

LIFE HISTORY AND SECONDARY PRODUCTION OF *CHEUMATOPSYCHE* SPP.
IN A SMALL APPALACHIAN STREAM WITH TWO DIFFERENT LAND USES
ON ITS WATERSHED

by

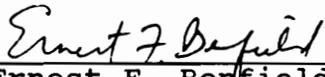
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Dissertation submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY
in
Biology

APPROVED:



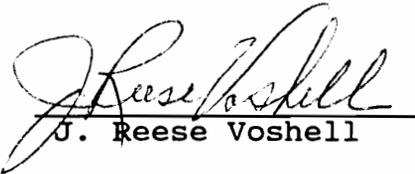
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May, 1996
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Key words: Life history, production, hydropsychids,
Cheumatopsyche.

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(ABSTRACT)

Ecological parameters of hydropsychid caddisflies are very important for production dynamics of stream ecosystems, due to the abundance and biomass of these collector-filterers in many stream types. I studied life history and secondary production of *Cheumatopsyche* spp. (Trichoptera: Hydropsychidae) in Stroubles Creek, a 3rd order stream near Blacksburg, Virginia, in order to compare life histories and production dynamics in two reaches with different land-use in a watershed. The upstream section was influenced by urban and agricultural activities. The channel showed evidence of disturbance related to both geomorphological processes and agricultural activities. There was higher annual accumulated degree days, and stream substrate particles were mostly mid and coarse gravel. The downstream section was surrounded by forest, with little evidence of human activities and

disturbance and with a more diverse distribution of particle size ranges in the streambed.

Cheumatopsyche pettiti (Banks) was the only species of the genus that developed the whole life cycle in the upstream site, while *C. pettiti* and *C. oxa* Ross were both abundant downstream. There were three other *Cheumatopsyche* species collected with light traps in the area.

Cheumatopsyche larvae and other aquatic insects were more abundant downstream, probably in relation to higher habitat availability. *C. pettiti* was determined to be bivoltine at the upstream site, perhaps related to high thermal input. However, only a fraction of the two *Cheumatopsyche* species could develop a 2nd generation downstream, overlapping with continuous emergence of the overwintering larvae during the summer.

Cheumatopsyche production in Stroubles Creek was higher than in forested, low-order streams of North America but similar to some values obtained at streams in agricultural areas and large rivers. Production was less than from sites below food-enriched reservoir releases or from snag habitat in southeastern, coastal-plain rivers. Detritus was the greatest component of the diet of *Cheumatopsyche* at the two sites, but detritus and animal food had similar contribution to production downstream. The adjustment in life history and production dynamics in the two reaches showed the ecological

plasticity of *Cheumatopsyche* and the importance of
hydropsychids in the energy flow of moderately disturbed
streams in mountainous regions.

ACKNOWLEDGMENTS

I thank Dr. Albert C. Hendricks for his guidance and support as my major advisor. He gave me direction and assistance, not only for this work but for my whole graduate program. I appreciate his attention to my personal situation, and his help with requirements beyond academic duties.

I also thank the other members of my committee, Drs. E.F. Benfield, A.L. Buikema, J.R. Voshell, and J.R. Webster, who were always available and willing to answer questions and orient my work. I have special thanks to Dr. O.S. Flint, Jr. from Smithsonian Institution, who has helped me with the identification of caddisflies for this work as well as with my interest in neotropical caddisflies which he knows better than anybody else.

I thank Mr. Dave Morton and Dr. Jeff Waldon, Department of Forestry of Virginia Tech, who gave me valuable information and maps regarding land uses in the study area.

I am specially thankful to Alicia S. Schultheis for her help with chemical analysis and for her stimulating ideas and enthusiasm for ecological studies. It has been a pleasure to share research and academic work with Alicia.

I also thank the Universidad Surcolombiana at Neiva, Colombia, the Fulbright Commission and LASPAU, since these institutions provided the scholarship for my graduate program at Virginia Tech.

Finally, I thank my wife Margarita for being my company and affectionate support during these years, in addition to her patient and valuable help in field and laboratory work. She and my daughters, Cristina and Luz Angela, have been my permanent inspiration and motive for my efforts.

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INTRODUCTION

Life history and production of freshwater invertebrates are parameters of considerable ecological importance, because knowledge of these processes allows interpretations of essential pathways of energy flow in aquatic ecosystems. Life history of a species or a population has been defined "as events that govern the reproduction (and survival) of the species or population" (Oliver 1979, p.319), and such events have great influence on structure and function of communities in flowing waters. Secondary production represents "the living organic matter, or biomass, that is created or produced by an animal population during an interval of time" (Benke 1984, p.289). These two parameters show strong interaction due to obvious relationships among reproductive events and the successful establishment and development of populations.

Low-order (1st-3rd) streams in mountainous regions are thought to have communities with low taxonomic diversity, especially in forested areas where dense canopy inhibits primary production and high-gradient channels limit habitat stability (Hynes 1970; Allan 1995). The River Continuum Concept (Vannote et al. 1980) postulates that shredder and collector invertebrates codominate the headwaters where

there is major importance of allochthonous organic inputs as coarse and fine particles transported to the stream. Within the collector-filterer functional group (Cummins 1973), caddisflies of the family Hydropsychidae usually comprise an important portion of the invertebrate biomass, especially in streams where geomorphological features or alteration processes favor the dominance of fine particles in the seston. These particles are efficiently retained by hydropsychid catch-nets (Wallace et al. 1977)

Some Hydropsychidae genera such as *Hydropsyche*, *Cheumatopsyche* and *Macronema* accounted for the majority of the secondary production in studies on different stream types of southeastern United States (Benke and Wallace 1980; Cudney and Wallace 1980; Parker and Voshell 1983; Diamond 1986; Smock and Roeding 1986; Willis and Hendricks 1992). However, there is a lack of knowledge on their taxonomy and life history for some species in these genera, thus making it difficult to evaluate their trophic status in stream ecosystems. Probably, this limitation contributed to the wide range in values of secondary production of hydropsychids that has been reported in these and other studies from other North American regions (Rhame and Stewart 1976; Neves 1979; Mackay and Waters 1986; Smock and Roeding 1986).

Knowledge on the life history of common hydropsychid species has been obtained only in recent years, and the review by Waters (1977) on secondary production listed only one species of this family. Due to the abundance and more accurate taxonomy of the genus *Hydropsyche*, recent studies have focused on *Hydropsyche* species from different types of lotic systems in North America. Mackay (1979) determined the basic life history of five *Hydropsyche* species from the Humber and Credit Rivers, Ontario. Other studies dealt with similar species of *Hydropsyche* and one *Cheumatopsyche* species in other streams (Mackay 1984, 1986). Life histories of other abundant net-spinning caddisflies have also been studied in a wide range of habitats that included low-order streams and larger rivers (Oswood 1976; Cudney and Wallace 1980; Parker and Voshell 1982; Freeman and Wallace 1984; Elliott 1986; Morin and Harper 1986). Some of these studies included net-spinning species of families other than Hydropsychidae such as Philopotamidae and Policentropodidae (Benke and Wallace 1980; Benke et al. 1984). Results of these studies have shown the importance of caddisflies for estimating secondary production of lotic systems, demonstrating important variations in life history among widespread species in different habitats.

Despite interest in the role of hydropsychids in lotic energy flow, secondary production estimates frequently face limitations due to the difficulty found in larval taxonomy and cohort separation. For example, early-instar larvae of *Cheumatopsyche* rarely can be sorted as separate species, and there is still no reliable technique available for complete larval identification (Mackay 1978; Armitage and Pretzman 1995). In addition, multivoltinism with overlapping generations also occurs in many habitats (Cudney and Wallace 1980), making it difficult to separate actual cohorts, which is necessary for survivorship determinations. In general, most of studies on life history and production of hydropsychids show more precise estimates for univoltine *Hydropsyche* species than for unidentified and multivoltine populations. Little is known about life history patterns and production of *Cheumatopsyche* populations.

Since laboratory studies do not allow realistic determinations of life history and production, changes in stream habitat conditions may be useful to interpret variations in these ecological parameters. Many southern Appalachian streams have received significant impacts from different land use in their watersheds (Swank and Bolstad 1994). Such impacts are thought to affect benthic populations, thus changes in life-history patterns and

production of hydropsychids can be studied in relation to environmental influences from the surrounding land use. *Cheumatopsyche* is frequently an abundant genus in these streams, but its species are only identified by adult genitalia (Ross 1944; Gordon 1974). Therefore, specific life histories are not easily distinguished when several species coexist, but small streams with one or few species may allow determinations of life-history patterns and their variations.

The objectives of the present study were:

1. To identify the life history of *Cheumatopsyche* spp. in Stroubles Creek, Virginia, and variations in life-history events at two stream sites with contrasting land-use.
2. To estimate secondary production by *Cheumatopsyche* populations at the two stream sites in relation to site-specific habitat conditions and life-history adjustments, which may influence production factors such as larval abundance, development time, habitat availability and food sources.

LITERATURE REVIEW

Taxonomy

Net-spinning caddisflies of the family Hydropsychidae are some of the most conspicuous collector-filterers in different stream types. This family is widespread through all biogeographic realms with specially high diversity in temperate and tropical regions (Flint 1991). However, three of the four subfamilies (Arctopsychinae, Diplectroninae and Macronematinae) have rather restricted distribution in the stream continuum (Unzicker et al. 1982). The other subfamily, Hydropsychinae, includes the most generalist species which are known to occupy very diverse aquatic habitats and to use multiple food sources. They feed either by collecting in their nets or by direct consumption through grazing on producers or capturing animal prey (Wiggins and Mackay 1978).

Two genera of nearctic Hydropsychinae, *Hydropsyche* and *Cheumatopsyche*, are frequently the dominant caddisflies in streams of eastern United States (Wiggins 1977), and they are considered as ecological equivalents of the genus *Smicridea* which is usually the dominant caddisfly in neotropical streams (Flint 1974, 1978). Despite the abundance of these taxa, little is known about the biology

of many common species, and identification of immature stages is far from accurate because it is usually only possible with adult specimens (Merritt and Cummins 1984). For neotropical caddisflies it is nearly impossible to identify the immature stages beyond the genus (Flint 1981), and for some North American genera, such as *Cheumatopsyche*, there is no available larval key for species separation (Unzicker et al. 1982; Scheffer and Wiggins 1987; Armitage and Pretzman 1995).

Adults of Hydropsychidae genera are commonly identified with the keys by Ross (1944) and regional descriptions of species. The dominant genera, *Hydropsyche* and *Cheumatopsyche*, can be separated by venation and genitalia characters (Gordon 1974), but species identification usually requires assistance of taxonomic specialists. In Virginia, some *Hydropsyche* species were described by Flint et al. (1979). Parker and Voshell (1981) listed 28 species of *Hydropsyche* and 17 of *Cheumatopsyche* reported from the state. The studies by Gordon (1972, 1974) associated males and females of *Cheumatopsyche*, described 39 known nearctic species, illustrating male and female genitalia, and provided groups and phylogenetic relations among these species.

Immatures of Hydropsychidae genera have received different taxonomic attention. *Hydropsyche* species are relatively well known and their identification is possible for mature larvae in several regions, as it occurs in North and South Carolina where species can be separated in late instars with keys by Unzicker et al. (1982). Proximity and geographic similarity with Virginia may allow the use of this key, because most of species from the Carolinas have been also collected in Virginia (Parker and Voshell 1981).

Taxonomy of *Cheumatopsyche* larvae, in contrast, is less well developed and even identification of the genus may be difficult for small individuals. Late instars (III-V) are frequently distinguished from *Hydropsyche* by the uniform coloration of the head, the absence (or reduction) of the posterior sclerites in the prosternum, and the presence of a frontoclypeal notch in most of species (Wiggins 1977; Merritt and Cummins 1984). However, early instars (I-II) usually have not fully developed these characteristics. Mackay (1978) determined ranges of head width for common species of *Hydropsyche*, which are helpful in separating small larvae. She also identified the presence of long and tapered setae on the anterolateral borders of the pronotum in *Cheumatopsyche*, compared with the short and blunt ones in

Hydropsyche, that is probably the most reliable character for separating early-instar larvae of the two genera.

Given the taxonomic limitations and the reduced knowledge on biology of *Cheumatopsyche*, studies on ecological parameters with this genus require integration of data on different life stages. Larval collection in the field should be complemented with rearing in a laboratory to ensure identification, together with observation of adults and mature pupae that may have developed genitalic features (Metamorphotypes). In addition, small streams may be occupied by one or few species that allow more reliable taxonomic separation. Therefore, understanding life history patterns of *Cheumatopsyche* is essential for identification of the genus and for assessing its ecological parameters in streams.

Life histories

Determination of life histories of caddisflies has become an important objective in benthic ecology during the last two decades. Studies on several insect taxa from temperate regions may have led researchers to believe that univoltinism is the most common life history mode in Trichoptera (Hynes 1970; Wiggins 1977). But careful observations on even a limited number of species showed the

variability of life history patterns in Trichoptera (Oswood 1976; Rhame and Stewart 1976; Mackay 1979). Thus, the need for accumulating basic data on life histories as well as on factors influencing their patterns is well recognized (Rosenberg 1979; Butler 1984; Sweeney 1984). Waters (1979a) suggested that these data make significant contributions to research such as sampling, taxonomy and bioassays of aquatic invertebrates.

The importance of net-spinning caddisflies in stream ecosystems has stimulated studies on their life-history patterns, and wide distribution of some hydropsychid species allows comparisons among different stream habitats. Life histories of *Hydropsyche* and *Cheumatopsyche* species have been determined in low-order streams throughout the United States and Canada. Oswood (1976) reported univoltine life history of *H. oslari*, *H. occidentalis* and *C. gracilis*, while *H. cockerelli* was interpreted as bivoltine in Owl Creek, Montana. Univoltinism of most species also has been reported in small streams of Québec (Morin and Harper 1986), Minnesota (Mackay 1986), Virginia (Willis and Hendricks 1992) and even in a mid-size river of England (Elliott 1986). However, a shift to bivoltinism has been determined for some of the same species in warmer streams of North Carolina (Ross and Wallace 1983), Georgia (Benke and Wallace

1980; Freeman and Wallace 1984), and even in lower sites of mid-size rivers of Ontario where the species were univoltine at upstream locations (Mackay 1979).

Studies in larger rivers have shown more variability in life history patterns. Four *Hydropsyche* species and *C. pasella* were bivoltine in the lower Savannah River, Georgia (Cudney and Wallace 1980), and similar patterns were interpreted for two *Hydropsyche* species and an unidentified *Cheumatopsyche* spp. in the Satilla River, Georgia (Benke et al. 1984). Parker and Voshell (1982) found that three *Hydropsyche* species were trivoltine at 4-5th order sites in the North and South Anna Rivers of Virginia. These differences in life cycles have been related to differences in temperature regimes, but also interactions with high-quality food supply have been suggested as reasons for multivoltine life histories (Parker and Voshell 1982, 1983).

Life history events such as emergence, mating, oviposition and hatching of hydroptychids have been rarely described. Harris (1971) collected emergent adults of *Cheumatopsyche* and *Hydropsyche* from July to October in Illinois, and he also determined some flight periodicity with different light-trap attraction for the two sexes. Rhame and Stewart (1976) reported emergence of *C. campyla* from February through October and that of *C. lasia* and

H. simulans from March through September. They also found bimodal peaks of emergence that suggested bivoltine life histories. A review of emergence periods reported for hydroptychids in the Carolinas showed variations from a few days in mid-summer to a maximum of about 8 months from March through November (Unzicker et al. 1982). Periods of emergence for *C. pettiti* have been reported varying from 1-2 months (June-August) in Minnesota (Mackay 1986), to around a maximum of 6 months (April-October) (Parker 1980; Elliott 1986; Morin and Harper 1986; Floyd and Schuster 1990). Because this species is known for wide habitat tolerance (Ross 1944; Mackay 1986), and it has been found from streams to large rivers in the South East (Gordon and Wallace 1975), variations in emergence periods may be attributed to increases in thermal regimes along latitudinal or altitudinal gradients.

Very few observations have been made on mating and oviposition by hydroptychids. Fremling (1960) and Rhame and Stewart (1976) reported occasional swarms of *H. simulans* and *H. orris*. The latter authors described patterns of mating behavior, but swarms were not observed for *C. campyla* and *C. lasia*. These studies and the one by Deutsch (1984) observed that gravid females entered the water to oviposit on objects at the bottom at depths up to 2-3 m. Deutsch (1985) also

observed that hydropsychid females had modified tibiae and tarsi that are widened, concave when compared to other Trichoptera, and often with hair fringes. These were assumed to be swimming adaptations related to oviposition. Egg masses seem very similar for the family Hydropsychidae but important variations in eggs per mass have been observed, with fewer numbers for smaller species as *C. campyla* and *C. speciosa* (Rhame and Stewart 1976; Deutsch 1984) than for larger species such as *H. slossonae* (Willis and Hendricks 1992). Hatching of hydropsychid egg masses was observed in the laboratory by Rhame and Stewart (1976) and Elliott (1986), and in the field by Willis and Hendricks (1992). Incubation periods were estimated to be 9 to 17 days.

Recruitment and larval growth are frequently analyzed in life history studies to support interpretations on voltinism. The elaboration of instar-frequency histograms for each sample throughout the year constituted the basic evidence for deciphering the life-history patterns in the above mentioned studies. Relative abundance of instars during the year and timing of pupation also helped corroborate emergence data. Temperature has been the main factor observed to influence larval development and life-cycle periods. Conceptual frameworks such as the Thermal Equilibrium Hypothesis (Vannote and Sweeney 1980) predict

thermal effects on growth and distribution of aquatic invertebrates. In addition, Mackay (1984) suggested a particular trend to increased voltinism in hydropsychids for smaller species and for those that overwinter in later larval instars. Variation in life history patterns is poorly known for many hydropsychids including the *Cheumatopsyche* species that develop abundant populations in Appalachian streams.

Secondary production

Secondary production by hydropsychids has an essential role in the energy flow of lotic systems because of their abundance and growth in many stream types. Dominance of Hydropsychidae among collector-filterers has been observed in many small streams and large rivers (Neves 1979; Benke and Wallace 1980; Benke et al. 1984; Diamond 1986). Hydropsychids are reported to account for 39% of habitat-weighted production in Upper Ball Creek, North Carolina, with the highest contribution in bedrock outcrops and riffles (Huryn and Wallace 1988). Moreover, it represented more than 90 % of secondary production on snags that constitute the most productive habitat for invertebrates in rivers of the southeastern coastal plain (Cudney and Wallace 1980; Benke et al. 1984). However, determination of

hydropsychid production frequently faces uncertainty due to insufficient life-history information or to difficulties for sampling and identifying hydropsychid larvae.

Traditional methods for estimating secondary production are based on survival or mortality of synchronous individuals in a cohort (Benke 1984). Given the inability to separate actual cohorts in many stream invertebrate populations, as frequently occurs with overlapping generations of multispecies hydropsychid assemblages, most recent studies have used the size-frequency or Hynes method. The method was originally intended to produce acceptable estimates, in the correct order of magnitude, of total annual production of the whole benthic community (Hynes 1961; Hynes and Coleman 1968). Further adjustments of the method by Hamilton (1969) and Benke (1979) have rendered more accurate estimates and allowed its use for monospecific multivoltine populations. One of these adjustments on calculation of annual production arises from the use of the cohort production interval (CPI) of the "average" cohort, that can be determined from life-history information (Parker and Voshell 1983; Benke 1984; Mackay and Waters 1986).

Results of hydropsychid production obtained by this method have shown a wide range of values from low-order streams to large rivers. Forested streams in Massachusetts

(Neves 1979), North and South Carolina (Ross and Wallace 1983; Smock and Roeding 1986) and Georgia (Benke and Wallace 1980) generally have production lower than 1 gDM/m²/yr. This production has been related to reduced seston supply and low food quality. Low food quality has been attributed to paucity of critical nutrients with consequent decrease in the quality of detritus. Values several-fold higher have been reported in streams flowing through opened areas and sometimes with inputs from agricultural activities. Hydropsychid production in these disturbed streams reached more than 10 gDM/m²/yr in rock outcrops of Rose Creek, Georgia (Freeman and Wallace 1984), up to 40 gDM/m²/yr below pond outlets in Valley Creek, Minnesota (Mackay and Waters 1986), and more than 5 gDM/m²/yr for one *Hydropsyche* species in the 1st-order Mill Creek, Virginia (Willis and Hendricks 1992). In general, streams of moderately disturbed areas are believed to have higher collector-filterer production than streams in woodland areas, due to nutrient-enriched seston, higher autochthonous primary production, and higher biomass turnover ratios of consumers (Iversen 1988).

