AN ABSTRACT OF THE THESIS OF

Robert John Steedman for the degree of Master of Science

in Entomology presented on May 16, 1983

Title: Life History and Feeding Role of the Xylophagous Aquatic Beetle, Lara avara LeConte (Dryopoidea: Elmidae)

Abstract approved: Redacted for Privacy

Norman H. Anderson

The purpose of this study was to document the life history of the xylophagous elmid beetle, Lara avara, and to estimate its contribution to wood degradation in Oregon streams. Field collections, mark-recapture, and laboratory rearing were used to determine details of the life cycle. Laboratory feeding studies and field population estimates were used to estimate fecal production by natural populations of Lara larvae.

The life cycle was found to be four to seven years long, with all but two to three months of that spent in the larval stage. Adults live approximately three weeks, and occur from May to August. Female adults lay 100 - 150 eggs on submerged wood. Larvae grow through seven instars, taking about one year for instars one to three, and from three to six years for instars four to seven. Last-instar larvae leave the water in the spring, and burrow into moss at the edge of the stream. Pupation occurs when the moss dries in early summer. The pupal stage lasts at least two

weeks.

I found Lara to have a mean abundance of 34 mg/m^2 stream bed, or 57 mg/kg wood, in the Coast Range streams that I sampled. Variation in abundance was not related to variation in size or density (mg/cm^3, an index of decay) of the wood used by Lara as habitat.

Lara larvae probably obtain nutrition from decaying wood by absorbing substances that have been liberated by fungal exoenzymes, and by digesting and absorbing the contents of fungal and bacterial cells. Lara larvae do not produce their own cellulase, nor do they have a symbiotic gut flora similar to that of xylophagous craneflies. Assimilation efficiency is probably less than 10%.

Fecal production of Lara larvae averaged 9% of their body weight per day in laboratory culture. When extrapolated to field population levels, this corresponds to a fecal production of 1.1 $gm/m^2/yr$ in Coast Range streams.

LIFE HISTORY AND FEEDING ROLE OF THE XYLOPHAGOUS AQUATIC BEETLE, *Lara avara* LeConte (DRYOPOIDEA: ELMIDAE)

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of
Master of Science

Completed May 16, 1983

Commencement June 1984

APPROVED:

Redacted for Privacy

Professor of Entomology in charge of major

Redacted for Privacy

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Date thesis is presented May 16, 1983

Typed by Robert John Steedman

ACKNOWLEDGEMENTS

To Norm Anderson, for good advice, long chats, and for this opportunity, I offer sincere thanks and appreciation. To Chuck Hawkins, who also taught me a thing or two, my thanks for friendship and community structure.

I thank the members of my committee: Jim Hall, Victor Brookes, and William Simonson, for helpful discussions and thorough editing.

I also wish to thank the following people: Lin Roberts for help with field collecting, and for sharing her "Lara lore"; Gary Peters for loaning me his personal collection of Lara adults; and Harley P. Brown, for valuable correspondence and advice.

Special thanks to my wife, Gillian, for patience, humor, and for drafting the figures.

Financial assistance was provided by National Science Foundation grant DEB 78-10594, and by the Department of Entomology.

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INTRODUCTION

Wood debris is a major component of headwater stream channels in the Pacific Northwest. Swanson et al. (1976) measured standing crops of large wood debris (> 10 cm diameter) of up to 40 kg/m^2 in headwater streams flowing through old growth Douglas-fir (*Pseudotsuga menziezii*) stands in the Cascade Range of Oregon. When present in such amounts, wood has an important role in the geomorphology, habitat complexity, and biotic structure of the stream ecosystem (Swanson et al. 1976, Keller and Swanson 1979, Anderson et al. 1978, Anderson and Sedell 1979, Dudley and Anderson 1982).

Although it constitutes an abundant source of organic carbon in streams, wood contains little nitrogen, and is a poor food source. In spite of this, it supports a diverse insect fauna. Dudley and Anderson (1982) listed 56 insect taxa as being closely associated with wood debris in western U.S. streams, and 124 taxa as facultative users of wood debris as habitat. Only a few of the xylophilous species listed by Dudley and Anderson use wood as a primary food source. The most important of the obligate xylophages are *Lara avara*, *Lipsothrix* spp. (Diptera: Tipulidae), and several species of Chironomidae (Diptera) (Pereira et al. 1982).

Most other wood-associated insect taxa ingest some wood while scraping aufwuchs from the wood surface.

Lara avara LeConte, a large elmid beetle, is found in western montane streams. The larvae feed on the surface of submerged wood, creating grooves and shallow depressions as they progress. This method of feeding has been described as "gouging" by Anderson et al. (1978).

Lara avara is of interest as a representative of the group of stream insects that have specialized on stream wood debris for food and habitat. Preliminary information about Lara avara's life history, population levels, and feeding rates, has proved useful to our understanding of the adaptive strategies used by xylophagous stream insects, and their role in the processing of wood debris in streams.

The objectives of this thesis were an improved understanding of Lara's life history, and refined measurements of its feeding activity in Oregon streams. In view of the low nutritional value of wood, I was interested in ecological and physiological mechanisms that enabled Lara to complete its life cycle. While Lara seemed in some ways to be an unusual aquatic insect, I hoped that the results of this research would contribute to a generalized understanding of life-history adaptations of stream detritivores.

Lara avara: Background Information

Lara avara was once considered to be a very rare beetle (Fletcher 1905), but has since been found to be relatively common in the appropriate habitat. Brown (1975) records it from British Columbia, Washington, Oregon, California, Idaho, Montana, Utah, Wyoming, and Colorado. The genus Lara is the only member of the Nearctic Larinae; worldwide there are 107 species of this subfamily in 20 genera (Brown 1981).

Much of the ecological information available for Lara was obtained by Anderson et al. (1978), in the course of three year's field collecting and laboratory studies. Adults occur in July and August, and are frequently found just above the waterline on damp wood. The number of larval instars was unknown, but presumed to be more than five. Based on the presence of several size classes of larvae in all seasons, and laboratory evidence for slow growth, the life cycle was believed to be three or more years long. In laboratory culture, the larvae produced 10 - 30% of their body weight in feces per day, but did not appear to grow. After examining wood debris from several Oregon streams, Anderson et al. estimated Lara abundance at 1 - 21 mg/m^2. Its contribution to wood degradation in Oregon streams was estimated to be 0.6% of the wood standing crop per year.

Lara may be unusual among elmid beetles for its large size and long life cycle. Other aspects of its life

history, however, seem to be shared with its close relatives. Perez (1863) suggested a one- to two-year life cycle for Machronychus quadrituberculatus (Elmidae), which he found on wood in the River Adour in France. In Quebec, LeSage and Harper (1976a) found that Machronychus glabratus, also xylophagous, spent two years growing through six larval instars, and lived one year as an adult. In the same study, non-xylophagous elmid beetles from sand, moss, and gravel were found to have life cycles similar to that of M. glabratus. Also in Quebec, Anchytarsus bicolor (Ptilodactylidae), a xylophagous beetle closely related to the Elmidae, spends three years growing through ten larval instars, and has a short lived, terrestrial adult (LeSage and Harper 1976b). In Kentucky, Stenelmis sexlineata (Elmidae) had a one- to two-year life cycle in the field, and a six- to seven-month life cycle in the laboratory (White 1978). It was not apparent from White's paper whether food or temperature was responsible for the shorter life cycle in the laboratory.

Lara's taxonomic standing has been changed several times. The genus Lara was erected by LeConte (1852), based on a single adult specimen from Sacramento, California, and placed in the family Parnidae (= Dryopidae). He later erected the tribe Larini, with Lara avara as the only species (LeConte 1861). West (1929) described and figured a larva from Montana, which he tentatively but correctly identified as Lara avara on the basis of its size, and

location of collection. Böving (1929), apparently unaware of West's work, erected the family Lariidae after examining a larva from Portland, Oregon, which was missing the gills and operculum from its ninth abdominal segment. In a later paper Böving and Craighead (1931) lowered the Lariidae to subfamily status (Larinae) within the family Dryopidae. Hinton (1939) transferred the Larinae from the Dryopidae to the Elmidae, and suggested that tribal rank (Larini and Elmini) was justified when dealing with the adults. He emphasized, however, that in spite of the morphological similarity of adult Larini and Elmini, there was an interesting ecological divergence:

> "The only character which I have been able to find that can be used to divide the Elmidae without exception into two tribes concerns their method of respiration. The Larinae are not truly aquatic, but enter the water accidentally or when ovipositing. The entire body is clothed with ordinary hydrofuge hairs, and when they enter the water the whole body is surrounded by a film of air. The Elmini are truly aquatic beetles, seldom or never leaving the water or even coming to the surface.... When these are submerged the entire body is never covered by a film of air, but a film is restricted to certain tracts of fine matted hairs or scales known as tomentum."

Brown (1981) separated the two groups at the subfamily level in his recent survey of the Dryopoidea of the world.

Hatch (1965) included Lara avara amplipennis Darlington, and Lara gehringi Darlington, in addition to Lara avara avara LeConte, in his treatise "The Beetles of the Pacific Northwest". His source was Darlington's (1929)

descriptions of Lara avara amplipennis and Lara gehringi, which were based on a series of adults, in which Lara avara avara was also present, collected from North Bend, Washington. Darlington separated the three taxa by differences in body size, shape of the pronotum, and male genitalia.

I found that Darlington's key did not work well with specimens of Lara available to me at Oregon State University, including those in the M.H. Hatch collection. Although there were definitely two types of pronota, corresponding to Darlington's avara and gehringi types, I questioned the validity of Darlington's classification of Lara into two species. In an attempt to resolve this question, I sent all Lara adult specimens at my disposal to Dr. H.P. Brown for comparison with his specimens. He concluded that the material represented a single species, Lara avara, in which there is a range of individual variation.

The distribution of adult specimens that I have examined (Fig. 1) suggests that the avara facies occurs throughout the range of Lara, while the gehringi facies is limited to the Coast Range. As I was unable to distinguish between larvae of Lara from the different regions, I have considered all the larvae examined in this study to be of one species, Lara avara.

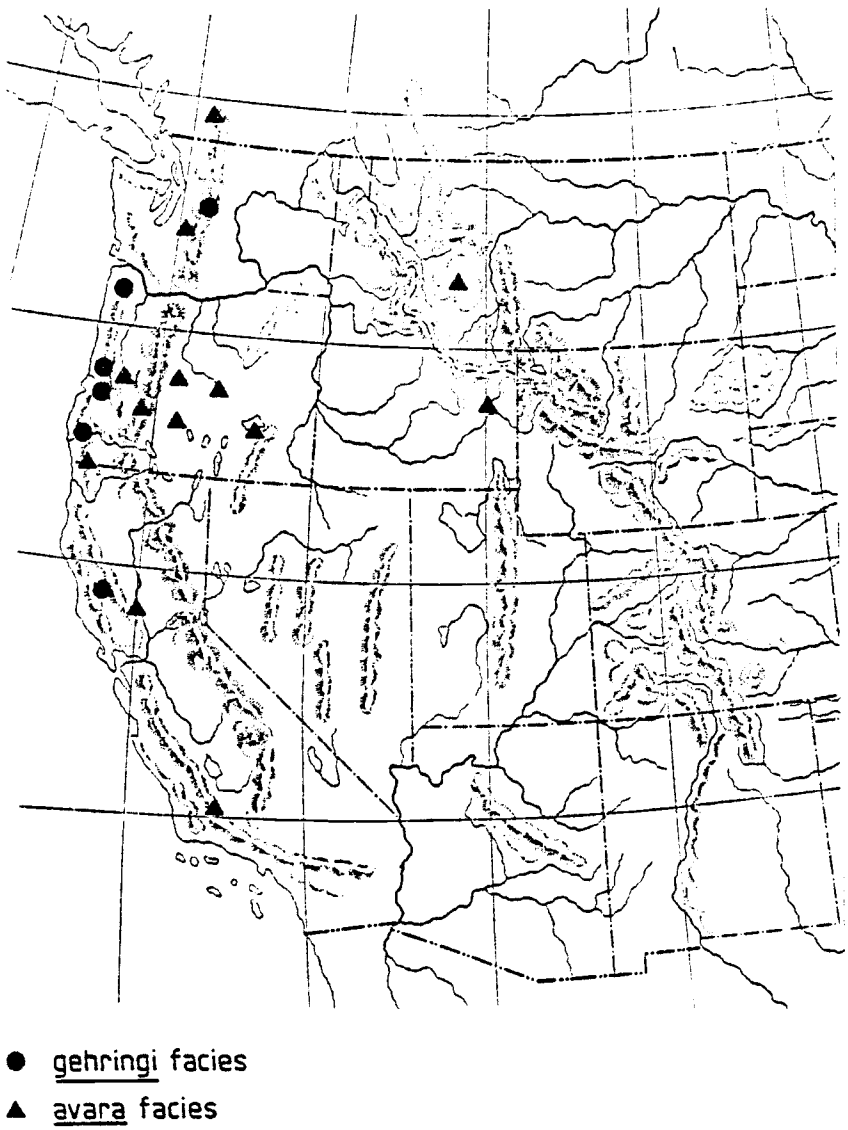

Figure 1. Map of western United States, showing distribution of Lara avara morphotypes.

METHODS

Description Of Study Sites

Most of my field sampling sampling took place in the Coast Range of Oregon, at Berry, Flynn, and Yew Creeks, from October 1980 to October 1982.

Berry Creek (Benton Co.) is a second order stream that drains foothills on the eastern edge of the Coast Range, 15 km north of Corvallis, Oregon. It was chosen as the main study site because it supports high densities of Lara. Samples were taken from the 460 m controlled-flow section, where it passes through a dense stand of red alder (Alnus rubra) and big leaf maple (Acer macrophyllum). This section of Berry Creek is especially suitable as Lara habitat because a diversion dam at the upstream end has prevented freshets for the last 22 years, allowing branch wood to accumulate in the channel. Warren et al. (1964) provide a more complete description of Berry Creek.

Flynn Creek (Lincoln Co.) is a second order stream on the western side of the Coast Range, 16 km from the Pacific Ocean and 50 km west of Corvallis. The riparian zone consists mainly of red alder, salmonberry (Rubus spectabilis), and Douglas-fir. There is a large annual variation in streamflow, with freshets occurring from November to February (Hall and Lantz 1969).

Yew Creek (Benton Co.) is a second order stream draining a watershed on the south side of Mary's Peak,

about 20 km south-west of Corvallis. The riparian vegetation consists mainly of second growth big leaf maple and red alder. The flow pattern is probably similar to that of Flynn Creek. A first order tributary of Yew Creek approximately 500 m upstream of Highway 34 also was sampled.

Occasionally, I collected at Lobster and Little Lobster Creeks (Benton Co.), 65 km south-west of Corvallis.

Field Studies

Field collections of *Lara* were required to provide information about its life cycle and population levels, and to provide specimens for laboratory studies. The larval stage is the most important in terms of feeding and growth, and was the main object of my sampling efforts, although I often encountered adult *Lara* while collecting larvae in the spring and summer.

Collecting Methods

Lara larvae live on submerged pieces of wood, and are not readily collected with devices designed to sample the benthic habitat. While collecting for *Lara*, I examined any suitable piece of wood that I found in the stream. For this reason, my sampling effort was not standardized, and abundance data from successive sampling dates were not comparable.

I started out using the collecting methodology of

Anderson et al. (1978), who removed pieces of wood debris from streams and examined them in the field for larvae. The efficiency of this "field picking" method was reduced on dim, cloudy days, and when examining highly grooved wood. Even under the best of conditions, very small larvae were often missed. This method had the advantage, however, of providing live specimens, and not destroying the stick as Lara habitat. After sampling, the stick could be replaced into the stream, as was required for certain of my field experiments.

I later found that all sizes of larvae could be collected by slowly drying sticks in the laboratory. If each stick, while drying, was placed in a separate bucket, the Lara population on that stick could be easily collected and counted. This "stick drying" method, which at least temporarily ruined the stick as Lara habitat, and often killed many of the larvae, was used to estimate field population size and age-structure.

I examined 11 sticks from Berry Creek in the field, and then dried them in the laboratory, to determine the relative efficiency of the two sampling methods. Only 54% of the larvae were removed by field picking (Fig. 2). After one week of drying, an average of 96% of the Lara had left the sticks, and by two weeks all of them had left. The efficiency of field picking was lower for large sticks (Fig. 3).

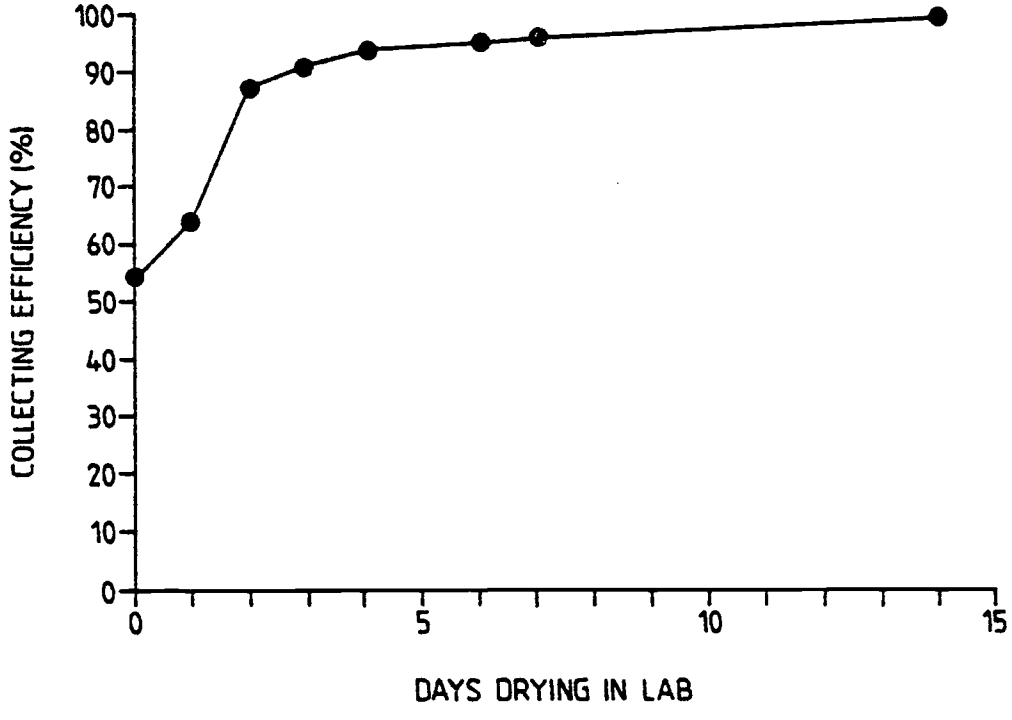

Figure 2. Efficiencies of "field picking" and "stick drying" methods of collecting Lara avara larvae (means of 11 sticks from Berry Creek). Results for "field picking" are plotted at Day 0.

