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## LARVAL DEVELOPMENT OF *HIODON TERGISUS* LESUEUR WITH COMPARISONS TO *HIODON ALOSOIDES* (RAFINESQUE)

ROBERT WALLUS

Tennessee Valley Authority

### ABSTRACT

Mooneye (*Hiodon tergisus*) larvae were collected in the Tennessee and Cumberland River systems from 1973 to 1977. Mooneye spawned in this portion of the Tennessee Valley, apparently beginning mid-to-late March with a peak in April when water temperatures ranged from 8-14 C. Protolarval goldeye (*Hiodon alosoides*) lack postanal pigmentation while mooneye possess postanal melanophones dorsally, ventrally, and in the caudal region. Protolarval and mesolarval goldeye have  $\geq 23$  postanal myomeres and mooneye have  $\leq 23$ . Metalarval mooneye have 12-13 dorsal rays and 27-29 anal rays while goldeye range from 10-11 and 31-33, respectively.

### INTRODUCTION

The mooneye, *Hiodon tergisus* Lesueur, and the goldeye, *H. alosoides* (Rafinesque) are the only two species in the monogeneric family Hiodontidae. They are sympatric in the Mississippi and Ohio River basins and both have been collected from the Tennessee River although the goldeye has disappeared from the upper reaches of the Tennessee system (Lee et al., 1980).

The overlaps in distribution and the occasional occurrence of mooneye and goldeye larvae in ichthyoplankton samples necessitates well-defined taxonomic descriptions of early development for both species. Battle and Sprules (1960) discuss the reproductive biology of the goldeye and provide an excellent description of larval development. Several authors have studied or reported on aspects of mooneye life history (Johnson 1951; Van Oosten 1961; Hargis 1966; Scott and Crossman 1973; and Glenn 1975a, 1975b, 1976, 1978), but little information is available on spawning and early development. Fish (1932) described and illustrated two specimens as *H. tergisus*, which was the only information available on larval mooneye until recently. Moreover, one of those specimens had the characteristics of a cyprinid and is deemed an error in identification (Snyder and Douglas 1978). Hogue et al. (1976) briefly described larvae in the family Hiodontidae and provided a key to distinguish mooneye and goldeye larvae. Snyder and Douglas (1978) described mooneye protolarvae.

In this paper I provide a detailed description of post-hatching development of mooneye  $> 9.0$  mm total length (TL) and compare it with goldeye development. Also included is a discussion of spawning times for mooneye populations from the Tennessee and Cumberland River systems.

### METHODS

Mooneye in all phases of development were collected by Tennessee Valley Authority (TVA) fisheries personnel in

the Tennessee and Cumberland River systems. Most of the 65 specimens ranging from 9.0 to 33.0 mm TL used for describing mooneye development were collected during the period 1973 through 1977 from Wheeler Reservoir, a mainstream impoundment of the Tennessee River in northern Alabama. Goldeye larvae were also collected by TVA workers from the Mississippi River (near Memphis, Tennessee) and the Ohio River (near Paducah, Kentucky). Additional larvae of goldeye from the Missouri River and of both species from the lower Mississippi River were obtained from other investigators. Specimens were initially fixed in 10 percent formalin, and then transferred to 5 percent formalin buffered with marble chips to approximately pH 7.5 for permanent storage. All specimens used in this study are currently housed in TVA's Regional Larval Fish Identification and Information Center at Norris, Tennessee.

Specimens were examined with a stereo-microscope equipped with an ocular micrometer and polarizers. Morphometric and meristic characters examined were: total length, distance from tip of snout to end of caudal fin or finfold; standard length, distance from tip of snout to the posterior tip of the notochord or the hypural complex once it was completely developed; predorsal length, distance from the tip of the snout to anterior margin of the base of the first dorsal pterygiophore; preanal length, distance from back of anus to tip of snout; greatest body depth (excluding finfold); number of complete preanal myomeres, those from back of anus to nape including any bisected by an imaginary vertical line at back of anus; number of complete postanal myomeres; number of dorsal and anal pterygiophores; and number of fin rays. Lengths given in the text are total length (TL) unless stated otherwise. Developmental terminology follows Snyder (1976). Illustrations were made using a camera lucida.