High values of hydropsychid production have been found in large, southeastern rivers, perhaps related to abundant supply or nutrient enrichment of seston. Cudney and Wallace (1980) reported values higher than 40 gDM/m²/yr in the lower

Savannah River, Georgia and more than 20 gDM/m²/yr were obtained in the Satilla River by Benke et al. (1984). Parker and Voshell (1983) reported the highest known value of hydropsychid production, approximately 325 gDM/m²/yr below a reservoir in the North Anna River, Virginia. Again, elevated seston supply, zooplankton-enriched releases from reservoirs, multivoltine life histories, and availability of habitat locations such as snags, have been established as factors determining high production in these areas.

Factors known to cause variation in secondary production of stream invertebrates can be related to life history patterns and to habitat influences. A review of life history influences on production by Waters (1979b) identified voltinism and length of aquatic life as essential parameters that determine the level of production. Variability in life-history patterns of Hydropsychidae, that was described above, account for part of high production. Small, cold streams are likely to have univoltine populations while in warmer rivers larval growth is increased and multivoltine species are more frequent (Parker and Voshell 1982; Mackay 1984). In addition, length of aquatic life may become shorter by faster larval growth stimulated by higher temperature or favorable habitat

locations such as rock outcrops or snags (Freeman and Wallace 1984; Benke et al. 1984).

Quantity and quality of food constitute major habitat influences on production through effects on larval density and biomass. Large amounts of seston, as well as better quality due to enrichment of the animal fraction by releases from reservoirs, have been correlated with increases in benthic production (Cudney and Wallace 1980; Parker and Voshell 1983; Mackay and Waters 1986). High alkalinity and hardness are known to stimulate periphyton growth (Hill and Webster 1982; Smock and Roeding 1986), flocculation of dissolved organic matter that becomes more available to filterers (Krueger and Waters 1983), and dense macrophyte beds (Allan 1995), and all these mechanisms may interact to produce high invertebrate production.

Several analyses of the trophic basis of production have been conducted with hydropsychids, and some of them have determined a high contribution of animal food (Benke and Wallace 1980; Ross and Wallace 1983). It is not only the relative abundance of animal material in the diet, but also its high assimilability (McCullough et al. 1979). However, such a high contribution of animal food has been found for some hydropsychid species but not for others (Benke and Wallace 1980; Ross and Wallace 1983; Smock and Roeding

1986). Animal food had major contribution to production in particular habitat conditions in which animal-enriched seston was readily available (Parker and Voshell 1983). In addition to the quality of food sources, specific characteristics of mesh size of hydropsyche nets are known to affect abundance and microdistribution of these caddisflies and consequently their efficiency to retain some size ranges of seston (Wallace and Malas 1976; Ross and Wallace 1982). In general, models that analyze factors influencing secondary production have found high correlation of production with temperature and individual weight, the former factor influencing life history and the latter related to quantity and quality of food (Benke 1993).

Most of the production work has been done with *Hydropsyche* rather than *Cheumatopsyche*. This probably reflects the more precise information on taxonomy and life history of *Hydropsyche*, as well as its larger size and diversity of identifiable species in immature stages. *Cheumatopsyche* in production studies usually included several species, and their production calculated as a whole was usually lower than *Hydropsyche*. However, in some cases production of *Cheumatopsyche* was higher than *Hydropsyche* as occurred at mid velocity ranges in the Savannah River, Georgia (Cudney and Wallace 1980). *Cheumatopsyche* had higher

production than *Hydropsyche* in Cedar Creek, South Carolina, but it had considerably lower production than *Macronema carolina* (Smock and Roeding 1986). General trends mentioned for the family regarding production, i.e., increases in production from small cold streams to larger warmer rivers, have been also suggested to occur in *Cheumatopsyche* populations.

The scarcity of life history data and production estimates of *Cheumatopsyche* support the general purpose of the present study. Given the taxonomic problems and the fact that *Cheumatopsyche* larva has one of the smallest body size of hydropsychids, its production dynamics may provide further insights in the ecological roles of these abundant collector-filterers. The trophic status of this genus and its life-history adjustments also can be affected by habitat disturbance in Appalachian streams, such as those disturbances related to different land uses on Stroubles Creek watershed.

SITE DESCRIPTION

Stream morphology

Study sites for this work were established in Stroubles Creek, a tributary of the New River located in Montgomery County, Virginia at $37^{\circ} 12' 20''$ N of latitude and $80^{\circ} 27' 30''$ W of longitude (Fig. 1). The stream headwaters form in several springs and lead to two main tributaries which run through the town of Blacksburg. The springs are at an elevation of approximately 670m, and the stream collects runoff water mostly from paved surfaces. These two headwater streams are covered under part of the town area, and they join in a shallow artificial impoundment (Duck Pond) on the Virginia Tech campus.

Below this impoundment, the stream flows NE-SW through pasture and urban areas with some box-culverts for about 1.5 km, and for other 2.5 km through agricultural areas used for crops and cattle management. In this upper section, the stream receives three main tributaries which collect runoff water from the agricultural fields and also from small farm ponds built for livestock use.

The lower section of the stream flows through a forested area composed of mixed coniferous and deciduous trees. This forest surrounds approximately the lowest 9 km

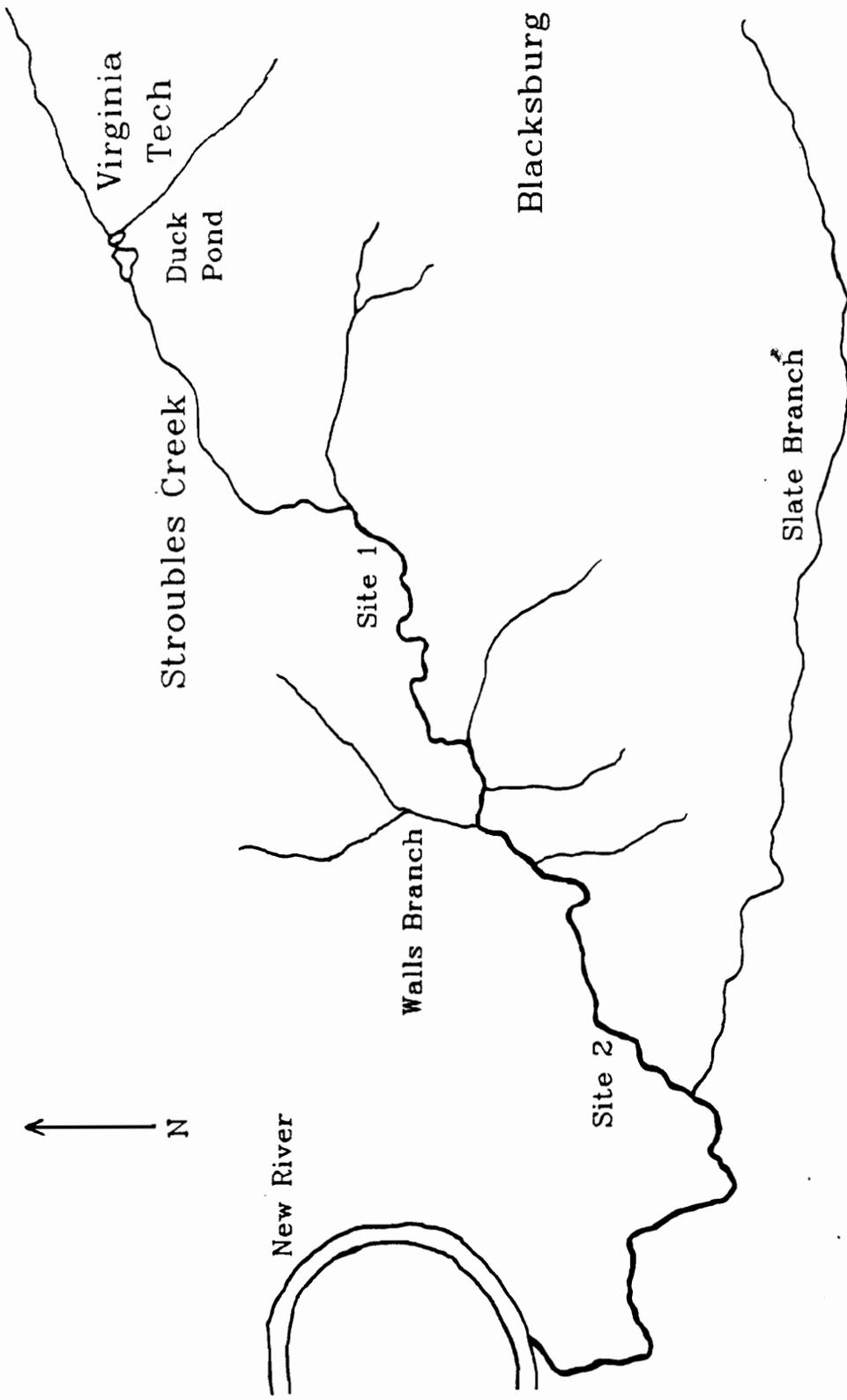


Fig. 1. Map of the Stroubles Creek system showing tributaries and study sites.

of the stream until its confluence in the New River at an elevation of 518 m. The total length of the main course of Stroubles Creek is approximately 15 km, with an average gradient of 10 m/km that corresponds to gentle slopes lower than 2% (Rosgen 1994). In the lower course, the stream receives 5 small tributaries that originate in the forested area, and another (Walls Branch) from a urban zone in the northern portion of the watershed. Finally, the largest tributary, Slate Branch, which also drains agricultural and forested areas, joins the main channel 3 km upstream from the confluence with the New River.

Stroubles Creek watershed lies within the Valley and Ridge physiographic province of Virginia. The geology of the Blacksburg area was described by Ritter (1969), and it includes mainly ancient sedimentary formations which range in age from Cambrian to Mississippian. Rocks composition is mostly dolomites and limestones mainly located in the upper section of the watershed. Sandstones and siltstones are found in the mid-and-lower sections of the watershed (Ritter 1969). Surface materials of recent, quaternary origin are also present in alluvial deposits that include calcareous and sandstone pebbles and cobbles. The dominant carbonaceous materials are known to be easily removed and transported by

runoff, and the unprotected soil surfaces are easily eroded due to effects related to urban and agricultural land uses.

Human activities are widespread on Stroubles Creek watershed, and such activities are reflected in land use patterns as well as in morphological characteristics of the stream channel. High density of buildings and roads is common on the headwater area, which has an approximate gradient of 27 m/km along the first 2 km of the stream. Urban structures are likely to generate quick runoff from paved surfaces and facilitate increases in the amount of materials transported to the stream (Swank and Bolstad 1994). Channelled and covered sections of the stream are also present in this uppermost area, which may allow fast movement of particles and scarcity of retentive structures in the stream bed.

The agricultural area is located in the mid-course of the stream, approximately between the 2nd and 6th km. Through this area, the channel has a gradient nearer to 4.5 m/km which is less than half of the average gradient for the whole course. This lower slope can contribute to sediment deposition in the stream, but most of materials transported from the urban area are already deposited in the Duck Pond at Virginia Tech. Sediment-free water, however, has a high carrying capacity, so the stream is able to degrade the

channel banks. Many areas of bank erosion can be observed along this mid-section, since very few banks are protected and the channel shows evidence of agricultural activities and cattle disturbance. Incision of the stream channel is also visible, and qualitative observations, such as one made after melting of a heavy snowfall, indicated increases of water level of approximately 1 m at some excavated banks.

The lower section of the stream shows less degradation because the channel is protected by the surrounding forest. There are few buildings and roads near the stream. This lower course has a gradient of 8.9 m/km, close to the general average, and most banks show gentle slopes with little evidence of channel incision. Some military installations, with buildings and roads, are located in the New River margin around the confluence area, but they probably have limited effects due to the restricted activities and access that are allowed.

Land use classification

The influence of land use on habitat conditions in the stream can be related to dominant land cover types on the main sections of the watershed. The following classification has been incorporated in the Virginia Gap Analysis Project (David Morton, Department of Forestry Virginia Tech,

unpublished data), based on criteria from Anderson et al. (1976). Results of this project are synthesized in a map of land cover types that includes the Stroubles Creek watershed (Fig. 2).

Urban (Red). Urban land use comprises areas defined by intense human use, such as cities, residential areas, transportation, factories, shopping centers and commercial complexes. In the map (Fig 2), a 30m-wide strip at each side of main roads also has been included as urban area. These areas are concentrated on the eastern portion of the watershed, basically around Blacksburg, with other marked surfaces on the north along Price's Fork Road and on the west beside the New River.

Agriculture (Yellow). Agricultural land use corresponds to lands that are used predominantly for production of food and fiber, generally defined by their herbaceous ground cover. This type includes uses such as croplands, orchards, horticultural areas, pastures and even recreational lawns, clear cuts and forest openings. These agricultural areas cover roughly 30-40% of the watershed, specially on the north and east sections and they extend to the central section.

Shrub (Orange). Shrublands are typically a successional stage between herbaceous (agriculture) and forest. This type

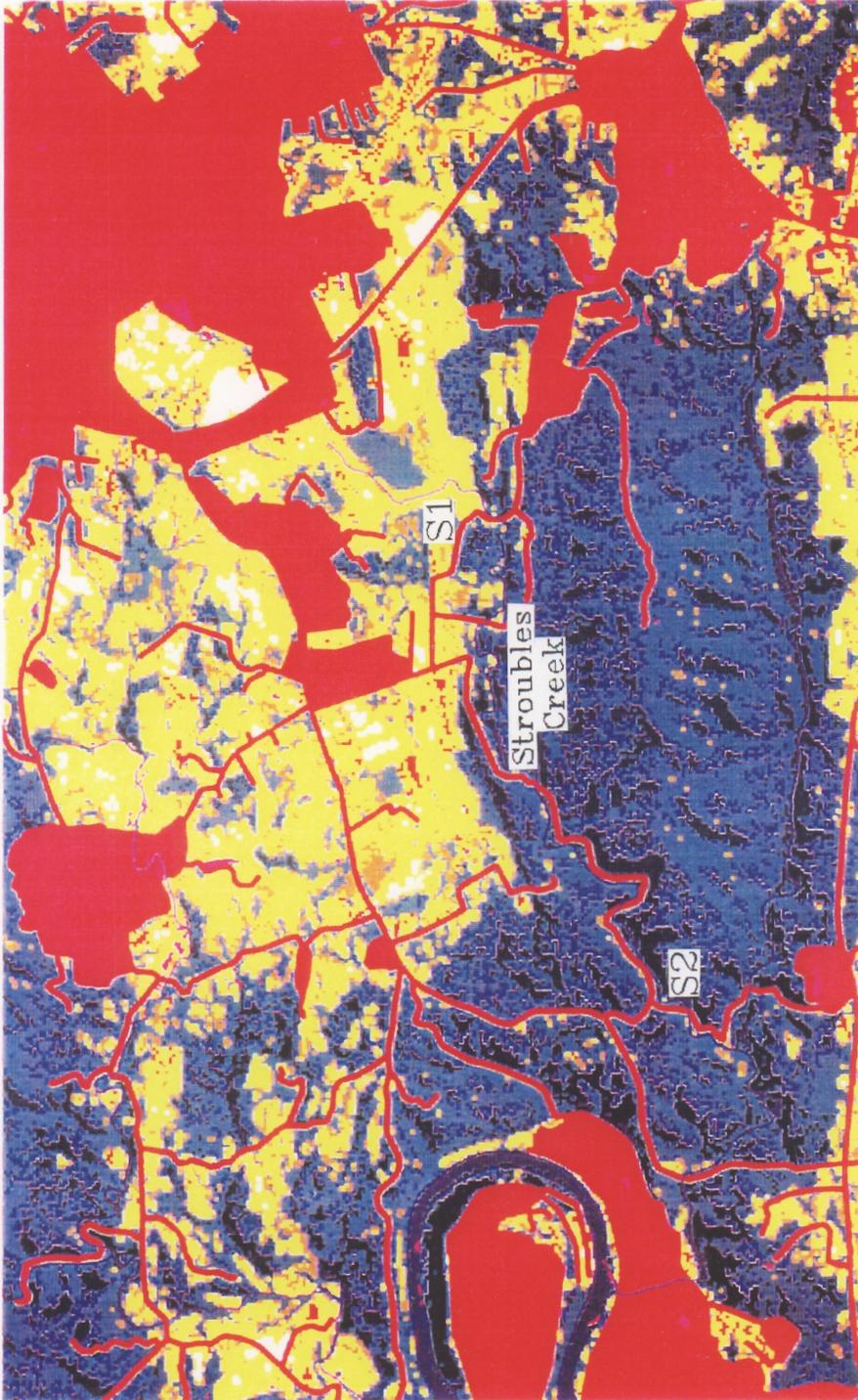


Fig. 2. Map of land cover types in the Stroubles Creek watershed.
See color code in text.

is characterized by woody vegetation less than 3 m tall, that is scattered within urban, agricultural and forest surfaces in the mapped area.

Forest (Green). Forest land use comprises areas dominated by woody vegetation over 3 m tall, with tree basal area greater than 10%. This type include sub-classes with color tones in the map that represent coniferous forest (dark green), dominated in 70% or more by evergreens; deciduous forest (light green), containing over 70% deciduous trees; and mixed forest (light blue-green) that includes less than 70% of each coniferous and deciduous. Forest constitutes the largest land cover around Stroubles Creek with more than 40% of the watershed surface, mainly located on the south and west sections.

Water (Dark blue). This color represents open water areas larger than the minimum mapping unit (1 ha), including lakes, reservoirs, streams and rivers. Main water courses located in the map are the New River, Stroubles Creek with its largest tributary Slate Branch, and the watercourses of the northern watershed of Tom's Creek.

Other types. Two more land cover types are represented in small areas. Wetlands (purplish) occur in areas such as the shallow farm ponds, which can be assimilated to areas with the water table at, near, or above the ground for a

significant part of most years. Finally, white represents small barren areas that include bare rock, bare soil, quarries or mines.

Study sites

Two study sites were established for collecting biological material and environmental data from Stroubles Creek (Fig. 1). These two sites were selected in order to assess contrasting influences from the surrounding watershed on the stream habitat. The first Site (S1) was chosen in the upper mid section of the stream system, within the pasture and agricultural area, in a 3rd order reach with gentle gradient and relatively incised channel. The second Site (S2), also in a 3rd order reach, is in the center of the forested area, surrounded by the typical land cover of mixed coniferous and deciduous forest.

Riffle units at both sites were used for sampling and measurements. At Site 1, the scarcity of riffles restricted this selection to a stream section of approximately 6 m long and 4.3 m wide that contained adequate substrate of gravel, cobbles and some small boulders. The stream banks had the typical incision described for this area and showed some evidence of depositional processes such as small bars and sandy areas. The riffle was limited by shallow pool areas,

and the stream margins showed tracks and other signs of cattle activity. Site 1 is located approximately 300 m upstream from the bridge of Route 657, and around 3.5 km downstream from the Duck Pond at Virginia Tech.

Site 2 was near the junction of Routes 659 and 619, approximately 5.3 km downstream from Site 1, 4.5 km after the stream flows through the forested area and 1 km upstream of the confluence of Slate Branch. The sampling area was a riffle approximately 15 m long and 4.5 m wide, limited upstream by a shallow run and downstream by some continuous small pools. The streambed has gentle banks with the exception of a bend close to the road which forms a steep bank around 2 m above the streambed. The substrate also consists of gravel and cobbles, with higher abundance of boulders than at Site 1. The presence of trees on the stream margins produced abundant shading over the water course, except for one section at the upstream end of the riffle, where there was an open lawn.

General observations of the study areas showed environmental differences related to geomorphological conditions and land use activities in the watershed. At Site 1, the lower gradient and runoff from urban and agricultural areas were probably responsible for high amounts of suspended particles in the water and deposition of sand bars

and small islands in the streambed. Cattle management around streams contributes to erosion of streambanks, eliminates riparian vegetation and increases sediment load (Armour et al 1991). These disturbances probably affect habitat parameters such as seston and available resources for caddisfly larvae. In addition, the absence of riparian cover allows increases in temperature and higher development of algae and macrophytes that were observed as layers on rocks surface.

In contrast, Site 2 showed less evidence of erosion or deposition. Shading of the streambed reduces algal development and thermal input, and average water temperature recorded from January 1995 to January 1996 was 12.4°C compared to 13.4°C at S1. The presence of forest cover certainly supplies more organic detritus through litterfall input. In general, S2 has environmental conditions closer to those typical of mountainous, southeastern streams, than conditions at Site 1 which has received noticeable alterations due to human impacts on the watershed.

MATERIALS AND METHODS

Preliminary collection

Due to the limited knowledge on taxonomy of *Cheumatopsyche* larva, some preliminary collections were required in order to become familiar with identification of several life stages of the genus. *Cheumatopsyche* species have been described only from adult material (Gordon 1974): No larval identification keys are available for this genus. (Unzicker et al. 1982). Therefore, observations of juveniles and adults, collected from the study sites, were performed to verify distinctive features of the genus and to determine the species occurring in the watershed.