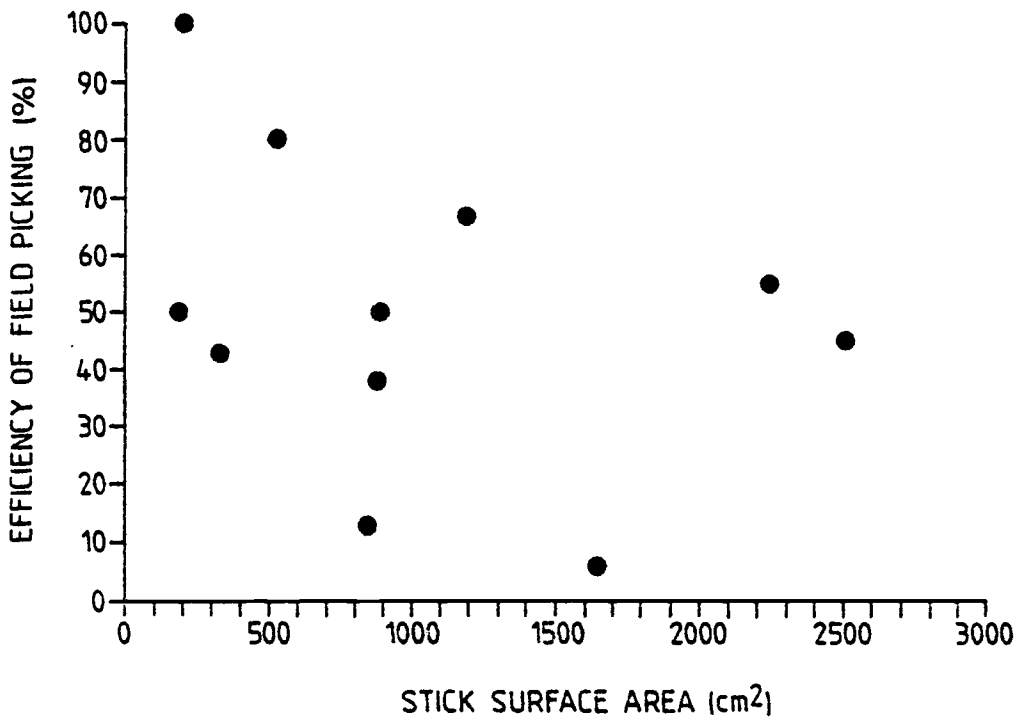

Figure 3. Effect of stick surface area on efficiency of "field picking" method of collecting Lara avara larvae.

Number and Timing of Larval Instars

Although different types of field collections were intended to provide data about different aspects of the larval stage, measurement of head-capsule widths with an ocular micrometer at 25X was the first step in each analysis. I prepared size-frequency histograms of head-capsule measurements from Berry and Yew Creeks, after pooling several monthly samples to provide a large data set. I determined the number of instars, and their size ranges, by inspecting peaks in the frequency distribution. Monthly data on head-capsule size from the various study sites could then be examined for seasonal changes in the abundance of each instar.

Instar Duration

Although Anderson et al. (1978) found that Lara larvae grew very slowly, if at all, in laboratory culture, I felt that growth under natural conditions could be measured if many larvae were observed over a long period of time.

I conducted a long term mark-recapture program at Berry Creek to estimate the duration of Lara's larval stage in the field. The fundamental assumption of the mark-recapture method of estimating instar duration was based on the nature of insect growth, i.e. a larva will retain a paint mark only until its next moult. When a marked larva moults, it loses its mark, and cannot be "recaptured". My experience indicated that properly applied marks could last for many months. Improperly applied marks fell off within

minutes, and could be replaced before the larvae were returned to the field.

The interval between the initial marking and the date of recapture is a minimum estimate of instar duration. This is the simplest interpretation of the data, since it uses information from only one recapture. Other analyses will be considered in the Results section.

I conducted the mark-recapture study at Berry Creek from March 1981 until July 1982. In March 1981, I collected approximately 100 Lara. These were transported to the laboratory in small jars of water, and kept at 5°C until processing was completed. Each larva was measured for head-capsule width, and marked on the thorax with red nail polish in a positional code that indicated the date of capture. The larvae were returned to Berry Creek the next day, and placed on one of five sticks from which I had previously removed all visible Lara. The sticks were marked with flagging for easy recognition.

At subsequent monthly intervals until January 1981, I collected as many marked and unmarked larvae as possible from the flagged sticks, along with enough larvae from other parts of Berry Creek to bring the total to aproximately 100. Because the "field picking" method was used, only a few early-instar larvae were collected. The larvae were returned to the laboratory, and measured as described above. The marking date of previously captured larvae was recorded, and unmarked larvae were marked

according to the current date. After processing, all larvae were returned to the flagged sticks.

Between samples, unmarked larvae could occur on the flagged sticks because of moulting of marked larvae, or because of immigration of unmarked larvae from upstream. Just prior to the January 26, 1982 sample, I placed a net at the upstream end of the riffle containing the flagged sticks to prevent immigration as a source of unmarked larvae. Commencing with the January 26, 1982 sample, I restricted my mark-recapture collecting to the flagged sticks, so that no new larvae were introduced into the riffle. This allowed me to monitor, in subsequent collections, moulting and drifting rates of the Lara population on the flagged sticks.

Drift of Marked Larvae

The presence of marked larvae in Berry Creek also provided an opportunity to monitor drift for reasons not related to the measurement of instar duration. I was interested in drift as a dispersal mechanism, and as a potential means by which Lara larvae left the stream prior to pupation. Brusven (1970) had found Lara larvae in drift samples from Idaho, and N.H. Anderson had noticed that some Lara larvae were able to float.

To test the hypothesis that last-instar larvae might drift actively in the spring, I monitored the drift of Lara larvae in Berry Creek, from January 6 to June 15, 1982, by

placing a 250-micron mesh drift net at the bottom of the riffle containing the flagged sticks. The contents of the net were collected and examined two or three times a week. Because the net clogged quickly, it functioned efficiently for only a portion of the period between collections.

Field Population Levels

To assess the importance of *Lara* as a wood processor, information about its abundance was required. In 1982 I collected a total of 50 sticks from Berry, Flynn, and Yew Creeks, and determined the *Lara* abundance on them using the "stick drying" method. The sticks ranged in size from 2 to 10 cm in diameter, and 27 to 200 cm in length. Hardwood and conifer sticks in a range of decay states were included in the collection. I measured the surface area, weight, and density of the sticks in an attempt to relate *Lara* abundance to physical aspects of its habitat. The surface area of each stick was estimated by fitting the stick dimensions to a cylinder, truncated cone, or rectangular prism model. Volume was estimated by displacement, after soaking each stick to reduce water absorption during the measurement. The regression relation in Appendix 1 was used to calculate *Lara* biomass from head-capsule measurements.

Laboratory Studies

I conducted laboratory studies to provide information

about aspects of Lara's life history, such as pupation, oviposition, feeding rates, and digestive mechanisms, that were not easily addressed in the field. Data from the feeding studies, which extended over several months, could also be used to estimate larval instar duration and growth rate.

Laboratory Rearing

Pupae In June, 1982, I placed final-instar larvae from Berry Creek in plastic dishes containing a thin layer of soil, and a few sticks covered with damp moss. The containers were moistened, and allowed to dry slowly over a one- to two-month period, to encourage pupation. I killed and preserved some of the pupae, and reared the others to eclosion.

Adults I was able to obtain approximately 25 adults by field collecting and rearing pupae in the laboratory. I kept most of these in aquaria containing partially submerged sticks, for observation of longevity, feeding, and oviposition behavior. The others were killed and preserved for dissection or taxonomic studies.

Estimates of Larval Feeding Rate

Waldbauer (1968) indicated that three measurements are necessary to estimate the feeding rate and assimilation efficiency of an insect: 1) weight of food ingested, 2) weight of feces produced, and 3) weight gain of the insect. The measurement of ingestion requires an estimate of the

fresh weight of food eaten, which must be converted to a dry weight based on the proportion of dry material present in an aliquot of similar food. This can be done for shredders, using paired leaf disks (i.e. Anderson and Grafius [1975]), but is not practical with sticks, as stream-conditioned wood is heterogeneous, and Lara feeds only on a thin surface layer. My approach with Lara was therefore limited to the collection of fecal material, which could be accomplished accurately using larvae reared in drippery trays. If Lara has a low assimilation efficiency, as is suggested by its simple gut and lack of digestive symbionts (Anderson et al. 1978), then fecal production, which I can easily measure, is a good estimate of ingestion, which I cannot easily measure.

I measured larval fecal production in the Aquatic Entomology wet-lab at Oak Creek, 9 km north-west of Corvallis. Twenty 15 cm x 38 cm plastic trays were arranged in a four-tiered drippery (Anderson 1973), which was supplied with filtered stream water. Temperature measured with a maximum-minimum thermometer at one- to three-day intervals was used to calculate a "mean" water temperature for each run. In each tray approximately 10 large or 20 small larvae were allowed to feed on a single piece of stream-conditioned wood for one to two weeks. Trays containing sticks without larvae were used to control for non-feeding particle production.

In 1981, Douglas-fir, hemlock, and alder sticks, which

had been in Berry Creek for five years, were used as food in the fecal-production studies. No large cracks or grooves were present on the surface of any of these sticks. Seven trays of each wood type were prepared: two with large larvae, two with medium larvae, one with small larvae, and two as controls. Four nine-day runs were made in each of June and July, 1981 and October and November 1981, to provide data from warm and cool temperatures.

In 1982, six 4-cm diameter pieces of alder were obtained by cutting up a well-conditioned alder branch from Berry Creek. These pieces were slightly larger, and of considerably more complex surface texture than the Douglas fir, hemlock, and alder sticks. Five replicates with Lara larvae were prepared: two with large larvae, two with medium larvae, and one with small larvae. One tray containing a piece of alder branch was used to measure fecal production of Heteroplectron californicum McLachlan (Trichoptera: Calamoceratidae), so that comparisons with Lara could be made. In 1982, control measurements were made for each tray before larvae were added. Five 12-day runs with Lara and Heteroplectron were made during April, May, and June, 1982. Two more runs with Heteroplectron alone were made in November, 1982.

At the end of each run the sticks were removed from the trays, and all particulate material filtered out of the water with a millipore apparatus and glass fiber filters. The number of exuviae resulting from moults during the run

was recorded for each tray. Missing larvae were replaced with individuals of similar size, from stock kept at 10°C in an aquarium. Dry (48 hrs at 60°C) and ashed (12 hrs at 450°C) weights of the particulate material were determined on an analytical balance, and corrected for control weights.

The larvae used for measurement of fecal production in 1981 were blotted dry and wet-weighed as groups on an analytical balance before and after each run. The regression relation in Appendix 1 was used to calculate dry weights from live weights. Instantaneous growth rates were calculated from the initial and final mean individual weight for groups of larvae that lasted through a three- or four-run sequence (30 to 40 days) without losing any larvae from the drippery trays.

Larvae used for measurement of fecal production in 1982 were individually weighed, as described above, at the beginning and end of the 62-day measurement period. Instantaneous growth rates were calculated from initial and final individual weights.

Digestive Strategy of Larvae

Since I intended to use fecal production as an estimate of ingestion, I at least wanted qualitative evidence that Lara larvae assimilated only a small proportion of the wood that they consumed. The evidence that I looked for was short gut-residence time, little

visible alteration to wood particles as they passed through the gut, and an inability to digest cellulose.

Gut Retention Time Lara larvae were allowed to feed for 48 hours at 12°C on an alder branch dyed with a 10% solution of safranin. The larvae were then transferred to small pieces of unstained alder in individual dishes of water, and allowed to feed in the dark. At one- to two-hour intervals fecal pellets were collected with an eye dropper, and examined under a dissecting microscope for traces of dye. Gut residence time was considered to be the interval from the beginning of feeding on the undyed wood, to the time when fecal pellets were free of dyed wood particles. Five groups of four larvae were monitored in this manner.

Appearance of Gut Contents The gut contents of Lara larvae and larvae of other aquatic xylophagous insects were examined for visual evidence of alteration by digestion. Fresh mounts were made of the larval foregut, midgut, and hindgut contents of ten Lara, three Heteroplectron californicum, four Lipsothrix nigrilinea Doane (Diptera: Tipulidae), and one Austrolimnophila badia (Diptera: Tipulidae), and examined under a compound microscope for differences in particle size, cellular integrity, and gut flora.

Effect of Digestion on Ash Content of Wood Fifty Lara larvae were allowed to feed for ten days on a piece of Douglas-fir stick or alder branch in a pan of aerated

water. The feces were then collected, and a thin layer of conditioned wood was scraped from each stick. The ash content of the feces and conditioned wood was calculated from their dry and ashed weights.

Assay of Gut Tissue for Cellulase Cellulase assays based on the detection of glucose released from hydrolysed cellulose were conducted by John Patt of the Forest Service Laboratory in Corvallis. Guts were removed from 100 large Lara larvae which had been starved for 72 hours, and from 50 large larvae with full guts. Fifty of the empty guts were rinsed by injecting them with cold citrate buffer from a 50 microliter syringe. The three treatments were kept on ice until they could be flash-frozen in liquid nitrogen, and stored at -80°C in a deep-freeze.

On the day of the assay, gut tissue was thawed, wet-weighed, and mechanically homogenized in cold citrate buffer. The homogenate was briefly centrifuged to remove suspended tissue, and the resulting supernatent incubated with fine particulate cellulose (Avicel) in citrate buffer at 37°C for four hours. Standards were run using commercially-supplied fungal cellulose. Controls consisting of gut extract without cellulose substrate were provided to correct for glucose that may have been present in the gut tissue. At the end of the incubation period the samples were run through an ion-exchange column to stop the reaction. The glucose fraction was then analysed with a hexokinase/glucose-6-phosphate assay (Sigma glucose assay

no. 15-UV). In this reaction NADH is produced in proportion to the amount of glucose in the sample, and can be measured as an increase in absorbance at 340 nm.

Respiration Rate of Larvae

I measured the oxygen uptake, using a Gilson differential respirometer, at both 10°C and 15°C of fifth-, sixth-, and seventh-instar Lara larvae. Five ml of dechlorinated water and a 1 x 1 x 3 cm piece of Douglas-fir stick were placed in a 15 ml reaction flask. One ml of 10% KOH solution was added to the side arm to absorb carbon dioxide. Oxygen uptake of the wood was measured for three to four hours, Lara were added, and oxygen uptake measured again for three to four hours. Three flasks with five seventh-instar larvae, three flasks with seven sixth-instar larvae, and two flasks with eight fifth-instar larvae were used at each temperature. Controls consisted of water alone (six flasks), and water plus wood (one flask). The regression relation in Appendix 1 was used to calculate dry weights from head-capsule measurements.

RESULTS AND INTERPRETATION

I will introduce the Results section by summarizing *Lara avara*'s life cycle as I now understand it. This summary is followed by sub-sections that describe field and laboratory observations on the life history of the adult, pupal, and larval stages. The last section in the Results deals with estimates of the importance of *Lara* larvae to wood processing in Oregon streams.

Life Cycle Summary

The life cycle of *Lara* is four to seven years long, with all but two to three months of that spent in the larval stage. Adults live approximately three weeks, and are found in the field from May to August. Adult females lay 100 - 150 eggs on submerged wood. Approximately one month is required for embryonic development. The larvae grow through a total of seven instars, taking about one year for instars one to three, and from three to six years for instars four to seven. Last-instar larvae leave the water in the spring, possibly by drifting with the aid of abdominal air sacs, and burrow into moss at the edge of the stream. Pupation occurs when the moss dries in the early summer. The pupal stage lasts a minimum of two weeks.

Observations of the Adult Stage

Adult *Lara* were found in the spring and summer, above the water surface on sticks and logs in streams where larvae were present. For specimens that I examined, the extreme dates of collection were May 26 (1952) and August 27 (1937). Adults were most abundant in June (Fig. 4).

Females are larger and heavier than males. The mean dry weight of two gravid females was 5.81 mg (SE = 0.280). The mean dry weight of four males was 3.55 mg (SE = 0.438).

At eclosion, females that had been reared from pupae in the laboratory had no ovarial development, suggesting that time and/or feeding were necessary to mature eggs. Two gravid females collected in the field contained 100 - 150 eggs, which were white, ovoid, approximately 0.54 x 0.42 mm, and had a mean dry weight of 0.013 mg.

Both field-collected and laboratory-reared adults lived two to three weeks in aquaria containing partially submerged sticks, and fed by sweeping the surface of moist wood with their mouthparts. The mandibles of adult *Lara* are thinner and more blade-like than those of the larvae (Fig. 5), and appear to be more suited to grazing than to gouging. The gut contained fungal spores, fungal hyphae, and diatoms, but little wood tissue.

Although captive adults copulated frequently, neither field-collected nor laboratory-reared females laid eggs on wood in the aquaria.

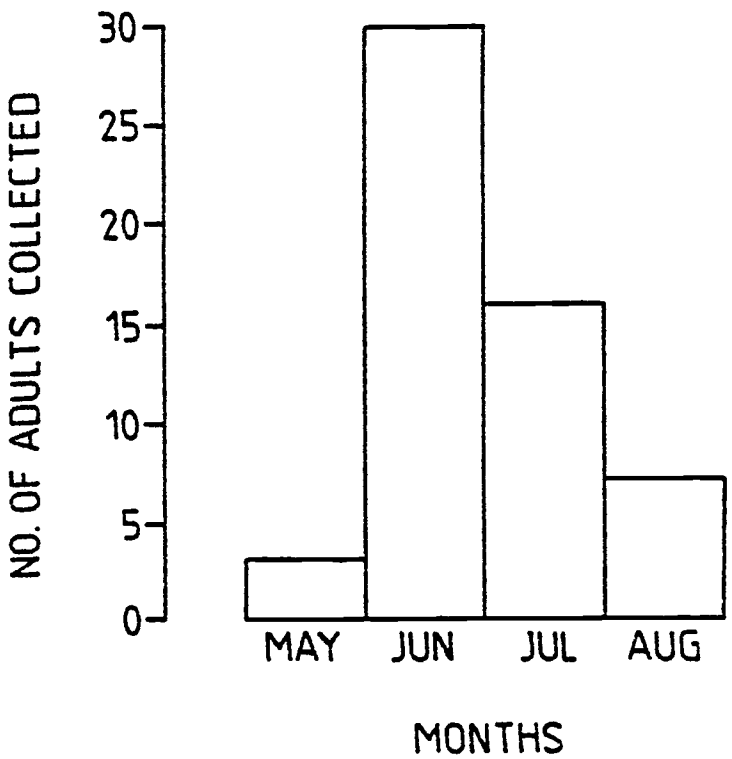

Figure 4. Frequency distribution of Lara avara adult collection records.