### RESULTS AND DISCUSSIONS

#### Spawning

Johnson (1951) reported that mooneye spawn in Lake Erie and Lake St. Clair in April and May, and Scott and Crossman (1973) reported spawning in the spring (April-June) in Lake Erie. Hargis (1966) stated that mooneye spawning began April 18 in the Clinch and Emory River embayments of Watts Bar Reservoir (Tennessee River system) and that all mooneye examined for gonad condition between May 23 and May 27, 1966, had completed spawning. Water temperatures associated with spawning were not reported in those references. Assuming mooneye larvae hatch at about 7.0 mm total length (Snyder and Douglas 1978), inferences for spawning temperatures would be difficult to make from Table 1, since the smallest larvae captured from the Tennessee River were 9.0 mm in length. However, hiodontid eggs

**Table 1. First occurrence of Larval *Hiodon tergisus* in collections by Tennessee Valley Authority in 1976 and 1977.**

Year, Reservoir	Dates	First Occurrence		
		Water Temp. (c)	Number of Specimens	TL Range (mm)
1976				
Wheeler <sup>1</sup>	8 Apr	16.6	3	11-13
Guntersville <sup>1</sup>	5-7 Apr	14.6-16.5	7	9-14
Barkley <sup>2</sup>	20-21 Apr	12.5-20	2	12-13
1977				
Wheeler	13 Apr	18.0	11	10-14
Guntersville	12 Apr	15.4-16.1	1	10
Old Hickory <sup>2</sup>	28 Apr	12.5	1	11

1 - Tennessee River

2 - Cumberland River

were collected from the Hiwassee River, a Tennessee River tributary, on April 22, 23, 27 and 28, 1976, when water temperatures ranged from 10.5-15 C. They were assumed to be mooneye eggs because extensive surveys in the Hiwassee River have not revealed the presence of adult or larval goldeye. The spawning period in the Tennessee Valley area appears to begin in late March with the peak occurring in April, probably at temperatures ranging from 8-14 C.

#### Development

Mooneye protolarvae between 9.0 and 9.5 mm long have rather large eyes and a head still slightly deflected over the yolk sac. Nares, auditory vesicles with otoliths, and three to four gill arches are present, and on some specimens, the stomodeum is visible. Between 10.0 and 12.0 mm (Fig. 1),

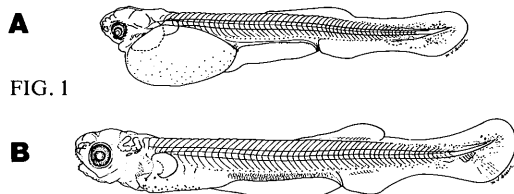


FIG. 1

the mouth and lower jaw appear and by 16.0 mm the mouth is well developed, the premaxilla extending posteriorly approximately one-third the eye width (Fig. 2B). Opercular development is slow, and the gills are not completely covered until larvae reach a length of about 27.0 mm.

Early mooneye protolarvae have a large oval yolk sac. The oil globule is located in the anterior one-third of the yolk sac, but may be difficult to see due to a yellowish-brown yolk covering. The yolk sac gradually becomes cylindrical and disappears posteriorly as yolk is absorbed. Specimens 13.0 to 13.5 mm TL have a greatly reduced yolk sac (Fig. 2A). At 16.0 mm oil is no longer visible, and the yolk gradually disappears by 21.5 mm TL.

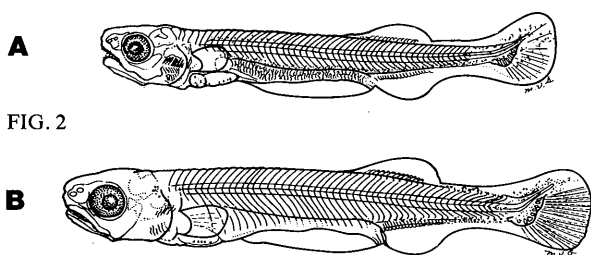


FIG. 2

#### Pigmentation

Protolarval mooneye have dark eyes and melanophores scattered ventrally and ventrolaterally on the yolk sac. Postanal pigment is plentiful along the ventrum to the urostyle where it outlines the urostyle and is present dorsally on the posterior one-third to one-half of the caudal peduncle (Fig. 1A). On some specimens melanophores may be somewhat scattered on the finfold near the caudal peduncle, especially around the urostyle. One to several melanophores may be present on the caudal peduncle along the horizontal myoseptum, especially posteriorly. Visible internal pigment consists of an anterior continuation of ventral postanal pigment dorsally along the gut.

As the yolk is absorbed on early mesolarval specimens, the ventral pigmentation on the yolk sac becomes concentrated (Fig. 1B). This concentration continues and pigment gradually disappears as the yolk is absorbed, until by 10.0 mm only two or three small melanophores remain (between the pectoral fin bases). Further pigment development in the mesolarval phase is marked by the appearance of a double row of small melanophores, ventrally, posterior to the anus ( $\approx$ 19.0 mm); appearance of scattered melanophores over the brain ( $\approx$ 21.0 mm); and increased dorsal pigmentation resulting in a double row of melanophores on either side of the median finfold and by the end of the mesolarval phase scattered melanophores dorsolaterally around the dorsal fin base.

Metalarval development is characterized by a gradual increase in dorsal pigmentation until, by the juvenile period, scattered melanophores extend the entire length of the dorsum with small melanophores profusely scattered dorsolaterally almost to the horizontal myoseptum. Dorsal pigment is plentiful on the head, covering the brain and scattered on the tip of the snout (Fig. 3B).

