LIFE HISTORY AND VARIABILITY OF SECONDARY PRODUCTION ESTIMATES FOR CORYDALUS CORNUTUS (MEGALOPTERA: CORYDALIDAE) IN AN OZARK STREAM

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ABSTRACT

In the Mulberry River, Arkansas, Corydalus cornutus (Megaloptera: Corydalidae) had a univoltine life history with ten larval instars. Secondary production estimates (size-frequency method) from three adjacent riffles ranged from 0.37 to 2.98 g/m²/yr dry weight, and annual P/B ratios ranged from 7.4 to 9.0. Production estimates calculated from reduced sample sizes yielded variable results but in general did not decrease production estimates. Production estimates for two of three riffles changed little when sample size was reduced by one-half. This study suggests that single riffle sampling regimes are inadequate and may produce misleading results. A proposal for a stratified, inter-riffle sampling design is offered.

Key Words: Corydalus cornutus, life history, secondary production, variability, Ozarks, Megaloptera, Corydalidae.

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The predaceous stream insect Corydalus cornutus L. (Megaloptera: Corydalidae) has been the subject of numerous life history and secondary production studies. While life history has been investigated for the species at both northern and southern locations (Chandler 1956, Brown and Fitzpatrick 1978), secondary production studies have been limited to southern regions. With the exception of studies in Georgia (Benke et al. 1984) and South Carolina (Smock et al. 1985) all previous production estimates are from Texas streams (Brown and Fitzpatrick 1978, Epperson and Short 1987, Short et al., 1987). Moreover, scant attention has been paid to variation in production estimates for C. cornutus. Epperson and Short (1987) estimated annual production for C. cornutus from five widely spaced sites in Guadalupe River, Texas, and Short et al. (1987) determined annual production for the species from four different south Texas streams. However, no one has addressed inter-riffle variation in production estimates from a limited stretch of stream, or investigated sampling effort with regard to optimizing production estimates.

The purpose of this paper is to examine the life history and inter-riffle variation in the abundance, standing stock biomass and secondary production of C. cornutus from a limited stretch of an Ozark stream. Variability of production estimates calculated from reduced sample sizes is also examined on an intra-riffle basis.

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METHODS AND MATERIALS

The Mulberry River, Arkansas, is one of the few Ozark streams that remains in a near pristine condition because the stream flows almost entirely through the Ozark National Forest and therefore receives little anthropogenic disturbance. A third order (Strahler 1957) stretch of the Mulberry River between Wolf Pen Recreational Area and Yale in Johnson County, Arkansas (Secs. 27 - 28, T 12 N, R 25 W), was selected as the study location. All samples and physical measurements were taken from three consecutive riffles at this location (riffles A, B and C from downstream to upstream). Large pools, approximately 30 m in length, separated the riffles. The three riffles were very similar in their physical characteristics including temperature, velocity, discharge and substrate (Table 1). A few large boulders were scattered about the stream channel. The riparian canopy was well developed, and aquatic vegetation was sparse.

Benthic samples were collected with a modified Hess sampler (0.1 m²; 243-μm mesh) (Waters and Knapp 1961) from August 1985 until 1986. On each sampling date, 12 samples were collected from riffle A, and six each were collected from riffles B and C. Samples were collected twice monthly May through October and monthly from November through March. No collections were made during April due to high water levels. The total annual number of samples collected was 216 from riffle A and 108 each were collected from riffles B and C.

Samples were preserved in the field with 10% formalin and returned to the laboratory where they were sorted under 10X magnification. All C. cornulus larvae were removed and enumerated, and the head capsule widths were measured (mm) at the eyes with an ocular micrometer mounted in a dissecting microscope. Specimens were grouped by instar and dried at 100° C for 24 h, cooled in a desiccator for an additional 24 h, and then weighed.

Secondary production was estimated using the size-frequency method (Benke 1984). The methodology of Krueger and Martin (1980) was used to calculate 95% confidence intervals. The cohort production interval (CPI) (Benke 1979) was estimated at 11 months. Portions of the life cycle not spent in productive stages including eggs until hatching and prepupal and pupal periods were subtracted from the life history length to arrive at the CPI. Values of 2 weeks for egg development until hatching and 1 week each for the prepupal and pupal stages were obtained from Brown and Fitzpatrick (1978).

In order to observe the effect of a reduction in sample size on production estimates, each sample from each riffle and sampling date was assigned a number (1-12 riffle A; 1-6 riffles B and C), and then randomized (Montgomery 1984) by sampling date. A group of three samples was then selected from the random order for both riffles B and C while groups of three, six and nine samples were chosen for riffle A. The data from these reduced sample groups were then used to estimate production assuming that mean instar weight remained constant.