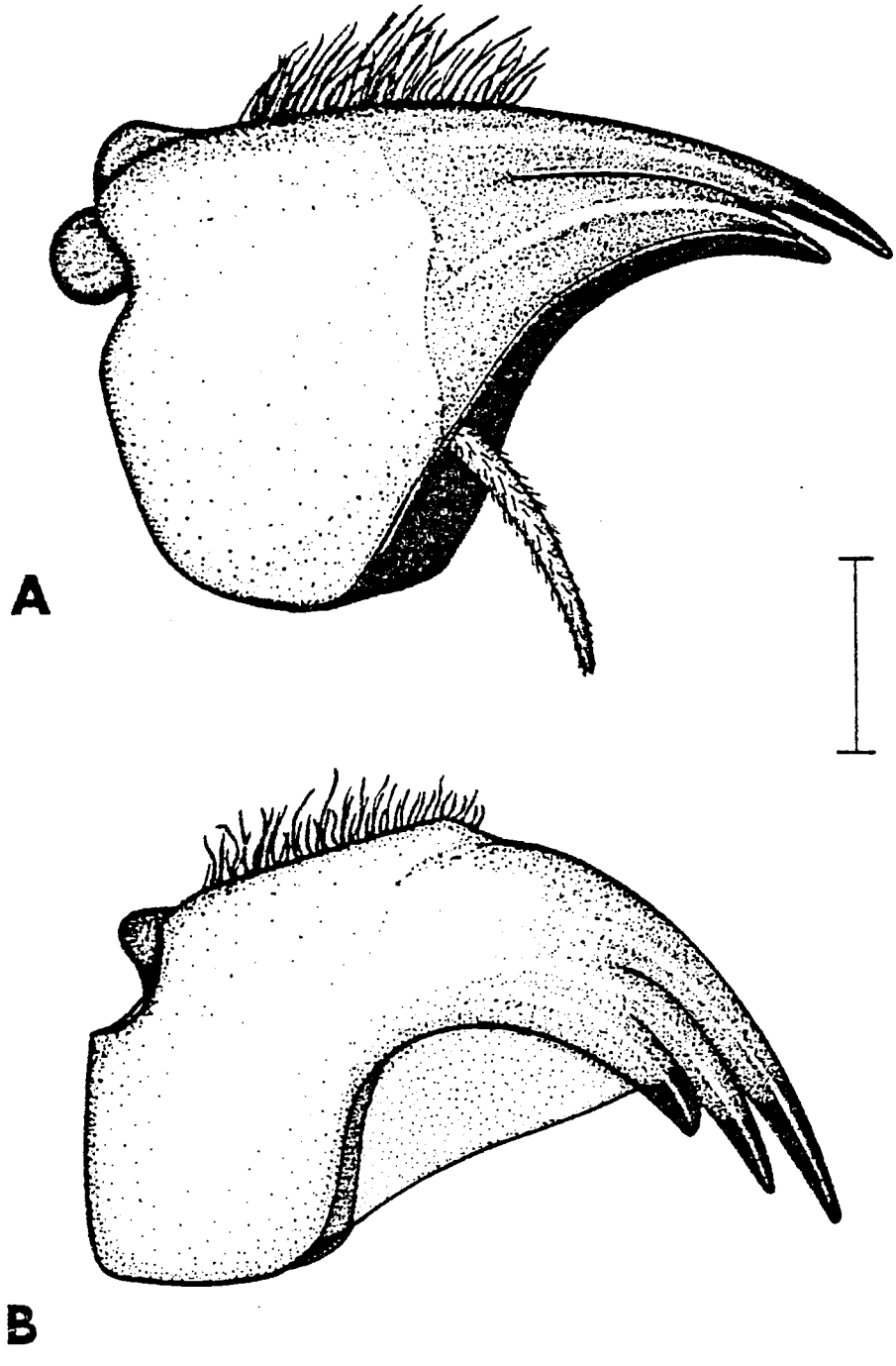

Figure 5. Mandibles of Lara avara (left, dorsal view) A) larva B) adult. Bar = 0.1 mm.

Observations of the Pupal Stage

Lara pupae were first discovered by N.H. Anderson and R.W. Wisseman (Dept. of Entomology OSU) in Berry Creek on June 25, 1981, under moss on the upper surface of a partly submerged log. The pupae were in 1.5 cm-long chambers in damp soil below the moss layer, and were found with seventh-instar larval exuvia. Pupae of *Ametor latus* Horn (Hydrophilidae) were also present. Three of the six *Lara* pupae were allowed to emerge as adults in the laboratory, to confirm the identification. At 12°C, the adults emerged nine days after collection, or about seven days after the elytra darkened. On June 28, 1981, I found another pupa at Berry Creek, in the same type of habitat as the first six pupae. A description of the pupa of *Lara* can be found in Steedman (1983), included as Appendix 2.

A total of eight larvae pupated in the laboratory in 1982. In all cases, the pupation occurred when the wood and moss had dried to the point where no surface moisture was present. This suggests that the onset of dry weather in the early summer may trigger pupation in *Lara* larvae that have been out of the stream for some time. Five pupae (three male, two female) were found on July 6, 1982, more than two months after 30 - 40 larvae had been placed in a plastic container. On August 4, 1982, after a second drying cycle, three more pupae were found. On September 9,

1982, after a third drying cycle, one male pupa was found. Pupal development took about two weeks at 12°C. The mean dry weight of three preserved pupae was 5.8 mg.

Number of Instars

Size-frequency histograms of larval head-capsule measurements were used to determine instar boundaries. There were seven instars in the frequency histogram for Berry Creek (Fig. 6). In the histogram for Yew Creek (Fig. 6) the last instar was divided into two peaks, which may indicate sexual dimorphism; *Lara* adult females are generally larger than males.

The instar boundaries from the two streams were similar (Table 1). The third column in Table 1 shows the boundaries that were used to create the monthly instar frequency histograms presented in Fig. 7. These boundaries, which were based on an earlier, smaller, data set from Berry Creek, differ slightly from those obtained from Figure 6.

My interpretation of the size-frequency histogram is consistent with the geometric progression predicted by Dyar's Law (Dyar 1890). The ratios of the mean head capsule measurement for successive instars are 1.36, 1.32, 1.32, 1.30, 1.23, and 1.25. Other supporting evidence is provided by observations of egg - larva and larva - pupa transformations in the laboratory. Head capsules of first-instar larvae reared from eggs collected by N.H. Anderson

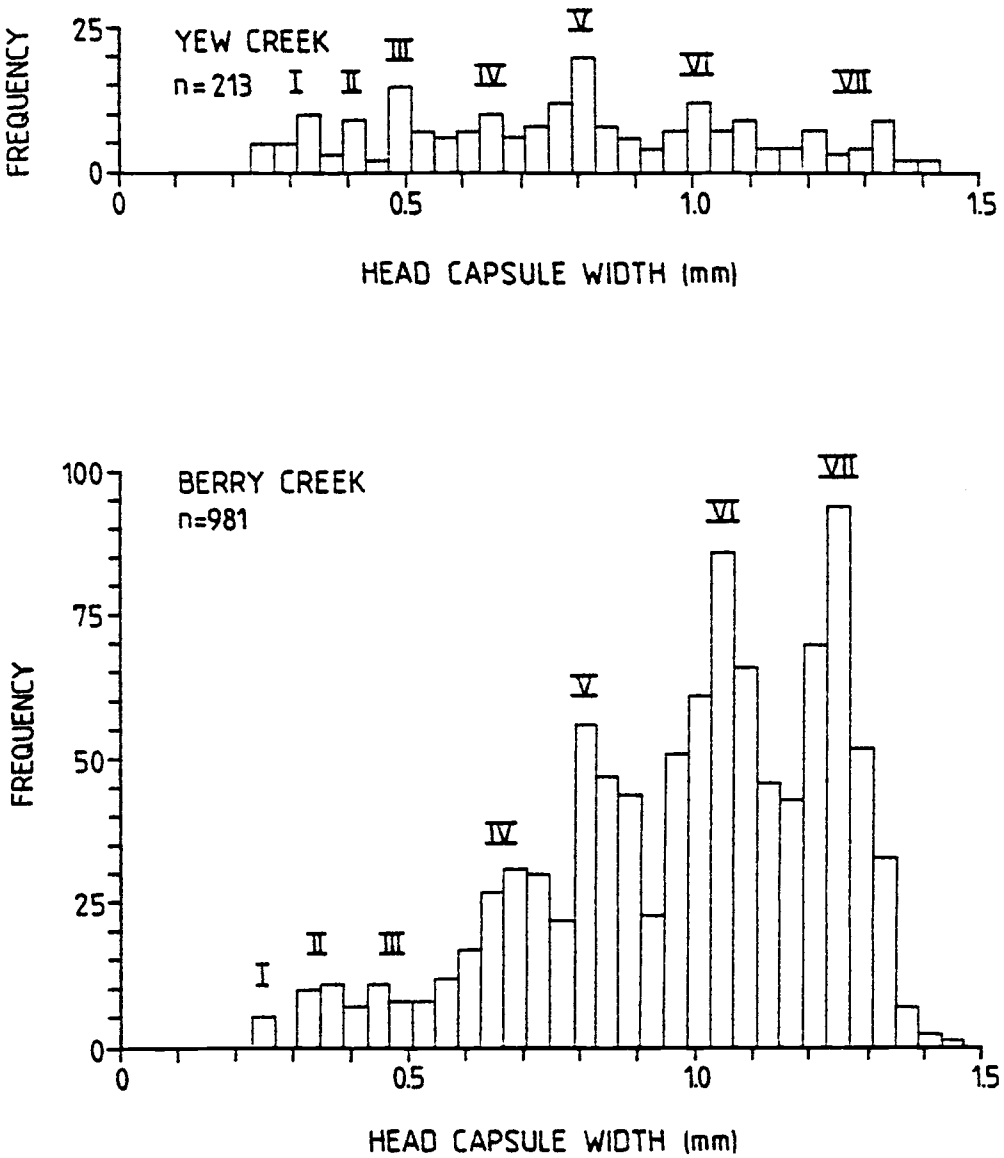

Figure 6. Frequency distributions of larval Lara avara head-capsule measurements.

Table 1. Instar boundaries of *Lara avara*, based on head-capsule width (mm). Data derived from size-frequency histograms in Fig. 8.

Instar	Berry Creek (n=981)	Yew Creek (n=213)	Values used to generate instar-frequency histograms
1	0.24 - 0.30	0.24 - 0.35	0.24 - 0.32
2	0.30 - 0.42	0.35 - 0.45	0.32 - 0.44
3	0.42 - 0.54	0.45 - 0.58	0.44 - 0.56
4	0.54 - 0.76	0.58 - 0.70	0.56 - 0.76
5	0.76 - 0.94	0.70 - 0.93	0.76 - 0.96
6	0.94 - 1.16	0.93 - 1.15	0.96 - 1.16
7	1.16 +	1.15 +	1.16 +

measured 0.28 mm, which corresponds with the smallest size of field-collected larvae (Fig. 6). Larval exuviae associated with laboratory-reared pupae had head-capsule widths of 1.30 - 1.40 mm, which is in the upper range of the seventh-instar (Fig. 6).

Timing of Instars

A total of 2203 *Lara* larvae, mostly fourth- to seventh-instars, were collected in monthly samples from Coast Range streams. All instars were present in all seasons, and in most months (Fig. 7), but the first three instars were absent from some samples, especially in the spring. There was, however, a correspondence between months where early-instar larvae were poorly represented, and months where no sticks were brought to the laboratory for drying. The only evidence in Figure 7 for annual cohort recruitment is the peak in relative abundance of second-instar larvae in August and September, which is probably due to young of the year that hatched one to two months earlier. Seasonal changes in the relative abundance of sixth- and seventh-instar larvae will be discussed in connection with drifting by last-instar larvae.

Some unpublished data made available to me by N.H. Anderson proved useful in my analysis of seasonal changes in instar abundance. The data provided several years of seasonally-measured weights and counts of *Lara* larvae

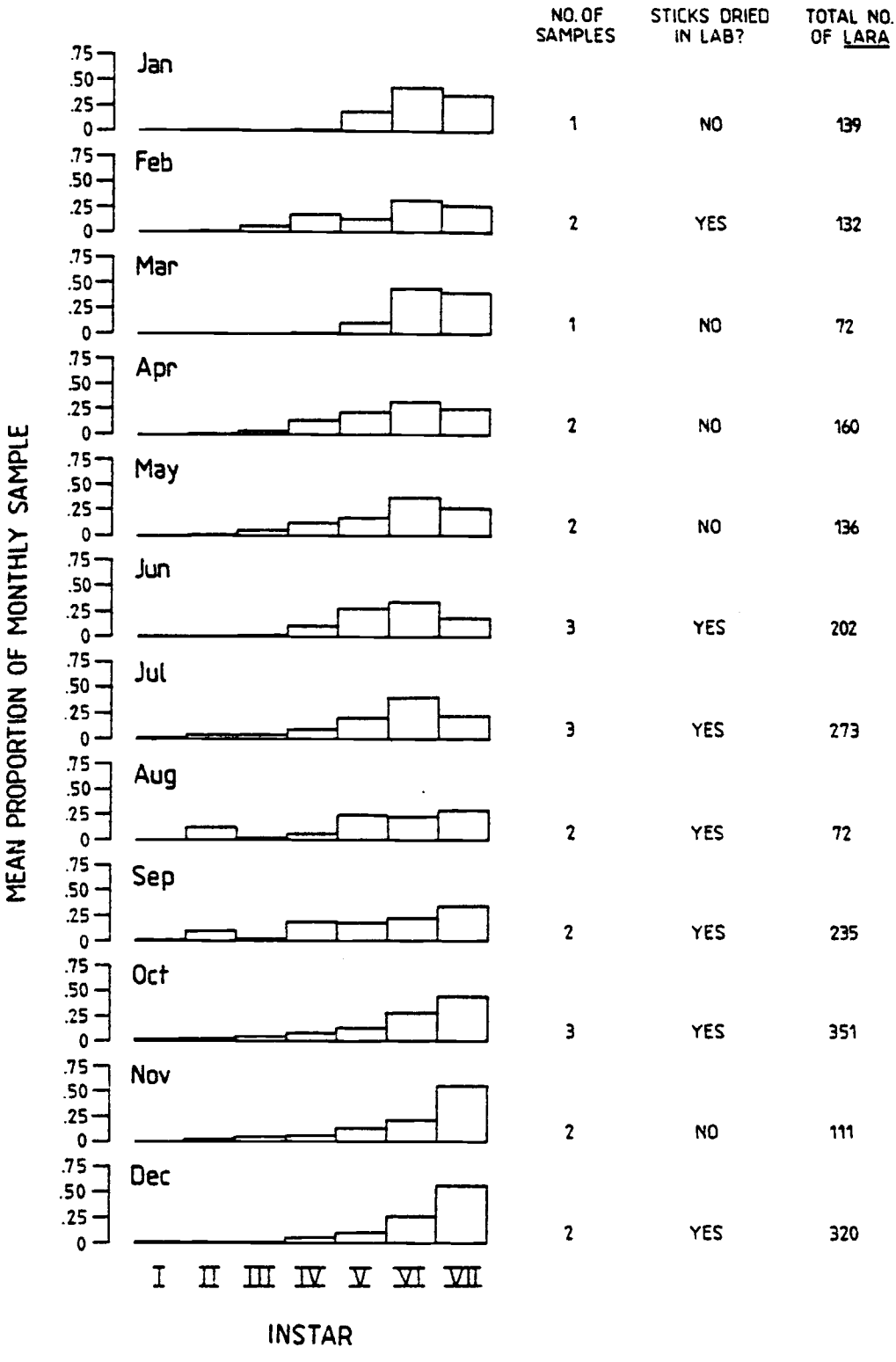

Figure 7. Monthly changes in relative abundance of Lara avara instars, on sticks collected from Coast Range streams, 1981 - 1982.

washed from tethered sticks in Berry, Flynn, and Mack Creeks. Using a regression equation that related dry weight and head capsule measurements (Appendix 1), I was able to estimate the instar of a larva, given its weight. Because the specimens were pooled for weighing, only those Lara that occurred alone in a sample could be assigned to an instar. This was possible for 265 of the 972 larvae that were collected in Anderson's study. These data also showed that all instars were represented in all seasons, except for first-instar larvae, which were absent from spring samples (Fig. 8).

Instar Duration

One of my major objectives was the estimation of instar duration by some indirect means, since my expected tenure at OSU was considerably shorter than the expected life span of Lara. Three field estimates, based on the mark-recapture study in Berry Creek, and two laboratory estimates based on observations of larvae used in the fecal production studies, are described below. Raw data for the mark-recapture study is contained in Appendix 3.

Field Estimates of Instar Duration

Oldest Mark The oldest mark recovered in each instar provided an under-estimate of maximum instar duration. This method under-estimated instar duration for the larva carrying the oldest mark, since the mark was

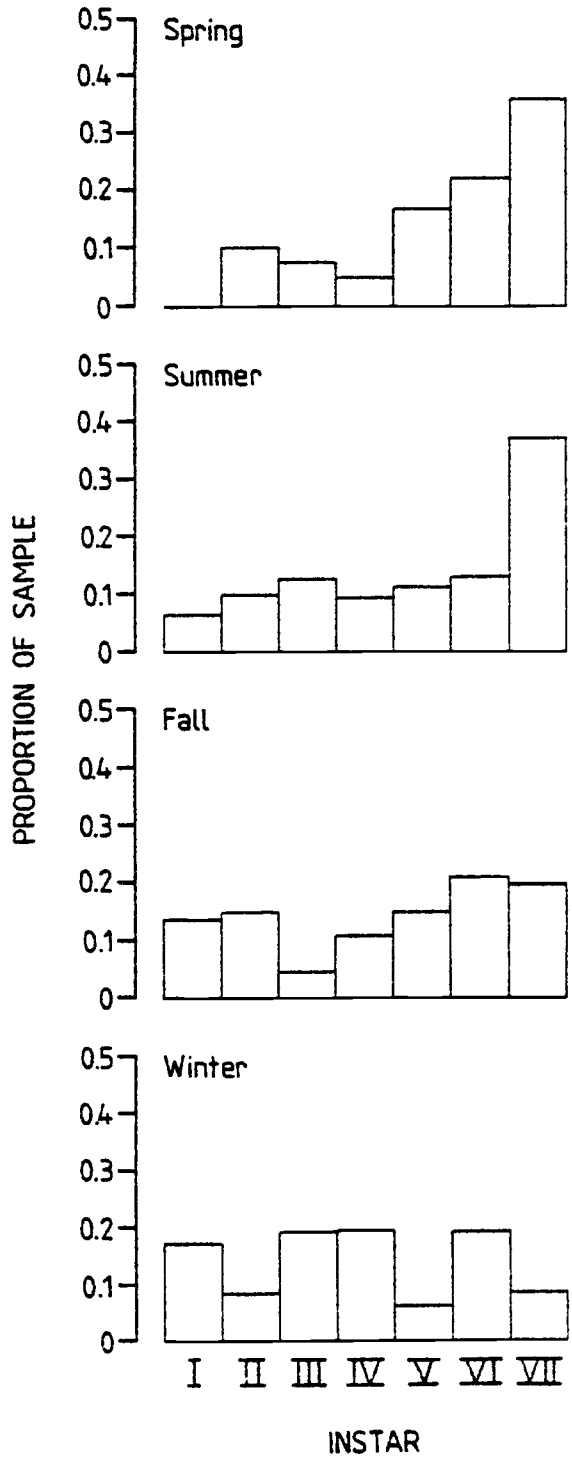

Figure 8. Seasonal changes in relative abundance of Lara avara instars, on tethered sticks in Oregon streams (N.H. Anderson, unpublished data). See text for details of calculation.

applied after the start of the instar. However, this method may over-estimate mean instar duration for a population of Lara larvae, if the larvae with the oldest marks are slow-growing. The age of the oldest mark recovered in each instar was 2 months for fourth-instar, 11 months for fifth-instar, 15 months for sixth-instar, and 15 months for seventh-instar.