Larvae were initially collected in the stream with a Hess sampler and by hand picking from rocks. Hess samples were preserved in the field in 10% formalin. Invertebrates were sorted and identified to the genus in the lab. Hand-picked larvae were placed in stream water and transported to the lab for rearing. Six rearing chambers were built with plexiglass. (Mackay 1981). These chambers were installed in a temperature-controlled room at 20-22 °C with continuous air supply, and 1-6 mature larvae were placed in each chamber to obtain reared adults for identification. Aquarium

food was provided daily and adults emerging were captured in plastic bags placed over the chambers.

Generic larval identification was done under a dissecting scope by using general keys for the family (Wiggins 1977; Merritt and Cummins 1984). Separation of *Cheumatopsyche* from *Hydropsyche* is more complicated for early instars, since distinctive features such as the frontoclypeal notch or the prosternal sclerites are not fully developed before III instar. Thus, the diagnostic character for *Cheumatopsyche* in instars I-II was basically the long and tapered setae on the anterolateral border of the pronotum, as opposed to the short and blunt ones of *Hydropsyche* (Mackay 1978).

Eggs and adults of hydropsychids were collected during emergence and oviposition periods reported for the family (Wiggins 1977; Mackay 1979, 1986; Unzicker et al. 1982; Parker and Voshell 1982; Morin and Harper 1986). Eggs were removed from rocks, placed in Petri dishes with stream water and maintained in the Lab at 24°C for determining hatching periods. Adults were collected mainly with light trap, identified using the descriptions and keys by Gordon (1974), and species confirmations were obtained from Dr O.S. Flint at the National Museum of Natural History in Washington D.C.

Habitat conditions

Some physical-chemical measures of the stream habitat were done to assess environmental influences on variations in life history between the two study sites. Water temperature was continuously recorded with Ryan tempentors (thermographs) placed in the stream. Water samples were taken for laboratory analysis that included pH measured with a Corning digital pH meter, alkalinity and hardness determined by titration methods, and heavy-metal concentrations determined using a Perkin-Elmer model 1100 atomic absorption spectrometer (Methods for Chemical Analysis of Water and Wastes 1985). Seston measures were obtained by filtering 1-2 liters of stream water, drying, ashing and weighing the filters and determining total dry mass and ash-free dry mass of seston in the water. Finally, Chlorophyll-a concentrations were determined in water samples by the monochromatic method with a Perkin-Elmer model 55E spectrophotometer (Wetzel and Likens 1991).

Effects from hydraulic and geomorphological features on the composition of the stream bed were evaluated in the two study sites by the Pebble Count Procedure described by Harrelson et al. (1994) with some minor modifications. The selected reach was the one where insect sampling took place. The Hess sampler was used to establish areas where diameter

of all particles larger than 8 mm was measured. This procedure was repeated until 120 particles were measured. In addition, a subjective evaluation of habitat quality was conducted. I performed this evaluation by applying the Habitat Assessment Matrix utilized by EPA Rapid Bioassessment Protocols (Plafkin et al. 1989). The complete procedure requires comparison with a regional reference stream that was not available. However, I used this application only for a relative comparison of habitat influences on the caddisfly populations. Current velocity and discharge were measured at the two sites during fall 1995 using a Marsh McBirney model 2000 portable flow meter.

Life history

Stages and development of the life history of *Cheumatopsyche* in Stroubles Creek were determined simultaneously with the sampling program used for secondary production estimates. Timing of the emergence period and species composition were established with adult collections, and the incubation period was estimated by observing hydropsychid eggs in the stream and the laboratory.

Samples of immatures were taken at the study sites at 2-week intervals between May and September and at monthly

intervals between October and April. Three subsamples were collected with a Hess sampler of 0.1 m² area and 200-um mesh size. Samples were preserved in the field in 10% formalin and transported to the lab for sorting and identifying under a dissecting scope. Aquatic insects collected were identified to the genus for most taxa, using general taxonomic keys (Pennak 1953; Brigham et al. 1982; Merritt and Cummins 1984). *Cheumatopsyche* larvae were counted and their head widths measured with an ocular micrometer to the nearest 0.025 mm. Larval instars were determined by plotting the size frequency distribution of all head widths to obtain width ranges for instars I through V and to generate regression lines of larval growth through instars I-V for the two sites (Mackay 1978).

Pupae collected in samples were used for taxonomic study as well as for determining the timing of this stage in the life history. Abundance of immature stages were used to elaborate frequency histograms for each sample date and the general instar-frequency distribution in the two sites during the study period.

Adult collections were done weekly from June to September 1994 and again from early May to late September 1995 until no more adults were obtained. A black-light trap was located during 1-hour dusk periods at stream margins by

the two study sites. Adults were preserved in the field in 70% ethanol and identified in the lab using the descriptions and keys by Gordon (1974). Two emergence traps of 0.1 m² were placed one night per week in each site, during June and July 1995, and examined the following morning to collect adults that might have emerged.

Eggs of the family Hydropsychidae were observed during the emergence periods in both natural and artificial substrates. Egg masses on cobbles were collected for hatching in the lab and for determining mean number of eggs per mass. Artificial substrates (bricks) were placed in the stream and checked daily in order to determine the incubation period. Unfortunately, only three of the masses observed were from *Cheumatopsyche*.

All data obtained from collections of immature and adult *Cheumatopsyche* were used for the description of life history in Stroubles Creek. Given the inability to identify the species of larvae present in the stream, actual cohorts developing could not be established. However, the relative abundance of adults collected will be used to help explain variations in life history between the two study sites.

Secondary production

Determinations of secondary production of

Cheumatopsyche were performed by the size-frequency or Hynes method (Benke 1984), because the lack of larval specific identification did not allow me to establish actual cohorts required for the removal-summation or other cohort methods (Hynes and Coleman 1968; Hamilton 1969). Data on head width of instars and timing of life history events were used to determine size fractions and cohort production interval. Environmental influences in the two sites, such as water temperature, habitat structure, seston and chlorophyll concentration, helped explain variations in larval production.

Mean numbers of individuals per instar were calculated from all samples collected during the study period. Larvae of the instars obtained in each sample were dried for 24 hours at 60°C and weighed in a Cann electrobalance to the nearest 0.001 mg. Average dry mass of 10-15 larvae was obtained for each instar when these numbers were available in a sample, but fewer numbers of some instars were used in sample dates of low abundance and for instars I-II that were frequently underrepresented in samples. Average dry-mass for each instar was used to calculate mean biomass and biomass losses for production estimates. Due to the low numbers of instars I-II collected, some negative values were obtained for production losses of these early instars, even though in

some samples the number of instar I was determined from egg-mass size.

Growth and development of mature larvae in the two sites were also assessed by lipid accumulation of V-instar individuals. To measure lipid contents, some larvae were dried overnight, weighed and placed in ethyl ether for 48 hours, then dried and weighed again to calculate percentage of mass loss that represents the amount of lipids extracted.

Gut content analysis was done monthly by the method described by Cummins (1973) with some modifications similar to those performed by Snyder and Hendricks (1995). Foreguts from 4-6 larvae from each site were pooled and filtered onto a 0.45-um gridded filter for estimating relative volume of three food types: animal, detritus and algae. Three grids were counted at 100X magnification and the area occupied by each food type averaged and converted to a percent of total area.

Mean annual production was calculated by the Hynes method for the year August 1994-August 1995. However, assuming the cohort production interval estimated from field and laboratory observations and from literature sources, the production value was adjusted to the number of generations with the CPI correction factor (Hamilton 1969; Benke 1979; Benke and Wallace 1980). Finally, the relative importance of

food sources was evaluated by using the gut content analysis and reported values of assimilation and net production efficiency (McCullough et al. 1979; Benke and Wallace 1980). This analysis was then used to assess the effects on growth and production of *Cheumatopsyche* that can be attributed to different habitat conditions at the two study sites in Stroubles Creek.

RESULTS

Habitat conditions.

Differences in physical features were determined between the two study sites. In addition to general environmental influences due to the contrasting land use on the watershed, records of temperature, seston and streambed configuration showed noticeable differences between the two stream reaches.

Mean water temperature and accumulated degree days (ADD) at the two sites are shown in Fig. 3. Annual ranges of mean daily temperature were quite similar, 0.3-24.6 °C at S1 and 0.1-23.9 °C at S2, but lower daily values were recorded for more days at S2 and, conversely, higher values were more abundant at S1. Accumulated degree days totalled 4891.3 at S1 compared to 4508.7 at S2.

Ranges of pH and averages of alkalinity, hardness and heavy-metals concentration appear in Table 1. Most of these parameters were similar for the two sites. Concentrations of heavy metals were quite low and they are considered below chronic effect concentrations (Quality Criteria for water 1986). Total alkalinity and total hardness showed maximum values and averages higher at S1 than S2, and a similar higher value upstream was observed in Mg concentration

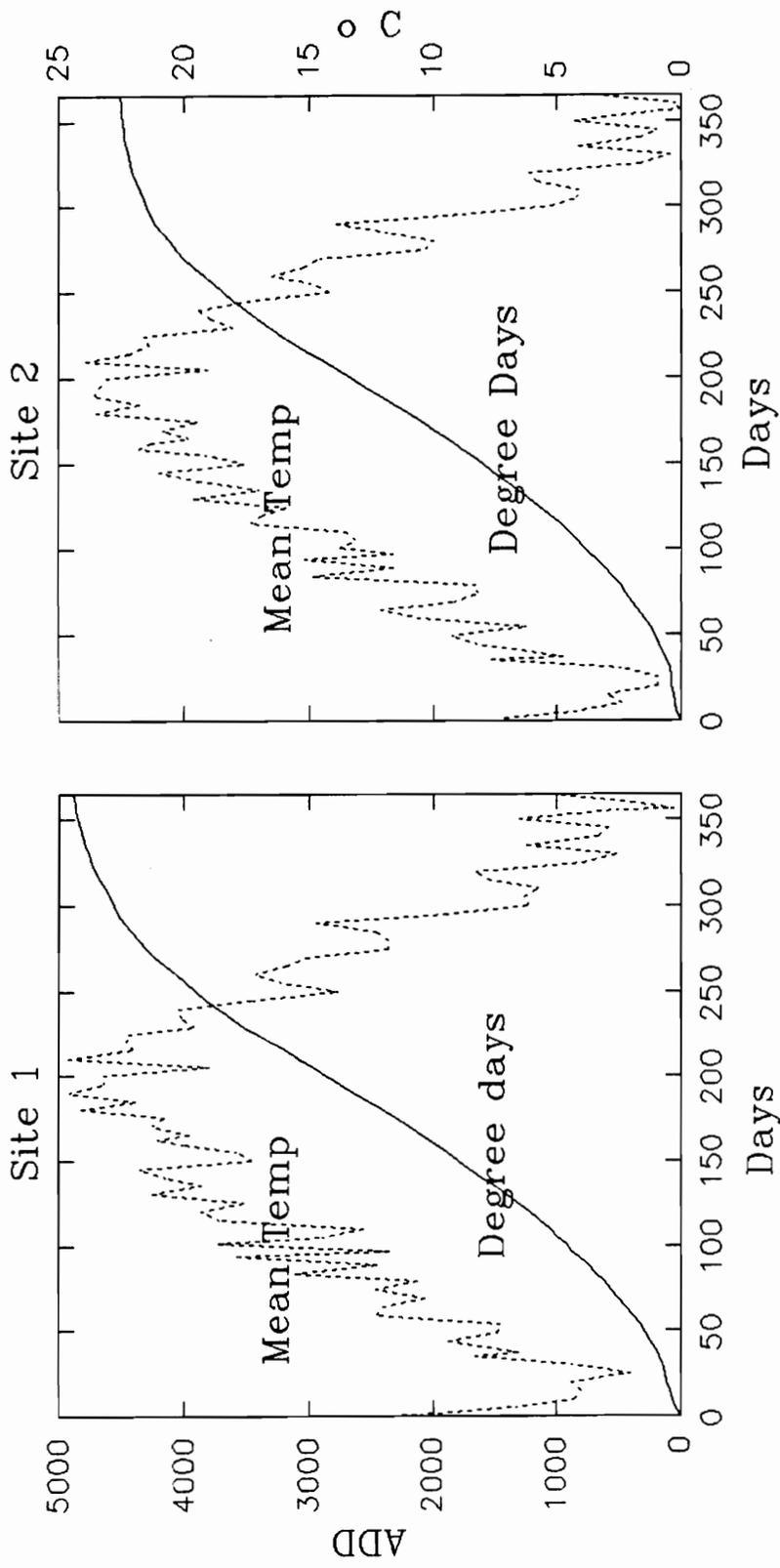


Fig. 3. Accumulated degree days (ADD) and mean temperature ($^{\circ}\text{C}$) at two sites in Stroubles Creek. January 17, 1995 to January 16, 1996.

Table 1. pH ranges, alkalinity, hardness and metal concentrations at two sites in Stroubles Creek.

Parameter (Units)	S1		S2	
	Mean	± 95% C.I.	Mean	± 95% C.I.
pH (range)	7.90-8.42		7.90-8.77	
Total alkalinity (mg CaCO ₃ /L)	207.44	13.23	173.25	14.88
Total hardness (mg/L as CaCO ₃)	120.00	27.69	106.00	20.70
Mg (mg/L)	20.11	5.10	16.59	4.28
Fe (mg/L)	0.29	0.11	0.25	0.11
Mn (mg/L)	0.06	0.02	0.06	0.02
Zn (mg/L)	0.05	0.02	0.06	0.02
Cu (ug/L)	0.66	0.59	0.33	0.29
Pb (ug/L)	1.66	1.19	1.60	1.14

(Methods for chemical analysis of water and wastes 1985).

The amount of seston carried by the stream showed different influences from the watershed at the two sites (Fig. 4). Total dry-mass seston at S1 was between 2 and 20 times higher than at S2 from August 1994 to April 1995. The value at S1 in October was not completely drawn because it was abnormally high (76.0 mg/l) due to cattle activity in the streambed just before sampling. Lesser differences between sites were observed during summer periods, but the values at S1 were again higher in fall 1995.

The ash-free-dry-mass (AFDM) seston showed similar temporal variations, but the difference was only 2-3 fold for S1 relative to S2. This variation was produced by a higher percentage of AFDM seston in relation to total seston, that was 35.2% at S1 and 47.2% at S2.

Results of the Pebble Count Procedure for the two sites are summarized in Fig. 5. At S1, there was evident concentration of the number of particles in the range of medium and coarse gravel (8-32 mm), while the distribution at S2 was more uniform for the gravel ranges with higher numbers in the range of very coarse gravel (32-64 mm). In contrast, there were about three times more small and medium cobbles (64-128 mm) at S2 than at S1, even though large and

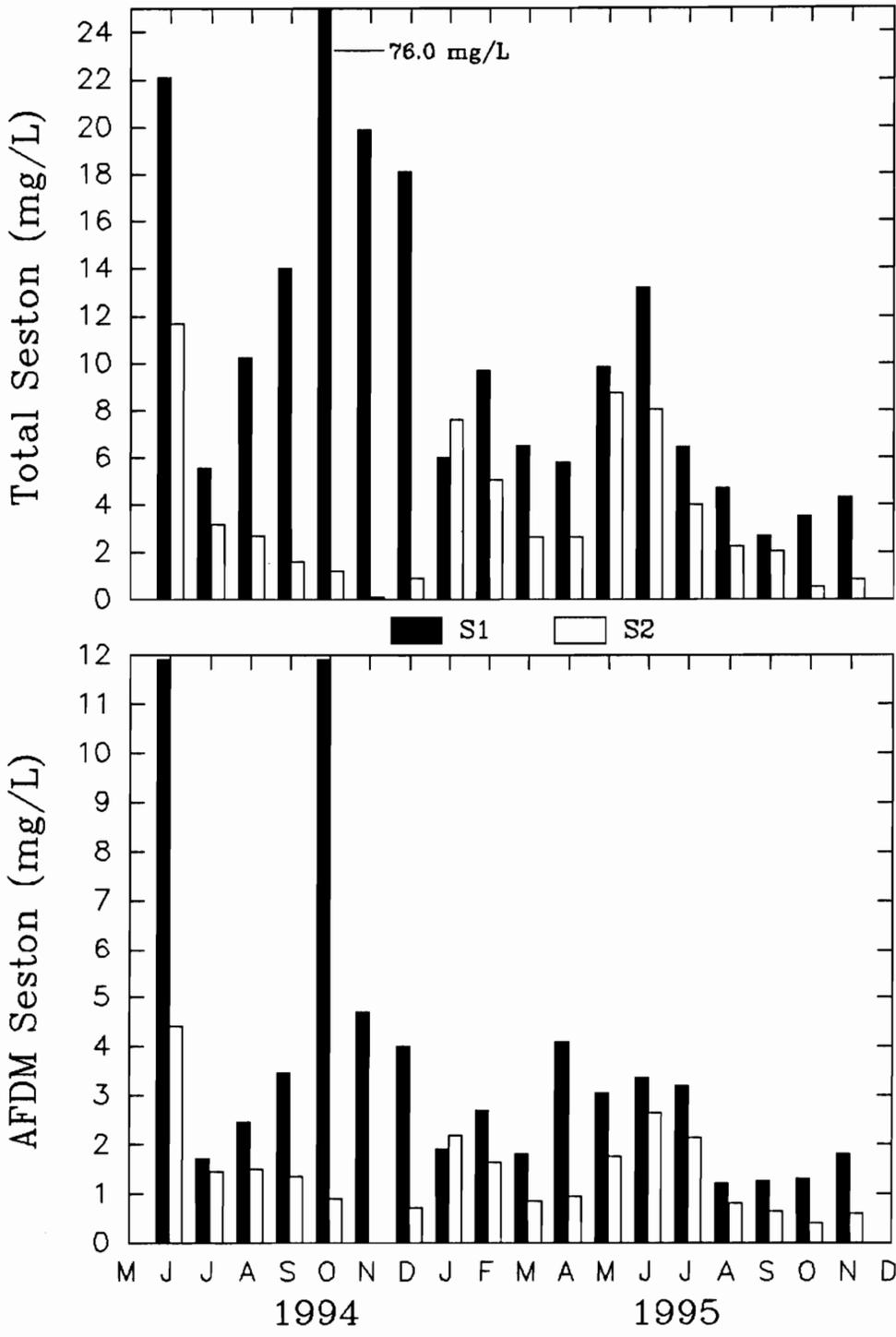


Fig 4. Monthly averages of total dry mass and ash free dry mass seston in Stroubles Creek.

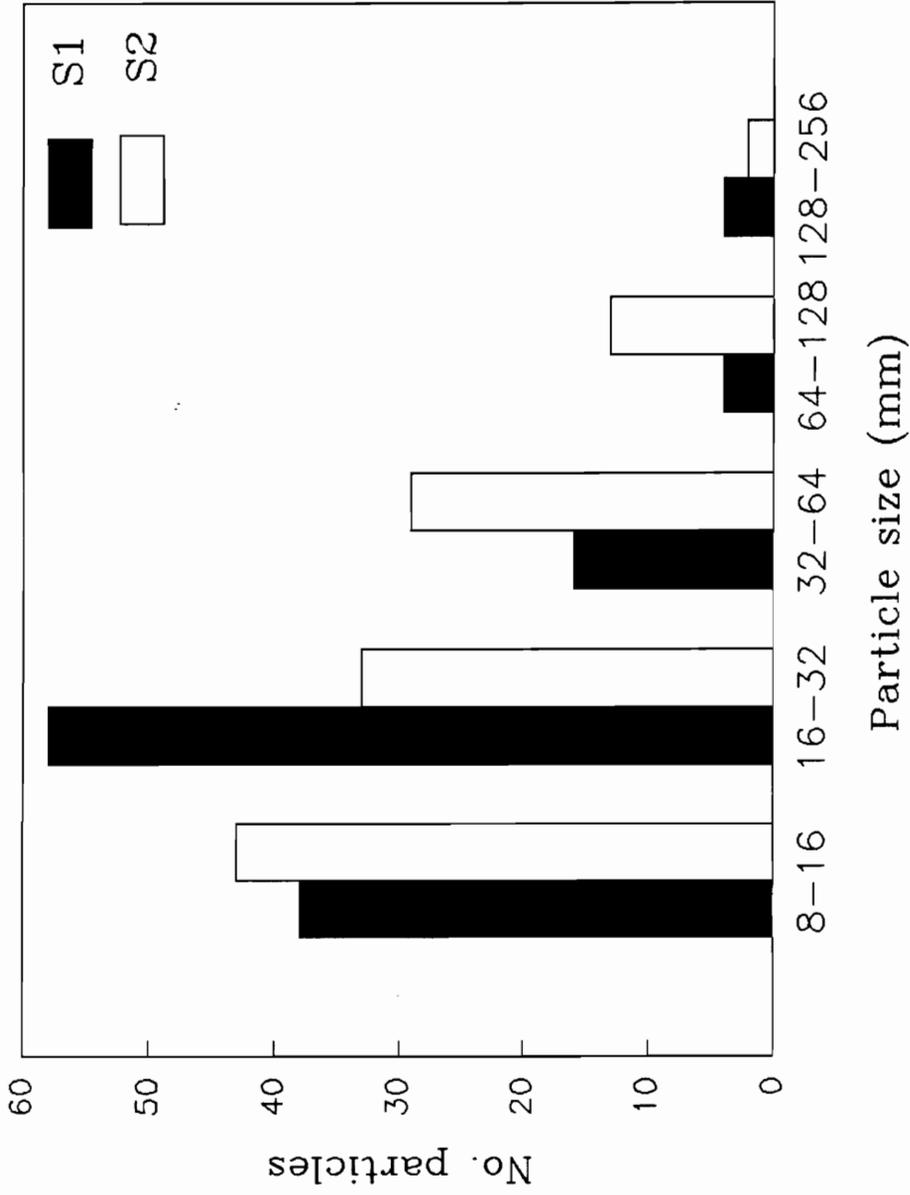


Fig. 5. Size distribution of substrate particles at two sites in Stroubles Creek.

very large cobbles (128-256 mm) were more abundant at S1, but they represented a quite low fraction of the substrate composition.