#### Fin Development

On 9.0 to 10.0 mm specimens, the median finfold has its dorsal origin near midbody, extends around the slightly upturned urostyle, and continues ventrally to the posterior margin of the yolk sac (Fig. 1A). Undulations in the profile of the finfold are present at the relative positions of the dorsal and anal fins. Pectoral fin buds are visible on some specimens. Some 10.0 mm specimens have opaque areas along the base of the finfold, indicating beginning differentiation of the dorsal, anal, and caudal fins. Hypurals and dorsal and anal pterygiophores first appear on specimens between 10.5 and 11.0 mm long. The first caudal rays appear as early as 12.0 mm but usually around 13.0 mm, marking transition from protolarval to the mesolarval phase. Also, between 12.0 and 13.0 mm incipient rays begin developing in the pectoral fins.

By 16.0 mm (Fig. 2B) the finfold disappears completely on the dorsum anterior to the dorsal fin and is greatly reduced posteriorly. The ventral finfold remains prominent, and the caudal fin is fan shaped with eight or nine hypurals and 15 to 17 rays. By 17.0 mm the caudal fin is slightly bilobed and pelvic buds are present. At 20.0 mm only the prominent preanal finfold and small portions anterior to the caudal fin remain (Fig. 3A). Hypural development is complete or nearly so by 23.0 mm, at which point the adult complement of fin rays is present in the dorsal, anal, and caudal fins, thus marking transition to the metalarval phase. By approximately 25.0 mm, the adult complement of pectoral rays has formed, and by approximately 30.0 mm the pelvic fins have a full complement of segmented rays. On specimens this size the ventral finfold has decreased in length, extending from the anus approximately to the midgut region (Fig. 3B). The preanal finfold

is still present between the pelvic fins and the anus at 40.0 mm, having not yet completely disappeared into the fleshy keel characteristic of mooneye.

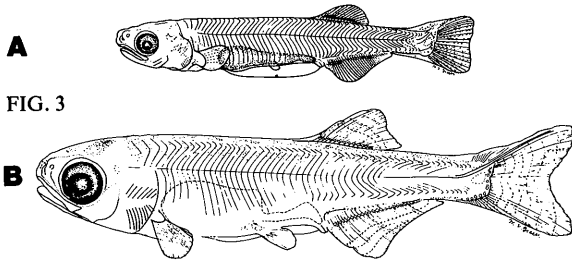


FIG. 3

#### Diagnosis

Differentiation of protolarval and mesolarval hiodontids to species is accomplished readily, in most instances. Goldeye larvae in these phases normally lack postanal pigmentation while mooneyes exhibit postanal pigmentation dorsally, ventrally, and in the caudal region (Fig. 4). Also, once pterygiophore development establishes relative positions of the dorsal and anal fins (late protolarvae/early mesolarvae) identification to species level is possible. The dorsal fin origin is anterior to the anal fin origin on mooneye, but is above or posterior to the anal fin origin on goldeye (Fig. 4). Although this character is occasionally dif-

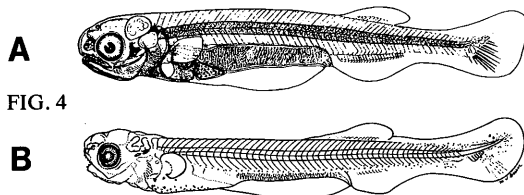


FIG. 4

ficult to see, morphometric data in Table 2 (percent TL values of predorsal and preanal lengths) are supportive.

Dorsal and anal fin meristics as well as dorsal fin position are diagnostic for mesolarval (pterygiophore counts) and metalarval hiodontids (Table 2). Dorsal and anal fin ray

counts of 10-11 and 31-33, respectively, are typical for goldeye, while 12-13 dorsal rays and 27-29 anal rays are common for mooneye.

There is a difference in the origin and in the rate of diminution of the preanal finfold in metalarve. The preanal finfold of the mooneye originates slightly anterior to midway between the pelvic and pectoral fins while on goldeye it originates near the base of the pectoral fins. By about 30 mm (Fig. 5), the preanal finfold is notably more reduced in the mooneye.

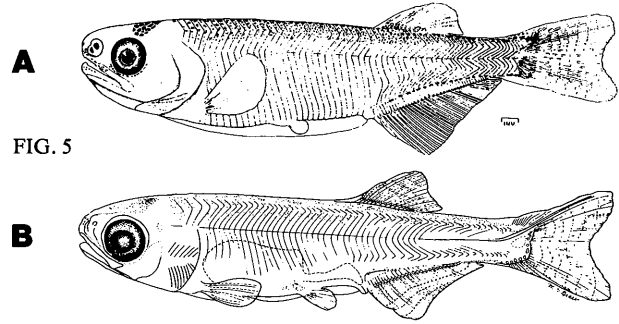


FIG. 5

Postanal myomere counts can be used to identify hiodontid specimens unless an overlapping count of 23 is obtained. In Hogue et al. (1976), hiodontid larvae with fewer than 24 postanal myomeres were identified as *H. tergisus*. This diagnostic character was based on myomere counts from mooneye collected in the Tennessee River and goldeye data collected in Lake Claire, Alberta, by Battle and Sprules (1960). The present study reveals that postanal myomere counts of 23 are not uncommon for goldeye (Table 3). Counts of 23 postanal myomeres for mooneye were observed only on protolarvae but were common (50 percent, N=10) for specimens examined in this phase of development.

