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Author(s): Clay Runck and W. Blinn

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Secondary production by *Telebasis salva* (Odonata) in a thermally constant aquatic ecosystem

CLAY RUNCK AND DEAN W. BLINN

Department of Biological Sciences, Northern Arizona University, Flagstaff,
Arizona 86011-5640 USA

Abstract. Annual production for the odonate *Telebasis salva* ($7.9 \text{ g dry weight [dw] m}^{-2} \text{ yr}^{-1}$, $\pm 2 \text{ SE} = 1.2$) was found to be an order of magnitude higher in the thermally constant ($21 \pm 4^\circ\text{C}$) ecosystem of Montezuma Well, Arizona, than production for multi-species damselfly assemblages in other aquatic ecosystems. *Telebasis salva* was univoltine in Montezuma Well; larval development took 270.1 d in the laboratory (21°C). Both production ($2.1 \text{ g dw m}^{-2} \text{ yr}^{-1}$) and mortality (62.2%) were highest for individuals 2-3 mm in body length. Mean annual biomass was 0.78 g dw/m^2 , annual P/B ratio was 10.0, cohort P/B was 7.5, and annual energy production for *T. salva* was $1.58 \times 10^5 \text{ J m}^{-2} \text{ yr}^{-1}$. Density, standing stock biomass, and production of *T. salva* were higher in the top 50 cm of the littoral water column than in the 50-100 cm stratum. Densities of a major prey (*Hyaella montezuma*, Amphipoda) and predator (*Belostoma bakeri*, Heteroptera) of *T. salva* nymphs were also estimated. Macroinvertebrate community production, trophic structure, and energy transfer in Montezuma Well are presented. Constant warm water temperature, abundant food, absence of fish, and high predation by invertebrates contribute to the high production rates of *T. salva* in Montezuma Well.

Key words: production, Odonata, damselfly, predation, energy, *Telebasis salva*, thermally constant, amphipod, *Belostoma*.

Few studies have examined secondary production of larval damselflies (Odonata:Zygoptera) despite the importance of these insects in freshwater communities (Lawton 1971, Benke et al. 1984, Gaines 1992, Dudgeon 1989a). In general, production estimates for odonates are fewer for lentic species than for lotic species (Table 7) which is surprising given the common occurrence of odonates in the littoral zone of lentic ecosystems. Larval damselflies are often abundant in such littoral zones and are both important generalist predators as well as prey for invertebrates and fish. Consequently, larval damselflies contribute to community production and are important intermediate links in food webs of freshwater littoral communities.

Telebasis species (Coenagrionidae) are widespread in southern and southwestern USA and are commonly associated with submerged macrophytes (Smith and Pritchard 1956, Pennak 1978, Westfall 1984). *Telebasis salva* is the most common of the two species in North America, but production estimates for this species are lacking.

Telebasis salva is the most abundant predaceous aquatic insect in the littoral zone of Montezuma Well, Arizona (Blinn and Sanderson 1989). High secondary production estimates have previously been reported for a predaceous

heteropteran, *Ranatra montezuma* (Runck and Blinn 1990), and an amphipod prey, *Hyaella montezuma* (Dehdashti and Blinn 1991), in the thermally constant environment of Montezuma Well. We undertook a study of secondary production by *T. salva* to compare production estimates of an odonate in a fishless, thermally constant environment with production estimates of odonates in other aquatic ecosystems. We also examined the role of *T. salva* in the trophic structure of Montezuma Well.

Study Site

Montezuma Well is a circular (112-m diameter), collapsed, travertine spring mound in north-central Arizona. The Well has a surface area of 0.76 ha, a mean depth of 6.7 m, and a maximum depth of 17 m. It has an isothermal water column with a mean annual water temperature of $21 \pm 4.0^\circ\text{C}$. The littoral zone (0.32 ha) is restricted to a 10-20-m wide shelf around the perimeter of the Well with an average depth of 1 m and supports a dense stand of *Potamogeton illinoiensis* Morong (Boucher et al. 1984). The absence of fish is presumably due to high dissolved CO_2 concentrations $>550 \text{ mg/L}$ (Cole and Watkins 1977, Boucher et al. 1984). Additional physiochemical data on Montezuma Well

were given by Cole and Barry (1973) and Boucher et al. (1984).