The subjective evaluation conducted with the habitat assessment matrix used by EPA (Plafkin et al. 1989) produced ranges that fit in the scale of fair habitat condition at S1 and good condition at S2. Main parameters that may affect habitat quality at S1 were less available cover in the substrate, channel alterations such as bars and islands, scouring and deposition of sediments, reduction of riffles, lower bank stability and the reduced streamside cover due to the grass vegetation. In only one determination of flow, I found lower values at S1 (discharge $0.457 \text{ m}^3/\text{s}$; velocity 0.31 m/s) than at S2 (discharge $0.575 \text{ m}^3/\text{s}$; velocity 0.47 m/s).

Aquatic insects

Even though the essential purpose of the study was to determine ecological parameters of *Cheumatopsyche*, other aquatic insects collected in the Hess samples were also sorted and identified to the generic level for most taxa, but only to family for Diptera and Coleoptera. Monthly values of number of taxa and insect density are shown in Fig. 6 during the study period.

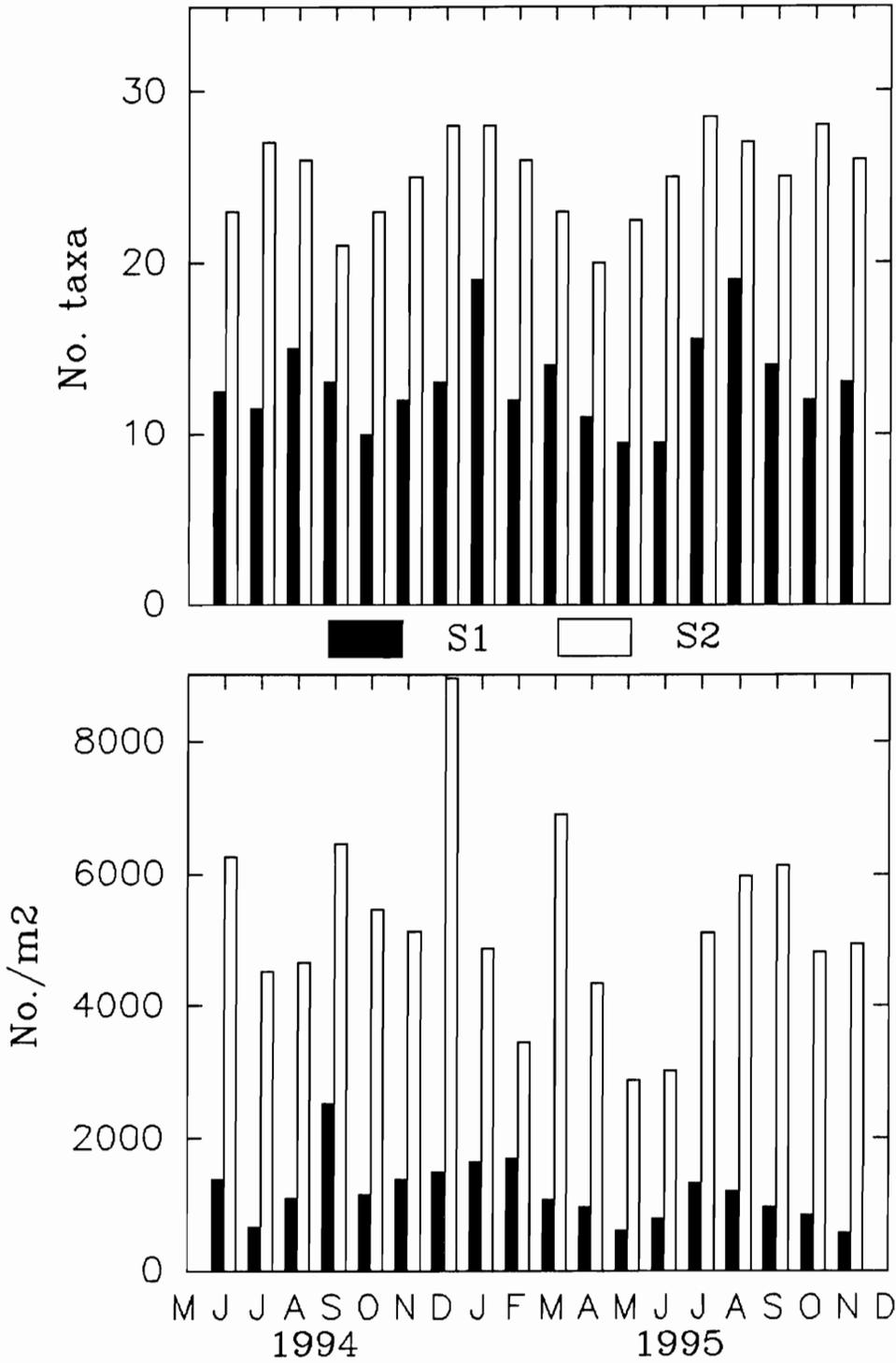


Fig. 6. Monthly number of taxa and density of aquatic insects at two sites in Stroubles Creek.

Number of insect taxa ranged between 8 and 21 at S1 and between 19 and 30 at S2. This marked difference of insect taxa downstream was produced by the presence of more genera in several orders. Among the Trichoptera, I found 2 species of *Hydropsyche* at S1 and 3 at S2, and the genera *Nyctiophylax*, *Neophylax*, *Rhyacophyla*, *Polycentropus* and *Glossosoma* were found only at S2, but *Chimarra*, *Hydroptila* and *Helicopsyche* were collected at both sites. Similarly, 6 genera of mayflies and 3 of stoneflies were collected at S1 while these orders were represented by 9 and 6 genera respectively at S2. Six families of Diptera and 3 of Coleoptera were found at both sites, but the presence of all these families was more frequent in the downstream samples. In general, the number of taxa collected was consistently higher at S2 than at S1 (Fig. 6), even though many of the taxa apparently could occur at both sites.

Overall density of aquatic insects collected was also consistently higher at S2 (2137.9-8951.0/m²) than at S1 (532.8-2577.4/m²) (Fig. 6). The average densities were approximately 4.4 times higher at S2 (5156.8/m²) than at S1 (1176.5/m²). *Cheumatopsyche* was one of the taxa that was more abundant downstream. Other caddisflies such as *Hydropsyche* and *Chimarra* were also observed with higher density at S2 than at S1, and a similar trend was observed

for mayflies and stoneflies. Diptera and Coleoptera seem to be more similar in density between sites.

Adult collections.

Total *Cheumatopsyche* adults collected with light traps during the emergence periods were 385 at S1 and 810 at S2. Males represented a minor portion at both sites, 6% at S1 and 18% at S2, which suggests that females were probably more attracted by the light, since the two sexes had approximately the same proportion in reared specimens.

All males from light collection were identified to species as well as most of females. However, when collections had more than 20 females a subsample of 20%, but not fewer than 10 females, was used to determine the proportion of species due to the long time required for female identification. Table 2 shows the number and percentages of *Cheumatopsyche* adults collected and reared from the two study sites.

The majority of males collected from S1 were *C. pettiti* (Banks) (78%) and there were a few specimens of *C. ela* Denning (13%) and *C. minuscula* (Banks) (9%). The females were mostly *C. pettiti* (92%) with small numbers of *C. oxa* Ross (5%) and *C. ela* (3%). In total numbers, Fig 7 shows

Table 2. Number and relative abundance of Cheumatopsyche collected and reared in lab chambers from two sites in Stroubles Creek.

species	S1			S2		
	male	% female	Total %	male	% female	Total %
Light trap collection						
pettiti	18	78	327	90	345	89
oxa			23	6	23	6
ela	3	13	12	4	15	4
minuscula	2	9		2	1	1
Rearing chambers						
pettiti	11	100	12	100	23	100
oxa						
Emergence traps						
pettiti	1	100	5	100	6	100
oxa						
	2	100	6	100	8	100

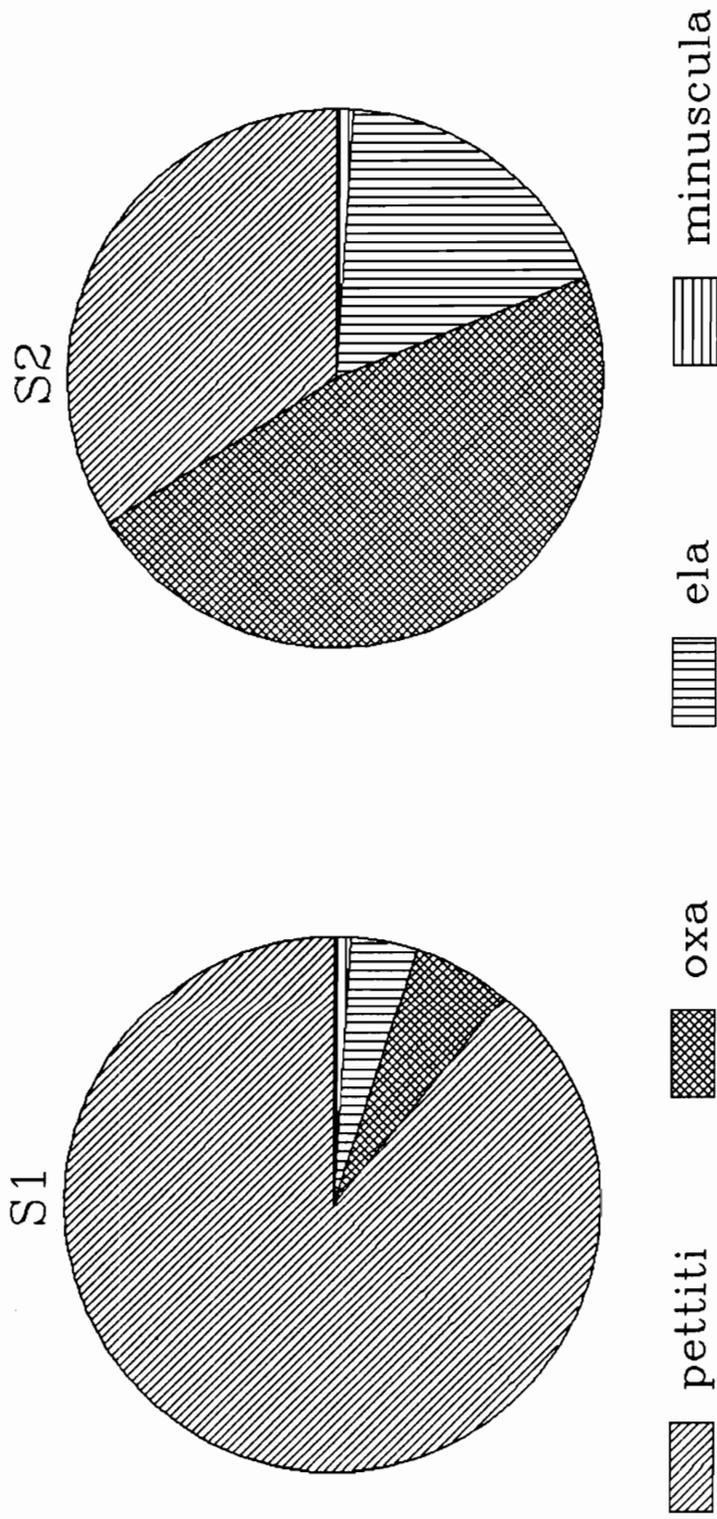


Fig. 7. Relative abundance of *Cheumatopsyche* species collected with light trap at two sites in Stroubles Creek.

that *C. pettiti* was the dominant species from S1 with almost 90% of the adults collected.

From S2 the males collected were mostly *C. ela* (62%) and *C. pettiti* (25%) with fewer *C. minuscula* (2%), *C. oxa* (11%) and just one adult *C. sordida* (Hagen). On the other hand, females showed higher abundance of *C. oxa* (57%) and *C. pettiti* (34%) and fewer *C. ela* (8%) and *C. minuscula* (1%). In general, both *C. oxa* (47%) and *C. pettiti* (34%) seem to be dominant species of *Cheumatopsyche* at S2 (Fig 7).

In the rearing chambers, 23 larvae from S1 and 20 from S2 were successfully reared to adults and identified (Table 2). All from S1 were *C. pettiti*, but from S2 *C. pettiti* and *C. oxa* were obtained in similar numbers. In emergence traps all adults collected at S1 were *C. pettiti* and all at S2 were *C. oxa*.

Immatures of *Cheumatopsyche*

Density of *Cheumatopsyche* larvae showed a noticeable difference between the two study sites. At S1, the average monthly number of larvae ranged from 10 to 817.5/m², while at S2 this range was 234.8 to 1944.7/m² (Fig. 8). In the upstream site, the highest density was obtained in June 1995, when the only egg mass collected was used to calculate I-instar larvae. The highest number in the downstream site

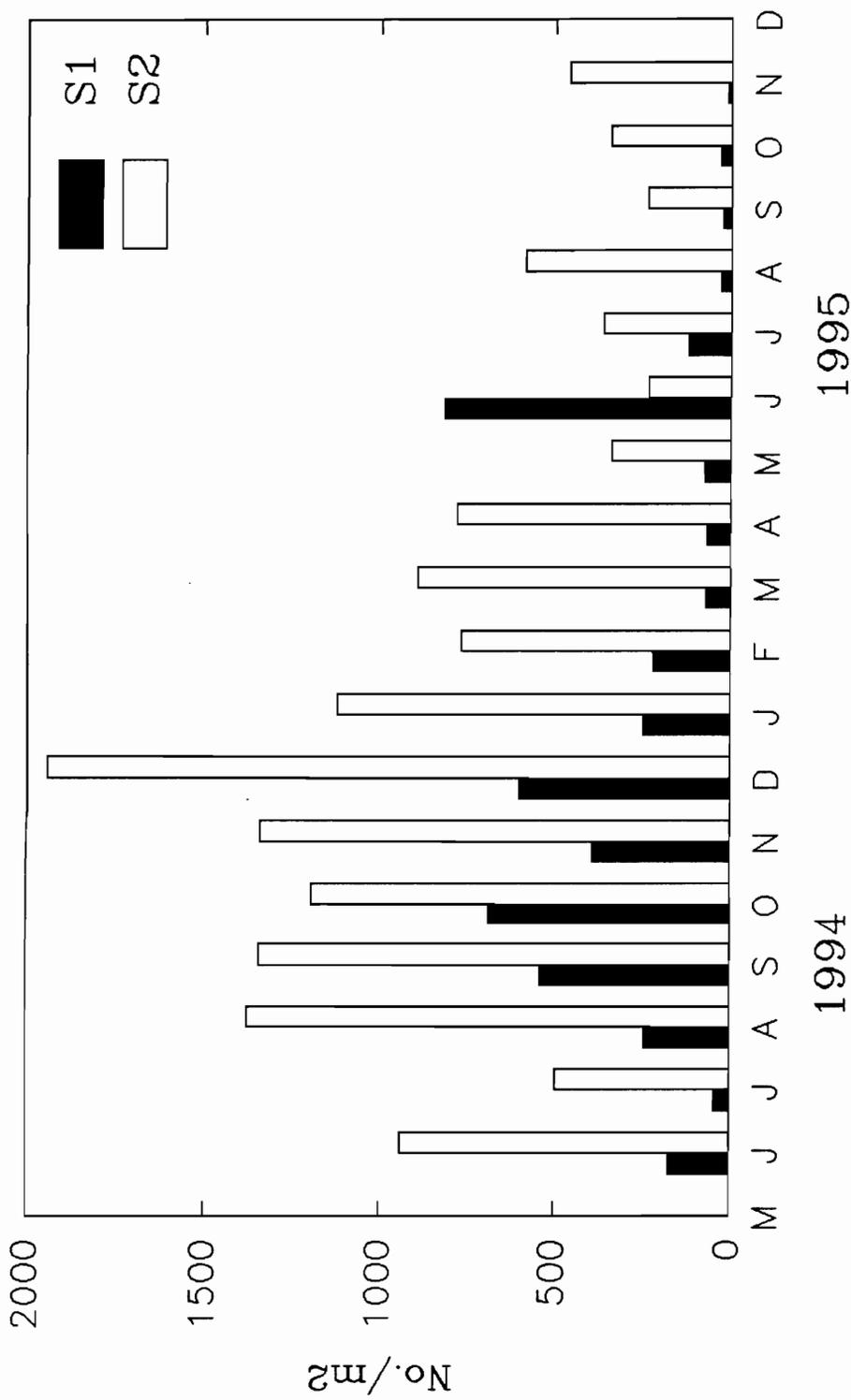


Fig. 8. Monthly density of *Cheumatopsyche* larvae at two sites in Stroubles Creek.

was obtained in December 1994, and this value corresponded to late-instar larvae which were in overwintering stages.

Head widths of 8212 larvae were used to determine size ranges of larval instars. Fig. 9 shows the relative abundance of head widths and their size ranges that correspond to the identified instars I-V of *Cheumatopsyche*. Due to sample limitations, large larvae (Instars III-V) were collected in higher numbers than small size (I-II). However, the use of egg masses to calculate hatched larvae allowed me to obtain better estimates of I-instar abundance, but the number of instars II and III seem to be underestimated.

The weighed means of head width per instar from the two study sites are shown in Table 3. Instar I to IV showed similar ranges of head widths at the two sites, but V-instar larvae from S1 had wider heads than the same instar from S2 on most sampling dates. Paired T-tests performed for head widths of each instar from the two sites produced a highly significant difference between the means of V-instar head width during the overwintering period ($P < 0.005$). Similarly, a general lineal model procedure was conducted to test the null hypothesis that the mean head width of V-instar larvae from the two sites were equal and the alternative that they were significantly different (Sokal and Rohlf 1995). The ANOVA table from this analysis (Table 4) shows

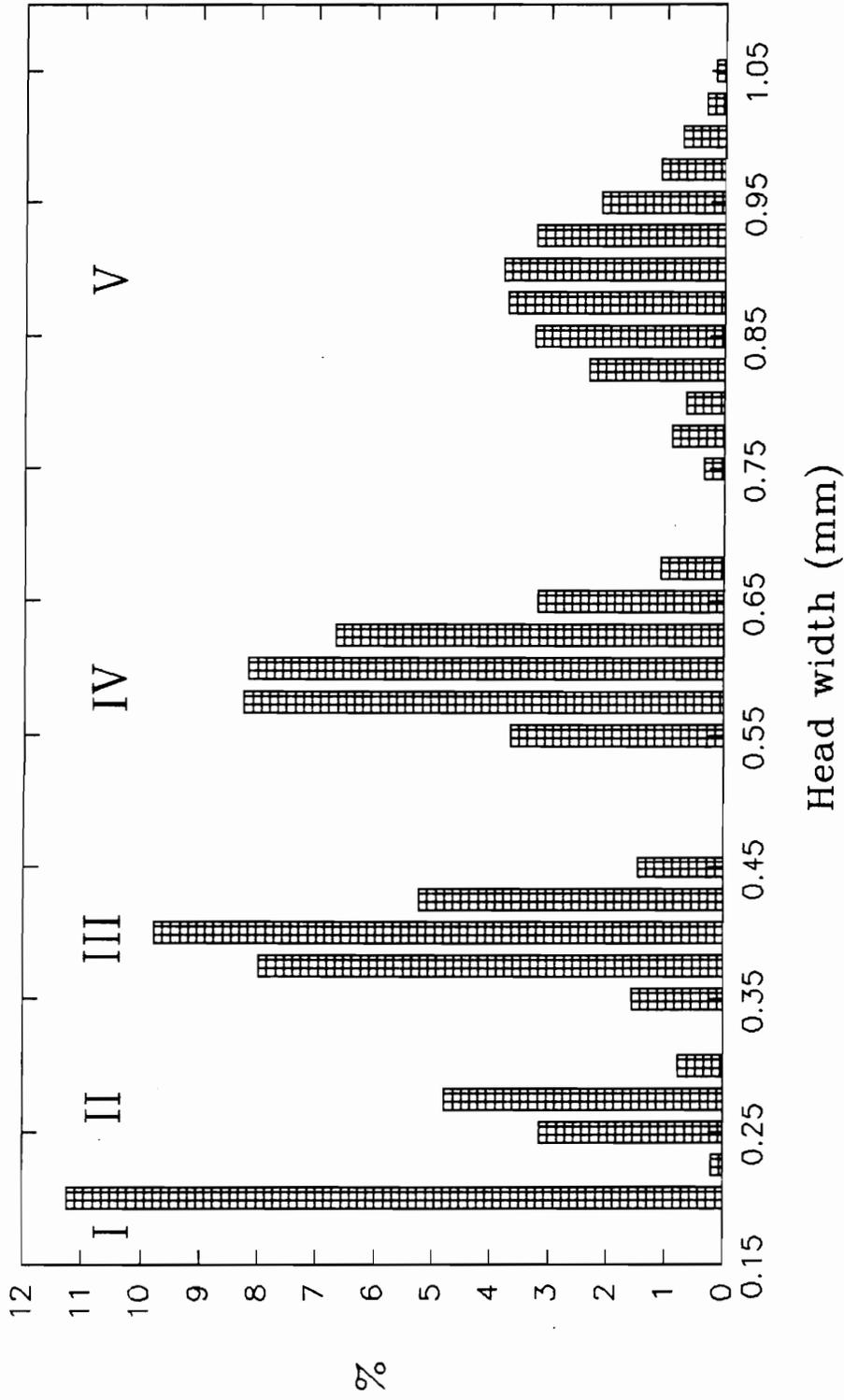


Fig. 9. Relative abundance of head width (%) and instars of *Cheumatopsyche* in Stroubles Creek.