Postanal myomere counts for mooneye reported by Snyder and Douglas (1978) were similar to those in this study, but myomere counts by Battle and Sprules (1960)

Table 2

Selected morphometrics and meristics for larvae of *Hiodon tergisus* (mooneye) from the Tennessee River and *H. alosoides* (goldeye) from the Mississippi and Ohio Rivers

Characteristics	Protolarvae		Mesolarvae		Metalarvae	
	Mooneye	Goldeye	Mooneye	Goldeye	Mooneye	Goldeye
Number of Specimens	10	5	23	9	8	7
Total Length (TL) Range	9.25-12.99	10.83-12.99	13.16-22.82	13.33-22.82	23.16-30.32	23.82-31.15
Measurements as Percentage of TL						
Standard Length	96	96	92	92	88	86
Predorsal Length	-	62	55	60	53	57
Preanal Length	61	59	60	57	56	54*
Greatest Depth	9	17	15	16	18	21
Counts (Range)						
Caudal Rays	0-6	0-7	6-18	8-18	18	18
Dorsal Pterygiophores	0-12	0-9	10-13	6-11	12-13	10-11
Dorsal Rays	0	0	0-13	0-11	12-13	10-11
Anal Pterygiophores	0-15	0-23	13-28	13-34	27-28	32-33
Anal Rays	0	0	0-25	0-31	27-28	31-33
Pectoral Rays	0	0	0-11	0-11	11-13	11-12
Pelvic Rays	-	-	0	0	0-7	5-7

for goldeye (after adjustment for different counting techniques) were high when compared to my counts. Some variation in myomere counts may result from the difficulty of accurately counting extreme anterior on posterior myomeres. Yet there seems to be a possibility of

geographical variation in numbers of postanal myomeres for goldeye. Postanal myomere counts for goldeye from the middle Missouri River slightly higher than counts for specimens from the lower Ohio and lower Mississippi Rivers (Table 3) would also support such an hypothesis.

**Table 3.**

Myomere Counts for Mooneye (*Hiodon tergisus*) and Goldeye (*H. alosoides*) Larvae from the Tennessee, Ohio, Missouri, and Mississippi Rivers

Length Range (mm TL)	9-10.99	11-12.99	13-14.99	15-16.99	17-18.99	19-20.99	21-22.99	23-24.99	25-29.99
<i>Hiodon tergisus</i> (From the Tennessee River)									
Number of Specimens	5	5	5	5	5	5	3	3	-
Preanal Myomeres	33-34	33-35	34-36	34-36	34-36	34-36	35-36	34-35	-
Postanal Myomeres	20-23	21-23	18-22	19-20	17-20	18-20	19-20	19-20	-
<i>Hiodon tergisus</i> (From the Lower Ohio and Lower Mississippi Rivers)									
Number of Specimens	*	*	5	3	*	*	2	*	*
Preanal Myomeres	-	-	35-36	35-36	-	-	34-36	-	-
Postanal Myomeres	-	-	19-22	20	-	-	19-20	-	-
<i>Hiodon alosoides</i> (From the Lower Ohio and Lower Mississippi Rivers)									
Number of Specimens	1	4	4	*	1	3	2	1	3
Preanal Myomeres	32	35-36	34-36	-	35	35-36	33-34	33	32-33
Postanal Myomeres	23	23-24	23-24	-	23	23	23-24	23	23-24
<i>Hiodon alosoides</i> (From Middle Missouri River)									
Number of Specimens	8	4	2	4	4	4	3	3	3
Preanal Myomeres	32-34	32-34	32-34	33-34	33-35	34-35	34-35	34-35	33-34
Postanal Myomeres	25-27	24-26	24	23-24	23-24	24-25	23-24	23-24	24-27

\*Specimens unavailable in this length category.

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### PRODUCTION ECOLOGY OF INVERTEBRATES IN SMALL EXPERIMENTAL PONDS

ROBERT M. CUSHMAN  
PAUL J. FRANCO  
JONATHAN C. GOYERT<sup>a</sup>  
PETER A. LESSLIE<sup>b</sup>

Oak Ridge National Laboratory  
Oak Ridge, Tennessee 37831

<sup>a</sup>Present address: Science Applications International Corporation, Oak Ridge, Tennessee 37830.