Methods

Population dynamics

We tested three collection methods for sampling *Telebasis salva* nymphs in the macrophytes. The high standing crop of submerged *Potamogeton* (annual range = 86–450 g dw/m², Runck and Blinn 1990) and a deep littoral water column in Montezuma Well made sampling difficult to perform at certain times of the year, e.g., early summer through fall. *Telebasis* species are characterized as climbers on aquatic macrophytes and *T. salva* nymphs have never been observed in littoral dredge samples in Montezuma Well.

The first method employed a stove pipe (20 × 50 cm) which harvested vegetation with associated fauna. The stove pipe was lowered over the vegetation to a depth of 50 cm, the enclosed vegetation was cut from below with grass clippers, and a tight-fitting lid was immediately placed on the bottom of the stove pipe. The central portion of the lid was nylon mesh (0.16 mm), which allowed water to drain but retained all organisms. The second and third methods employed a plankton net (154 μm mesh, 20 cm in diameter) to collect *T. salva* nymphs from two strata of the littoral water column: 0–50 cm and 0–100 cm. To perform the vertical net tows, the net was lowered to a depth of either 50 or 100 cm and pulled vertically to the water's surface along a different path from which it was lowered. The plankton net tows and the stove pipe sampled the same area (314.1 cm²), but the 50-cm tow and the stove pipe sampled half the volume (15.7 L) of the 100-cm tow (31.4 L).

Twelve stove pipe samples and 12 each for 50-cm and 100-cm tows were collected at 3-wk intervals (\bar{x} = 21 d between sample dates, range = 15–28 d) from 4 January 1990 to 31 December 1990 (18 dates, 362 d). Samples were collected at approximately equidistant points within the littoral zone around Montezuma Well between 1000 and 1430 h. Samples were preserved with FAA (formalin-alcohol-acetic acid, Pennack 1978) and sorted in the laboratory. Body length (excluding caudal lamellae) of *T. salva* nymphs was measured to the nearest 1 mm and nymphs were separated into 14 1-mm size classes.

Mortality of *T. salva* nymphs was calculated

as the percent loss between size classes, e.g., $1 - (n_{j+1}/n_j) \times 100$. Total larval mortality was calculated as the percent loss between the 1–2-mm and 12–13-mm size-classes, e.g., $1 - (n_{12}/n_1) \times 100$.

Densities of the primary prey (*Hyaella montezuma*, Crustacea:Amphipoda) and a major predator (*Belostoma bakeri*, Heteroptera:Belostomatidae) of *T. salva* nymphs in Montezuma Well were estimated in the littoral zone. Densities of juvenile (≤ 3 mm body length) and adult (≥ 4 mm) *H. montezuma* were estimated from 12 samples each for the 50-cm and 100-cm tows for only 17 of 18 dates. Density of *B. bakeri* was estimated from stove pipe, 50-cm, and 100-cm tow samples, 12 samples for each, for 18 dates.

Annual production

Thirty-four 1–2-mm *T. salva* nymphs were collected in May 1990 and reared in the laboratory to determine developmental time. Nymphs were reared individually in plastic dishes (53 mm diameter, 37 mm deep) with 40 mL of filtered water from Montezuma Well. Nymphs were maintained at $21 \pm 1.0^\circ\text{C}$ on a 16:8 h L:D photoperiod at a light intensity $18 \mu\text{Ein m}^{-2} \text{s}^{-1}$. Nymphs were fed ad libitum a mixture of amphipods (*H. montezuma*) and copepods collected from Montezuma Well. Prey were replaced daily and water was changed every 2 d. Molting events were recorded and nymphs were measured to the nearest mm. Sex of adults was also recorded.