Attrition of Mark Cohorts Larvae that were marked for the first time in any given month of the study could be considered as a mark cohort, and followed in succeeding months. "Mark survivorship" curves for instars four to seven, with several mark cohorts plotted on the same time scale, are shown in Figs. 9 - 11. Loss of marks or marked individuals from the cohort could occur from moulting, drifting, or accidental mark loss. The estimate of instar duration is based on the rate of mark-loss that is attributable to moulting. To do this, I corrected for the rate of loss due to drift, and assumed that the rate of accidental mark loss was negligible.

For instars four to seven, the mean proportion remaining for each of the first six months was calculated over nine cohorts initiated from March to December, 1981 (Table 2). For each instar, the natural logarithm of the mean proportion remaining at each month was regressed on time in months. The resulting coefficient of regression is the instantaneous rate of loss of marked larvae from the cohort. This rate still needed to have the rate of loss

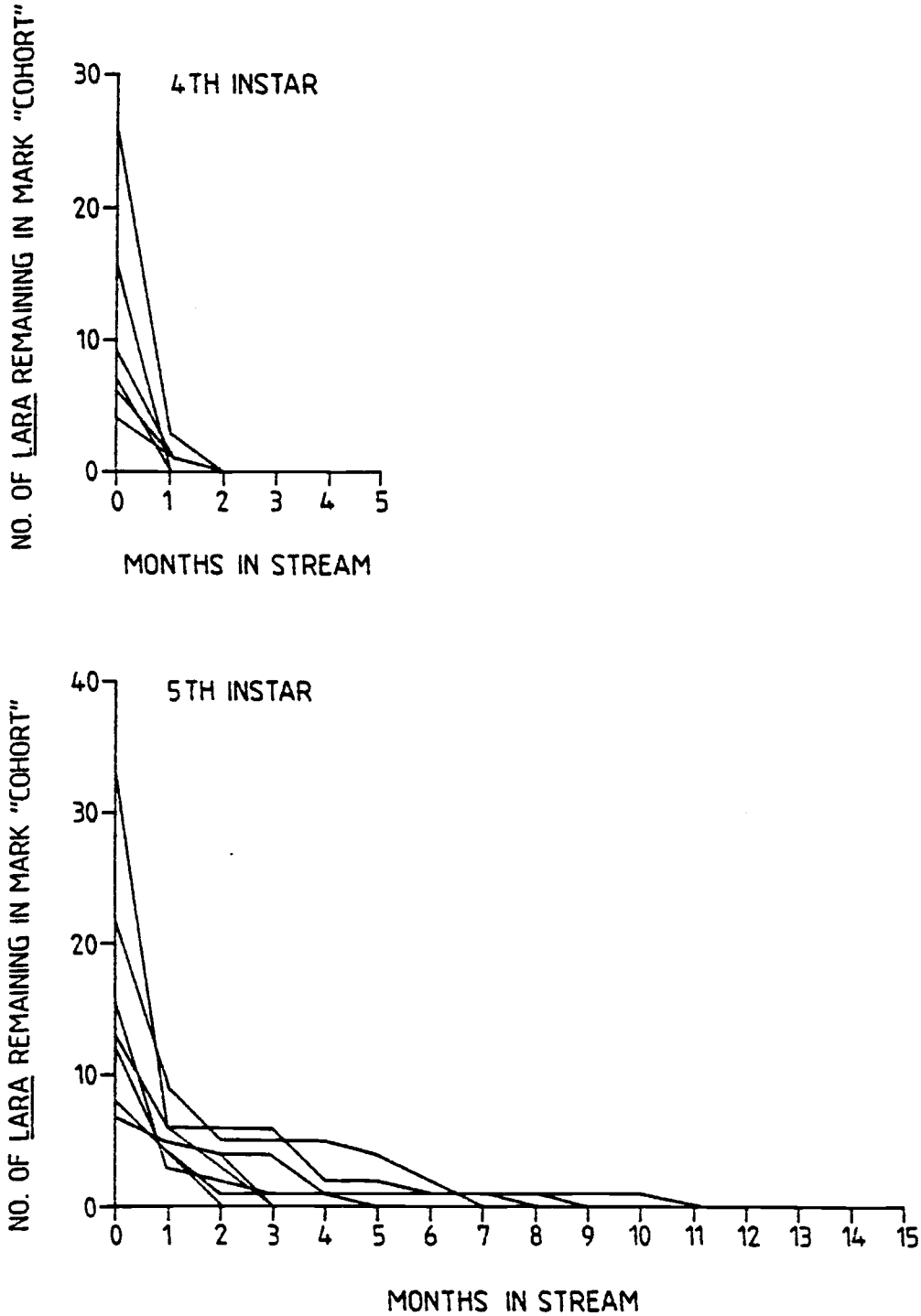

Figure 9. Attrition of 4th- and 5th-instar Lara avara mark cohorts in Berry Creek.

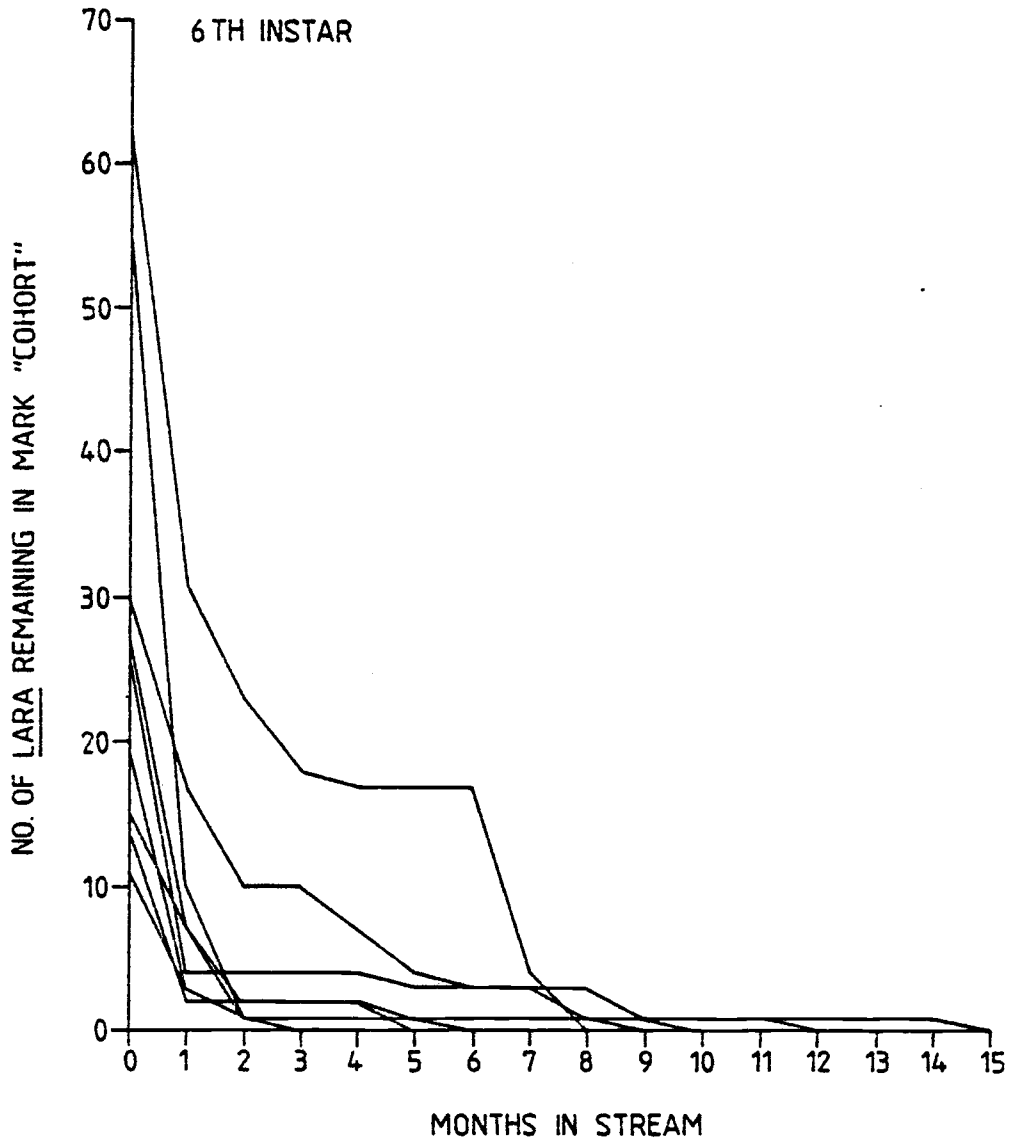

Figure 10. Attrition of 6th-instar Lara avara mark cohorts in Berry Creek.

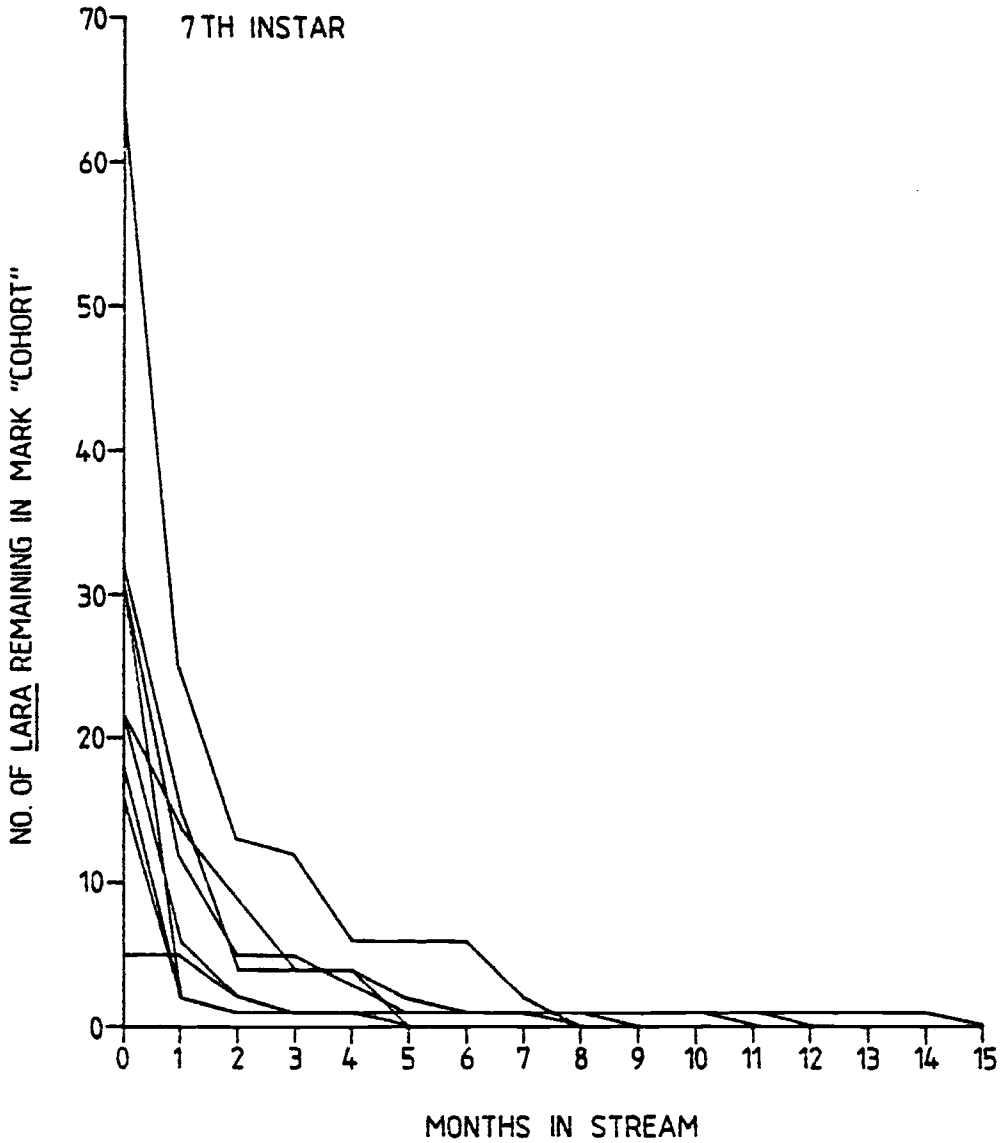

Figure 11. Attrition of 7th-instar Lara avara mark cohorts in Berry Creek.

Table 2. Mean (SE) proportion remaining at one month intervals, of 4th- to 7th-instar Lara avara mark-recapture cohorts initiated from March - December, 1981 (n = 9 cohorts).

	Instar			
Month	4*	5	6	7
1	0.108 (0.0398)	0.326 (0.0687)	0.299 (0.0564)	0.384 (0.0993)
2	0.000 (0.0000)	0.201 (0.0653)	0.147 (0.0414)	0.171 (0.0476)
3		0.164 (0.0714)	0.128 (0.0390)	0.118 (0.0226)
4		0.080 (0.0291)	0.114 (0.0315)	0.100 (0.0197)
5		0.068 (0.0272)	0.081 (0.0295)	0.046 (0.0112)
6		0.044 (0.0196)	0.070 (0.0302)	0.041 (0.0098)

* n = 6 cohorts

due to drifting subtracted from it.

The drift rate of each instar was estimated during the period when the riffle containing the flagged sticks was blocked with a screen at the upstream end. Within an instar:

$$\Delta N = M^+ - M^- - D$$

where

ΔN = net change in abundance of larvae of that instar

M^+ = moults into the instar

M^- = moults out of the instar

D = number of larvae drifting from the stick

ΔN, M^+, and M^- could be obtained from the monthly collection data. Drift onto the stick was assumed to be zero. Drift rate was highest for seventh-instar larvae (28.9%/month), and lower for fifth- and sixth-instar larvae (22.7 and 18.6%/month respectively). No evidence of drift was indicated for fourth-instar larvae (Table 3). The value of D, expressed as a proportion per month, was used to calculate an instantaneous rate that could be subtracted from the total attrition rate. The drift-corrected slope was then used to calculate the time, T_a, (a for attrition) required for the mark-cohort to disappear due to loss by moulting, which is an estimate of instar duration. Instar duration was calculated to be 1.1 months for fourth-instar larvae, 10.9 months for fifth-instar larvae, 15.9 months for sixth-instar larvae, and 16.5 months for seventh-instar larvae (Table 4).

Table 3. Estimated effects of drift and moulting on abundance of 4th- to 7th-instar *Lara avara* larvae from flagged sticks in Berry Creek, with upstream net in place. Data from January - May, 1982 (n = 5 months). See text for details of calculations.

Instar	Mean % drift/month (SE)	Mean % moulting/month (SE)	No. *Lara* observed/month
4	0 (0)	31.3 (18.75)	1 - 4
5	22.7 (8.93)	15.3 (8.91)	9 - 25
6	18.6 (7.00)	3.2 (1.38)	28 - 61
7	28.9 (4.80)	N.D.	22 - 48

Table 4. Instar duration of 4th- to 6th-instar Lara avara larvae, calculated from results of regression of ln(proportion remaining) on (months) using data from Table 3. T_a = estimated time in months when an average of one individual remains in the mark-recapture cohort, after the regression slope has been corrected for the effect of larvae lost by drifting from the stick. See text for calculation of slope correction.

Instar	r^2	Intercept	Slope	Slope (corrected for drift)	T_a (months)
4*	1	0	-2.2256	-2.2256	1.1 (91% attrition)
5	0.95	-0.4001	-0.4795	-0.2221	10.9 (94% attrition)
6	0.83	-0.6274	-0.3873	-0.1815	15.9 (97% attrition)
7	0.94	-0.3806	-0.5130	-0.1719	16.5 (96% attrition)

* No 4th-instar larvae with marks older than one month were recaptured. This line includes data for only two points.

A relatively high proportion of marks was lost by each mark cohort in the first month, compared with later months. Possible explanations include: accidental loss of fresh marks, or unusually high drifting rates following marking. The exponential model of mark loss did not completely account for this, and the initial data point (month = 0, proportion remaining = 1) tends to lie above the regression line for each instar. As a result, the antilogarithms of the Y-intercepts for each instar (Table 4) are less than the expected value of 1, and the estimates of instar duration are biased downwards.

Accumulation of Unmarked Larvae While the upstream net was in place, unmarked larvae were likely to occur on the flagged sticks only as a result of mark loss or moulting. The inverse of the frequency of moulting per individual per month, within an instar, is an estimate of instar duration. Instar duration was calculated to be 4.0 months for fourth-instar larvae, 5.2 months for fifth-instar larvae, and 18.5 months for sixth-instar larvae (Table 5).

Laboratory Estimates of Instar Duration

Collection of Exuviae The inverse of moulting frequency (monitored by collection of exuviae from the drippery trays) is an estimate of instar duration. Instar duration was calculated to be 5.5 months for fourth-instar larvae at 7°C, 17.3 months for fourth-instar larvae at 17°C, and 4.2 months for sixth-instar larvae at 7°C (Table

Table 5. Instar duration of 4th- to 6th-instar *Lara avara* larvae, calculated from accumulation of unmarked larvae on Berry Creek flagged sticks, while upstream net was in place (February to September, 1982). One moult was assumed for each unmarked larva that appeared.

Moult	No. Moults	*Lara*-months	Months/moult
4th-5th	3	12	4.0
5th-6th	13	67	5.2
6th-7th	11	203	18.5

6). The estimate obtained at 17°C is less reliable than the others, as it was based on fewer moults, over a shorter observation period (Table 6). However, the indication of slower growth at the higher temperature is probably correct.