Table 3. Weighted means of head width (mm) per instar of Cheumatopsyche at two sites in Stroubles Creek.

Date	S1					S2				
	I	II	III	IV	V	I	II	III	IV	V
6/16			0.39	0.59	0.89	0.21	0.27	0.41	0.62	0.91
6/30	0.20		0.40	0.60	0.89	0.21	0.27	0.40	0.58	0.89
7/14				0.60	0.87		0.29	0.41	0.59	0.84
7/27			0.43	0.60	0.85	0.23	0.28	0.41	0.59	0.82
8/10		0.27	0.41	0.61	0.87	0.20	0.27	0.40	0.60	0.80
8/24		0.27	0.41	0.61	0.88		0.27	0.41	0.61	0.81
9/6	0.23	0.27	0.42	0.60	0.88	0.21	0.27	0.41	0.61	0.84
9/21		0.28	0.41	0.62	0.89	0.23	0.26	0.40	0.62	0.88
10/18		0.26	0.39	0.60	0.96	0.20	0.26	0.39	0.72	0.89
11/15		0.26	0.41	0.59	0.98		0.28	0.39	0.59	0.86
12/13		0.28	0.39	0.59	0.96		0.27	0.38	0.58	0.89
1/12			0.40	0.62	0.96		0.26	0.38	0.61	0.89
2/20		0.28	0.38	0.61	0.97		0.27	0.38	0.59	0.91
3/17				0.65	0.94			0.38	0.59	0.87
4/17				0.60	0.93				0.58	0.86
5/11				0.65	0.95				0.59	0.85
5/25			0.44	0.64	0.95			0.44	0.62	0.85
6/14	0.20	0.25	0.43	0.60	0.89	0.20	0.29	0.41	0.62	0.87
6/30		0.26	0.41	0.62	0.90	0.20	0.28	0.39	0.60	0.86
7/18		0.26	0.38	0.60	0.93	0.21	0.28	0.40	0.61	0.87
7/30		0.28	0.40	0.62	0.89	0.21	0.27	0.40	0.57	0.78
8/15					0.88	0.20	0.27	0.39	0.59	0.78
8/30			0.43	0.59	0.88	0.22	0.26	0.40	0.60	
9/14		0.28	0.40	0.68	0.89	0.21	0.27	0.40	0.61	
9/27	0.20	0.25	0.45	0.65	0.94	0.21	0.27	0.40	0.61	0.89
10/30			0.43	0.65	0.92	0.21	0.27	0.39	0.58	0.88
11/28				0.63	1.01		0.25	0.40	0.58	0.89

Table 4. Anova Table from the analysis of the mean head width of *Cheumatopsyche* larvae at two sites in Stroubles Creek. June 16, 1994 to March 17, 1995.

Source	DF	Sum of Squares	Mean Square	F value	P
SITE	1	0.01679	0.01679	19.57	0.0002
DATE	1	0.01311	0.01311	15.28	0.0007
DATE*SITE	1	0.00309	0.00309	3.61	0.0696
Model	3	0.03301	0.01100	12.82	0.0001
Error	24	0.02059	0.00085		
Corrected Total	27	0.05360			

that the effects explained by the regression model were highly significant ($P=0.0001$) and that the means of head width from the two sites were also significantly different ($P=0.0002$).

By using the mean head width of instars III-V a regression line was obtained for the increase of head width at each site (Fig. 10). The slope of the regression line represents the increase between molts, thus a corrected head width for instars I and II may be determined from the equation (Mackay 1978). Values of corrected head width for these early instars were very similar at the two sites: 0.1832 mm (S1) and 0.1869 mm (S2) for instar I, and 0.2741 mm (S1) and 0.2743 mm (S2) for instar II. A synthesis of data used to determine the mean head widths during the study period, and the range and average of the head width mean, is presented in Table 5.

The faster larval growth at S1 compared to S2 was also suggested by the lipid content of mature larvae (Fig. 11). Accumulation of lipids in larvae were higher at S1 during the overwintering period (October to March), but this difference was not consistent during the whole year period (Paired T-test, $P=0.053$).

Results of the relative frequency distribution of instars through a 1-year period, and the periods when pupae

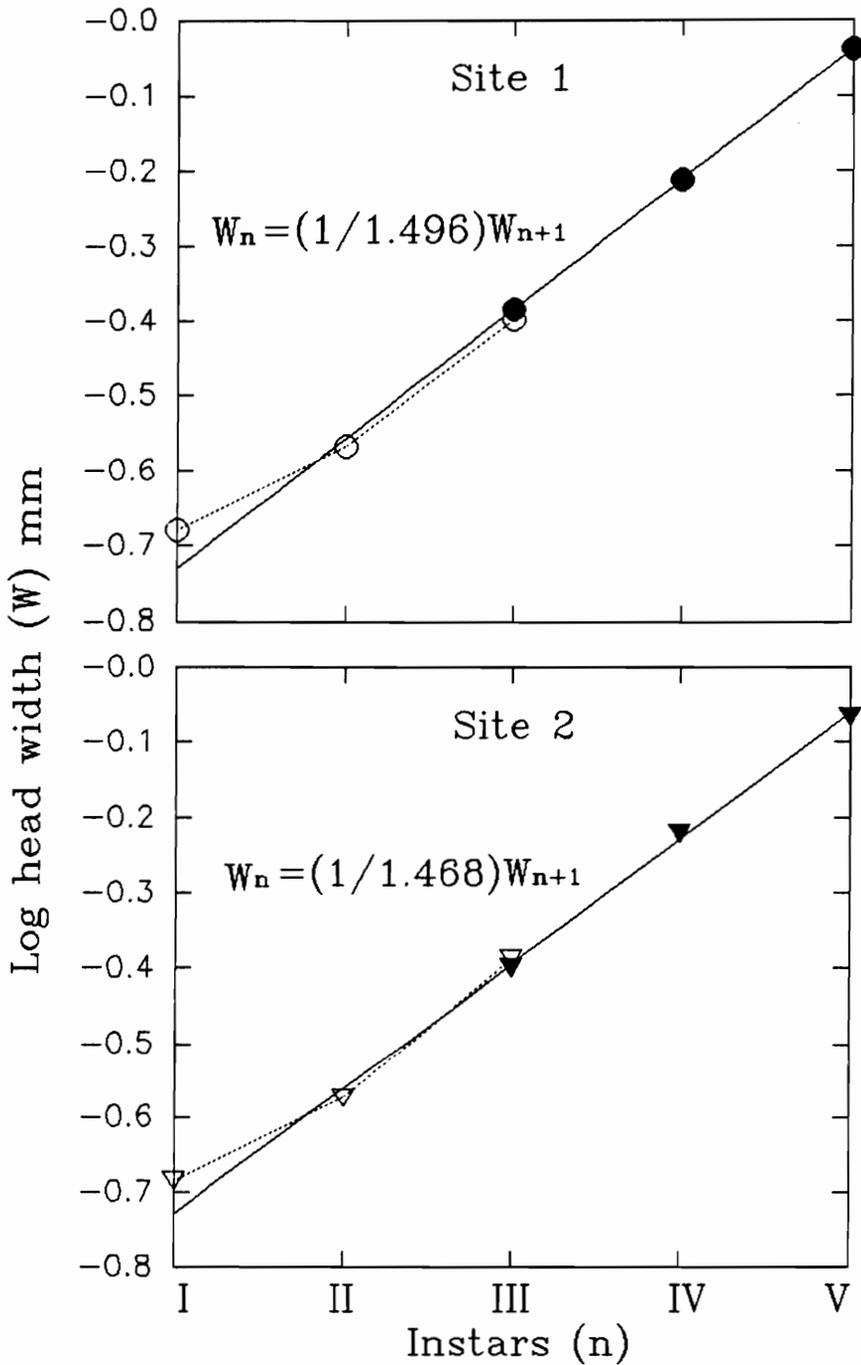


Fig 10. Changes in head width per instar of *Cheumatopsyche* larvae in Stroubles Creek. Solid line: regression from instars III, IV, V. Dashed line: actual data for instars I, II.

Table 5. Synthesis of head width mean of Cheumatopsyche larval instars at two sites in Stroubles Creek.

Site	Instar	Total larvae measured	Number of means	Range of head width mm	Average of head width means (mm)
Site 1	I	383	4	0.200-0.225	0.206
	II	275	14	0.250-0.300	0.267
	III	130	21	0.350-0.450	0.409
	IV	690	26	0.550-0.675	0.616
	V	460	27	0.750-1.050	0.916
Site 2	I	559	16	0.200-0.225	0.209
	II	441	23	0.250-0.300	0.271
	III	2024	25	0.350-0.450	0.399
	IV	1864	27	0.550-0.675	0.602
	V	1386	25	0.750-1.075	0.859

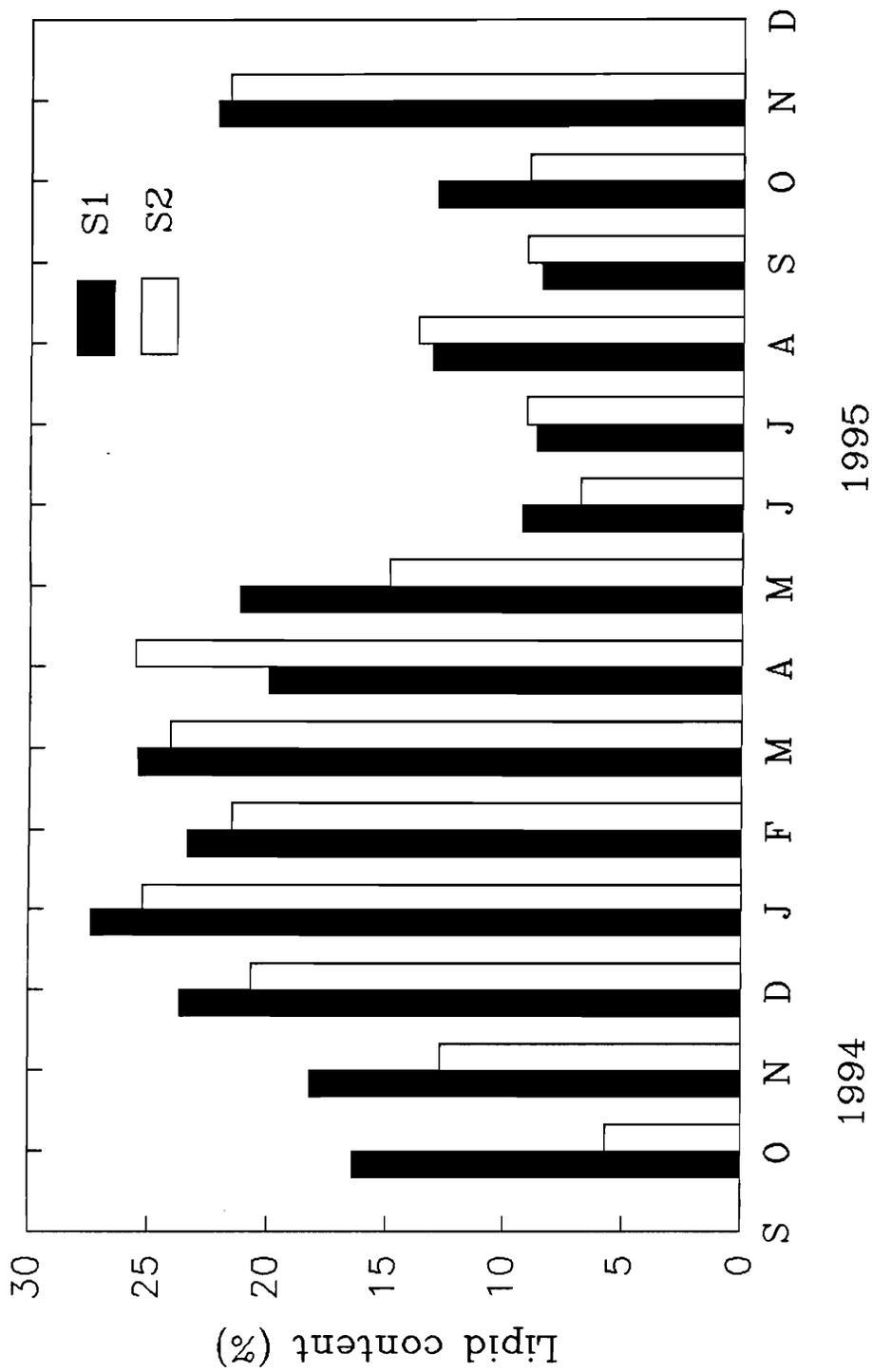


Fig. 11. Monthly lipid content (% dry mass) of *Cheumatopsyche* at two sites in Stroubles Creek.

and adults occurred, are represented for the two sites in Figs. 12 and 13 respectively. *Cheumatopsyche* eggs are only represented at the sampling dates when they were identified, despite the presence of Hydropsychidae eggs from May to September.

There were marked differences in overwintering and summer growth of larvae between the two sites in Stroubles Creek. At S2, from December to March, larvae had similar abundance of instars III-IV-V, and instars IV and V became predominant in April (Fig 13). At S1 instars IV and V were both abundant until December, but instar V was completely dominant from January to April (Fig 12). During the summer, the faster growth at S1 was also observed, after the only collection of eggs (interpreted as instar I) in June 15, instar IV and V were again dominant in July and August (Fig 12). At S2, instar I was present throughout all summer months and most larvae were in instar II and III, but instar V was also always present (Fig 13). By September, instar IV was dominant at S1 but both instars III and IV had similar abundance at S2. The annual distribution of instars at S1 seems to be the consequence of the two generations, despite overlap observed by the presence of late instars during most of the year. At S2, the bivoltinism is less clear because late instars were constantly present and little recruitment

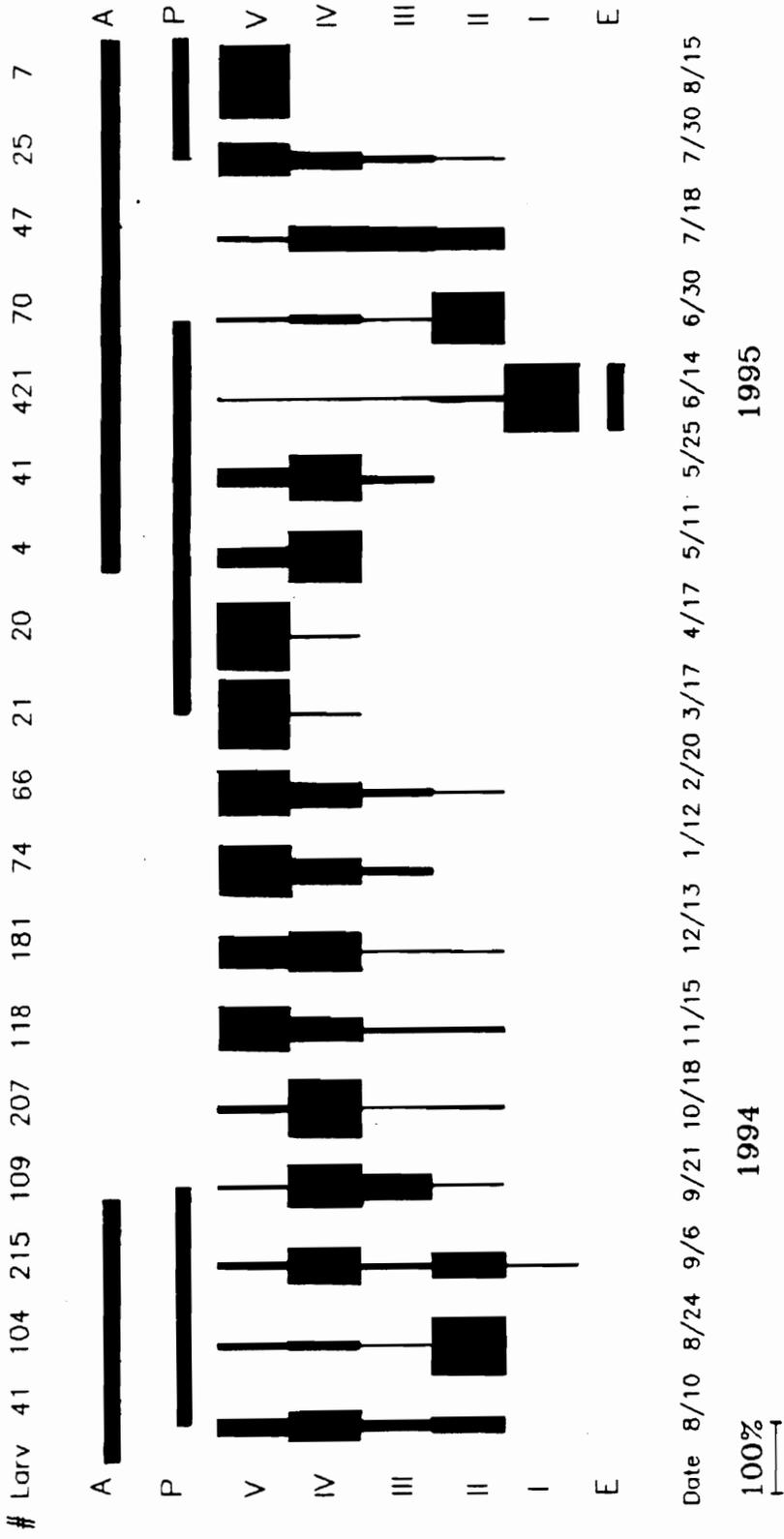


Fig12 Life history of *Cheumatopsyche pettiti* in Stroubles Creek at Site 1
 Width of bars indicates relative abundance of larval instars I - V.
 Solid horizontal lines indicates presence of eggs (E), pupae (P),
 and adults (A) collected with light trap.