The size-frequency method (Hynes and Coleman 1968, Hamilton 1969, Benke 1979, Hynes 1980, Waters and Hokenstrom 1980) was used to estimate annual production of *T. salva* following the procedures of Menzie (1980) and Krueger and Martin (1980):

$$P = \sum_{j=1}^{c-1} (N_j - N_{j+1}) \times (M_j \times M_{j+1})^{0.5} + (N_c) \times (M_c),$$

where P is the annual production, M_j is the mean mass of size-class j , c is the number of size classes ($j = 1$ to c), and N_j is the number of individuals that developed into size-class j during the year. Because the duration of each size class was unequal (i.e., non-linear growth), the P_c/P_s correction was used (Hamilton 1969, Menzie 1980). Menzie (1980) estimated N_j by:

TABLE 1. Comparison of the average areal and volumetric densities of *Telebasis salva* nymphs for the stove pipe, 50-cm net tow, and 100-cm net tow.

Method	n	Areal density (No./m ²)		Volumetric density (No./m ³)	
		\bar{x}	±SE	\bar{x}	±SE
Stove pipe	216	3947 ^a	±336	7892 ^a	±672
50-cm net tow	216	5118 ^b	±388	10,234 ^b	±776
100-cm net tow	216	4045 ^a	±315	4045 ^c	±315

Areal density: $F_{2,594} = 8.452$, $p < 0.001$. Letter superscripts indicate results of Student-Newman-Keuls Multiple Range test ($\alpha = 0.05$). Significant differences among means are indicated by different letters.

Volumetric density: $F_{2,594} = 61.688$, $p < 0.001$. Letter superscripts indicate results of Student-Newman-Keuls Multiple Range test ($\alpha = 0.05$). Significant differences among means are indicated by different letters.

$$N_j = n_j \times P_e/P_a \times (\text{growth period/CPI}) \times c,$$

where n_j is the mean number of individuals in size-class j , c is the number of size classes, P_e is the estimated proportion of the life cycle spent in each size class ($1/c$), p_a is the actual proportion of the life cycle spent in a particular size class, "growth period" is the number of days during the year over which production is estimated (362 d), and CPI is the cohort production interval (time from hatching to the attainment of the largest aquatic size class). We substituted Menzie's (1980) N_j term for the n_j term of Krueger and Martin (1980) in the production formula.

The duration of size classes obtained from rearing *T. salva* at 21°C was used to estimate P_a for each size class. Annual CPI of *T. salva* was estimated using laboratory rearing data for total larval duration of the first 12 size classes at 21°C. Production was calculated for nymphs ≤12–13-mm size class because all nymphs reared in the laboratory emerged to adults at or before this size class and nymphs >13 mm composed <1% of the annual larval population.

Individuals of each *T. salva* size class were collected from Montezuma Well and dried at 40°C to obtain mean individual dry weight (dw) biomass. Mean individual mass-at-loss was calculated as the geometric mean $(M_j \times M_{j+1})^{0.5}$ of two successive individual mass determinations of adjacent size classes (Krueger and Martin 1980). However, mean annual biomass (\bar{B}) was calculated using all 14 size classes of nymphs to avoid underestimation.

A 95% confidence interval (±2 SE) was computed for the secondary production estimate after the method described by Krueger and Martin (1980). To calculate the means and variances

described by Krueger and Martin (1980), and to incorporate the P_e/P_a data, we multiplied the raw field data (n_j per size class, sample, and date) by $P_e/P_a \times \text{growth period/CPI} \times c$, as described by Menzie (1980). This product can be viewed as a size-class-specific constant. Krueger and Martin (1980) described the following equation for the calculation of variance for the production estimate as:

$$v(P) = a^2 \times [G_1^2 \times v(n_{.1}) + \sum_{j=2}^{a-1} (G_j - G_{j-1})^2 \times v(n_{.j}) + (W_a - G_{a-1})^2 \times v(n_{.a})],$$

where a is the number of size classes (see Krueger and Martin 1980 for definition of all other terms). Since Menzie's (1980) calculation of N_j included the number of size classes (c), we deleted the a^2 term from the variance formula. We also substituted the N_j term described by Menzie (1980) for the n_j term of Krueger and Martin (1980) in the variance formula.