Weight Gain of Larvae Unlike the other methods described above, which are based on measurement of moulting frequency, this estimate of instar duration was calculated from the growth rate of larvae, measured as a weight gain over time. As will be described more completely in a later section, "Larval Growth Rates", a growth rate can be used to calculate instar duration, and vice versa, given that the weight gain during that instar is known. Instar durations corresponding to the growth rates of larvae in the fecal production study were 11 months for fourth-instar larvae, 11 months for fifth-instar larvae, 10 months for sixth-instar larvae, and 31 months for seventh-instar larvae, all at 7°C.

An estimate of the length of the larval stage can be arrived at by considering information from several sources. My preliminary observations indicated that some Lara larvae, kept on stream-conditioned wood at 12°C, required at least three months for each of instars one and two, and at least four months for each of instars three, four, and five. The estimated time required to grow through instars four to seven ranged from 2.7 to 5.8 years (Table 7), using

Table 6. Instar duration of 4th- to 6th-instar *Lara avara* larvae, calculated from frequency of moulting in Oak Creek drippery. Months/moult = instar duration

Moult	No. moults	*Lara*-months	Months/moult	Mean temp. (°C)
4th-5th	17	94.4	5.5	7
4th-5th	3	51.8	17.3	17
6th-7th	21	87.9	4.2	7

Table 7. Summary of instar duration estimates (months) for 4th- to 7th-instar Lara avara larvae.

	Method	Instar			
		4	5	6	7
Field	1) Oldest mark	2	11	15	15
	2) T_a (corrected for drift)	1	11	16	17
	3) Accumulation of unmarked individuals	4	5	19	N.D.
Lab	4) Weight change in drippery	11	11	10	31
	5) Frequency of moulting	6	4	N.D.	N.D.
	Range of instar duration	1-11	4-11	10-16	17-31

the field and laboratory methods described above. If one year is added for growth through instars one to three, the estimated length for the entire larval stage of Lara, rounded to the nearest year, is four to seven years.

Pre-pupation Behavior of Last-Instar Larvae

Like many other stream insects, Lara larvae can occur in the drift (Brusven 1970). They may drift accidentally, or intentionally for the purpose of locating new food sources or terrestrial pupation sites. While all instars appear to be capable of colonizing artificial substrates, which presumably requires some sort of drifting ability, I feel that drift by last-instar larvae deserves special consideration. N.H. Anderson and others had observed that some Lara larvae were able to float. This prompted dissections, and led to the discovery of tracheal air sacs in the abdomens of large larvae (Fig. 12). Further, my observations suggest that air sacs are possesed only by last-instar larvae, and may be important in pre-pupation behavior. Air sacs have been reported in other elmid beetles (i.e. Hinton 1940), but no systematic study of their occurrence has been attempted.

When dissecting 35 sixth- and seventh-instar larvae, I found that the smallest larva with air sacs had a head capsule width of 1.08 mm, and the largest larva without air sacs had a head capsule width of 1.16 mm. Of 19 larvae that fell within that range, 12 had air sacs, and 7 did

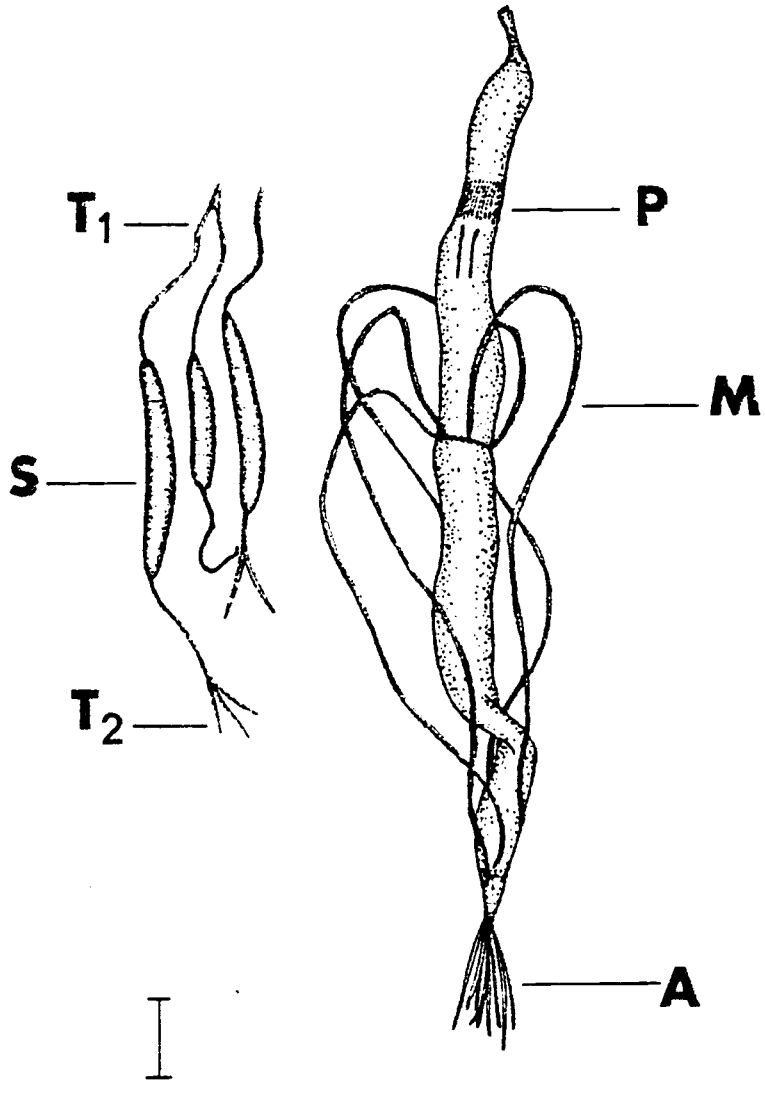

Figure 12. Gut and air sacs of 7th-instar Lara avara larva. A = anal gills M = malpighian tubule P = proventriculus S = air sac T_1 = trachea leading to body wall T_2 = trachea leading to gut. Approximately 30 - 40 air sacs, situated ventral to the gut, are present in each 7th-instar larva. Bar = 1 mm.

not. This range of size includes the graphically determined boundary between 6th and 7th instar larvae (1.15 to 1.16 mm).

Lara larvae that possess air sacs are able to control their buoyancy in some manner that is both rapid and reversible. Since the air sacs are merely an enlarged section of trachea and are not muscular, I propose, as did Perez (1863) for Machronychus quadrituberculatus (Elmidae), that buoyancy is controlled by the tergo-sternal muscles, and that the air sacs serve to reduce the density of the larva by displacing haemolymph with air. To float, the larva need only relax the tergo-sternal muscles, which allows the air sacs to expand to their full size. This increases volume, but not mass, and reduces the density of the larva. To sink, the muscles are contracted, reducing volume, and increasing the density of the larva. In vitro, the action of the tergo-sternal muscles can be replaced by external pressure on the abdomen. If sufficient pressure is exerted on the stopper of a vial of water containing a floating Lara larva, the larva will sink. When the pressure is released, the "cartesian dryopoid" will rise.

I suggest that air sacs, and the ability to float, may be associated with pre-pupation behavior, since they are present only in last-instar larvae. Pre-pupal larvae must leave the stream to reach terrestrial pupation sites, and an ability to float would appear to facilitate this.

There are two indications that last-instar larvae

drift more frequently just prior to pupation. The first is based on seasonal changes in relative abundance of last-instar larvae in two types of samples; the second is based on drift collections in Berry Creek.

In Figures 7 and 8, the ratio of the relative abundance of seventh-instar to sixth-instar larvae shifts on a seasonal basis. In my field collections, the ratio is >1 for the period from August to December, and <1 from January to July. This trend is reversed for N.H. Anderson's stick colonization data, which represents short-term colonization by Lara larvae, probably via drifting. Considered together (Fig. 13), these data suggest that last-instar larvae leave the larval habitat and become active in the water column sometime during the late winter or early spring.

Of 52 Lara larvae that were captured in drift collections from Berry Creek from January 26 to June 15 1982, 49 were 7th instar. Most of these larvae (40) were captured in one sample from February 4 - 19, 1982. This period was one of heavy rainfall (11.4 cm) and warm air temperatures (up to 15^{o}C). The pulse of drifting last-instar larvae could have been due to an environmental cue, such as photoperiod plus an increase in temperature, that prompted competent larvae to seek terrestrial pupation sites.

The following anecdotal observations suggest that last-instar larvae leave the stream during the late winter

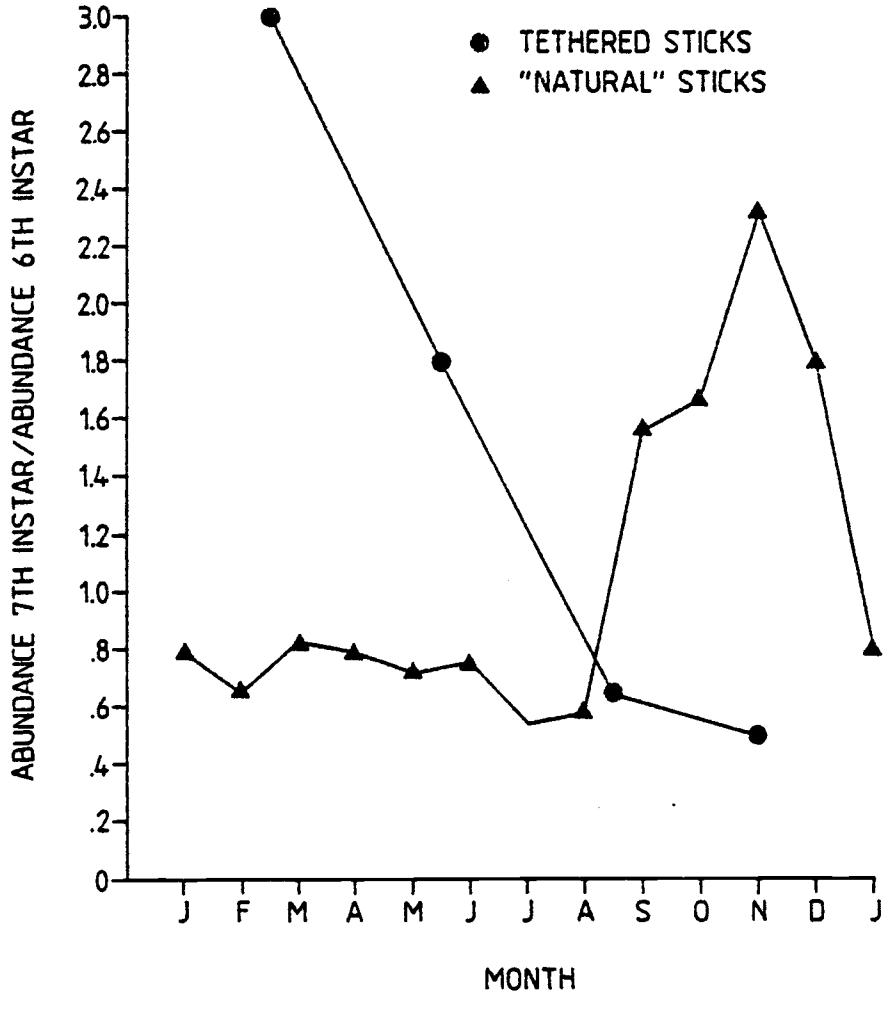

Figure 13. Seasonal changes in ratio of 7th-instar/6th-instar relative abundance, for Lara avara larvae on "natural" sticks and N.H. Anderson's tethered sticks.

or early spring, and that they may spend a month or more in moss at the edge of the stream, before they pupate. On July 3, 1981, I found a seventh-instar Lara larva in moss one meter above the water surface, on a large rock in Lobster Creek. On May 1, 1982, Jeff Witcosky (Department of Entomology, OSU) found a seventh-instar Lara larva in moss on the bank of Woods Creek, near Philomath, Oregon, 8 km west of Corvallis. On March 12, 1983, Kelly Moore (Department of Fisheries and Wildlife, OSU) found several seventh-instar Lara larvae in an emergence trap in Mack Creek, in the Cascade Range of Oregon. The larvae had crawled up the side of the trap, and into a glass container at the top. In all of these instances, the larvae were probably pre-pupal.

Some feeding and growth may occur between the time when last-instar larvae leave the stream, and the time when they pupate, as I often saw evidence of feeding in laboratory pupation experiments, even though the larvae had been out of water for several months.

Feeding and Digestion

My observations of gut structure and function in Lara larvae suggest a digestive strategy based on rapid throughput, and limited mechanical and biochemical disruption of wood particles. Such a strategy would place a premium on readily assimilable nutrients derived from

microbial activity, rather than on the more refractory structural polysaccharides of the wood.

Wood particles are not subjected to intense mechanical disruption during feeding and passage through the gut. Lara larvae have robust, scoop-shaped mandibles (Fig. 5a) that slice off, but do not grind, thin pieces of wood. The proventriculus (Fig. 12) is weakly developed, as is typical of most larval Coleoptera (Crowson 1981), and does not contribute to further reduction in particle size.

The rest of the larval gut (Fig. 12) is a straight tube, with no diverticula or "fermentation chambers" that could support a symbiotic gut flora. I was unable to see any evidence of a dense gut flora in Lara, although such a flora was quite evident in larval hindguts of the aquatic xylophages Lipsothrix nigrilinea and Austrolimnophila badia (Diptera: Tipulidae). The simple structure of Lara's gut also limits the residence time of ingested wood particles. Gut residence time was 8 hours at 12°C (n = 23, SE = 0.5 hours).

Very low cellulase activity (0.001 - 0.007 µg glucose/mg protein/hr) was found in extracts of both gut tissue and gut contents of Lara larvae. The levels of activity were low enough to suggest the possiblity of spurious, or non-specific enzyme activity, such as that attributable to amylase. It is not likely that Lara produces its own cellulase, nor that the observed level of activity is physiologically useful. Monk (1976) found

slight cellulase activity (3 - 12 μg glucose/mg protein/hr) in the guts of various aquatic insects, and higher activity (8 - 67 μg glucose/mg protein/hr) in the guts of amphipods and aquatic molluscs. Kesler (1982) found cellulase activities of 0.60 - 2.04 μg glucose/mg protein/hr in whole-insect extracts of caddisflies. Methodologies of cellulase determinations are far from standardized, however, and it is not clear whether observed cellulase activity is endogenous or derived from ingested material.

The proportion of ash contained in feces produced by Lara larvae feeding on alder and Douglas-fir wood (3 - 4%) was similar to that of the original conditioned wood that was eaten (Table 8), indicating that little carbon was removed by Lara. In another experiment, I found that the inner, unconditioned wood of Douglas-fir, hemlock, and alder sticks contained less than 1% ash. Apparently, Lara's contribution to the mineralization of wood tissue is minimal compared to that already accomplished by fungi and bacteria.

An indirect estimate of assimilation efficiency, based on my measurements of respiration, growth, and fecal production, was 12% for fourth-instar larvae, and 5% for sixth-instar larvae (Table 9).

Larval Growth Rates

Daily instantaneous growth rates of fourth- to seventh-instar Lara larvae were calculated from instar

Table 8. Ash content of wood before and after ingestion by *Lara avara*.

	Wood		Feces	
	Wt. collected (mg)	% ash	Wt. collected (mg)	% ash
Alder branch	560.13	4.14	358.16	3.85
Douglas-fir stick	398.93	3.04	556.53	3.11

Table 9. Calculation of assimilation efficiency of 4th- and 6th-instar *Lara avara* larvae. All values in mg/day.

		Instar	
		4th	6th
	Respiration (R)*	0.0032	0.0114
+			
	Growth (G)	0.0137	0.0071
=	Assimilation (A)	0.0169	0.0185
+			
	Fecal production (F)	0.1215	0.3204
=	Ingestion (I)	0.1384	0.3389
	Assimilation Efficiency (= 100 x A/I)	12%	5%

* assuming 0.9 liters O_2 at STP required to metabolize 1 g of carbohydrate/protein food (Schmidt-Nielsen 1979)

duration estimates, and from measurements of larval weight gain during the Oak Creek fecal production runs. As mentioned earlier in the "Instar Duration" section (p. 34), instar duration and growth rate during that instar are interconvertible, if the weight gain that occurs during that instar is known. If estimates of any two of:

a) mean weights of successive instars (W_i, W_{i+1})

b) instar duration (t)

c) instantaneous growth rate (G)

are known, then the remaining number can be calculated:

$$G = [\ln(W_{i+1}/W_i)]/t$$

In my calculations, I have added the weight of the exuviae lost in the moult from instar i to instar i+1, to the weight of instar i+1 (Table 10).

Daily instantaneous growth rates calculated from instar duration, and from weight gains in the Oak Creek drippery, were similar. In the discussion that follows, I use relative growth rate (%/day), which is very nearly equivalent to instantaneous growth rate x 100, at the low levels exhibited by Lara. Growth rates calculated from instar duration were: 0.62 - 3.72 %/day for fourth-instar larvae, 0.35 - 0.95 %/day for fifth-instar larvae, 0.11 - 0.13 %/day for sixth-instar larvae, and 0.22 - 0.25 %/day for seventh-instar larvae (Table 11). Growth rates calculated for larvae feeding on Douglas-fir, hemlock, and alder sticks in the 1981 fecal production runs were lower at 17°C (0.10 - 0.19 %/day) than at 7°C (0.25 - 0.40 %/day)

Table 10. Weights, in mg, of 1st- to 7th-instar *Lara avara* larvae and their exuviae. Total change in weight (including exuviae) from one instar to the next is shown.

Instar (I)	Mean dry wt. (SE) n	Mean exuvia wt. (n)	Total wt. change (I to I+1)
1	0.052 (0.0070) 17	0.007 (1)	0.077
2	0.122 (0.0098) 21	0.027 (2)	0.212
3	0.307 (0.0318) 18	0.062 (2)	0.564
4	0.813 (0.0583) 39	0.141 (2)	1.719
5	2.303 (0.1642) 40	0.287 (16)	1.765
6	3.687 (0.2504) 24	0.582 (17)	6.584
7	9.689 (0.5929) 30	1.666 (6)	

Table 11. Summary of growth rate estimates (%/day) for 4th- to 7th-instar *Lara avara* larvae.