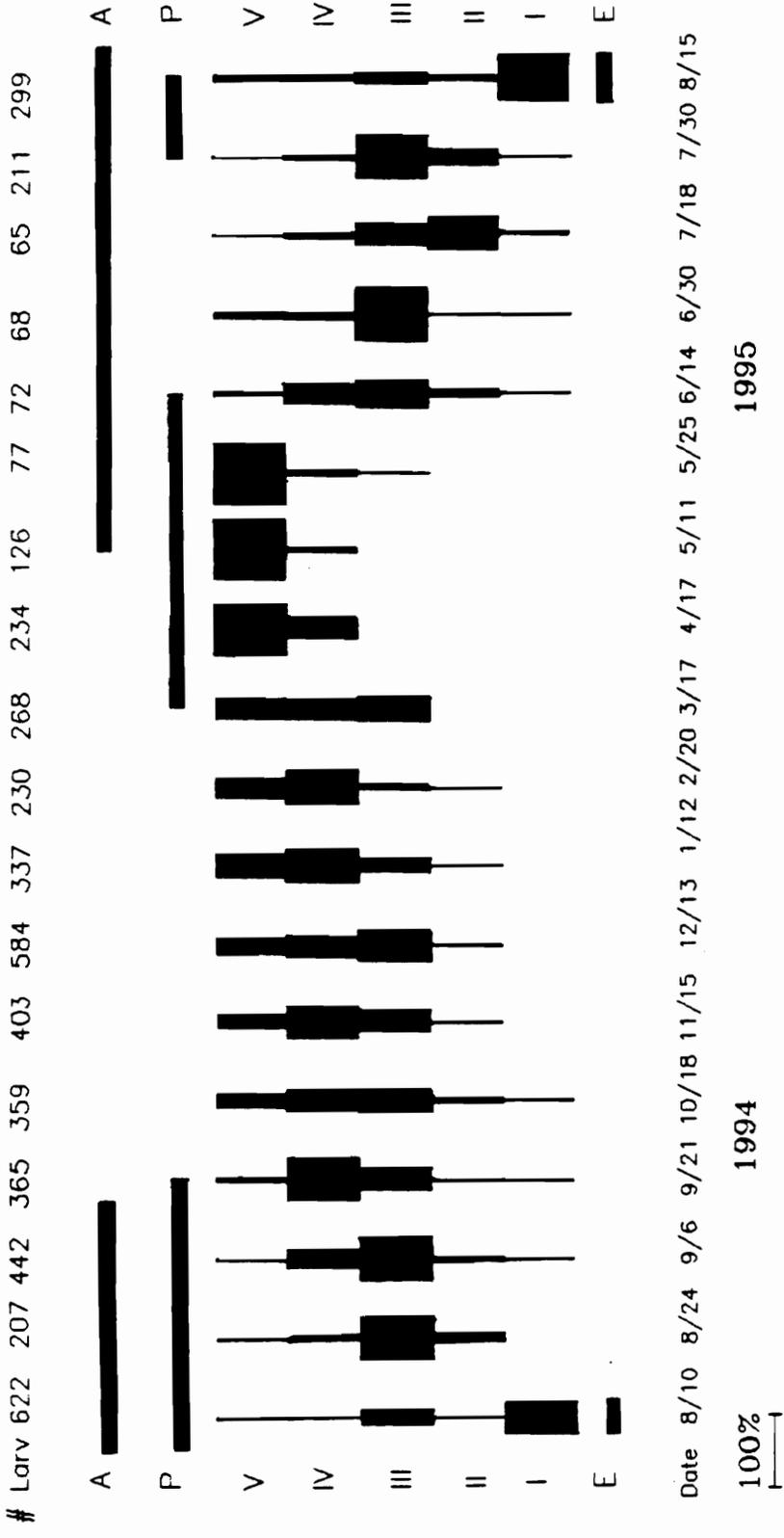


Fig13 Life history of *Cheumatopsyche* spp. in Stroubles Creek at Site 2.
 Width of bars indicates relative abundance of larval instars I - V.
 Solid horizontal lines indicates presence of eggs (E), pupae (P),
 and adults (A) collected with light trap.

occurred in late spring, thus only a fraction of the population was assumed to develop the second summer generation.

Hydropsychid eggs were found in the stream from mid June to late September 1994, and again from May to September 1995. Twenty five egg masses were collected at S2 in 1994, but only one of them was identified as *Cheumatopsyche*. In the second summer (1995), collections were made at both sites. Most eggs were found at S2, 38 egg masses, but only 5 egg masses could be collected at S1. From all these egg masses, just one from each site could be identified as *Cheumatopsyche*.

Measurements of eggs with the ocular micrometer showed that individual eggs ranged from 0.45 to 0.50 mm long and 0.2 to 0.3 mm wide. The three *Cheumatopsyche* egg masses observed had fairly constant egg dimensions, which were 0.45 mm long and 0.2 mm wide. Calculating the total area of these egg masses allowed an estimate of 330 eggs on August 10, 1994 and 180 eggs on August 15, 1995 at S2; while the egg mass collected at S1 on June 14, 1995 had an estimate 380 eggs. By observing egg masses on bricks, a hatching period of 10-12 days was determined for hydropsychids in this stream, which was similar to the maximum hatching time for eggs collected from rocks and placed in the lab.

Cheumatopsyche pupae were not abundant in the Hess samples but they were collected at both study sites. In 1994, prepupae and pupae were observed in preliminary collections by April and May at S1 but not at S2. During the regular sampling program, these stages were collected from June 30 until September 21, 1994 and from March 17 to August 30, 1995.

At the upstream site, 2 prepupae and 8 pupae were collected in 1994 and 4 and 13 respectively in 1995. These pupal stages were found in two periods in 1995, the first period from March 17 to June 14, and the second one from July 31 to August 30. At the downstream site, 2 prepupae and 3 pupae were found in 1994, and 19 and 20 respectively in 1995. In total, these stages were observed in 14 sampling dates at S1 and in 11 sampling dates at S2.

Some of the pupal stages had already developed genitalia and species could be identified. From S1, a total of 6 metamorphotypes were found and identified as *C. pettiti*. From S2, 15 metamorphotypes were found, 11 *C. oxa* and 4 *C. pettiti*.

Production of *Cheumatopsyche*.

Hynes production calculations were performed with all larvae collected from August 1994 to August 1995 at the two

sites (Table 6). Total annual production calculated by the summation of positive values with the correction factor for the number of size classes (instars) is called Hynes production (Parker and Voshell 1983). This first correction factor used (X5) accounts for losses of every size group or instar at all time periods as it was corrected by Hamilton (1969) in the original method. The negative values obtained for some instar losses (II-III) were probably the result of their being underestimated in samples. Thus, they were not included in the production summation as has been adopted in other production studies (Benke and Wallace 1980; Parker and Voshell 1983). The exclusion of these negative values increased the annual production by 12.5 % at S1 and 4.8 % at S2, increases similar to those reported by Benke and Wallace (1980).

Assuming bivoltine populations with overlapping generations, as was suggested by the presence of adults, egg and pupal stages, it is necessary either to calculate production separately for each cohort or to use a sort of "average cohort". This average cohort has been used to determine the Cohort Production Interval (CPI) by adding the life period of all instars in univoltine populations (Mackay and Waters 1986). However, for overlapping generations, when separation of larvae for each cohort is not possible, the

Table 6. Size-frequency calculations and annual production of Cheumatopsyche in Stroubles Creek. Sampling period 08/24/94 - 08/15/95. Values in mg dry mass.

	Mean Ins. density Ind/m2	Mean Indiv. biomass mg	Mean stand. stock mg/m2	No. lost Ind/m2	Indiv. biomass at lost mg	Total biomass loss mg/m2	Corr. factor X 5 mg/m2/yr
Site 1							
I	74.63	0.005	0.34				
				22.92	0.01	0.29	1.47
II	51.71	0.021	1.10				
				29.58	0.06	1.68	8.41
III	22.13	0.092	2.05				
				-95.20	0.21	-20.11	-100.55
IV	117.33	0.330	38.72				
				44.27	1.06	47.10	235.48
V	73.06	1.798	131.35				
				73.06	1.80	131.35	656.74
N = 338.88		B = 173.55		Hynes production =			902.10
							CPI correction factor x 2.22
							Total annual production = 2002.66
Site 2							
I	39.37	0.007	0.26				
				-14.30	0.02	-0.23	-1.15
II	53.67	0.026	1.37				
				-235.45	0.06	-13.09	-65.43
III	289.12	0.086	24.75				
				15.87	0.22	3.55	17.76
IV	273.26	0.362	98.93				
				77.18	0.94	72.26	361.28
V	196.08	1.510	296.16				
				196.08	1.51	296.16	1480.81
N = 851.50		B = 421.47		Hynes production =			1859.84
							CPI correction factor x 1.62
							Total annual production = 3012.94

CPI can be calculated by subtracting from 365 the number of days of non-productive stages (e.g. eggs, pupae and adults), and then dividing the difference by the number of generations to obtain the average CPI (Parker and Voshell 1983). Finally, this second correction factor ($365/\text{CPI}$) is applied to the value of Hynes production to obtain the total annual (corrected) production (Benke 1979). In Stroubles Creek, the complete bivoltinism was assumed at S1, but only half of the population was interpreted as bivoltine at S2. Thus, the number of generations used were 2 at S1 and 1.5 at S2 to calculate the CPI correction factors of 2.22 and 1.64 respectively (Table 6).

In general, production calculations for the two sites had a higher value at S2 relative to S1, which corresponded to the higher density of V-instar larvae collected that accounted for the majority of biomass. However, the faster larval growth at S1, that was observed in individual head width and biomass and suggested the bivoltine life history, made this increase in production of only 50.4% at S2 compared to S1.

The feeding habit of *Cheumatopsyche* larvae in Stroubles Creek was determined by gut content analysis, and the relative abundance of three main food groups is shown in Fig. 14. Detritus was the dominant source of food in both

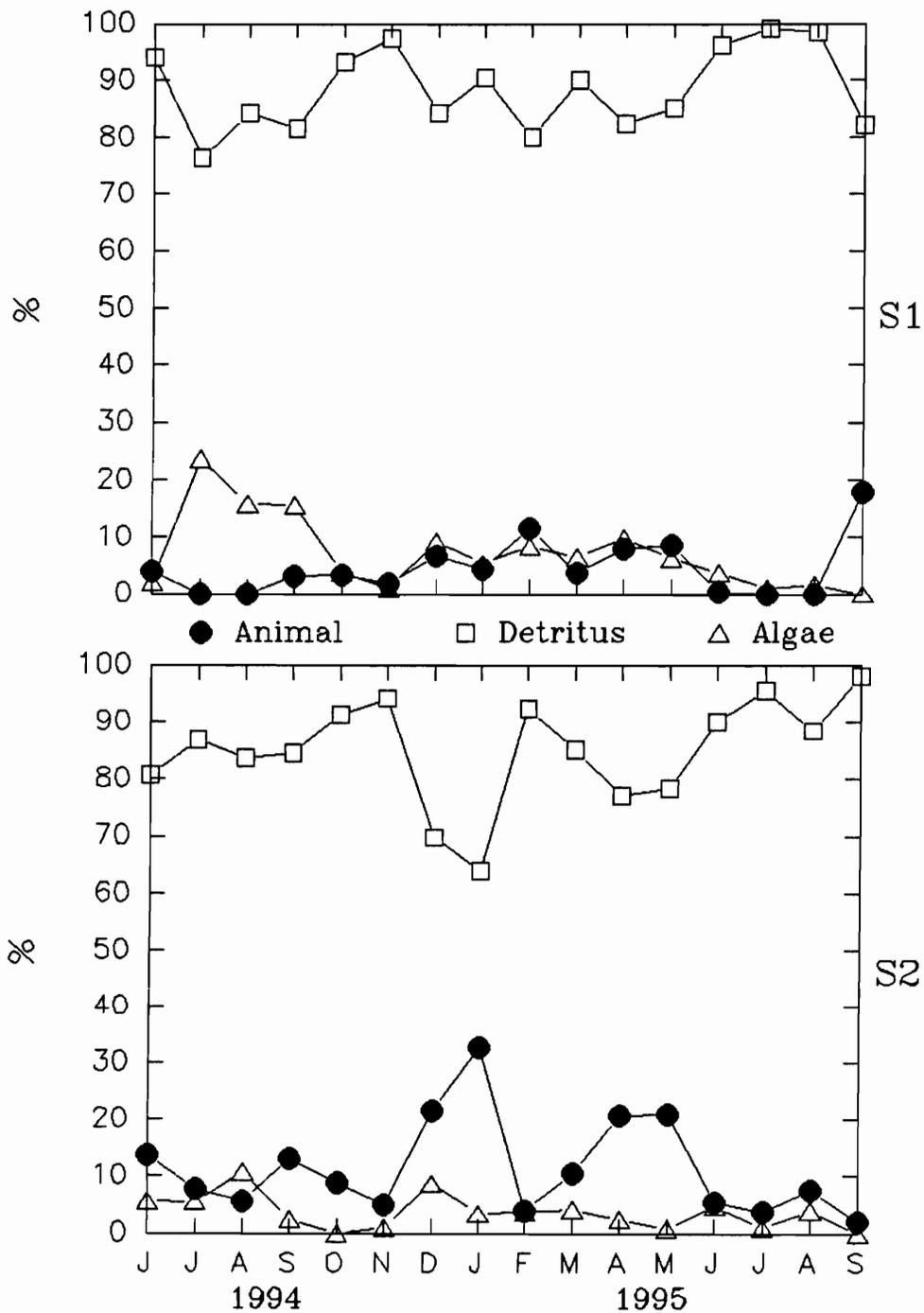


Fig. 14 Monthly relative volume (%) of food types in foregut contents of *Cheumatopsyche* larvae at two sites in Stroubles Creek.

sites, ranging from 76 to 98% at S1 and from 64 to 98% at S2. Animal food was found in higher percentage, up to 33%, at S2, while algae was the least consumed fraction but it was found in higher percentage at S1 with maximum of 24%. Paired T-tests performed for each food type between the two sites showed that animal food had significantly higher consumption at S2 ($P=0.012$), and algae had significantly higher consumption at S1 ($P=0.028$). However, no significant differences in consumption of the detrital fraction were found between the two sites ($P>0.2$).

Differences in consumption of certain food types might be related to different availability between the two sites. In general, the animal source was observed to be more abundant at S2 due to higher numbers of taxa and individuals (Fig. 6). In contrast, a thicker periphyton layer was observed on pebbles at S1 compared to S2, and the data of chlorophyll-a concentration showed significantly higher average at S1 than at S2 in most samples (Paired T-test, $P=0.036$) (Fig. 15). Therefore, differences in larval production between the two sites can be also related to different availability and quality of food.

The trophic basis of production of *Cheumatopsyche* was estimated using results of the gut content analysis. Table 7 shows the calculation of production attributed to each food

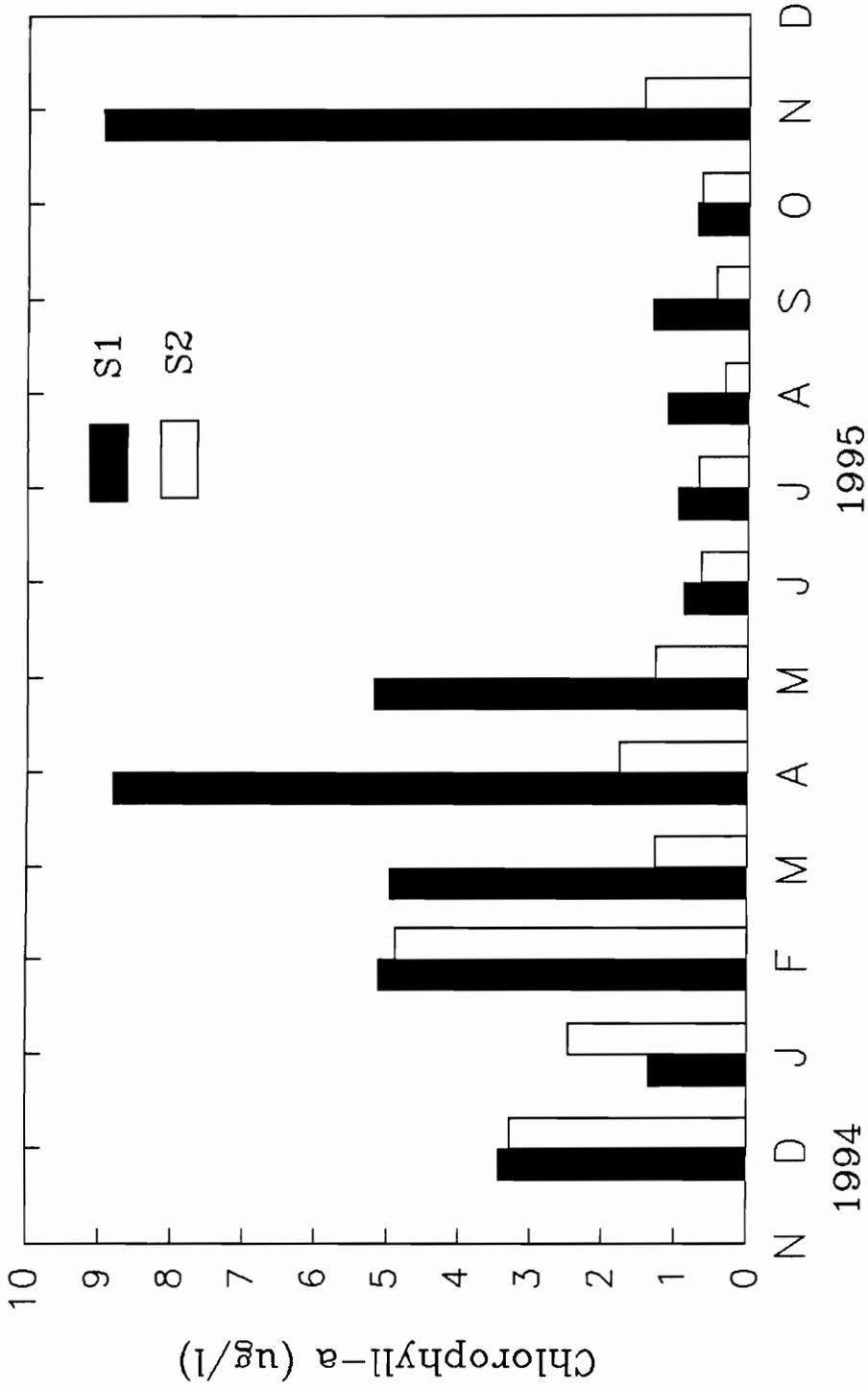


Fig. 15. Monthly chlorophyll-a concentration at two sites in Stroubles Creek.

Table 7. Calculation of Cheumatopsyche production attributed to each food type at two sites in Stroubles Creek.

	Food type	S1		S2	
		Detrit. Animal	Algae	Detrit. Animal	Algae
a. % food type in foregut		88.4	4.5	7.1	3.6
b. Assimilation efficiency (AE)		0.1	0.7	0.3	0.3
c. Net production efficiency (NPE)		0.5	0.5	0.5	0.5
d. Relative amount to production (a x b x c)		4.4	1.6	1.1	0.5
e. % attributed to food type		62.6	22.3	15.1	6.2
f. Production attributed to food type (mgDM/m ² /yr)		1253.8	446.8	302.1	185.3
		1458.4	1369.2		

type at the two study sites, in which the values of assimilation and net production efficiency are the most frequently used in studies with hydropsychids (McCullough et al. 1979; Benke and Wallace 1980; Parker and Voshell 1983; Smock and Roeding 1986). Detritus had the highest contribution at both sites, but animal food was nearly as important at S2. Algae had relatively higher contribution at S1 even though it was the least important fraction in determining production. This result can be related to the generalist feeding habit attributed to hydropsychids. It reflected the different availability of food fractions at the two sites.

DISCUSSION

Life history

The importance of natural history approaches to explain community level processes has been well established (Rosenberg 1979). Waters (1979a) pointed out that knowledge on benthic life histories can be used to improve sampling techniques, taxonomic methods and bioassays. Waters (1979b) also reviewed effects of life history features such as voltinism and length of aquatic life on production estimates. Therefore, my results on life history patterns of *Cheumatopsyche* in Stroubles Creek may be useful in explaining the dynamics of hydropsychid caddisflies in this type of stream ecosystem.

Adults abundance. Adult light-trap collections of the five species of *Cheumatopsyche* identified in Stroubles Creek occurred through a relatively long period, from May to September. However, the two dominant species, *C. pettiti* and *C. oxa*, were the ones collected on most of light-trapping occasions, while *C. ela*, *C. minuscula* and *C. sordida* were only occasionally collected.

The species composition obtained for the two sites showed an important difference, since probably only

C. pettiti has established a permanent population at S1, while both *C. pettiti* and *C. oxa* were abundant at S2 (Fig. 7). Given that S2 is approximately 3 km upstream of the confluence of Stroubles Creek and the New River, other species from this larger river are likely to have reached this site. Reports of several collections by Gordon (1974) suggest that *C. ela* and other related species are more abundant in larger rivers. Rhame and Stewart (1976) found *C. campyla*, which has a close phylogenetic relation to *C. ela* (Ross 1944; Gordon 1974), was the dominant species at a 10-m-wide riffle in the Brazos River, Texas, and it has been reported in the New River (Gordon 1974). Due to the proximity of the study sites, and to the recognized ability of hydroptychid adults to fly several kilometers in their search for mates and oviposition sites (O.S. Flint, personal communication), *C. ela* and other species probably flew from the New River where they are abundant. Furthermore, a single collection made during this study, close to the confluence of Stroubles Creek and the New River, showed that *Cheumatopsyche* collected were mostly *C. ela*, with the presence of very few individuals of *C. pettiti* and *C. minuscula*.

The two species considered as developing permanent populations at the study sites, *C. pettiti* and *C. oxa*, are

common in small headwater streams throughout eastern United States and Canada (Ross 1944; Gordon 1974; Mackay 1986; Morin and Harper 1986). Gordon and Wallace (1975) found *C. analis* (syn. *C. pettiti*) among dominant hydropsychids in streams of the lower headwater region of the Savannah River Basin, within 200-600 m of elevation, in an altitudinal range that corresponds to the study sites. In addition, Ross (1944) attributed a wide ecological tolerance to *C. pettiti*, and Mackay (1986) considered that it tolerates a broad range of stream types and water temperatures. Therefore, at the more altered habitat of S1, *C. pettiti* seems to be more successful, while at S2, where more abundant habitat locations may be available, both *C. pettiti* and *C. oxa* have developed stable populations, despite the presence of adults of other species around the stream.

