temperature acclimation in bees and dragonfly nymphs respectively, but then stated that "In spite of these cases it is believed that insects may be relatively poor in ability to compensate." Bullock's opinion was reiterated by Keister and Buck (1964).

Edwards (1957) reported that *Chironomus plumosus* does not show acclimation to temperature.

Whether or not insects as a group characteristically show metabolic compensation to temperature is unknown. The most likely candidates are aquatic forms, such as *C. cornutus*, that live at least 1 yr in temperate zones.

The relationship between body weight and O_2 consumption has received considerable attention (e.g., Needham 1942, Edwards 1946, 1957, Bertalanffy 1951, 1957, Bertalanffy and Krywienczyk 1953, Zeuthen 1953, Kleiber 1961) and will not be reviewed here. The values for the slope b in *C. cornutus* reported here (0.61-0.82; $\overline{X}$ = 0.70; Table 19) accord with the "Three-Fourth's Power Law" (Kleiber 1961) and are similar to the values reported by McDiffett (1970) for *Pteronarcys scotti* nymphs (0.71, 0.83 and 0.84 at 5, 10 and 15 C respectively), by Lawton (1971a) for *Pyrrhosoma nymphula* at 5, 10 and 16 C (0.867), and by Edwards (1957) for *Chironomus riparius* at 10 and 20 C (0.70).

The interaction effects between weight and determination temperature, and weight and acclimatization temperature (Tables 6 and 7) probably result from greater sensitivity of smaller larvae to acute temperature changes and less ability to acclimatize to seasonal temperature changes. Edwards and Irving (1943a) observed a similar relationship in the sand crab, *Emerita*, and later Edwards (1946) reported the same

results for the click beetle, *Talorchestia*. Dame (1972) observed this phenomenon in the American oyster *Crassostrea virginica*.

Production

The annual cohort production estimate reported here may be slightly lower than the actual production. Recruitment from hatching over a relatively long period continually lowered the mean weight of the cohort which concomitantly reduced the apparent growth rates (G), and production estimates for the sampling intervals during the hatching period.

Because numerous intrinsic and extrinsic factors influence production, actual production estimates are not readily comparable among species, localities, habitats etc. and even vary several orders of magnitude among riffles of the same stream within the same species (Pearson and Kramer 1972). Waters (1969) and Waters and Crawford (1973) reported that annual turnover ratios ($P/\bar{B}$) of freshwater benthic invertebrates are relatively constant, falling between 2.5 and 5 and are roughly comparable to the instantaneous life-cycle growth rates (Eq. 10). The turnover ratio for hellgrammites (9.96) and instantaneous growth rate (8.96) are considerably higher than those reported by Waters. This is probably due to three factors considered by Waters (1969): (1) the extremely high mortality of early instars (which contributes a considerable amount of production and results in a low mean annual standing

crop); (2) the small N m^{-2} of the final population in relation to its initial size; and (3) the small initial weight relative to the final weight of individuals. Waters' turnover ratio estimates were based on model cohorts with a higher survivorship than that of *C. cornutus* with the final N m^{-2} between 5 and 20% of the initial and with an initial individual mean weight 1-2% of their final weight. The final N m^{-2} of hellgrammites was less than 3% of the initial, and the initial weight was only 0.01% of the mean final instar weight.

Feeding Study

The rates of C, F and A in *C. cornutus* were influenced by temperature and size (Tables 15, 16 and 17), and the patterns of these values are generally similar to those of the respiration rates. The AE values for *C. cornutus* are about equal to the mean value reported by Lawton (1970) for carnivorous damselfly larvae (*P. nymphula*) when fed chironomids (84%). Lawton (1970) also reported that temperature had no effect on AE values; however, he found that AE decreased with increasing weight of the larvae. The AE values for *C. cornutus* are in general agreement with values reported for most invertebrate carnivores (e.g., Fewkes 1960, Phillipson 1960, Paine 1965, Lasker 1966, Brocksen et al. 1968, Dutton 1968). These values are much higher than those (20-40%) reported by Fischer (1966) for *Lestes sponsa* (Odonata) or the maximum AE proposed by Engelman (1966) for poikilotherms in general (30%). The

reported AE values for vertebrate poikilothermic carnivores (e.g., Merchant 1970, Müeller 1970, Fitzpatrick 1973a, b) and homeothermic carnivores (e.g., Golley 1960, Davis and Golley 1963, Buckner 1964, Golley et al. 1965), are approximately equal to those reported here for the carnivorous hellgrammite.