<sup>b</sup>Computing and Telecommunications Division, Martin Marietta Energy Systems, Inc., Oak Ridge, Tennessee 37831

#### ABSTRACT

Production of invertebrates is estimated for a series of small experimental ponds in Tennessee. Annual dry weight

production of predator insects is about 4.5 g/m<sup>2</sup> and of herbivore-detritivore insects about 3.8 g/m<sup>2</sup>; insects whose trophic position could not be classified account for an an-

nual dry weight production of about 0.3 g/m<sup>2</sup>. Annual dry weight production of zooplankton is about 14.5 g/m<sup>2</sup>, of annelids 25.4 g/m<sup>2</sup> and of snails 3.1 g/m<sup>2</sup>. Our data are consistent with published information that the predator insects probably depend on a variety of energy sources to support their estimated production rate.

#### INTRODUCTION

Freshwater ponds have been used in ecological research for a number of purposes. For example, Hall et al. (1970) studied community interactions in ponds in which they manipulated nutrients and predation; Benson et al. (1980) studied energy flow; Kormondy and Gower (1965), Benke and Benke (1975), and Benke (1976) reported on odonate (dragonfly and damselfly) life histories, species interactions, and production ecology; and Boyle (1980), Cushman and Goyert (1984), and Giddings et al. (1984) studied the effects of toxicants on pond ecosystems. Ponds are attractive for aquatic ecology research for several reasons: (1) they represent a common aquatic habitat and at the same time simulate embayments and coves of lakes and reservoirs, containing many of the ecological complexities (e.g., predation, competition, recruitment) of larger aquatic ecosystems; (2) because of their small size, they are amenable to experimental manipulation (such as nutrient or toxicant addition, or predator removal) and easy to sample with limited field gear; and (3) they can be cleaned up and restored, for future research.

A basic understanding of the ecology of the pond systems is a prerequisite to the interpretation of pond studies, especially studies involving perturbations. The interactions of populations (e.g., competition and predation) within pond ecosystems may be especially important in defining indirect responses to manipulations. One important aspect of ecology is production (i.e., elaboration of biomass), which determines the amount of energy potentially available for utilization by higher trophic levels. As shown in Water's (1977) review of freshwater secondary production, relatively few studies have estimated the production of an entire zoobenthos, and these have been for lakes, reservoirs, and large rivers, rather than ponds. In this paper we estimate the production ecology of the major invertebrate groups (insects, rotifers, crustaceans, annelids, and snails) in a series of shallow, experimental ponds.

In this study we used two of the methods available for calculating secondary production: for insects, the size-frequency method (Hamilton 1969), which allows estimates to be obtained when individual cohorts can not be determined; for the other invertebrates, the turnover ratio, or P/B ratio, method (Waters 1977). Other methods, not employed in this study, include the removal-summation, increment-summation, instantaneous growth, and Allen curve methods (Waters 1977).

#### MATERIALS AND METHODS

The eight Roane County, Tennessee, ponds used in this study have been described previously (Cushman and Goyert 1984). The ponds are 21 to 30 m<sup>2</sup> in surface area, with a maximum water depth of 73 to 80 cm. In this paper we consider results from all eight ponds from December 1980 through June 1981. Because a synthetic oil was applied to six of the ponds in July 1981 as described in Cushman and Goyert (1984), we consider results from only the two control ponds from July until October 1981; thus, in this paper we only describe the production ecology of undisturbed ponds.

Sampling for benthos was described by Cushman and Goyert (1984). In summary, 15- by 15-cm Ekman samples, four per pond, were taken every other month from December 1980 through October 1981. The samples were sieved (0.5-mm mesh opening) and insects picked from the samples, preserved in a 70% ethanol/5% glycerine solution, identified, measured, dried, and weighed in size-class groupings to establish length-weight regressions. Annelids were similarly processed, except that they were not measured, and for each sample period a single total weight was taken separately for both oligochaetes and leeches. The measured dry weights of insects and annelids were increased by 25% to compensate for weight loss in preservative (Benson et al., 1980). Snails (*Physa gyrina* and *Helisoma trivolvis*) in the December 1980, February 1981, August 1981 (one pond only), and October 1981 (one pond only) samples were measured for shell length; shell-free dry weights were calculated from the length-weight regressions reported for the same genera by Stein et al. (1984). Snails with a shell length of less than 3 mm generally were not counted or measured. As shown by Stein et al. (1984), weight for these taxa is a function of the shell length to about the 2.5 power, and many snails in our samples were longer than 10 mm; maximum measured lengths were 14.8 mm for *P. gyrina* and 17.3 mm for *H. trivolvis*. Although the unmeasured snails probably contributed relatively little to the standing crop in our ponds, actual standing crops were certainly somewhat greater than our estimates thereof.