Wide environmental tolerance and plasticity of life history in *Cheumatopsyche* are reflected in results of emergence of some species. *C. campyla* was found to emerge from April to October in Illinois (Ross 1944), but its emergence period started as early as February in Texas (Rhame and Stewart 1976). The emergence period was only from June to August in high-elevation streams of Utah (Alstad 1979). Adults of *C. parentum* and an unidentified group of species were found to emerge from March through October in

the North Anna River of Virginia (Parker 1980). *C. lepida* emerged from June to August in the River Leven, England (Elliott 1986). However, the scarcity of reports of *C. pettiti* emergence suggests that its emergence period is shorter, probably in relation to colder habitat in small streams. It emerged from late May to August in Montreal (Morin and Harper 1986) and apparently from June to August in Minnesota (Mackay 1986). Floyd and Schuster (1990) reported emergence of *C. pettiti* from April to September and that of *C. oxa* from April to August in Buck Creek, Kentucky. The observed period in Stroubles Creek, from early May through September, appears to represent life history adjustment to a warmer habitat and probably to watershed modifications around the stream.

Studies including emergence of *C. pettiti* have reported unimodal distribution of emergence (Morin and Harper 1986; Mackay 1986) in contrast to bimodal peaks of other *Cheumatopsyche* species (Rhame and Stewart 1976; Parker and Voshell 1982). In Stroubles Creek, relative abundance of all adults peaked by June and July as did the relative abundance of females, but male abundance was concentrated in two periods: from May to mid June and from early August to September. Since it has been reported that females can be attracted earlier during the light-trap period (Harris

1971), the reduction in male collection could represent the emergence of a summer generation. However, sex ratios of *Cheumatopsyche* have been reported to deviate from the expected 1:1 in light traps compared to emergence traps (Roy and Harper 1981), as occurred in Stroubles Creek comparing light-trap collections to reared adults (Table 2). Thus, it is difficult to attribute emergence peaks to different generations based only on the relative abundance of adults.

Another observation on emergence is related to the adult body size during the emergence period. *C. pettiti* and *C. oxa* have been described with a length ranging between 7-12 mm and 7-9 mm respectively (Ross 1944; Gordon 1974). However, most individuals of the two species collected in Stroubles Creek had overlapping body length that ranged 7.5-8.7 mm for *C. pettiti* and 6.8-8.5 mm for *C. oxa*. Other species of the genus have been observed to exhibit seasonal variability in length, mainly because adults with later emergence tend to be smaller (Rhame and Stewart 1976). In this study, length variability was observed especially for *C. oxa* which averaged 8.3 mm in May 1995 but only 6.8 mm in September. *C. pettiti* showed lower variation because its average length decreased only from 8.5 to 7.8 mm in the same period.

Relationships between emergence variation or seasonal body length with voltinism of *Cheumatopsyche* populations in Stroubles Creek are very difficult to establish, given the multispecies collection and the limited emergence-trap verification. However, the above mentioned reports on activity and distribution of some species of this genus, especially through observations on tolerance and life history plasticity of *C. pettiti* (Ross 1944; Mackay 1986), agree with the interpretation that this species is able to adjust to habitat variations at S1, while both *C. pettiti* and *C. oxa* have stable populations at S2.

Oviposition and hatching. There were very few observations of oviposition and hatching of *Cheumatopsyche* in Stroubles Creek, and previous studies of the species found in the stream have not included descriptions of these stages. A detailed work on oviposition of hydroptychids in the Susquehanna River, Pennsylvania (Deutsch 1984), described characteristics of egg masses, ovipositing behavior and habitat preferences of *C. speciosa* which is a smaller species abundant in large rivers (Gordon 1974). Deutsch (1984) found that oviposition occurred from May to September with preference for the tops of objects on the bottom at 1-2 m depth; and it occurred more frequently at

slow current (0.15m/s). Hydropsychid eggs in Stroubles Creek were found mainly on the sides of cobbles and bricks, which is probably related to the shallow depth and faster current of the stream.

Egg size and number of eggs per egg mass appear to be higher for *C. oxa* and *C. pettiti* in Stroubles Creek than those values reported for other *Cheumatopsyche* species, but the low number of egg masses found inhibits further precision. Smaller species such as *C. campyla* (Rhame and Stewart 1976) and *C. speciosa* (Deutsch 1984) are likely to produce fewer number and smaller eggs than larger species such as *C. pettiti* and *C. oxa*. The hatching period in Stroubles Creek for hydropsychid eggs on bricks (10-12 days) was shorter than reported by Rhame and Stewart (14-17 days at 18°C), probably because of higher temperatures in Stroubles Creek. The hatching period for *C. lepida* in the River Leven, England, was 9-15 days at temperatures from 18-22 °C (Elliott 1986).

Larval Growth. Due to the presence of instars I-V in many samples and to limitations of sampling techniques, interpretations about recruitment, molts, survival and completion of larval growth in Stroubles Creek are not conclusive. However, relative abundance and head width

changes of instars provided some clues for establishing a general view of the life history of *Cheumatopsyche* in the two study sites (Fig. 12 and 13).

Recruitment for the overwintering generation of larvae may have occurred in Stroubles Creek since June, but the abundance of instars I and II from August to October suggests that most recruitment occurred in late summer and early fall. These early instars were similarly predominant during the same period in the univoltine life history reported for *C. pettiti* in Minnesota and Montreal (Mackay 1986; Morin and Harper 1986). *C. lepida* showed a shorter recruitment period in England (Elliott 1986), with instars I-II present only from June to August and most larvae overwintering in instar V. Short periods of recruitment were observed for the bivoltine *C. pasella* in the Savannah River, Georgia (Cudney and Wallace 1980), with a summer generation from April to September, early instars again abundant from August through October and larvae overwintering in instars III-V. A different pattern was observed for *C. gracilis* in Owl Creek, Montana (Oswood 1976), where recruitment occurred apparently from June to August but larvae overwintered entirely as instar III. Oswood (1976) suggested that this pattern was reflected divergence as a result of competitive pressure from other abundant hydroptychids.

The difference in relative abundance of instars between the two sites cannot be compared to reports on the same species. Parker and Voshell (1982) interpreted *C. parentum* in the North Anna River as bivoltine, because of a growth pattern similar to that described at S2, including the presence of pupae in August and September. For species of the genus *Hydropsyche* in the Humber and Credit Rivers, Ontario, Mackay (1979) determined bivoltinism at downstream stations, with similar variations in overwintering instars. Therefore, patterns of relative abundance and growth of larvae suggest the adjustment of life histories, with the development of bivoltinism by part of the population, probably in higher proportion at S1 than at S2.

Periods of growth for the five larval instars are consequently affected by the total length of the larval growth period. However, early instars, with short growth periods, have probably less variation than late instars in which most of the growth occurs. Instar I larvae are supposed to last a very short time, and (Elliott 1986) determined 4-7 days for *C. lepida* at 18-22°C in lab. Instar I larvae from Stroubles Creek lasted 5-12 days after hatching in the lab at 20-22°C. Elliott (1986) also reported swimming and drifting behavior of this instar, which he believed explained the difficulty for collecting these

minute larvae on the substrate. In the present study, similar limitations made it difficult to collect instar I larvae. By using lab-hatched larvae, instar II lasted between 10-20 days and instar III started molting as soon as 18 days later. Unfortunately, attempts to track the whole cycle in the lab from the hatched eggs were not successful. Rhame and Stewart (1976) determined total development time of larvae hatched in the lab, to be a minimum of 61 days for *C. lasia* and 73 days for *C. campyla* at 20-24°C. A few larvae from Stroubles Creek were reared until they reached instar V, lasting up to 182 days at 20-22 °C, but they never started pupation.

The most evident variation in larval growth between the two study sites was observed in the mean head width of the last instar, that showed statistically significant difference between sites (Tables 3 and 4). The geometric progression in the increase of larval head width can be observed through the following ratios obtained between successive instars at S1 and S2 respectively: 1.30 at both sites for II:I; 1.53 and 1.47 for III:II; 1.51 at both sites for IV:III; 1.49 and 1.43 for V:IV. These values are within the range stated by Dyar's rule for species having 5 larval instars (Mackay 1978). The lower value of this ratio obtained for instars II:I was probably caused by irregular

collection of these early instars with fewer individuals on a few sample dates. In general, ranges and means of head widths for the five instars (Table 5) were similar to values reported for *Cheumatopsyche* species such as *C. lepida* (Elliott 1986), *C. analis* (Ferrier and Wissing 1979), and especially those by Mackay (1978) for a group of mixed larvae including *C. pettiti*, *C. campyla* and other *C.* species. However, head widths in this study were lower than those reported by Alstad (1979) for a group of *Cheumatopsyche* species including *C. campyla* and *C. gracilis*.

As a general overview, the pattern of larval growth in Stroubles Creek seems to be an adjustment of the life history to habitat condition, through a main shift towards bivoltinism by significant portion of the *Cheumatopsyche* population. This growth pattern was more evident at S1 where the two generations were clearly detected (Fig 12), and the presence of only one species made the adjustment in life history more uniform. In addition, the measurement of head width showed that late instars reached the upper values of common ranges determined for these stages easier, because instar V larvae became dominant throughout the winter. At S2, the pattern was not as straightforward to determine as it was upstream, since early instars were abundant during a longer time, and instar V larvae was only dominant in spring

(Fig 13). However, relative distribution of instars and pupal stages also showed the occurrence of a summer generation, probably by a small portion of the population.

The definite bivoltinism at S1 can be compared with that described by Mackay (1979, 1984) for some *Hydropsyche* species in the lower, warmer stations of the Credit and Humber Rivers. At S2, the pattern is more similar to those reported for *Cheumatopsyche* species in larger southeastern Rivers (Cudney and Wallace 1980; Parker and Voshell 1982), and also to the pattern of *Hydropsyche sparna* in a headwater stream of Georgia (Benke and Wallace 1980), where it was assumed that a small second generation developed during the summer.

Voltinism. Results on relative abundance of instars and development of pupal and adult stages support the interpretation of a shift to bivoltinism of *Cheumatopsyche* in Stroubles Creek, with the development of a second generation after oviposition by a small number of early emergent adults. However, not enough evidence was available to fully assess the seasonal timing of life history events for the two generations. Phenology and behavioral patterns of some critical stages, such as oviposition or pupal development (Butler 1984), require more detailed

observations and taxonomic resolution than were possible to attain in this study.

Effects of temperature on life-history patterns have been widely recognized (Ward and Stanford 1979; Sweeney 1984). The observed high thermal regime at S1 represented 16% more accumulated degree-days (ADD) compared to S2 from September to April. This higher thermal input at S1 could induce a higher portion of the overwintering larvae to early maturation, so the separation of the two generations was clearly detected. At S2, the lower number of ADD occurred mainly during the overwintering period (September-April), and therefore fewer larvae of the winter generation had probably reached maturity by the spring. During summer, a more similar temperature regime was observed at the two sites, with 2467.2 ADD at S1 and 2414.6 ADD at S2 from May to August. This suggests that only adults with early emergence, probably occurring in April and May, laid eggs that could develop the small second generation that emerged by August and September at S2, overlapping with continuous emergence of the winter generation throughout the summer. Despite the variation in the fraction of the population that completed the two generations, even a partial shift to bivoltinism may represent adaptive advantages supported by

the increase in opportunities for reproductive success and genetic variability.

Effects of temperature on length of life cycle occur through various events, but the main effect is reduction of larval growth periods as has been established for several insect taxa (Sweeney 1984). The Thermal Equilibrium Hypothesis postulated "that incrementing ambient winter temperatures would result in early emergence and diminished adult size" (Vannote and Sweeney 1980, p. 677). The effect on larval growth appeared evident in the faster emergence at S1 in Stroubles Creek, because more larvae could reach the size threshold required for emergence. The effect on adult size could not be tested in this study, due to the qualitative adult collection with light trap and the reduced emergence trapping.

The values of ADD accumulated during the summer at both sites are similar to values calculated for summer generations of hydropsychids in larger southeastern rivers (Cudney and Wallace 1980; Parker and Voshell 1983). However, the overwintering period (September-April) only allowed the accumulation of similar number of ADD at S1, because of the higher insolation of the stream compared to the forested downstream site. Thus, the reduced thermal input at S2 may explain the decrease in the portion of the larval population

that emerged and oviposited early enough to develop the summer generation.

Another limitation for deciphering the voltinism pattern at S2 could probably arise from the presence of two congeneric species. Previous studies on life history of *Cheumatopsyche* usually have dealt with several unidentified species (Rhame and Stewart 1976; Cudney and Wallace 1980; Parker and Voshell 1983), and references to species found in Stroubles Creek only described univoltine populations of *C. pettiti* (Mackay 1986; Morin and Harper 1986). Because this species was predominant at S1, I assumed that it can develop bivoltinism in warmer habitats as it was suggested by Mackay (1986). No successful separation of larvae or pupae of *C. pettiti* and *C. oxa* was possible at S2, but the presence of a few metamorphotypes of the two species in May-June and again in September, indicated that both may have developed the small summer generation.

In general, bivoltinism of *C. pettiti* in Stroubles Creek seems to be evident at S1. This adjustment in the life-history pattern is consistent with the Thermal Equilibrium Hypothesis of Vannote and Sweeney (1980). The result was not similarly clear-cut for *C. pettiti* and *C. oxa* at S2, perhaps due to the lower thermal regime. Furthermore, these results are compatible with the trend observed by

Mackay (1979, 1984) "that hydropsychid species overwintering in the final instars rather than earlier ones are likely to be bivoltine" (Mackay 1986, p. 23). Similarly, the maximum head width reached by larvae in Stroubles Creek is less than the maximum predicted for hydropsychid species that could develop bivoltinism in the warm water of Ontario rivers (Mackay 1979). Thus, the life-history patterns of *Cheumatopsyche* species found in Stroubles Creek have developed adjustments in larval growth and phenology that can be related to environmental variations in the stream habitat.

Secondary production

Production levels. The estimates of secondary production of *Cheumatopsyche* in Stroubles Creek that were done with the size-frequency or Hynes method required site-specific treatment according to assumptions established for the method as well as to life history features of the studied caddisfly populations. Results in Table 6 could be interpreted as approximations of actual production values, as was intended in the original formulation of the method (Hynes 1961, Hynes and Coleman 1968). However, further adjustments of the method, and modifications used in comparable studies, were taken into account to obtain more precise production estimates. Since determination of actual cohorts was not possible in Stroubles Creek, even in the assumed monospecific population at S1, no method based on cohort survival could be applied, and current calculations constitute the only process available to assess the secondary production.

Limitations and assumptions in the method were stated by Hamilton (1969) relative to voltinism, maximum size and growth of studied organisms. For multivoltine species, the estimate of annual production must be multiplied by the number of generations per year or by a correction factor based on the CPI of an average cohort (Parker and Voshell

to the same maximum size in order to avoid overestimates of production (Waters 1977). The assumption of linear growth is probably not completely true, but several authors have agreed that failure to adjust for nonlinear growth will not usually lead to large errors (Hamilton 1969; Benke 1984). Finally, the summation of losses per size-class or instars may produce negative values. Hamilton (1969) recommended that such values be added, but in more recent studies it has been suggested that they be discarded (Benke and Wallace 1980; Parker and Voshell 1983).

The partial bivoltinism described for the life history of *Cheumatopsyche* in Stroubles Creek did not allow me to assign a definite number of generations at the two sites. While at S1 results of larval growth and presence of eggs and pupae seem to support the identification of the two generations, at S2 the reduced number of early emergent individuals from the winter generation precluded a clear-cut interpretation of bivoltinism. Therefore, different correction factors were used in calculations of production in order to obtain annual values that reflected site-specific adjustments in life history.

The correction factors were based on the determination of the CPI of the average cohort at each site. Mackay and Waters (1986) recommended determining the CPI by summing

instar durations, because such durations could be established in the univoltine population of *C. pettiti* in Valley Creek, Minnesota. However, it was not possible in this study due to the overlapping generations, thus I calculated the average CPI after estimating the minimum length of nonproductive stages (e.g., egg, pupal, and adult stages) (Parker and Voshell 1983). Minimum hatching period of eggs observed was 10 days for the identified egg masses. Duration of the pupal stage was not established in this study, so the 6-day minimum period reported for *Cheumatopsyche* species was adopted (Parker and Voshell 1983). The adult life span of hydropsychids is probably short and eggs are laid as soon as 2-3 days after emergence (Fremling 1960; Jackson 1988). Thus, the minimum length of these nonproductive stages was assumed to be 18 days in Stroubles Creek, which provided a conservative correction factor for production calculations. This correction factor was calculated by multiplying the 18-day period by the voltinism, subtracting this product from 365 and dividing again by the voltinism to obtain the average CPI. Then, the correction factor recommended by Benke (1979) was the ratio $365/\text{CPI}$ used to adjust the sum of biomass losses in production calculations.

According to the previously reported periods, the average CPI was determined for each site by taking into account the respective adjustment in the life history described. At S1 the presence of two generations seems to be well established and this produced an average CPI of 164.5 days and a correction factor of 2.22. In contrast, the bivoltinism at S2 could occur only for a limited fraction of the population and, consequently, a larger average CPI must be used. According to the determined reduction of degree-days for the overwintering larvae (16%), I assumed that at least half of the population could emerge early enough to produce the second generation. Thus, a conservative estimate of 1.5 was used to replace the number of generations, that produced an average CPI of 225.3 days and a correction factor of 1.62. The CPI at S2 approached the 234 days reported for a partially bivoltine population of *C. harwoodi enigma* in the 1-4th order Dryman Fork, North Carolina (Ross and Wallace 1983).

The estimates of production at each site (Table 6) are within the range of hydroptychid production reported for low-order streams. However, comparisons are not very conclusive, since very few studies have determined *Cheumatopsyche* production (Fig. 16). In the only work that determined production of univoltine *C. pettiti* Mackay and

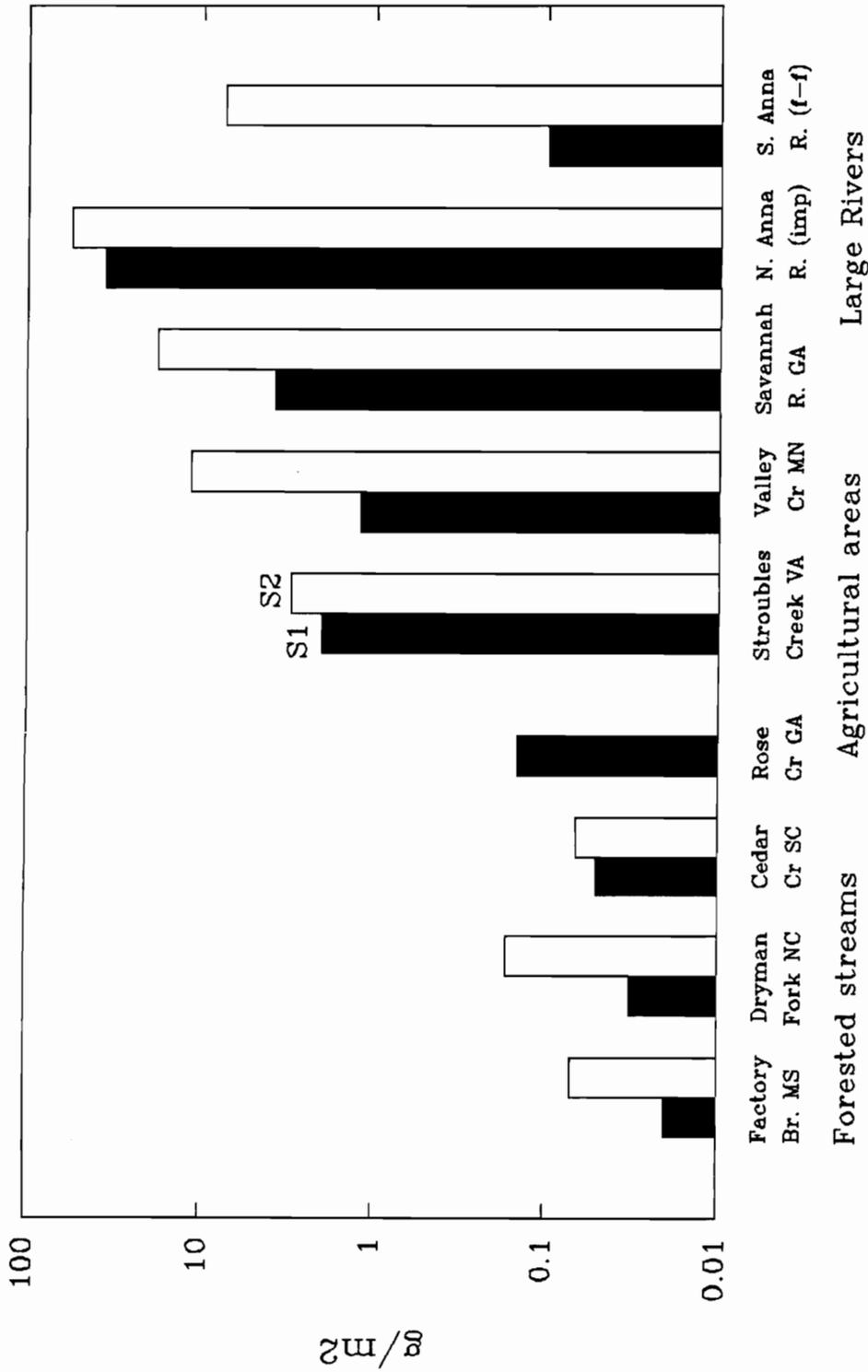


Fig. 16. Minimum and maximum values of annual production of *Cheumatopsyche* reported from different stream types.