A Phillipson Oxygen Microbomb Calorimeter (Gentry Instruments, Aiken, South Carolina) was used to determine the energy value (joules/mg dry weight) of *T. salva* nymphs. The calorimeter was calibrated using benzoic acid. Organisms were air-dried to a constant weight at room temperature (25°C) in a desiccator and ground and pressed into pellets weighing 14.0 ± 0.5 mg.

Multivariate analysis of variance (MANOVA) was used to test for the effect of method on areal and volumetric density estimates for *T. salva*, *H. montezuma*, and *B. bakeri* using SYSTAT v.1.05 (Wilkinson 1989) with method (3) and date (18) as blocks. The Student-Newman-Keuls Multi-

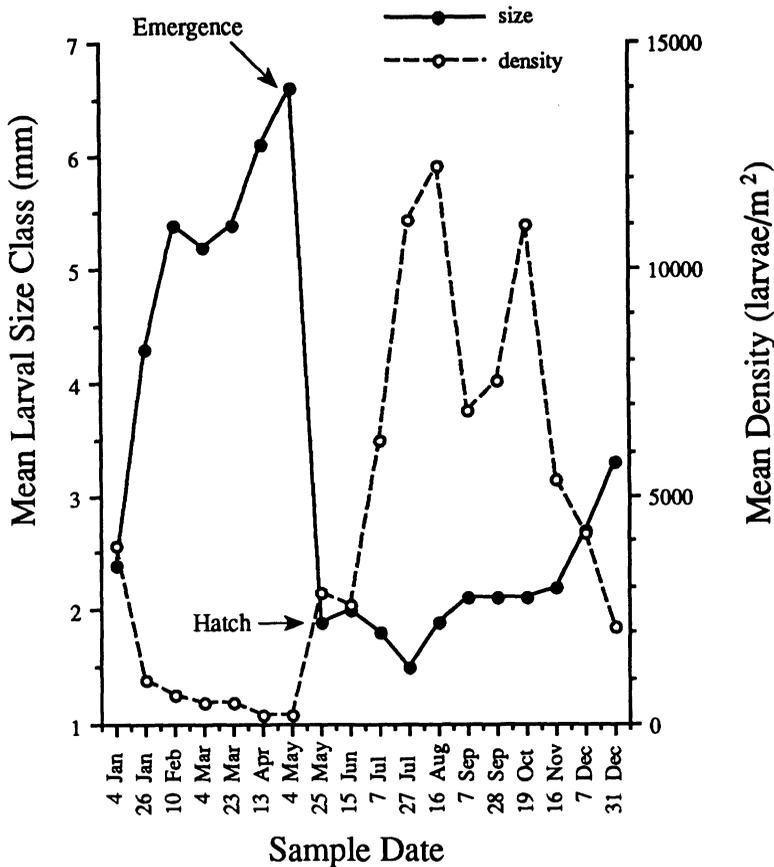


FIG. 1. Mean larval size-class (mm) and mean density (larvae/m²) for *Telebasis salva* by sample date in Montezuma Well, Arizona, 1990. Mean density is the pooled average for the three collection methods, based on 12 samples per collection method per sample date.

ple Range test (SNK MR test, $\alpha = 0.05$) was used to compare means among methods when indicated by MANOVA (Zar 1984).

Results

Statistical comparisons of the three collection methods revealed significant differences among estimates for areal ($p < 0.001$) and volumetric ($p < 0.001$) densities of *T. salva* nymphs (Table 1). The stove pipe, 50-cm, and 100-cm tow sampled the same area, but the 100-cm tow sampled twice the volume of the other two methods (see Methods). The estimated areal and volumetric densities of nymphs were significantly higher for the 50-cm tow than for either the stove pipe or 100-cm tow (SNK MR test). Areal densities estimated from the stove pipe and 100-cm tow

were equivalent (SNK MR test), but the volumetric density estimate was higher for the stove pipe than the 100-cm tow (SNK MR test). It was unclear which sampling method was the best with respect to estimation of *T. salva* density, so data for each method were pooled to avoid under- or overestimation. All results reported hereafter for *T. salva* are pooled results unless stated otherwise.