Zooplankton were sampled once every two weeks over a 4-month period from June to September 1981 with four samples taken from each pond on each sampling date. A plexiglass tube (4.3-cm ID by 94 cm long) with a closure at the lower end was submerged vertically, the closure was sealed, and a column of water (600 to 1200 ml) was removed. Samples were concentrated with a Wisconsin-type plankton bucket (80- $\mu$ m mesh) and preserved in a sucrose-formalin solution with methylene-blue dye. Zooplankton in aliquots of samples were counted, using a dissecting microscope. The proportion of the sample that was counted varied with total zooplankton density and detrital contamination of the samples. For each sample, the goal was to count at least 100 individuals. At least 20% of the sample was counted for those samples with high density and little detritus. As much as 50% was counted if the samples contained a large amount of plant detritus. Dominant zooplankters were identified to species. Immature stages of copepods and *Simocephalus vetulus* were enumerated separately from adults. Lengths of crustaceans and common rotifers were measured from subsamples, and mean individual dry weights were estimated from length-weight regressions (Dumont et al. 1975, Bottrell et al. 1976). Weights for some rotifer species were taken from Hall et al. (1970).

Production of each insect taxon was calculated by the size-frequency method (Hamilton 1969). This method was chosen because the bimonthly sampling was not adequate for discerning life histories of many of the insects. Dry weights of organisms of a given length were calculated from the length-weight regressions reported by Cushman and Goyert (1984). Univoltinism was assumed, except for *Chironomus decorus* and *Caenis* sp.

Several authors have observed multivoltinism in *C. decorus* (Ping 1917, Benson et al. 1980, Utberg and Sutherland 1982), with a generation time of about one month in New York and New Jersey. Because we observed *C. decorus* over five months, we assumed that there were five generations and multiplied our size-frequency produc-

tion estimate accordingly. Similarly, Hall et al. (1970) found that *Caenis simulans* had two generations per year, and we assumed the same for *Caenis* sp. in our ponds, correcting the production estimate accordingly. The trophic position of the various insects was determined from information presented in Merritt and Cummins (1978).

Monthly zooplankton productivities during the 4-month sampling period were estimated by multiplying monthly standing crops by the number of generations completed during the month (Winberg et al. 1971). The number of generations per month for each taxon was calculated from published relationships between life cycle duration and temperature using temperature data from the experimental ponds. Generation times for cladocerans were based on temperature/development-time regressions for our species or closely related species (Bottrell 1975). Data from Allan (1976) were used to estimate generation times for copepods and rotifers.

Zooplankton production for the remaining eight months of the year was estimated using the same procedures as above. Standing crops for these months were assumed to be equal to the mean biomass measured during the sampling period.

For annelids and snails, production was estimated by multiplying the mean annual standing crop by published values of turnover ratio (P/B). Waters (1977) reported P/B ratios for oligochaetes ranging from 0.7 to 12.5 and for leeches from 1.5 to 5.3; for our calculations we used the midpoint of each range, 6.6 for oligochaetes and 3.4 for leeches. Turnover ratios reported by Waters (1977) for pulmonate snails range from 0.3 to 6.5; we used the midpoint, 3.4, for our production calculation.

## RESULTS

Total annual secondary dry weight production of benthic insects is estimated to be about 8.6 g/m<sup>2</sup> (Table 1), of which about 4.5 g/m<sup>2</sup> is attributed to predators, 3.8 g/m<sup>2</sup> to herbivores or detritivores, and 0.3 g/m<sup>2</sup> to taxa that could not be positively classified as either predators or herbivores/detritivores. Most of the estimated insect production was accounted for by odonates (Libellulidae and Coenagrionidae) and the midge *Chironomus decorus*. Examples of the production calculations for the two dominant taxa are shown in Table 2.

Monthly productivity estimates for zooplankton are given in Table 3. Total annual dry weight production was 14.5 g/m<sup>2</sup>, attributable mostly to cladocerans and copepods. Even though rotifer generation times were much shorter than those of the other zooplankton, rotifer standing crops were an order of magnitude less than those of the crustaceans, and therefore the contribution of rotifers to production was relatively low.

The estimated annual dry weight production of oligochaetes was 23.7 g/m<sup>2</sup> and of leeches 1.7 g/m<sup>2</sup>, for an annelid total of 25.4 g/m<sup>2</sup> (Table 4). The estimated annual dry weight production of snails was 3.1 g/m<sup>2</sup> (Table 4).

## DISCUSSION

Production estimates are subject to sampling and calculation errors not unique to this paper. Errors due to sampling and processing typically result in underestimation of actual production. Mobile benthic and planktonic organisms may be undersampled by Ekman and tube-type samplers (Tonolli 1971, Benke and Benke 1975). Sieving and sorting of samples may cause the loss of the smallest individuals. (Weight loss due to sample preservation was corrected for as explained earlier).

**Table 1.**

Annual production of benthic insects in the experimental ponds, December 1980 through October 1981.