RESULTS AND DISCUSSION

The population of C. cornulus in the Mulberry River exhibited a univoltine life history with approximately ten larval instars (Figs. 1 and 2). Brown and Fitzpatrick (1978), Epperson and Short (1987) and Short et al. (1987) all observed 11 distinct instars for C. cornulus in Texas streams. Although the single specimen that had a
Table 1. Physical characteristics of riffles in the upper Mulberry River, Arkansas.*

<table>
<thead>
<tr>
<th>RIFFLE</th>
<th>TEMPERATURE (°C)</th>
<th>VELOCITY (m/sec)</th>
<th>DISCHARGE (m³/sec)</th>
<th>MAJOR SUBSTRATE TYPE</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>20.7</td>
<td>1.14</td>
<td>3.4</td>
<td>Pebble, Cobble</td>
</tr>
<tr>
<td></td>
<td>(6.0-32.0)</td>
<td>(0.33-2.34)</td>
<td>(0.10-7.76)</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>20.6</td>
<td>0.06</td>
<td>-</td>
<td>Pebble, Cobble</td>
</tr>
<tr>
<td></td>
<td>(6.0-32.0)</td>
<td>(0.27-2.10)</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>20.6</td>
<td>1.05</td>
<td>-</td>
<td>Pebble, Cobble</td>
</tr>
<tr>
<td></td>
<td>(6.0-32.0)</td>
<td>(0.26-2.24)</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

* Values are means with ranges in parentheses. Substrate classification follows Wentworth (1922).
Fig. 1. Head capsule width frequency for *Corydalus cornutus* larvae from the Mulberry River, Arkansas, with instars indicated.

Fig. 2. Instar frequency distribution for *Corydalus cornutus* on each sampling date from the Mulberry River, Arkansas, August 1985-August 1986.
head capsule width greater than 9.5 mm could possibly be considered an eleventh instar, a more conservative approach was adopted and it was grouped with the tenth instars. Evans and Neunzig (1984) reported that *C. cornutus* is likely to have a 10-12 instars over its entire geographic range.

Emergence of adult corydalids at the Mulberry River location was documented from June through August. Warren et al. (1963) reported a similar emergence pattern for dobsonflies in northwest Arkansas. Egg masses (Baker and Neunzig 1968) were common on overhanging riparian vegetation and large boulders from late June through August, and a single unhatched egg mass was observed as late as 26 October. First instars were most prevalent during July and August but were collected from May through October, suggesting a broad range for adult emergence and oviposition. Individuals that hatch and start larval development late in the season (e.g., October) probably require an additional year to complete their development (Brown and Fitzpatrick 1978). No prepupae or pupae were collected during this study.

The univoltine life history reported here corresponds to that accounted by Brown and Fitzpatrick (1978), Benke et al. (1984), Epperson and Short (1987) and Short et al. (1987) but contrasts with the two- to five-year life histories reported by Chandler (1956), Knight and Simmons (1975), and Evans and Neunzig (1984). Smock et al. (1985) estimated a two-year life history for *C. cornutus* in South Carolina. It therefore appears that *C. cornutus* may be principally univoltine at southern latitudes with longer life histories probably occurring at more northern locations.

Secondary production estimates of *C. cornutus* differed substantially among adjacent riffles (Table 2). Production was greatest in riffle C (2.98 g/m²/yr) while the estimates for riffles A and B were markedly lower (0.37 and 0.90 g/m²/yr, respectively). However, given the broad overlap of 95% confidence intervals, none of the estimates can be considered statistically different (P > 0.05). Production variance was lowest for riffle A (2.19) in comparison to riffs B (5.53) and C (53.45).

In addition to the differences observed between riffles in production estimates, it was observed that larval instars were not equally represented in the three riffles. Only riffle C had the full complement of ten instars; only the first nine instars were found in riffle A, and only the first eight were collected from riffle B.

The secondary production estimates calculated for *C. cornutus* in this study compare favorably with those reported in the literature (Table 3). Of these, only the study of Brown and Fitzpatrick (1978) did not use the size-frequency method for estimating production.