Waters (1986) found a range of 1.2-11.6 gDM/m²/yr in riffles located up and down outlets from farm ponds in Valley Creek, Minnesota. An early study on epilithic fauna in the 2nd order Factory Brook, Massachusetts, reported a low *Cheumatopsyche* spp. production of 6.8-69.5 mgDM/m²/yr (Neves 1979), but this study was done on experimental cobbles of 15 cm diameter so it did not include the whole larval population. Other production values obtained for *Cheumatopsyche* species in low-order streams were those estimated (using Waters 1977 AFDM-DM conversion factor) for *C. h. enigma* of 32-168 mgDM/m²/yr in Dryman Fork, North Carolina (Ross and Wallace 1983), for *Cheumatopsyche* sp. between 6-53 mg/m²/yr in Cedar Creek, South Carolina (Smock and Roeding 1986), and for *Cheumatopsyche* sp. of 145 mgDM/m²/yr in the 3rd order Rose Creek, Georgia (Freeman and Wallace 1984) (Fig. 16).

High values of production of *Cheumatopsyche* species have been determined in two studies performed in large southeastern rivers. Cudney and Wallace (1980) found annual production of *C. pasella* in the Savannah River, Georgia, ranging between 3.81 and 18.21 gDM/m² on snag surfaces (using Waters 1977 conversion factor). The highest value occurred in medium current velocity of 25-50 cm/s which corresponded to average velocity in Stroubles Creek. Parker

and Voshell (1983) reported the highest known values of annual production for *Cheumatopsyche* in the North Anna River, 400 m below Lake Anna, with 36.5 gDM/m² for *C. parentum* and 56.8 gDM/m² for other un-separated species including *C. pettiti*. In contrast, they found lower annual values of 0.07 and 2.3 gDM/m² respectively at a site 32 km downstream of the lake. At corresponding sites in the South Anna River they found annual production of 0.1 gDM/m² for *C. parentum* and 2.3-7.5 gDM/m² for other *C.* species (Parker and Voshell 1983). Thus, high values of annual production were found at the site below the lake outlet, while the site further downstream and corresponding sites on the free flowing affluent (South Anna River) showed values more similar to those reported for small streams.

Production levels determined for *Cheumatopsyche* in Stroubles Creek are in the upper ranges for small, southeastern streams and similar to some values obtained in larger rivers. This result was also reflected in the derived P/B ratios determined from summation of production and biomass in the size-frequency calculations.

Many studies have used cohort P/B and annual P/B ratios to support interpretations on life history and production, since the first ratio is related to growth and survivorship of the actual cohort and the second one to the biomass

turnover rate (Benke 1984, 1993). Waters (1977) explained that the common range of cohort P/B ratios is between 3 and 8 for most benthic invertebrates due to the usual ratio between maximum and minimum weight. He also criticized the assumption of the cohort P/B ratio as a constant (5) and gave several reasons for deviations from this number (Waters 1969, 1977). The annual P/B ratio is subject to variations caused by particular environmental conditions, especially those that are reflected in voltinism of insect populations. Univoltine species may have annual P/B ratios close to 5 while bivoltine ones have values around 10 (Waters 1977; Benke 1984).

Annual P/B ratios obtained in Stroubles Creek were 11.54 at S1 and 7.15 at S2, which corresponded to the different frequency of bivoltinism that was interpreted from the life history at the two sites. These values are higher than the 6.9 ratio reported for *Cheumatopsyche* in Factory Brook (Neves 1977) and also higher than the values of 3.6 and 6.0 obtained for the bivoltine *C. h. enigma* in Dryman Fork (Ross and Wallace 1983). However, my P/B values are lower than the ratio of 14.7 determined by Freeman and Wallace (1984) in a rock outcrop of Rose Creek, where a short development time was found. Values of annual P/B ratio for *C. pasella* in the Savannah River were 8.31, 8.27 and

10.53 at low, mid and high velocity respectively (Cudney and Wallace 1980), and this ratio averaged 10.2 for *Cheumatopsyche* species in the North and South Anna Rivers (Parker and Voshell 1983). The annual P/B ratio at S1 in Stroubles Creek (11.54) corresponded to the range of bivoltine species (Waters 1977). This ratio at S2 (7.15) reflected the assumed partial bivoltinism and was more similar to the values found by Cudney and Wallace (1980) at low and mid current velocities in the Savannah River, where patterns of instar-frequency distribution were similar to those observed in this study (See life history discussion).

Interpretation of annual P/B ratios in relation to voltinism involves some circular reasoning, since voltinism has already been used in the calculation of the CPI correction factor (Freeman and Wallace 1984). If cohort methods were used to determine production, then the cohort P/B ratios could give more precise insights when compared to annual P/B ratios, but those methods were not possible to implement in Stroubles Creek. However, if univoltinism were assumed, annual production by the Hynes method would be similar to cohort production, and the P/B ratio calculated without the CPI correction would be near the cohort P/B. Assuming univoltinism, annual P/B ratios in Stroubles Creek would be 5.2 at S1 and 4.4 at S2. Since this ratio is

roughly equivalent to biomass turnover rate (Benke 1984), then these values indicate faster replacement of biomass at S1 than at S2. The trend to a faster turnover rate can be interpreted as enhancing adaptive responses of hydropsychids due to the increase in possibilities of genetic variation.

Factors affecting *Cheumatopsyche* production. The production determined at the study sites in Stroubles Creek could be influenced by effects from life history adjustment and habitat conditions. No single factor can be used as explanation for production levels, since they are not independent in their effects, but a brief review of main influences is necessary in order to suggest an integrated explanation of variations in *Cheumatopsyche* production.

Higher density of larvae at S2 constituted the essential component that led to the higher production estimate at this downstream site when compared to S1. Higher *Cheumatopsyche* densities even through a short distance downstream were observed by Mackay and Waters (1986) in the small Valley Creek, Minnesota, and this trend has been related to efficiency of nets according to the availability of the adequate size fraction of seston particles and microhabitat locations for the net (Wallace et al. 1977; Ross and Wallace 1982). The higher density determined

downstream in this study is also related to the increase of habitat diversity that was estimated with measures of particle size distribution in the substrate (Fig. 5). The increase in taxa richness could be correlated with substrate heterogeneity, since significantly more taxa have been found in more heterogeneous substrate (Williams 1980). Thus, the presence of two *Cheumatopsyche* species at S2 may cause a more efficient use of resources which can sustain a greater density of the genus.

Differences observed in the life history between the two sites did, however, counterbalance to some extent the higher production downstream. The apparent bivoltinism at S1, compared with the estimate of partial development of the second generation at S2, produced a higher adjustment of the annual production value by the use of a shorter CPI for the average cohort at S1 (164.5 days) than at S2 (225.3 days). Furthermore, the faster growth observed at the upstream site originated more relative abundance of instar V larvae at S1 during the overwintering period, which increased the mean contribution of large-biomass larvae to the production calculation. I assumed the higher thermal input accounted for this faster growth, given the difference in ADD between sites.

Food constitutes the other factor of great importance that has been frequently shown to affect production levels. Both quantity and quality have been suggested to explain variations in production, as observed with the zooplankton-enriched food available in the seston downstream the impoundment in the North Anna River (Parker and Voshell 1983) or with the large amount of seston that constantly passes across sparse snag substrate in the lower Savannah River (Cudney and Wallace 1980). Organic seston concentrations in Stroubles Creek averaged 2.94 and 1.43 mgAFDM/L at S1 and S2 respectively during the study period (Fig. 4). These values can be considered within ranges reported from small southeastern streams (Webster et al. 1979; Merritt et al. 1982; Wallace et al. 1982), but Sedell et al. (1978) showed lower mean annual concentrations in four northern basins throughout the country. The range for Site 1 in Stroubles Creek (0.9-11.9 mg AFDM/L) is similar to ranges observed in larger rivers (Cudney and Wallace 1980; Voshell and Parker 1985). The lower seston concentration at S2 can be explained by the presence of a larger number of retentive structures in the streambed due to inputs from the forest. The higher concentration at S1 seemed to reflect abundance of transported material from urban and agricultural areas of the watershed.

The quality of seston was analyzed by Parker and Voshell (1983) as the main reason to explain the high value of production below Lake Anna. They suggested that higher percentage of animal material in the zooplankton-enriched seston and a size range of this fraction that fitted in the mesh size of caddisfly nets could account for the high production compared with other free-flowing river. Consistently higher production of hydropsychids was determined at riffles below outlets from small impoundments compared to upstream riffles in Valley Creek, Minnesota (Mackay and Waters 1986). However, no difference in seston composition was determined in that study. The presence of fecal particles produced by fish and waterfowl in ponds was suggested to cause increases in the fine particle seston and, indirectly, in the algae and macrophyte components due to nutrient-enriched releases (Mackay and Waters 1986). In Stroubles Creek, despite the lack of particle analysis of seston, direct effects from impoundments did not seem very important, because the small farm ponds and the recreational Duck Pond are relatively far from the study sites. The influence of pond releases has been interpreted as acting for relatively short distances, probably only for some hundred meters downstream (Parker and Voshell 1983; Mackay and Waters 1986; Willis and Hendricks 1992).

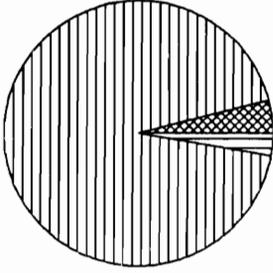
The relative importance of food types in the diet of *Cheumatopsyche* in Stroubles Creek may explain differences in production between the two study sites. While detritus was the most consumed fraction at both sites, algae had higher percentage of consumption at S1 and animal fragments were found more frequently in foreguts at S2 (Fig. 14). These variations were related to different availability of algal and animal sources at the two sites. The higher algal fraction at S1 was probably due to greater primary production in the open stream area as it has been observed in open sites in Dryman Fork, North Carolina (Ross and Wallace 1983). The higher availability of animal food at S2 was due to higher abundance and taxa richness of invertebrates (Fig. 6). Effects of different consumption of the two fractions can be observed in the relative contribution of food types to the *Cheumatopsyche* production (Table 7). The importance of the increase in animal food at S2 was detected in the contribution of this fraction to production which resulted very similar to that of detritus. The contribution of the algal fraction was higher at S1, but this food type represented the lowest contribution at both sites. Fig. 17 shows the relative contribution of food types to production in Stroubles Creek and to other estimates of hydropsychid production.

The relative importance of these food types to hydropsychid production has been determined in other southeastern streams with quite variable results. Benke and Wallace (1980) found the animal fraction had the highest contribution to production of some *Hydropsyche*, *Arctopsyche* and *Diplectrona* species in the 4th order Tallulah River, Georgia. Similar result was obtained for *Parapsyche* and *Hydropsyche* in Dryman Fork, North Carolina (Ross and Wallace 1983), but fine detritus had the highest contribution to *C. h. enigma* (54-67 %), even though the animal fraction also had a noticeable contribution (19-27%). A contrasting result was obtained in the low-gradient, 2nd-order Cedar Creek, South Carolina, which flows through a swamp system (Smock and Reading 1986). In this blackwater stream hydropsychid production was supported primarily by algae that contributed 61-79% of production, mainly due to the high production of *Macronema carolina*. Production of *Cheumatopsyche* sp. showed absence of the animal fraction at one swamp site yet high contribution of this food type at sites upstream and downstream (63 and 53 %). The study by Parker and Voshell (1983) showed the highest contribution of detritus for *Cheumatopsyche* production at three sites. However, at the site below the impoundment the animal fraction had the

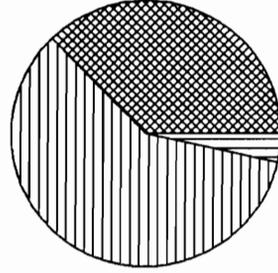
■ Detritus

▨ Animal

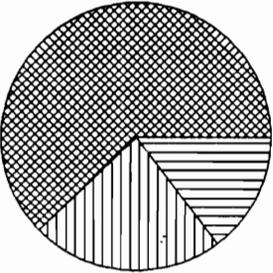
▧ Algae



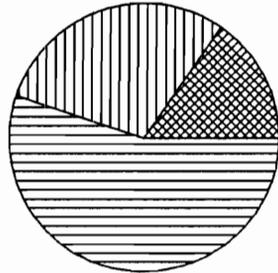
A. irrorata Tallulah R.



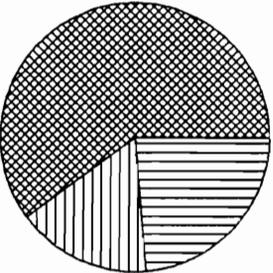
H. bronta Dryman Fork



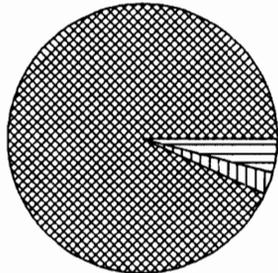
C. h. enigma Dryman Fork



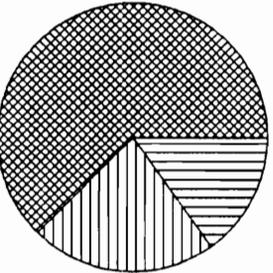
Cheumatopsyche sp. Cedar Cr.



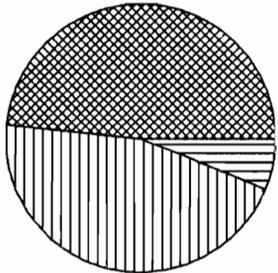
C. "notched" N. Anna R.



C. "notched" S. Anna R.



Stroubles Cr. S1



Stroubles Cr. S2

Fig. 17. Relative contribution of food types to hydropsychid production in different streams.

highest contribution for *C. parentum* but not for other *C. species*.

Predominant animal contribution in high-gradient streams has been attributed to the presence of coarse-mesh nets, such as those of *Arctopsyche*, *Parapsyche* and some *Hydropsyche* species (Smock and Reading 1986), that may be more efficient to capture drifting animals. In low-gradient streams fine-meshed nets such as that of *Macronema* would be more efficient at capturing fine detritus and algae (Wallace 1975). *Cheumatopsyche* nets have an intermediate mesh size between that of the large mesh-sized nets of *Arctopsyche* and some *Hydropsyche* and the small ones of *Macronema* (Wallace 1975; Wallace et al. 1977). Net mesh-size of instar V *C. pettiti* was reported as 81.4 x 43.3 μm (Ferrier and Wissing 1979) and little variation of mesh-size has been assumed for other species in the genus (Parker and Voshell 1983). The intermediate size of net mesh-size has been related to preference of *Cheumatopsyche* species for moderate current velocities (Fremling 1960; Cudney and Wallace 1980), and locations of retreats have been observed more frequently on sides and bottom of cobbles than on the top (Ferrier and Wissing 1979). Thus, microhabitat selection by *Cheumatopsyche* larvae, and corresponding mesh-size of nets, are probably determining the predominant range of particle

size that can be filtered out from the seston. In Stroubles Creek, the higher secondary production at S2 compared to S1 was probably influenced by the availability of habitat locations that allowed larger density of larvae than at S1. Similarly, production at S2 had higher contribution of animal food, which means that even with lower amount of organic seston than at S1 the availability of the animal food source would be able to support similar levels of production due to its superior quality.

A general overview on *Cheumatopsyche* production in Stroubles Creek supports the dominance of hydropsyhid caddisflies in this stream. *Cheumatopsyche* and *Hydropsyche* constituted the majority of individuals collected, and production values determined are well in the range of production levels of total insects in low-order streams. Values obtained in this study are higher than values from undisturbed Appalachian streams such as the Tallulah River, Georgia (Benke and Wallace 1980), Dryman Fork, North Carolina (Ross and Wallace 1983), and Rose Creek, Georgia (Freeman and Wallace 1984); and they are also higher than those from small streams in other regions such as Factory Brook, Massachusetts (Neves 1979) and the coastal-plain Cedar Creek, South Carolina (Smock and Reading 1986). Production values in this study are in the same order of

magnitude as values for *Cheumatopsyche* production in large, free-flowing rivers (Cudney and Wallace 1980; Parker and Voshell 1983). However, values from Stroubles Creek are clearly lower than those reported at sites below some food-enriched impoundment releases (Parker and Voshell 1983; Mackay and Waters 1986).

Differences in production between the two study sites appeared to be the result of combined influences from larval density, life history patterns, food supply and habitat availability. Higher density of *Cheumatopsyche* at S2 could be related to microhabitat availability as well as to the supply of animal food compared to S1. The combination of these factors made that numerical and total biomass components influenced the higher production estimate. However, faster larval growth and other life-history adjustments resulted in more evidence of bivoltinism at S1 than at S2. This difference in voltinism counter-balanced the annual production difference between sites that was 50.4% higher at S2 than at S1 while the average increase in larval density was as high as 151.3%. Finally, differences in physical habitat attributes between the two sites, specially through a major diversity of substrate particle size at S2 compared to S1, seemed to contribute directly to increase microhabitat availability for *Cheumatopsyche*

larvae, and indirectly to enhance animal food supply due to larger number of taxa and individuals at S2 than at S1. These combined influences can be related to the described land use patterns in the two sections of the watershed, since the general impacts from human activities are probably influencing life history and production dynamics on the entire stream ecosystem, but such impacts are more clearly recognized to affect the *Cheumatopsyche* population in the upstream section with urban and agricultural land covers surrounding the stream.

CONCLUSIONS

1. Life history and production information on *Cheumatopsyche* spp. in Stroubles Creek, Virginia, showed the importance of adjustment in life history events of hydropsychid caddisflies to habitat variations in a moderately disturbed stream.

2. Marked differences in habitat conditions were estimated between two stream sections as follows:

- Different land use on the two sections of the watershed consisted essentially of urban and agricultural uses upstream which generated dominant pasture cover around the stream, in contrast to a forest coverage in the downstream section with very low occurrence of other land uses.
- A noticeable increase in water temperature was recorded in the opened area of the upstream section, that reached 8.5% more accumulative degree days than at the downstream site during a 1-year period.
- Geomorphological conditions and disturbance processes on the upstream section were observed to affect streambed locations, specially through high relative abundance of substrate particles in some size ranges, compared to more

heterogeneous distribution of particles in diverse size ranges downstream.

3. Distribution and life history of *Cheumatopsyche* species had different patterns at the two study sites:

- Collection of adults and reared specimens showed that *C. pettiti* was the only species inhabiting Site 1, while both *C. pettiti* and *C. oxa* had permanent populations at Site 2. In addition, three other species of adults were collected beside the stream, but they were assumed to have flown from the larger New River.
- Larval density was lower at Site 1 than at Site 2, but larval growth was faster at Site 1 and it was attributed to the higher thermal input in the open section of the stream compared to the forest-covered section downstream.
- A definite bivoltinism of *C. pettiti* was determined at the upstream site, supporting the hypothesis of shift to bivoltinism for this species in warmer habitats. At the downstream site, bivoltinism also occurred but only to a fraction of the two-species population, since fewer proportion of overwintering larvae could reach maturation early enough to support the second summer generation.

4. Secondary production of *Cheumatopsyche* in Stroubles Creek was relatively high when compared to reported production of this genus in undisturbed streams of similar size in North America. However, production levels in this study are similar to those of hydropsychid species in streams in agricultural areas, and they are lower than values measured in large rivers or below impoundment releases.

5. Life-history patterns and habitat conditions interacted in effecting changes in *Cheumatopsyche* production. Elevated seston concentration at both sites contributed to the relatively high production. Higher larval density and better quality of food at Site 2 were the major influences for the production value, while at Site 1 the shorter length of aquatic life influenced in major proportion the estimate of production.

6. Overall effects of contrasting land uses on the two sections of Stroubles Creek watershed were qualitatively related to variations of *Cheumatopsyche*, essentially through habitat influences such as temperature, habitat availability and quality of food types. Tolerance and wide distribution of *C. pettiti* and other *Cheumatopsyche* species in North America may allow comparisons of its ecological parameters

among different streams. Results of this study supported the importance of adjustments in life history patterns for assessing the production dynamics of hydropsychids in this type of stream.

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