Individual Energy Budget

Although there is little difference among the three energy budgets given in Table 22, the energy budget shown in Table 22C is the most realistic because it does not overestimate rates of C in small larvae (see page 98, Results) and includes the rapid energy consumption of larvae immediately prior to leaving the stream to pupate. The difference in mean weight and biocontent between prepupae (372.5 mg; 2075 cal) and final instar larvae (341.2 mg; 1774 cal), which are assumed to be getting ready to leave the stream, indicates that there is a final rapid storage of energy (≃ 31.3 mg; 301 cal) which is a relatively large proportion (14.5%) of larval P_g.

The proportion of A allocated to P_g by *C. cornutus* is 5-26% ($\bar{X}$ = 12%) higher than values reported for other insects (Burlacu et al. 1967, Woodland et al. 1968, McDiffett 1970, Lawton 1971a, McNeill 1971, Bailey and Riegert 1972, Manga 1972, Schroeder 1972, Hofsvang 1973). The higher net growth efficiency in dobson flies may result from their ability to

conserve energy by metabolic compensation to seasonal temperatures, which, as discussed earlier, may be unique to insects such as *C. cornutus*. The total assimilated energy lost as P_{ev} by dobson flies (13.4%) falls within the range (2.7-14.7%) reported for other insects (Dutton 1968, McDiffett 1970, Lawton 1971a, Manga 1972, Bailey and Riegert 1972).

The fraction of C allocated to P_r by an adult female dobson fly (50.1%) is within the range of values (37-55%) reported by Mukerji and LeRoux (1969) for the adult stage of the terrestrial hemipteran predator *Podisus maculiventris*. This is the only paper I am aware of which provides precise P_r/C data for an individual insect. The ratio P_r/A would be more comparable, due to possible variations in AE; however, Mukerji and LeRoux's paper does not provide data for AE or R values. The only paper I am aware of that provides precise P_r/A data is for the salamander *Desmognathus ochrophaeus* Fitzpatrick 1973a). Female *D. ochrophaeus* allocate 48.3% and 68.5% of their annual A and P to P_r respectively compared to 53.7% and virtually 100% of a female dobson fly's adult A and P, respectively. Since the life expectancy (l_x) of a female dobson fly ($l_x = 0$) is much different from that for a female *D. ochrophaeus* ($l_x > 0$), their RE's are expected to vary. Dobson flies reproduce only once in their lifetime so their reproductive strategy, and their RE is expected to be similar to many other insects, salmon, etc.

Although there is considerable information on the theory and measurement of RE (e.g., Fisher 1930, Cody 1966, Williams 1966a, b, Tinkle 1969, Tinkle et al. 1970, Gadgil and Bossert 1970, Pianka 1970), few studies report more than instantaneous measurements of RE. These instantaneous measurements are only first approximations of the real RE and often cannot be used for comparison among taxa. Even the recent trend of using the ratio of calories stored in ova to biocontent of females (e.g., Tinkle and Hadley 1973, Vitt 1973) fails to account for the relative proportion of available resources allocated to P_r. Using "standing crop" values of ova calories and biocontent to measure RE is similar to equating production of a population to an instantaneous standing crop value. Since RE involves allocating resources within a time frame, instantaneous ratios or proportions may fail to assess the true RE and may even produce incorrect conclusions. The theory originally proposed by Fisher (1930) and discussed extensively by others (e.g., Lack 1954, Cody 1966, Williams 1966a, b, Tinkle 1969, Tilley 1970, Tinkle et al. 1970) that a female's RE should vary inversely with her life expectancy is intellectually pleasing and compatable with neo-Darwinian logic. However, an instantaneous measurement of RE may show the opposite from a time measurement of RE. For example, female rusty lizards, *Sceloporus olivaceus*, show a decrease in ova produced from the first through the fourth clutches during a given year in spite of a decrease in l_x during the same period

(from data in Blair 1960). Although ova cal/female biocontent may resolve this (see Derickson 1974), the proportion of A allocated to each clutch certainly would. Until RE's of a wide variety of taxa having different physiologies (i.e., poikilothermy vs. homeothermy) and existing under different r and K-selection regimes (see MacArthur and Wilson 1967) are measured in this way, meaningful comparisons within and among taxa, and testing of Fisher's theory will be tentative at best.