Decreasing the number of samples used to calculate production yielded variable results depending on the number of samples eliminated and the riffle sampled (Table 2). For instance, when nine random samples from the original 12 collected from riffle A were analyzed, the production statistics remained essentially the same. A similar response was observed for riffles B and C. For riffle B, standing stock biomass and production increased after a reduction from six to three samples because the three samples that were randomly selected contained the greatest densities of larvae. When the sample number for riffle A was decreased to six or three, the production statistics departed considerably from the original 12-sample estimate.
Table 2. Secondary production estimates for *Corydalus cornutus* from the Mulberry River, Arkansas. August 1985-August 1986.

<table>
<thead>
<tr>
<th>RIFFLE</th>
<th>NUMBER OF SAMPLES</th>
<th>NUMBER OF INSTARS PRESENT</th>
<th>( \bar{N} ) (No./m²)</th>
<th>( \bar{B} ) (g/m²)</th>
<th>( P^* ) (g/m²/yr)</th>
<th>PRODUCTION VARIANCE</th>
<th>ANNUAL ( P/\bar{B} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>12</td>
<td>9</td>
<td>0.15</td>
<td>0.05</td>
<td>0.37 (± 2.96)</td>
<td>2.19</td>
<td>7.40</td>
</tr>
<tr>
<td>A</td>
<td>9</td>
<td>9</td>
<td>0.23</td>
<td>0.05</td>
<td>0.38 (± 3.54)</td>
<td>3.13</td>
<td>7.60</td>
</tr>
<tr>
<td>A</td>
<td>6</td>
<td>9</td>
<td>0.09</td>
<td>0.05</td>
<td>0.29 (± 3.89)</td>
<td>3.78</td>
<td>5.80</td>
</tr>
<tr>
<td>A</td>
<td>3</td>
<td>6</td>
<td>0.08</td>
<td>0.01</td>
<td>0.05 (± 1.13)</td>
<td>0.32</td>
<td>5.00</td>
</tr>
<tr>
<td>B</td>
<td>6</td>
<td>8</td>
<td>0.37</td>
<td>0.10</td>
<td>0.90 (± 7.08)</td>
<td>12.53</td>
<td>9.00</td>
</tr>
<tr>
<td>B</td>
<td>3</td>
<td>8</td>
<td>0.42</td>
<td>0.15</td>
<td>1.17 (± 12.50)</td>
<td>39.08</td>
<td>7.80</td>
</tr>
<tr>
<td>C</td>
<td>6</td>
<td>10</td>
<td>1.25</td>
<td>0.34</td>
<td>2.98 (± 14.62)</td>
<td>53.45</td>
<td>8.76</td>
</tr>
<tr>
<td>C</td>
<td>3</td>
<td>9</td>
<td>1.23</td>
<td>0.34</td>
<td>2.43 (± 16.13)</td>
<td>65.02</td>
<td>7.15</td>
</tr>
<tr>
<td>ALL</td>
<td>24</td>
<td>10</td>
<td>0.66</td>
<td>0.21</td>
<td>1.94 (± 6.67)</td>
<td>11.13</td>
<td>9.24</td>
</tr>
</tbody>
</table>

* Oven dry mass.

†Values in parenthesis reflect 95% confidence limits.
The three-sample arrangement for riffle A yielded the smallest annual \( P/B \) and smallest production variance calculated in this study, but the standing stock biomass and production estimate were grossly underestimated. One might expect production estimates to more closely parallel the actual values as more samples are used in calculations. However, the possibility that production estimates can get closer to the actual value by a decrease in sample size cannot be ruled out.

An artificial reduction in sample size such as that used in this study may have exaggerated production statistics in certain instances. Production estimates based on artificially reduced sample size should not be strictly interpreted without considering comparisons of all possible random sample combinations. However, the use of selected randomized comparisons suggests that at least in some instances smaller sample sizes can yield equally reasonable estimates of production as larger samples sizes.

Production also was estimated from the combined total of all 24 samples collected on each sampling date (Table 3). The 24-sample estimate is an inter-riffle average of production for the three riffles. However, the inherent variability actually present among adjacent riffles would have been masked if the individual riffles had not been considered separately.

The heterogeneous physical environment of lotic ecosystems can result in patchy distributions of aquatic invertebrates, in turn creating an enormous number of questions and problems for the investigator (Benke 1984, Morin 1985, Resh 1977, 1979). In addition to the problems associated with sampling the physical environment of streams, there also are varying degrees of error in the production methodology itself that are presently impossible or exceedingly difficult to measure (Benke 1984). Among these are statistical questions such as the merits of confidence limits (Hynes 1980, Short et al. 1987). Because the underlying interest in sampling for secondary production studies is to obtain reasonably precise if not accurate estimates, sampling strategy is of utmost importance. The investigator should therefore attempt to maximize the degree of confidence in standing stock estimates on any given sampling date (Benke 1984). This is especially true considering that such a great potential for sampling error exists. Stratified sampling designs have been proposed to address the problems of physical heterogeneity in streams (Benke 1984, Resh 1977). However, these stratified designs have dealt only with intra-riffle concerns such as differences associated with substrate size, vegetation and other microhabitats. The problems in estimating production associated with inter-riffle variation have not been fully addressed.