	Method	Instar 4	5	6	7
Field	1) Oldest mark	1.86	0.35	0.13	0.25
	2) T_a (corrected for drift)	3.72	0.35	0.13	0.22
	3) Accumulation of unmarked individuals	0.93	0.76	0.11	N.D.
Lab	4) Weight change in drippery	0.34*	0.34*	0.20**	0.12**
	5) Frequency of moulting	0.62	0.95	N.D.	N.D.
	"Mean" growth rate	1.49	0.55	0.14	0.20

* fed on Douglas-fir, hemlock, and alder sticks; mean temperature 7°C
** fed on alder branch wood; mean temperature 11°C

(Table 12a). Growth rates for larvae feeding on alder branch wood in the 1982 fecal production runs were: 0.37 %/day for fifth-instar, 0.20 %/day for sixth-instar, and 0.12 %/day for seventh-instar (Table 12b)

The methods that I used to measure the growth rate of Lara larvae may have tended to give underestimates (see Table 13 for potential biases of each method), and as a result, my estimates of the duration of the larval stage are probably high. There was no clear correspondence between the expected bias of a method and the relative size of the estimate that it provided.

Larval Respiration Rates

During measurements of respiration rate, Lara larvae in the reaction vessels fed and defecated, in some semblance of normal behavior. The respiration rates that I obtained probably represent active, rather than basal metabolism. At 10°C, mean oxygen consumption was 0.15 µl/mg/hr for fourth- and fifth-instar larvae, 0.12 µl/mg/hr for sixth-instar larvae, and 0.13 µl/mg/hr for seventh-instar larvae. At 15°C, mean oxygen consumption for the same groups of larvae was 0.32, 0.32, and 0.19 µl/mg/hr (Table 14). The mean Q_{10} for the interval between 10° and 15° was 4.67 for fourth- and fifth-instar larvae, 7.39 for sixth-instar larvae, and 2.90 for seventh-instar larvae. The "grand mean" oxygen consumption was 0.13 µl/mg/hr at

Table 12a. Growth of 4th- and 5th-instar Lara avara larvae in Oak Creek drippery, 1981. Larvae were fed Douglas-fir, hemlock, and alder sticks. Weights in mg. Larvae weighed in groups of "n".

Instar	n	No. days	Temp. (°C)	Initial wt. (W_o)	Final wt. incl. exuviae (W_t)	Daily Instantaneous Growth Rate
4+5	20	48	7	57.12	69.32	0.0040
4+5	20	48	7	54.02	64.98	0.0038
4+5	20	34	7	53.99	58.88	0.0025
4+5	20	21	17	44.87	45.87	0.0010
4+5	20	21	17	42.21	43.91	0.0019
5	10	45	17	55.17	57.75	0.0010

Table 12b. Growth of 5th- to 7th-instar Lara avara larvae in Oak Creek drippery, 1982. Larvae were fed alder branch wood. Weights in mg. Larvae weighed individually.

Instar	n	No. days	Temp. (°C)	Initial wt. (W_o)	Final wt. incl. exuviae (W_t)	Daily Instantaneous Growth Rate
5	10	62	11	22.63	28.41	0.0037
6	16	62	11	73.92	83.69	0.0020
7	12	62	11	110.35	118.80	0.0012

Table 13. Possible biases associated with estimates of larval growth rate in this study.

Field Methods	Main Bias	
Oldest Mark	Over-estimate:	(for individuals) larvae marked after beginning of instar; some tendency to under-estimate mean population instar duration, due to potential for selection of slow-growing individuals.
T_a (corrected for drift)	Over-estimate:	part of observed attrition could be due to incomplete correction for drift, incomplete sampling of marked larvae, or lost marks.
Accumulation of unmarked Individuals	Under-estimate:	incomplete sampling of marked larvae; some tendency to over-estimate, due to lost marks.
Laboratory Methods		
Weight change in drippery	Under-estimate:	growth may be reduced due to imperfect rearing conditions.
Frequency of moulting	"	
Laboratory rearing	"	

Table 14. Respiration rates of 4th- to 7th-instar Lara avara larvae, at 10° and 15°C.

Instar	No. Larvae	Mean wt (mg)	10°C $\mu l O_2/mg/hr$	15°C $\mu l O_2/mg/hr$	Q_{10}
4+5	8	1.55	0.21	0.44	4.39
	8	1.98	0.09	0.20	4.94
6	7	4.17	0.11	0.33	9.00
	7	4.38	0.14	0.32	5.22
	7	3.86	0.11	0.31	7.94
7	5	8.66	0.19	0.20	1.11
	5	8.50	0.07	0.16	5.22
	5	9.26	0.13	0.20	2.37

$10^{o}C$, 0.27 µl/mg/hr at $15^{o}C$, with a Q_{10} of 4.31.

Feeding Impact of Natural Populations of Lara Larvae

This section presents the results of laboratory and field studies that were intended to estimate the effect of feeding by Lara larvae on wood debris in Oregon streams. The calculations required estimates of field population levels of Lara larvae, and estimates of per capita fecal production rate (itself an estimate of feeding rate; see the Methods section).

Population Estimates

The abundance of Lara larvae in stick collections from Coast Range streams is shown in Table 15. For simplicity, I will discuss only results expressed as biomass per kg wood. In the next section, which presents estimates of fecal production for natural populations of Lara, some of these results will be converted to biomass per m^2 of stream bed, using published estimates of wood abundance for Oregon streams.

Lara abundance in stick collections varied considerably, depending on the location of collection, and wood type. Lara biomass was 2 to 10 times higher on Berry Creek sticks (258 mg/kg) than on sticks from the other Coast Range streams: Yew Creek Tributary had 105 mg/kg, Yew Creek had 19 mg/kg, and Flynn Creek had 23 mg/kg. Lara biomass on hardwood sticks exclusive of Berry Creek (83 mg/kg) was more than twice as high as on conifer sticks (35

Table 15. Density and biomass (mg) of Lara avara larvae on sticks from Coast Range streams [mean (SE)].

	n (sticks)	No./m^2 wood	Wt./m^2 wood	No./kg wood	Wt./kg wood
All sticks	50	71 (13.9)	262 (58.7)	29 (6.9)	113 (36.0)
Sites other than Berry Ck.	36	51 (14.8)	168 (41.3)	17 (5.3)	57 (15.7)
Berry Ck.	14	124 (28.2)	501 (168.6)	60 (18.3)	258 (116.2)
Flynn Ck.	10	28 (14.8)	100 (40.9)	6 (3.0)	23 (8.6)
Yew Ck.	7	17 (7.8)	76 (54.4)	4 (1.9)	19 (13.8)
Yew Ck. trib.	16	88 (29.7)	279 (79.2)	33 (10.7)	105 (30.8)
Hardwood sticks	30	91 (16.6)	348 (86.4)	41 (9.8)	165 (57.1)
Hardwood other than Berry Ck.	16	61 (16.4)	213 (53.8)	24 (7.5)	83 (25.4)
Conifer sticks	20	43 (23.3)	133 (60.7)	12 (7.3)	35 (18.8)

mg/kg). Lara biomass did not appear to be related to the size or density (gm/cm^3, an index of decay) of the conditioned sticks that I collected. Larvae were found in similar abundance on large and small sticks, of widely varying decay states (Figs. 14, 15). One hardwood stick from Berry Creek and one conifer stick from Yew Creek Tributary had unusually high densities of Lara larvae, 1729 mg/kg and 371 mg/kg, respectively (Figs. 14, 15). These sticks were relatively small and had a complex surface texture with many feeding grooves, but did not appear to be unusual in any other way. I rarely found Lara on undecayed wood, and when I did, there was no evidence of feeding. The results of the stick collections indicate that Lara larvae, if present in the stream, may occur on virtually any type of submerged, partially decayed wood.

Fecal Production in Laboratory Culture

Individual estimates of fecal production by Lara larvae in the Oak Creek drippery ranged from 0 - 41% of body weight per day. The overall mean (Table 16) was 9%/day. During these measurements the water temperature ranged from 4 - 18°C.

On Douglas-fir, hemlock, and alder sticks, rates for fourth- and fifth-instar larvae (7 - 13%/day) were higher than those for sixth- and seventh-instar larvae (4 - 7%/day). On alder branch wood, the rates were higher than those on the sticks, and there was no difference between

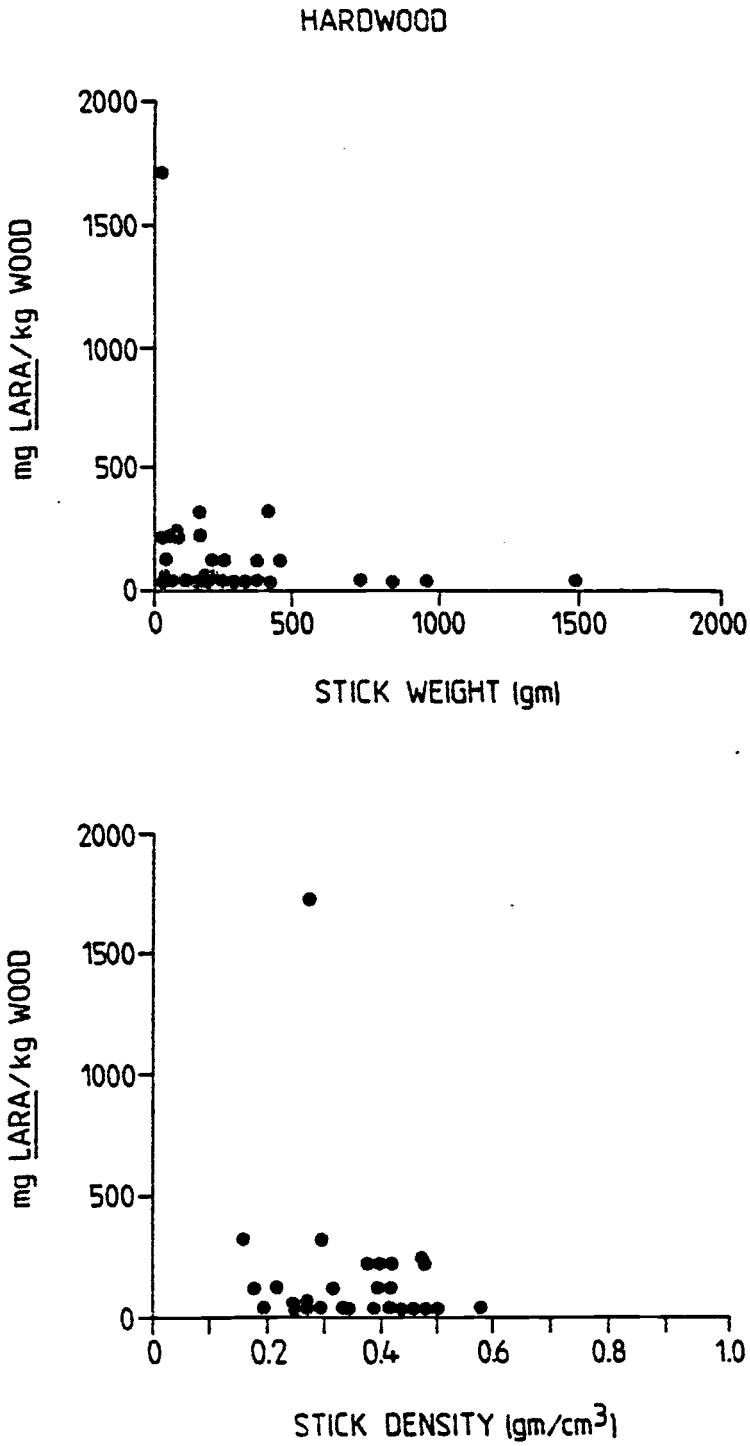

Figure 14. Effects of stick weight and stick density on abundance of Lara avara larvae in hardwood stick collections.

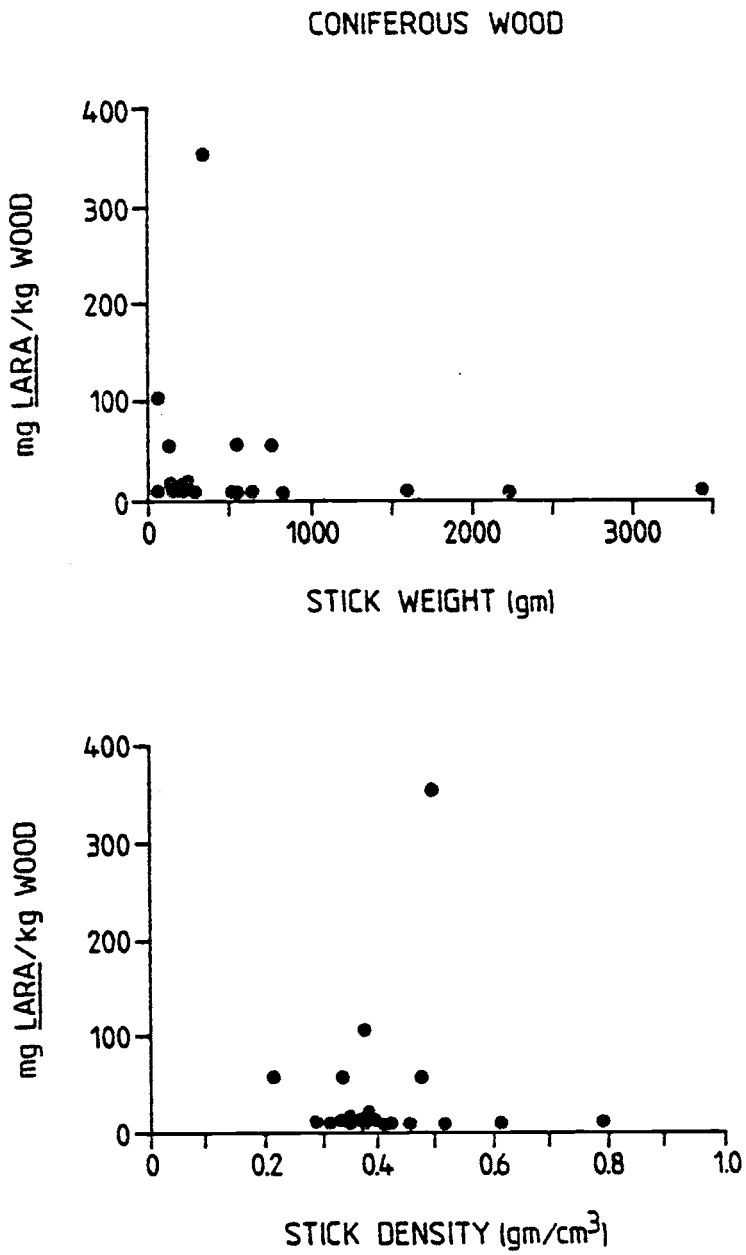

Figure 15. Effects of stick weight and stick density on abundance of Lara avara larvae in conifer stick collections.

Table 16. Fecal production (% body wt./day) by Lara avara larvae on Douglas-fir sticks (Df), hemlock sticks (Hm), alder sticks (Al), and alder branch wood (AlBr) [mean (SE) n]. All data from dry weights.

	Wood			
Instar	Df	Hm	Al	AlBr
4 + 5	13.2 (3.31) 6	17.7 (2.34) 6	7.1 (0.68) 7	16.4 (3.70) 5
6 + 7	7.4 (1.53) 26	7.2 (0.89) 21	3.8 (0.47) 26	14.4 (2.02) 20
	Grand Mean: 9.0 (0.74) 117			

instars. An additional estimate of fecal production rate for fifth-, sixth-, and seventh-instar larvae was provided by an experiment, discussed earlier in connection with larval feeding and digestion, that compared the ash content of Lara's food and feces. These estimates, obtained with much higher densities of Lara, were 17%/day on Douglas-fir sticks, and 9%/day on alder branch.

Analysis of Variance of the fecal production data (summarized in Table 17) indicated that there were no significant effects due to wood type (Douglas-fir, hemlock, alder) or temperature, on fecal production rate. Plots of mean fecal production rates (Figs. 16, 17) also show that effects of temperature on fecal production rate were small relative to other sources of variation.

Fecal production by Heteroplectron californicum larvae on alder branch wood was much higher than that for Lara, and appeared to increase over a range of temperatures from 5 - 18°C (Fig. 18). Fourth-instar Heteroplectron larvae (mean wt. 3.9 mg) produced 17% body weight per day at 9°C, and 91%/day at 18°C. Fifth-instar Heteroplectron larvae (mean wt. 9.5, and 14.2 mg) produced 28%/day at 5°C, and 42 - 45%/day at 8°C.

Feeding Impact

An estimate of Lara's fecal production in Oregon streams ($gm/m^2/yr$) can be calculated from estimates of wood abundance in Oregon streams (kg wood/m^2 stream bed) (Anderson et al. 1978), and my estimates of laboratory

Table 17. Summary of Analysis of Variance of fecal production data for Lara avara larvae.

	Factors				
	Instar	Temp. (°C)	Wood	Replicates/cell	Effects
3-way:	4+5, 6+7, 7	4,7,8,9	Df,Hm,Al	1 - 2	Instar: P < 0.005 (4+5 was higher)
2-way:	4+5, 6+7, 7	5,9,11,12,15	AlBr	1 - 2	no significant effects

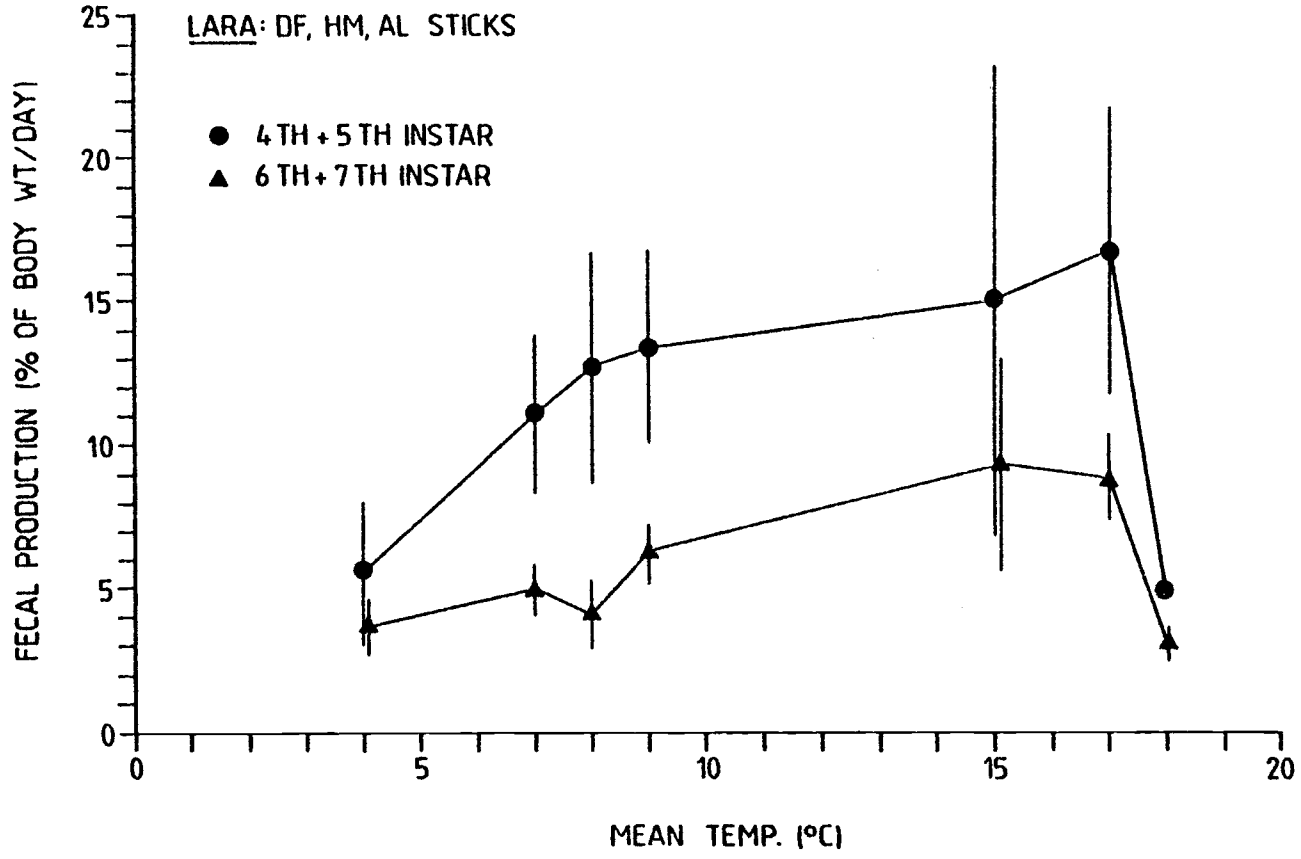

Figure 16. Effects of temperature on fecal production of Lara avara larvae feeding on Douglas-fir, hemlock, and alder sticks (mean ± SE).