Telebasis salva was univoltine in Montezuma Well (Fig. 1), and had a long flight season with adults observed from early March through mid-November. The first major increase in 1-2 mm nymphs occurred in early May and the 1-2-mm size class made up 30 to 76% of the larval population until mid-December (Table 2, Fig. 1). The average (± 1 SE) density of *T. salva* nymphs was 4264 ± 346 nymphs m⁻² yr⁻¹ ($n = 648$),

TABLE 2. Length frequency (% of total N) distribution among size classes for *Telebasis salva* in Montezuma Well, Arizona, during 1990.

Date	Size class (mm)														Total N (No./m ²)
	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	13-14	14-15	
4 Jan	27	50	12	3	3	2	1	1	<1	<1	0	0	0	0	3910
26 Jan	2	20	34	19	11	2	3	2	2	2	2	1	<1	0	957
10 Feb	<1	9	29	27	14	4	3	3	2	2	3	2	1	<1	643
4 Mar	0	4	21	29	19	8	5	1	2	2	2	2	3	2	479
23 Mar	0	4	21	29	25	8	3	2	<1	<1	2	<1	2	2	469
13 Apr	0	0	7	21	32	17	8	3	<1	1	<1	0	4	5	209
4 May	12	<1	3	15	25	15	7	8	2	5	1	1	1	3	215
25 May	73	16	5	2	1	1	<1	<1	<1	<1	<1	<1	<1	<1	2896
15 Jun	45	40	7	3	1	<1	<1	<1	<1	<1	<1	<1	<1	<1	2582
7 Jul	73	17	5	2	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	6268
27 Jul	76	18	2	1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	11,087
16 Aug	49	41	7	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	12,301
7 Sep	45	33	15	4	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	6889
28 Sep	42	35	13	6	2	<1	<1	<1	<1	<1	<1	<1	<1	<1	7575
19 Oct	49	30	10	5	5	1	<1	<1	<1	<1	<1	<1	<1	<1	10,984
16 Nov	45	33	9	4	4	2	1	1	<1	<1	<1	0	<1	0	5355
7 Dec	29	41	13	5	3	2	2	2	1	<1	<1	<1	0	0	4181
31 Dec	7	44	19	9	7	4	3	4	3	1	<1	<1	<1	0	2111

with a seasonal range of 209 to 12,301 nymphs/m². Nymphs ≤3 mm in body length made up 81% of the annual density. Larval development continued throughout the year in Montezuma Well based on the occurrence of successively larger size classes during the winter months.

TABLE 3. Average duration ($\bar{x} \pm 1$ SE d) of larval size classes and size at eclosion for *Telebasis salva* reared in the laboratory at 21°C. Rearing started with 34 1-2 mm nymphs. M = male, F = female.

Size class (mm)	Duration (d) $\bar{x} \pm 1$ SE	Size at eclosion (mm) number/size class
1-2	18.9 ± 1.6	
2-3	12.5 ± 1.2	
3-4	16.1 ± 1.1	
4-5	10.3 ± 0.9	
5-6	13.7 ± 0.9	
6-7	21.0 ± 2.2	
7-8	19.8 ± 1.5	
8-9	22.8 ± 1.8	2 (1 M, 1 F)
9-10	33.3 ± 2.2	14 (9 M, 5 F)
10-11	29.7 ± 2.2	10 (4 M, 6 F)
11-12	31.5 ± 1.4	3 (0 M, 3 F)
12-13	40.5 ± 0.4	2 (2 M, 0 F)
Total	270.1 ± 1.6	31 (16 M, 15 F)

The largest size class observed in the field was 14-15 mm before spring emergence of adults after overwintering.