Taxon	Annual production, P (g dry wt/m <sup>2</sup> )
<b>Predators</b>	
Libellulidae	2.71
Coenagrionidae	1.01
<i>Clinotanypus pinguis</i>	0.52
<i>Dromogomphus spoliatus</i>	0.12
<i>Tabanus</i> sp.	0.06
<i>Chaoborus puntipennis</i>	0.05
<i>Psectrotanypus</i> sp.	0.04
Others <sup>a</sup>	0.00
<b>Herbivores-Detritivores</b>	
<i>Chironomus decorus</i>	2.95
<i>Chrysops</i> sp.	0.50
<i>Agrypnia vestita</i>	0.18
<i>Trianenodes</i> sp.	0.10
<i>Caenis</i> sp.	0.05
Others <sup>b</sup>	0.06
<b>Undetermined</b>	
Ceratopogonidae	0.16
<i>Procladius</i> sp.	0.06
<i>Phryganea sayi</i>	0.03
Others <sup>c</sup>	0.03
<b>Total</b>	<b>8.6</b>

a Includes *Agabus* sp. and *Bidessus* sp.

b Includes *Callibaetis* sp., *Hexagenia* sp., *Dixa* sp., Orthocladiinae, *Einfeldia natchitochaeae*, *Pseudochironomus* sp., and other Chironominae.

c Includes *Tanytus neopunctipennis*, *Ablabesmyia peleensis*, *Oecetis* sp., *Polypedilum* sp., and *Oxyethira* sp.

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The accuracy of production estimates by the size-frequency method is affected by details of the life histories of the species (Waters 1979). By calculating production separately by taxon, we were unable to minimize the effect of overestimation caused by the assumption that all species in a group could achieve the maximum size of the largest species. Voltinism could also have affected the production estimates. If, for example, the odonates were hemivoltine rather than, as we assumed, univoltine, the actual production estimate for our data would be half of our calculated value. Kormondy and Gower (1965) found that a group of odonates in a Pennsylvania pond exhibited both univoltinism and hemivoltinism, although Benke and Benke (1975) found that the most abundant dragonfly species in a South Carolina farm pond were univoltine. We were not able to determine if correction for hemivoltinism would have been appropriate for our estimates.

The use of generation times to calculate zooplankton production requires the assumption that turnover of individuals is equivalent to biomass turnover. This holds true for rotifers, for which the weight of newly hatched individuals approximates that of adults, but may underestimate crustacean production (Winberg et al. 1971). The annual generation turnover ratios calculated from temperature/generation-time regressions were 16 to 30 for 5 cladoceran species and 22.4 for copepods. P/B ratios (annual biomass turnover ratios) for Cladocera and copepods from temperate lakes are 22 to 31 and 12 to 28.5, respectively (Waters 1977). Makarewicz and Likens (1979) listed P/B ratios of 10.1 to 19.1 for total zooplankton communities during vegetative periods. The P/B ratio for

**Table 2.**

Production calculations for the two dominant taxa in the experimental ponds, December 1980 through October 1981.

Length (mm)	Mean density (No./m <sup>2</sup> )	Loss (No./m <sup>2</sup> )	Length at loss (mm)	Dry wt. at loss (mg)	Dry wt. loss (mg/m <sup>2</sup> )	Times loss occurs	Annual production (mg dry wt./m <sup>2</sup> )
<b>(a) Libellulidae</b>							
1-3	13.2						
		-17.4	3.5	0.6	-11.12	7	-78
4-6	30.6						
		22.9	6.5	3.3	75.0	7	525
7-9	7.6						
		0.7	9.5	8.9	6.1	7	43
10-12	6.9						
		2.1	12.5	18.3	38.2	7	267
13-15	4.9						
		-1.2	15.5	32.2	-37.4	7	-262
16-18	6.0						
		5.3	18.5	51.3	273.0	7	1911
19-21	0.7						
		0.7	20.0	62.9	43.8	7	307
Total							2713
<b>(b) Chironomus decorus</b>							
3-4	84						
		-511	4.5	0.03	-17.2	5	-86.2
5-6	594						
		344	6.5	0.10	33.5	5	167.7
7-8	250						
		28	8.5	0.21	5.9	5	29.5
9-10	222						
		119	10.5	0.38	45.0	5	225.2
11-12	104						
		104	11.5	0.49	50.9	5	254.7
Uncorrected total							591
Corrected (for multivoltinism) total							2954

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zooplankton in our ponds over 4 months, using generation times to calculate production, was 13.2. Therefore, our estimates of turnover ratios are not greatly different from those in the literature.

Even if the annual production of undetermined taxa is added to that of herbivore-detritivore taxa, the sum is still far too low to account for production of predator insects. For example, it may be assumed that production of prey is about ten times that of their predators (e.g., Kormondy 1969) (the ratios of non-predator production to predator production of zoobenthos in a variety of reservoir, river, and lake ecosystems, as summarized by Waters (1977), ranged from 3:1 to 25:1). Under this assumption, our observed annual production of 4.5 g dry weight/m<sup>2</sup> of predator insects would require an annual production of prey of 45 g dry weight/m<sup>2</sup>; this latter figure is more than ten times the combined annual production we estimated for prey and undetermined insects. Furthermore, some of the production of prey insects in our ponds may have been exploited by fathead minnows (*Pimephales promelas*) (the only fish species present) rather than by predator insects. Thus, additional energy sources for production of predator insects must be invoked.