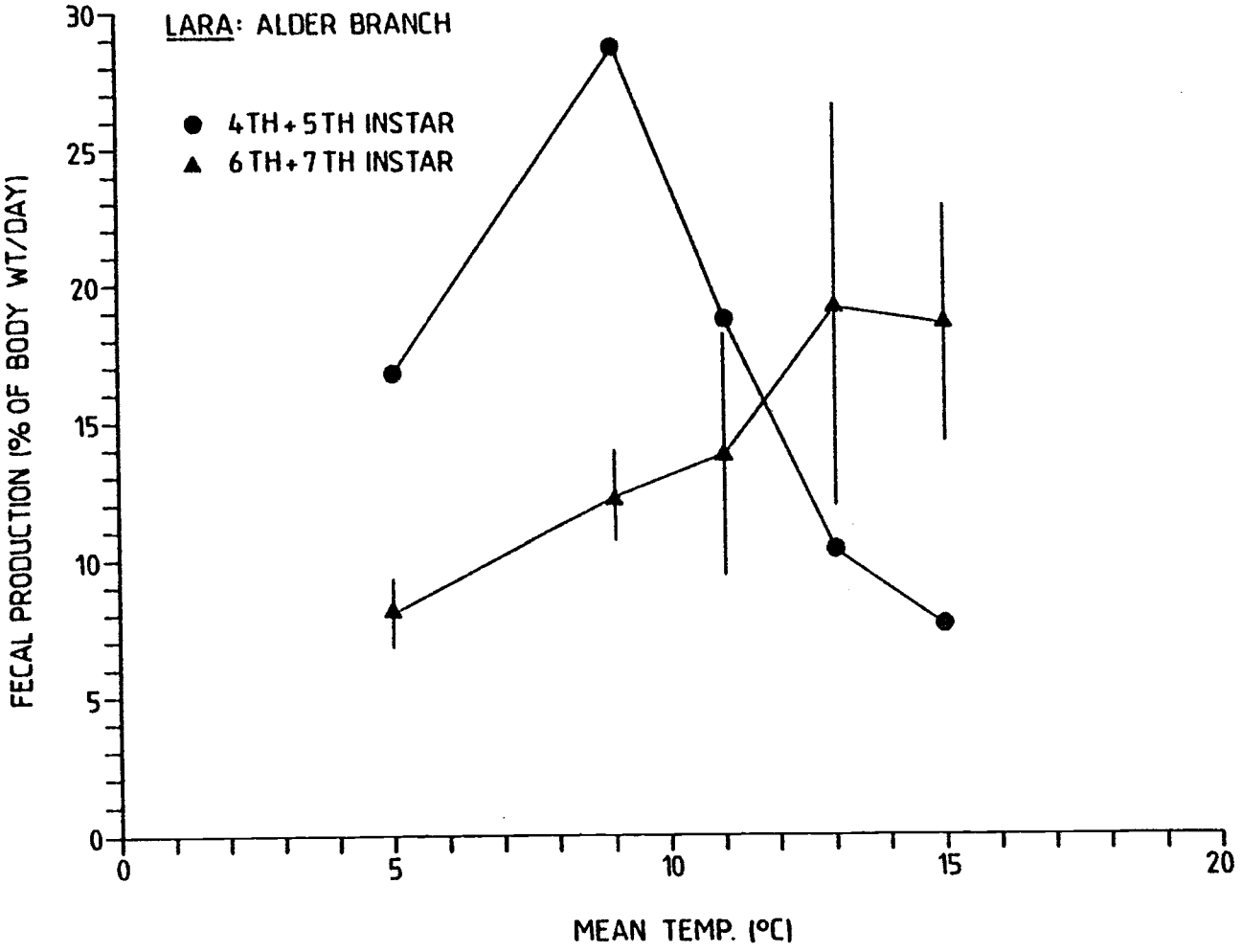

Figure 17. Effects of temperature on fecal production of Lara avara larvae feeding on alder branch (mean ± SE).

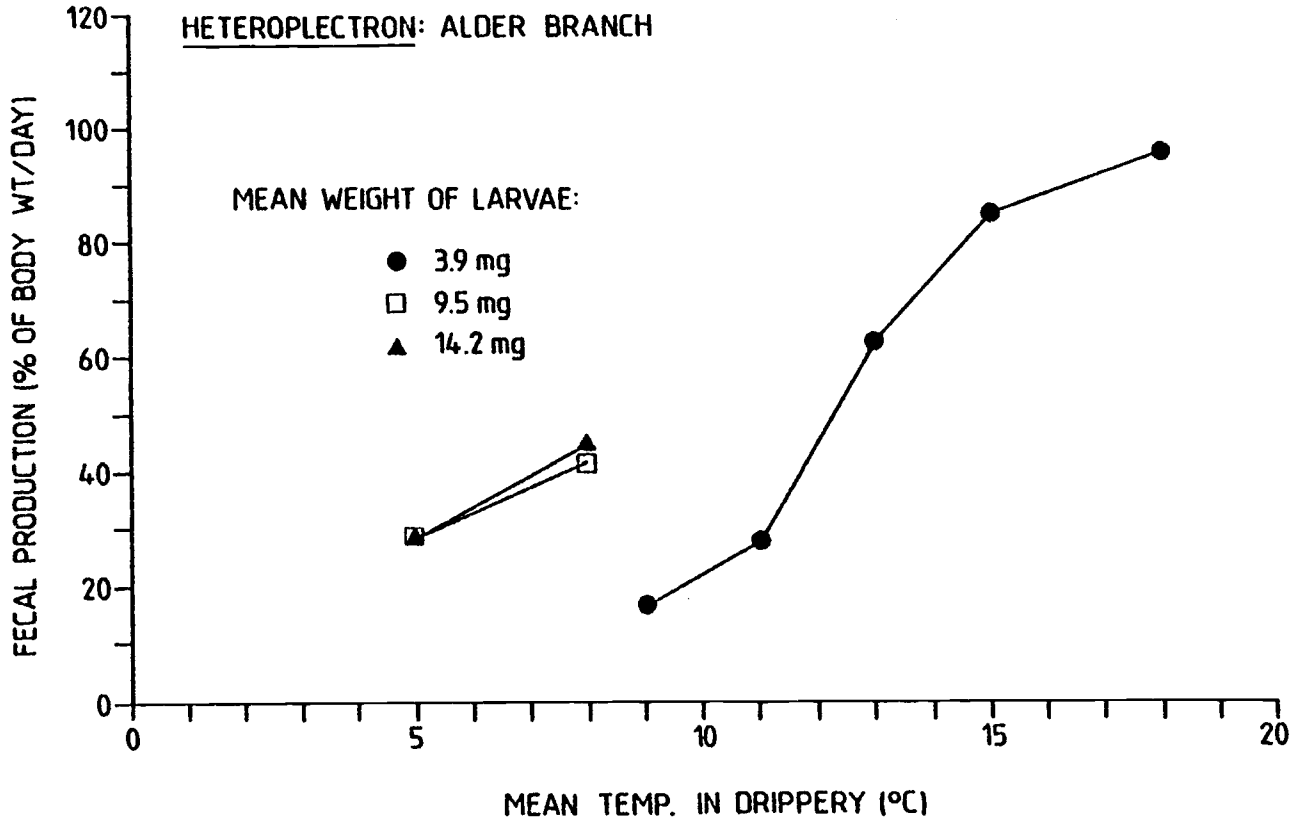

Figure 18. Effects of temperature on fecal production of Heteroplectron californicum larvae feeding on alder branch (mean ± SE).

fecal production (mg/mg/day) and field abundance of Lara (mg/kg) (Table 18). In Berry Creek, estimated fecal production by Lara was 2.5 $gm/m^2/yr$, or 0.8% of the standing crop of wood debris < 10 cm diameter, per year. The average estimate for Coast Range streams was 1.1 $gm/m^2/yr$, or 0.2% of wood standing crop per year.

Table 18. Estimated fecal production and feeding impact of *Lara avara* larvae in two Coast Range streams.

	Kg wood/m^2 streambed*	Mg *Lara*/m^2 streambed	Fecal production: gm/m^2 streambed/yr	Feeding impact: % of wood standing crop/yr
Berry Ck.	0.30	77	2.5	0.8
Flynn Ck.	0.86	20	0.6	0.1
Coast Range streams (mean)	0.59	34	1.1	0.2

* data from Anderson et al. (1978), for wood < 10 cm diameter

DISCUSSION

In the few studies that have been published, xylophagy in aquatic beetles was not necessarily associated with long life cycles (Perez 1863, LeSage and Harper 1976a,b). Other factors besides food quality, such as size at maturity, or temperature, may also be important determinants of growth rate and life cycle duration. One of my main objectives in this section is the consideration of factors that may contribute to Lara's long life cycle.

Pupation: Ending the Larval Stage

My data suggest that Lara's life cycle is long and quite variable. Pritchard (1978) indicated that, for a given cohort, the duration and timing of aquatic insect life cycles can be highly variable, depending on the quality and availability of food. Given that variation in food quality exists within and between decaying sticks in a stream, there is ample opportunity for Lara, with its four to seven year larval stage, to develop asynchrony within a cohort.

One consequence of asynchronous development is the necessity for synchronization of emergence and mating in insects that have short-lived adults. In Lara's case, this synchrony may be provided by factors that initiate the pupal moult.

At least some immature insects use body size as an

index of development. The tobacco hornworm, Manduca sexta, must reach a certain size before the endocrine events that trigger pupation can be initiated (Nijhout and Williams 1974, Nijhout 1975). The milkweed bug, Oncopeltus fasciatus, monitors its size via stretch receptors in its abdominal wall, and will metamorphose to the adult stage only if a certain critical size is attained (Blakely and Goodner 1978, Nijhout 1979). Last-instar Lara larvae may assess their competence for pupation in some similar manner, prior to seeking terrestrial pupation sites in the spring. Larvae that were too small to pupate would spend at least one more year feeding in the stream. In a given year, larvae of different ages may initiate the behavioral and physiological events leading to pupation.

Once Lara larvae have left the stream, the timing of the pupal moult and emergence probably depends on drying of the streambank. While most areas within a watershed would dry at similar times, local variation in soil moisture could delay, or even prevent pupation. The broad emergence peak shown by Lara adults may be caused by such variation in the timing of pupation.

Drying may be an important factor in the pupation of other elmids. White (1978) suggested that last-instar Stenelmis sexlineata larvae migrate to the water's edge during periods of high flow, and pupate after the water recedes. When Machronychus quadrituberculatus larvae are ready to pupate, they climb onto emergent portions of

decaying logs, and excavate small chambers in the wood (Perez 1863). Other elmids pupate out of the water, under debris at the sides of streams (Brown 1972, LeSage and Harper 1976a). The Elmidae are not unusual in this respect; most other aquatic beetles except for some Psephenidae have terrestrial pupae.

Wood As Habitat

A xylophagous aquatic insect such as Lara must deal with such problems as poor food quality and patchy habitat distribution. There are, however, advantages to living on wood. Decaying wood is available all year round, rather than in seasonal pulses like leaf litter, algae, or fine particles derived from these sources. Submerged wood decays slowly, and is likely to provide habitat for several years. While the low food value of wood may impose slow growth and a long life cycle, there may be relatively little risk of increased mortality involved because of the physical protection that wood affords a gouging insect. Compared with benthic habitats, which may be scoured several times a year, wood provides a safe place for an insect that must spend several years feeding.

As a xylophagous insect, Lara plays a role in the processing of wood debris in streams. Keller and Swanson (1979) discussed ways in which large bole wood contributed to stepped stream profiles, bank stabilization, and habitat diversity in Cascade Range streams. Insofar as it feeds on

bole wood, Lara may affect the role of large wood debris in stream geomorphology. However, I feel that Lara is most abundant on smaller, branch-sized wood. Small wood debris contributes less to structural aspects of the stream, but is known to be important as food and habitat for aquatic invertebrates (Anderson et al. 1978, Dudley and Anderson 1982, Pereira et al. 1982). In small streams, bole wood is too large to remain submerged at low flow, and may often be unavailable as habitat for aquatic insects. This could account for my inability to collect many Lara from bole wood, although careful examination of the undersides of large, immobile tree trunks was not often possible. Branch wood may also be favored because it is a better food source. Cowling and Merrill (1966) found that branch wood was likely to contain more nitrogen than bole wood.

Wood as Food

Although wood debris in streams offers an abundant supply of carbon to organisms capable of digesting cellulose or lignin, it is a poor source of nitrogen (N). Wood typically contains only 0.03 - 0.10% N by weight, as both protein and non-protein compounds (Cowling and Merrill 1966), while insects contain 1 - 14% N by weight, mainly as protein (DeFoliart 1975). Clearly, xylophagous insects must be able to obtain N in quantities and qualities suitable for the elaboration of animal tissue.

Lara larvae feed exclusively on wood that has been "conditioned", or colonized and partially degraded by fungi and bacteria. This feeding preference is analogous to that of leaf-shredding stream invertebrates (Kaushik and Hynes 1971, Bärlocher and Kendrick 1973, Iversen 1974). The decay-causing organisms in submerged wood are often of terrestrial origin, having colonized standing dead wood before it fell into the stream.

The protein content of wood increases with conditioning because the amount of microbial biomass relative to the amount of wood increases over time. Wood-rotting fungi are able to concentrate N obtained from wood in their mycelia (Merrill and Cowling 1966), and certain bacteria associated with decaying wood in streams are able to fix gaseous N (Buckley and Triska 1978). Fungal spores, protozoans, and small invertebrates may also be present in wood that is consumed by Lara. By eating wood that contains this community of organisms, Lara is able to ingest considerably more high quality N, and presumably more vitamins and sterols as well, than would have been available in unconditioned wood. Anderson et al. (in prep.) found that the soft, stained layer of wood that is eaten by Lara and other gougers contains about five times as much N as unconditioned wood.

The original N content of wood tissue is probably correlated with the abundance and quality of the microflora that will eventually colonize it. Alder wood is relatively

high in nitrogen compared with coniferous wood (Franklin and Waring 1979), and, after several year's conditioning in a stream, was found to have much higher respiration rates than similarly treated Douglas-fir or hemlock (R.J. Steedman and N.H. Anderson, unpublished data). Such nutritional considerations may explain the high abundance of Lara on hardwood, relative to coniferous wood.

A Strategy of Xylophagy

Mattson (1980) discussed adaptive syndromes that may allow herbivores feeding on poor quality food, such as wood, to obtain sufficient N to complete their life cycle. Several of these adaptations apply to a discussion of xylophagy in aquatic insects:

1) protracted life cycles to compensate for low growth rates.

2) increased body size, to provide mechanical advantages when proccessing woody material, or for reduced respiration per unit body weight.

3) protracted feeding periods and/or elevated feeding rates, to process large amounts of food.

4) modifications of the digestive tract (such as hindgut caecae) that allow the growth of cellulose-degrading symbiotic microorganisms.

5) dependence on "ectosymbionts", such as wood-rotting fungi, to concentrate N into a smaller volume of food.

6) switching to higher quality food, such as algae or animals, in portions of the life cycle that require rapid growth and storage of nutrient reserves.

Some of these adaptations appear to be used by Lara. In discussing them, I assume that nutritional consequences of

xylophagy are the most important adaptive hurdle faced by Lara. This may well be the case, but phylogeny, and non-nutritional selective agents such as biological interactions and the physical environment, are also possible explanations for my observations. Nitrogen requirements may become secondary to lipid requirements in late instars of at least some insects (Montgomery 1982, Hanson et al. 1983). However, the adaptive strategies proposed by Mattson are still appropriate in the case of Lara, since the problem is still one of obtaining adequate nutrition from a dilute source.

Lara's life cycle is certainly long, a phenomenon that can be attributed both to its slow growth, and to the relatively large size that it attains. The growth rates calculated for Lara in this study (0.1 - 0.7%/day for the larger instars) are lower than those for other aquatic insects from the same region: 0.9%/day for Heteroplectron californicum, a facultative wood gouger with a two year life cycle (Anderson and Cummins 1979), 2 - 3%/day for Lepidostoma spp., univoltive leaf-shredding caddisflies (Grafius and Anderson 1980), and 2 - 5%/day for Ephemerella spp., univoltine mayflies (Hawkins 1982). Some insects, such as terrestrial caterpillars, are capable of growth rates of 10 - 60%/day (Scriber and Feeny 1979). If its growth rate is limited by food quality, why doesn't Lara opt for a smaller body size, and a shorter life cycle? Given that large size is positively correlated with

fecundity, and that wood is a "safe" habitat for a long-lived insect, there would be little selective advantage to shortening the life cycle by reducing size at maturity. Large size may also provide for more effective feeding on woody material, and for increased efficiency of conversion of food to biomass because of reduced respiration rates. Lara's large size relative to other Nearctic elmid beetles may be due to phylogenetic affiliations, rather than its xylophagous habit. Published descriptions (i.e. Hinton 1940, Brown 1981a, LeSage and Harper 1976a,) indicate that the Larinae tend to be bigger beetles than the Elminae.

Continuous feeding during the larval stage is a behavioral adaptation suited to Lara's habitat and simple gut. The nature of wood debris in streams is such that feeding need not be interrupted by seasonal or diel changes in food availability and quality, as may happen with terrestrial herbivores. Lara stops feeding only when moulting, or when it encounters unsuitable food.