Selection of an individual riffle for a production study of an aquatic invertebrate can prove to be problematic. The variability encountered in this study exemplifies the potential problems that can arise. For instance, a production estimate based solely on samples collected from either riffle A or riffle C would have led to very different and perhaps erroneous conclusions in comparison to an analysis of all three riffle areas. Additionally, of the ten larval instars known to be present in this stretch of stream, only riffle C was represented by the full complement. Although the size-frequency method does not require the recognition of distinct instars (Benke 1984), the absence of particular instars when they are known to be present is an obvious source of error. The vast majority of secondary production estimates reported in the literature are based on single-riffle sampling designs.
Table 3. Summary of the secondary production literature for *Corydalus cornutus.*

<table>
<thead>
<tr>
<th>AUTHOR</th>
<th>METHOD†</th>
<th>VOLTINISM</th>
<th>( \bar{B} ) (g/m²)</th>
<th>P (g/m²/yr)</th>
<th>ANNUAL P/ ( \bar{B} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brown and Fitzpatrick (1978)</td>
<td>IGR</td>
<td>Univoltine</td>
<td>0.25</td>
<td>2.51</td>
<td>9.96</td>
</tr>
<tr>
<td>Benke et al. (1984)</td>
<td>SF</td>
<td>Univoltine</td>
<td>0.32</td>
<td>1.60</td>
<td>5.00 ‡</td>
</tr>
<tr>
<td></td>
<td>SF</td>
<td></td>
<td>(0.26-0.38)</td>
<td>(1.30-1.89)</td>
<td>-</td>
</tr>
<tr>
<td>Epperson and Short (1987)</td>
<td>SF</td>
<td>Univoltine</td>
<td>1.29 §</td>
<td>12.06</td>
<td>9.43</td>
</tr>
<tr>
<td></td>
<td>SF</td>
<td></td>
<td>(0.42-2.41)</td>
<td>(4.60-22.90)</td>
<td>(8.23-10.81)</td>
</tr>
<tr>
<td>Short et al. (1987)**</td>
<td>SF</td>
<td>Univoltine</td>
<td>0.82</td>
<td>8.21</td>
<td>10.02</td>
</tr>
<tr>
<td></td>
<td>SF</td>
<td></td>
<td>(0.19-1.46)</td>
<td>(1.62-13.19)</td>
<td>(8.60-11.90)</td>
</tr>
<tr>
<td>Smock et al. (1985)</td>
<td>SF</td>
<td>Semivoltine</td>
<td></td>
<td>0.05</td>
<td>2.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.002-0.84)</td>
<td>-</td>
</tr>
</tbody>
</table>

* Values are means with ranges in parentheses.
† IGR = Instantaneous growth method, SF = Size frequency-method.
‡ Estimated value.
§ Ash free dry mass.
** Based on four different Texas Streams.
Variability in benthic densities of aquatic invertebrates should ideally be estimated before undertaking a quantitative study such as secondary production estimation (Morin 1985, Resh 1979). However, time, energy and financial constraints generally prove pre-investigative work of this sort to be impractical. This particular study is not an exception. Use of a stratified sampling design that incorporates samples from several adjacent riffles may alleviate some of the problems. The number of samples collected from each of these areas would depend on factors such as size in area of the riffles, potential microhabitat and the time and financial limits of the study.

A reduction in sample size, as demonstrated in this study, need not have a negative impact on production estimates. For example, by artificially reducing the number of samples collected in this study to one-half of the actual number collected, a reasonable estimate of production was retained for two of three riffles. In other words, an approximation of the variability in inter-riffle production estimates could have been obtained with one-half of the sampling effort based on the random samples that were analyzed. The implications of such a reduction in sample size for other secondary production studies are obvious. The investigator should not necessarily decrease the number of benthic samples to be collected on a given sampling date but rather should not collect them all from one riffle. If the investigator elected to collect 12 samples per sampling data from a given stream, the samples should be taken from two or three riffles rather than from just one. The use of stratified, multi-riffle sampling regimes may provide more insight into the variability that can occur in production estimates among adjacent riffles. In turn, more confidence may be lent to future secondary production studies.

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