Population Energy Budget

Although the individual's energy budget and various efficiencies are in a sense absolute, the cohort's energy budget is not because it is basically only an extrapolation of the individual's C, AE and R relative to the densities of larvae in the riffle throughout the year; and these densities should vary among years, whereas the individual's energetics should be much more constant. Therefore, detailed discussion of differences between individual and cohort efficiencies will be limited to the P/R ratio, which is considerably higher for the individual. The effect of calculating the annual cohort energy budget (Table 26) varies considerably among the three methods because the large number of small larvae magnify the overestimation of C for the cohort. Conversely, the low density of large larvae reduce the effect of their high P_g, including the rapid assimilation by the final instars, which was considerable on the individual energy budget. Because

the cohort energy budget of *C. cornutus* is density dependent, absolute comparison with published energetics of other insect populations is less meaningful than with energetics of individuals.

McNeill and Lawton (1970) have examined the relationship between total annual production (P_{obs}) and annual respiration in animal populations. They logically divided the P/R ratios into groups of homeotherms, all poikilotherms and short-lived poikilotherms (less than 2 yr) and calculated regression equations for log P vs. log R for each group. The P/R relationship reported here for larval dobson flies is in general agreement with their equation for short-lived poikilotherms, although it is slightly higher. A more meaningful relationship between P and R might be shown by separating poikilotherms according to their acclimatization capabilities rather than life histories, although the two are probably related.

Summary

1) The rates, energies and associated efficiencies of C, F, A, R, P_{ev}, P_g and P_r, and the effects of season and temperature, and weight and metamorphic stage on them are given for a typical individual and a cohort of dobson flies (*Corydalus cornutus* L.) from a riffle section of Elm Fork of the Trinity River in north-central Texas (33°23'N, 97°5'W) during 1972-1973.

2) Dobson flies are apparently univoltine in the study area. Emergence, oviposition and hatching extended from late May through August and were centered on 24 June, 1 July and 14 July respectively. Larval growth rate, rapid from hatching until November, ceased until March, and then increased until the final instar larvae left the stream around 10 June to pupate.

3) Caloric values of various stages in the life cycle ranged from 4799 cal g^{-1} (17±12 mg larvae in September) to 6599 cal g^{-1} (ova) and definitely correlated with metamorphic stages and season of the year.

4) Temperature ranged from 0 C in winter, for brief periods, to 32 C in summer, was relatively stable between 25 and 30 C from June to September, and around 5 C from December to February. During fall and spring temperature was less predictable, passing through 10, 15 and 20 C rather quickly.

5) Larval dobson flies exhibited partial metabolic compensation to temperature that enables them to maintain relatively constant winter and summer rates of R, which conserve energy during winter when food is scarce and in summer when temperatures are relatively high.

6) Secondary production (2.51 g m^{-2}) was calculated for the cohort with Ricker's (1971) instantaneous growth method. The annual turnover ratio ($P/\overline{B}$ = 9.96) was about double that predicted by Waters (1969) but was roughly equal to the life-cycle instantaneous growth rate (8.96). Larval growth rates

calculated from sampling data were comparable to rates determined for larvae kept in cages in the riffles.

7) The energy budget for a typical dobson fly during its 47-wk existence as an aquatic larva was:

	cal	% of C	% of A
C	4,167	. .	. .
A	3,442	82.6	. .
F	725	17.4	. .
P_g	2,075	49.8	60.3
P_{ev}	198	4.8	5.8
R	1,169	54.5	34.0

Individual ova respired 0.107 cal wk^{-1}, prepupae 357 cal wk^{-1}, male pupae 509 cal wk^{-1}, female pupae 454 cal wk^{-1}, male adults 623 cal wk^{-1} and female adults 735 cal wk^{-1}. The prepupal and pupal exuviae had a biocontent of 144 and 120 cal respectively. Total P_{ev} was 13.4% of larval A and 20.3% of P_{obs} ($P_g + P_{ev}$). The average female produced 667 cal of eggs and 185 cal of egg case material (total P_r = 852 cal), which was 17% of her total lifetime energy flow and 54% of her adult energy flow (P + R). The adult female's C, F and A were estimated to be 1671 cal, 84 cal and 1587 cal respectively. Estimates were based on obvious energy requirements imposed by energy demands of P and R not explained by loss of carcass calories.

8) Annual energetics of the 1972-1973 cohort of larval dobson flies was:

	cal m^{-2}	% of C	% of A
C	39,518	. .	. .
A	32,642	82.6	. .
F	1,876	17.4	. .
P_g	13,052	33.0	40.0
P_{ev}	3,608	9.1	11.1
R	15,982	40.4	49.0

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