Lara's feeding rate, as estimated by fecal production (9%/day), is low compared to other xylophagous insects such as Heteroplectron californicum (20 - 95%/day [p. 76]) or Lipsothrix spp. (90-200%/day [Dudley 1982]). It may be constrained by a sluggish metabolism. As measured by uptake of oxygen, Lara's metabolic rate was lower than that of some other aquatic insects. Stoneflies of the genus Isoperla, and the caddisflies Lepidostoma spp. and Clistoronia magnifica have respiration rates 4 - 11 times

higher than Lara of comparable size (Table 19). Lara also tended to show a greater increase in respiration (Q_{10}) over the interval from 10 - 15°C, indicating that it incurred a greater relative increase in metabolic rate over that temperature range. As Lara's feeding rate did not increase over a similar temperature range, its reduced growth rate at 17°C relative to 7°C (Table 12) may be due in part to an decrease in growth efficiency at the higher temperature.

Lara could assimilate nutrients from ingested wood in the following ways:

1) Absorb soluble molecules previously liberated from the wood by fungal or bacterial enzymes

2) use its own enzymes to digest the contents of fungal, bacterial, or animal cells that were mechanically disrupted by feeding

3) use sequestered fungal enzymes (Martin 1979) to digest the wood

4) use symbiotic bacteria or protozoans in its gut to digest the wood

5) use its own cellulase to digest the wood

Insects generally include proteases and lipases in their repertoire of digestive enzymes (House 1973, Martin et al. 1981). Lara is almost certainly able to digest the microbial component of decaying wood, which, although not a concentrated food source, could be an adequate one. On the basis of my data regarding Lara's gut morphology (a simple tube), low assimilation efficiency (5 - 12%), cellulase (absent), and gut flora (absent), I feel that Lara utilizes a "passive" sort of digestive strategy based primarily on 1) and 2) above. This would mean that Lara relies on the

Table 19. Respiration rates (µl O_2/mg/hr) at 10° and 15°C of some aquatic insects. All data from Gilson differential respirometers.

Insect	Mean wt. (mg)	Respiration rate 10°C	Respiration rate 15°C	Q_{10}
Lara avara	1.8	0.15	0.32	4.7
	4.1	0.12	0.32	7.4
	8.8	0.13	0.19	2.9
Trichoptera				
*Lepidostoma unicolor**	3.3	0.96	1.40	2.1
*L. quercina**	1.7	1.39	1.48	1.1
*Clistoronia magnifica**	20.6	1.12	0.98	0.8
Plecoptera				
*Isoperla nana***	1.0	1.5	1.3	0.8
*I. namata***	2.9	1.1	1.7	2.4
*I. clio***	10.6	0.4	1.0	6.3

* Grafius (1977)
** Modlin and Jayne (1981)

microflora associated with decaying wood to digest and concentrate nutrients from the wood, rather than doing so in its own digestive tract using enzymes of animal, fungal, or gut-symbiont origin. Anderson et al. (1978) reached a similar conclusion based on preliminary studies of Lara, and concluded that such a strategy would necessitate a low metabolic rate, and a long life cycle.

I saw no indication that Lara is capable of switching to higher-quality food, such as animal or algal tissue, as has been observed for larval caddisflies (Brusven and Scoggan 1969, Winterbourn 1971, Anderson 1976), and for the elmid beetle Microcylloepus pusillus (Brown and Shoemake 1969).

Feeding Impact

Lara's role in the stream ecosystem is mediated most strongly through effects of feeding during the larval stage. These effects may be manifest in changes to the surface texture of wood debris, and in the conversion of wood debris to fine fecal particles. Feeding by Lara larvae also exposes new, unconditioned wood to fungal attack, speeding its decomposition.

Wood that has been fed upon by Lara larvae is often highly grooved and sculptured, a phenomenon that led Anderson et al. (1978) to describe "Lara sticks", which can be recognized by their firm surface texture and signs of

gouging activity. Lara's contribution to a complex, highly textured surface on wood debris may be one of the most important aspects of its ecological role. Many of the insects associated with wood in streams use the wood as habitat rather than as food (Dudley and Anderson 1982). A stick with a spatially complex surface is likely to support a more diverse invertebrate community than is a smooth stick, due to increased potential to avoid unfavorable interactions with other insects and with the physical environment. Anderson et al. (unpublished data) found that artificially grooved Douglas-fir, hemlock, and alder sticks were colonized more rapidly, and by a greater variety of aquatic insects than were smooth sticks.

Anderson et al. (1978) estimated that Lara, Heteroplectron, and Juga (a pleurocerid snail), the three most important wood processors in Oregon streams, consumed 1.8% of the standing crop of stream wood debris per year. Their estimates of Lara abundance, which were based on field-picked samples were lower than my estimates (22 mg/kg vs 57 mg/kg for Coast Range streams), and therefore their estimate of Lara's contribution to wood degradation is also low. Substituting my value for Lara's contribution to wood degradation (0.2% of wood standing crop per year) into their calculation, the total impact of Lara, Heteroplectron, and Juga, is 1.9% of wood standing crop per year. Lara is responsible for 11% of that impact.

After conversion to feces by Lara larvae, wood becomes

part of the particulate organic material (POM) carried by the stream. The fine particles of fecal material (about 100 x 200 microns) may be stored as sediment in depositional areas, fed upon by filter feeders or collectors, or transported from the system.

Lara is probably not a major producer of POM. A rough estimate of the contribution of Lara feces to the annual POM budget of Devils Club Creek, a first-order stream in the Cascade Range of Oregon (Table 20) was 0.03%.

Prognosis

This study has shown that Lara avara must feed for several years in order to complete its life cycle. The long feeding period is primarily a consequence of the low food value of wood, and Lara's inefficient digestive strategy.

While Lara represents only one of several possible models of xylophagy in aquatic insects, it has provided a clear example of the constraints imposed by specialization on stream wood debris for food and habitat. Study of other wood-eating aquatic insects, especially in the order Diptera, may show that short life cycles and xylophagy are not irreconcilable. Information about the life cycles, digestive physiology, and feeding rates of these insects should provide a more complete model of wood processing by aquatic insects.

Table 20. Estimated contribution of *Lara avara* feces to the annual particulate organic material (POM) budget of Devils Club Creek, in the Cascade Range of Oregon.

Lara feces production		Total POM production	
Stream bed area*	300 m^2	Mean flow*	0.0017 m^3/s
Lara density**	28 mg/m^3	Mean [POM]*	966 mg/m^3
Lara fecal prod.#	0.09 mg/mg/day	Annual POM prod.	51788 gm/yr
Annual fecal prod.##	138 gm/yr		

Contribution of *Lara* feces to annual POM budget: 138 gm/yr / 51788 gm/yr x 100 = 0.3%

* Naiman and Sedell (1979)
** Anderson et al. (1978); estimate corrected for field picking (x2)
\# *ibid*.
\#\# assuming 50% of stream bed area suitable as *Lara* habitat

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APPENDICES

Appendix 1. Size-weight relations of *Lara* larvae

I calculated functional linear regressions (Ricker 1973) for:

1. ln(head-capsule width) and ln(dry weight)
2. dry weight and live weight (blotted dry).

The head capsule/dry weight regression was based on 189 larvae. The wet weight/dry weight regression (data supplied by Lin Roberts, Department of Fisheries and Wildlife, OSU) was based on 98 larvae.

The equation relating dry weight (DW) to head capsule width (HC) is:

$$\ln(DW) = 1.30387 + 3.62884 \ln(HC)$$

The equation relating dry weight (DW) to wet weight (WW) is:

$$DW = -0.17788 + 0.37875\ WW$$

where DW and WW are in milligrams, and HC is in millimeters.

The wet weight/dry weight regression should not be used for wet weights < 2.00 mg., or dry weights < 0.70 mg.

Appendix 2. Manuscript:

Steedman, R.J. (1983). The pupa of the elmid beetle, Lara avara (Coleoptera: Dryopoidea: Elmidae). Aquatic Insects 5: 17-20.

The Pupa of the Elmid Beetle, Lara avara (Coleoptera: Dryopoidea: Elmidae)

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ABSTRACT

The pupa of the elmid beetle, Lara avara is described. This pupa is similar to other pupae in the Elmidae, differing mainly in its large size, and the presence of lateral projections on the abdominal tergites. A description of the pupal habitat is included. Diagnostic characters of pupae of the subfamily Larinae are discussed.

INTRODUCTION

Lara avara LeConte is a large elmid beetle associated with decaying wood in mountain and foothill streams in the western portions of Canada and the United States. *Lara avara* is the only Nearctic (*sensu* Brown 1981) member of the subfamily Larinae. Pupae of *Lara* are hitherto undescribed.

Two members of the Holarctic elmid pupae in the subfamily Larinae have been described, *Potamophilus acuminatus* Fabricus (Bertrand 1939) and *Hexanchorus gracilipes* Sharp (Hinton 1940). The Larinae are represented by 107 species in 20 genera worldwide (Brown 1981).

Bertrand (1936) constructed a key which suggested that pupae of the subfamily Larinae (then Potamophilini) had no pronotal filaments, and that this character could be used to separate them from pupae of the subfamily Elminae (then Helmini), which had two sets of filaments. Hinton (1939) later indicated that *Hexanchorus* pupae had two sets of filaments on the pronotum, and a concurrent paper by Bertrand (1939) showed *Potamophilus* with two sets of filaments as well.

In general, the pupa of *Lara avara* is similar to that of *Potamophilus* and *Hexanchorus*, and to pupae of the subfamily Elminae. It differs mainly in size (2-3 times as long as most other elmid pupae), and the presence of

lateral projections on the abdominal tergites. Hinton (1939) recognized the great similarity between adults of the Larinae and Elminae when he suggested that they only merited separation at the tribal level. Such similarity also appears to exist for the elmid pupal stage.

DESCRIPTION OF Lara avara PUPA (fig. 1)

Female: pearly-white in color, elytra darkening with development; length from front of pronotum to end of last abdominal segment: 9.4 mm; breadth at pronotum: 3.0 mm.

Head completely concealed from above by pronotum; 10 setae, about 0.13 mm long: 4 on frons, 2 above each eye, 1 at anterior margin of each eye; glabrous otherwise.
Pronotum four stout, sclerotized spines, or filaments, 0.75 mm long: 2 at anterior angles, 2 at lateral angles; 6 setae, 0.25 mm long: 4 near posterior margin, 1 dorsolateral on each side; other setae at base of filaments, and at apex of longitudinal ventrolateral ridge which connects anterior and lateral angles.
Mesonotum four setae, 0.1 mm long: 2 at base of each elytron.
Metanotum four setae, 0.1 m long: 2 at base of each wing.
Abdomen segments 1-8 with posteroir angles of tergites extended laterally about 0.5 mm to form spine-like processes, each with 6-8 setae along margins; abdominal spiracles located dorsolaterally near anterior bases of

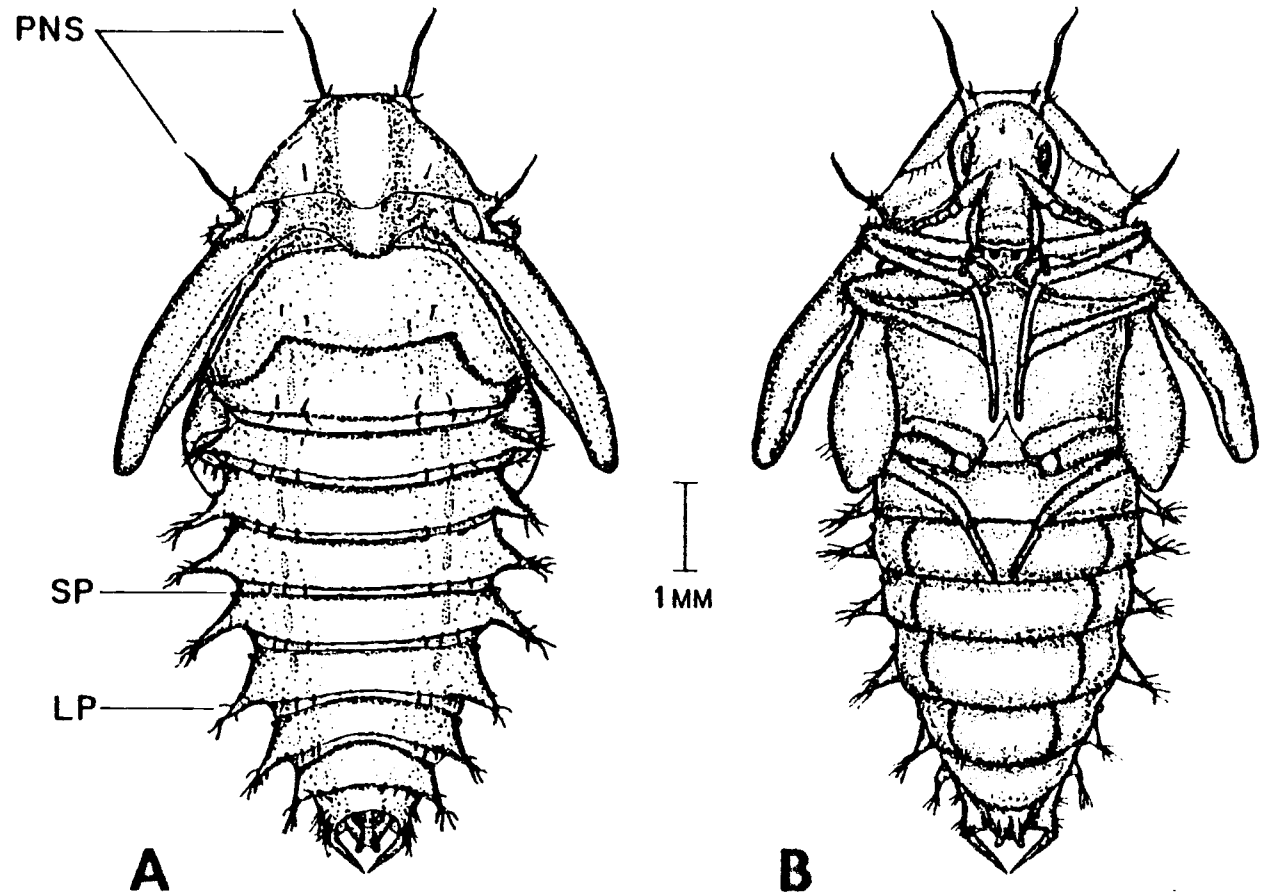

Fig. 1. Pupa of Lara avara, female. A) dorsal, B) ventral, PNS = pronotal spines, SP = abdominal spiracles, LP = lateral processes of tergites.

lateral processes on segments 1-7, at apices of small tubercles; first segment with 8 setae along posterior margin, in 2 groups of 2 on each side of the midline; segments 2-7 with 6 setae along posterior margin in a group of 3 on each side of the midline; eighth segment with 8 setae along posterior margin; ninth segment with several longer setae (0.4 mm) on lateral surface, and 2 terminal styli.

Wings elytra and wings extending to ventral side, attaining third abdominal segment.

Legs front pair extending to middle of metathorax; middle pair extending to posterior margin of first abdominal segment; hind pair extending to posterior margin of fourth abdominal segment.

Variations Males: length 8.9-9.0 mm, breadth 2.7-2.8 mm.

Material Examined 1 female, 2 males, 3 male pupal exuviae.

Remarks Our specimens were found in Berry Creek, Benton County, Oregon, on June 25, 1981, under moss on the upper surface of a partly submerged log. They were in small chambers (1.5 cm long) in damp soul below the moss layer, and were found with cast larval skins of Lara avara. Pupae of Ametor latus Horn (Hydrophilidae) were also present. The submerged portion of the log showed signs of feeding by Lara larvae. Several of the pupae were allowed to complete their development in the laboratory, and were identified as

Lara avara. At 15°C, the adults emerged 9 days after collection, or about 7 days after the elytra darkened.

ACKNOWLEDGEMENTS

I wish to thank R.W. Wisseman and Dr. N.H. Anderson for locating the pupal habitat and providing the first specimens. Dr. H.P. Brown reviewed the manuscript and provided helpful suggestions. The project was supported by NSF grant DEB 78-10594. This is Technical Paper No. 6310 of the Oregon Agricultural Experiment Station.

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Appendix 3. Raw data for Berry Creek mark-recapture study.

Each cell in the following table includes the number of unmarked larvae captured (top number), and the number and mark-age of recaptured larvae (lower numbers, where the number on the left of the colon is the mark age in months, and the number on the right is the number of larvae).

DATE	INSTAR				
	3	4	5	6	7
April 21/81	8	26	27	20	16
May 6	0 1:1	15 1:3	12 1:4	14 1:3	18 1:2
June 12	0	9	34 1:1	55 1:1 2:1	32 1:2
July 9	0	0 1:1	20 1:6	27 1:10 3:1	22 1:2
August 15	0	4	8 1:5 2:3	11 1:7 2:1	5 1:6
September 17	0	7 1:1	16 1:4 2:4 3:1	15 1:3 2:1 3:1 4:2	22 1:5 2:2 3:1
October 24	0	0	7 1:3	26 1:7 2:1	14 1:14 2:2 3:1
November 25	0	0	13 1:5 2:2	30 1:3 2:2	31 1:15 2:9
December 24	0	8 2:2	27 1:2 2:2 4:1	64 1:17 3:1 8:1	68 1:12 2:4 3:4 4:1 6:1 8:1
January 26/82	0	3 1:1	6 1:9 2:5 3:4 4:1	15 1:31 2:9 3:4 4:2	12 1:25 2:5 3:2 4:4
February 25	0	1 4:1	3 1:2 2:2 3:6 6:1	7 1:7 2:23 3:10 4:3 5:1	3 1:4 2:13 3:5 4:4 5:2 8:1 10:1
March 24	0	0 1:1	1 1:1 2:1 3:3 4:1 5:1 7:1	0 1:3 2:1 3:18 4:7 5:2 8:1	1 1:3 2:4 3:12 4:3 6:1 8:1 10:1 11:3
April 27	0	1 2:1	0 2:1 3:1 4:5 5:2 6:1	3 2:2 3:2 4:14 5:4 6:1 12:1	2 4:1 5:1 7:1 10:1
May 25	1 5:1	0 1:1 3:1	0 3:1 5:4 6:1 7:1 9:1	0 1:3 3:2 4:2 5:14 6:3 7:2 10:1 13:1	3 1:1 3:1 4:1 5:6 6:1 10:1 13:1
July 1	0	1 4:1	1 5:1 6:2 7:1 10:1	3 2:2 5:2 6:17 7:3 8:3 11:1 14:1	2 2:1 4:1 5:1 6:6 7:1 11:1 14:1
September 14	0	0	4 8:1	4 7:4 8:1 9:1	13 1:2 5:1 7:2 8:1 12:1