Many predator insects have been reported to feed on a variety of non-insect prey, and this alternative resource probably accounts for a significant part of the production of predator insects in our study. Pennak (1953) and

Johnson (1973) reported that odonates feed on microcrustaceans, although Benke (1976) estimated that the latter contributed no more than 5% to odonate intake. Odonates also have been reported to feed on annelids, mollusks, and protozoans (Pennak 1953). Non-insect prey also have been reported for other predator insects found in our study. For example, *Chaoborus* feeds on microcrustaceans (Cummins *et al.* 1978), *Clinotanypus* on oligochaetes and ostracods and *Psectrotanypus* on cladocerans (Cummins and Coffman 1978), *Tabanus* on "earthworms" and snails (Johannsen 1935), and dytiscids on "shrimps", "worms", leeches, snails, tadpoles, and small fish (Leech and Chandler 1971). Hurlbert (1975) reviewed a number of pond studies of insecticide toxicity that demonstrated the importance of predation of insects on non-insects. Our estimated annual production of zooplankton, annelids, and snails totals 43 g dry weight/m<sup>2</sup>; presumably, some of this production was exploited by the predator insects in our ponds. If this total is added to the combined estimates for prey and undeter-

**Table 3.**

Production calculations for zooplankton in experimental ponds, June through September 1981.

Month	Standing crop (g dry wt./m <sup>2</sup> )	Number of generations /month	Monthly production (g dry wt./m <sup>2</sup> )
<b>Cladocera</b>			
<i>Alona costata</i>			
June	0.040	2.3	0.09
July	0.023	2.8	0.06
August	0.044	2.5	0.11
September	0.026	1.7	0.04
<i>Chydorus sphaericus</i>			
June	0.025	4.3	0.11
July	0.039	5.0	0.20
August	0.028	4.6	0.13
September	0.071	3.4	0.24
<i>Simocephalus vetulus</i>			
June	0.110	2.7	0.30
July	0.176	3.1	0.55
August	0.379	2.8	1.06
September	0.632	2.0	1.26
<b>Other Cladocera</b>			
June	0.017	2.9 <sup>a</sup>	0.05
July	0.000	--	0.00
August	0.021	2.9	0.06
September	0.010	2.0	0.02
Total			4.28
<b>Copepoda</b>			
June	0.163	3.5 <sup>a</sup>	0.57
July	0.483	5.0	2.42
August	0.165	3.9	0.64
September	0.124	1.9	0.24
Total			3.87
<b>Rotifera</b>			
June	0.023	15.8 <sup>a</sup>	0.36
July	0.016	19.4	0.31
August	0.015	17.2	0.26
September	0.015	9.4	0.14
Total			1.07

<sup>a</sup>Group average number of generations per month

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**Table 4.**

Production calculation for annelids and snails in the experimental ponds, December 1980 through October 1981.

Month	Standing crop (g dry wt./m <sup>2</sup> )	Annual turnover ratio <sup>a</sup>	Annual production (g dry wt./m <sup>2</sup> )
<b>Annelids</b>			
Oligochaetes			
December 1980	5.92		
February 1981	5.02		
April	3.88		
June	2.23		
August	1.36		
October	3.13		
Mean	3.6	6.6	23.7
<b>Leeches</b>			
December 1980	0.42		
February 1981	0.52		
April	0.34		
June	0.42		
August	0.37		
October	0.99		
Mean	0.5	3.4	1.7
<b>Snails</b>			
December 1980	0.83		
February 1981	0.85		
August	0.25		
October	1.73		
Mean	0.9	3.4	3.1

<sup>a</sup>Derived from published values (see text).

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mined insects (4.1 g dry weight/m<sup>2</sup>), the resulting 47 g dry weight/m<sup>2</sup> is close to the required prey production cited in the preceding paragraph. Given the uncertainties inherent in the various production estimates in this study, the closeness of the two values is likely fortuitous; however, it does suggest that estimated prey production in the ponds could be sufficient to support the estimated predator production.

Benke (1976) found that odonate production depended on a rapid turnover of a small standing crop of prey (primarily chironomids and mayflies). Other food resources (zooplankton, annelids, and snails) probably also contributed to the production of predator insects in our experimental ponds. Our results underscore the need for an accounting of all possible prey sources for predator insects. This accounting would be particularly important, for example, if one were to explain (1) reduced abundance or production of predators as an indirect result of effects on prey or (2) increased abundance or production of prey as an indirect result of reduction of predator insects.

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