The average duration of larval development for *T. salva* from the 1-2-mm size class to adult emergence was 270 d in the laboratory at 21°C (Table 3), with ten instars before emergence. Rearing success was 91% in the laboratory, and sex ratio of adults was approximately 1:1. Nymphs molted into adults from four size classes. The largest size class observed in the laboratory was 12-13 mm, but most nymphs emerged as adults from 9-10-mm (45%) and 10-11-mm (32%) size classes, at 168 and 198 d, respectively. The number of days from the first appearance of 1-2 mm nymphs (early May) in Montezuma Well to the disappearance of adults (mid-November) is approximately 195 d. Therefore, a cohort of *T. salva* nymphs can complete development, i.e., 1-2-mm size class to adult emergence (9-11 mm), within this 195-d interval.

The pooled rate of production for *Telebasis salva* in Montezuma Well was 7.9 g dw m⁻² yr⁻¹ with a mean annual biomass of 0.783 g dw m⁻² (Tables 4 and 5). Based on the area of the littoral zone, the annual production of *T. salva* in Montezuma Well was 25 kg dw/yr. Production was highest for the 2-3-mm size class which ac-

TABLE 4. Correction of density estimates (n_j to N_j) for non-linear growth, as described by Menzie (1980), percent loss between size-classes, and mean annual biomass (\bar{B}) for *Telebasis salva* in Montezuma Well, Arizona, during 1990.

Size class (mm)	n_j (No./m ²)	% Loss ($n_j - n_{j+1}$)	M_j (mg dw/ animal)	\bar{B}_j (mg dw/m ²)	P_a	P_e/P_a	N_j (No./m ²)
1-2	2311.5		0.03	69.3	0.07	1.19	44,273.2
		52.2					
2-3	1104.3		0.07	77.3	0.05	1.80	31,980.5
		62.2					
3-4	417.3		0.13	54.2	0.06	1.40	9382.8
		56.9					
4-5	180.0		0.31	55.8	0.04	2.18	6326.2
		40.0					
5-6	107.9		0.54	58.3	0.05	1.64	2851.1
		54.4					
6-7	49.2		0.85	41.8	0.08	1.07	848.1
		41.9					
7-8	28.6		1.17	33.5	0.07	1.14	522.9
		30.0					
8-9	20.0		1.84	36.8	0.08	0.99	317.5
		30.0					
9-10	14.0		2.52	35.3	0.12	0.67	152.2
		15.7					
10-11	11.8		3.56	42.0	0.11	0.76	143.8
		22.0					
11-12	9.2		4.84	44.5	0.12	0.71	105.7
		—					
12-13	10.1		6.04	61.0	0.15	0.55	90.3
		—					
13-14	8.3		7.47	62.0			
		—					
14-15	13.5		8.27	111.6			
		—					
Σ	4263.9 larvae/m ²			783.4 mg dw/m ²			

n_j = mean number of larvae of size-class j /m², from field collections.

M_j = mean individual dry weight (dw) biomass (mg) of size-class j .

\bar{B}_j = mean standing stock biomass of size-class j [mg dry weight (dw)/m²].

P_a = actual duration of size-class j ($d = \text{days}$)/270.1 d.

P_e = expected duration of size-class j ($d = 1/12$).

$N_j = n_j \times (P_e/P_a) \times (362/270.1) \times c$; CPI = 270.1 d, c = number of size classes (12). N_j = the number of individuals that could be expected to develop into size-class j during the year.

% Loss = loss in number between size-class j and $j + 1$.

counted for 27.3% of the total annual production. Annual P/\bar{B} ratio was 10.0 and cohort P/\bar{B} ratio was 7.5. The rate of production for the stove pipe, 50-cm tow, and 100-cm tow was 6.7, 9.2, and 8.2 g dw m⁻² yr⁻¹, respectively.

The average (± 1 SE) energy value for *T. salva* nymphs was 20 ± 0.1 joules/mg dw ($n = 9$). The rate of annual energy production for *T. salva* was 1.58×10^5 J m⁻² yr⁻¹ and total energy incorporated into *T. salva* in Montezuma Well was 5×10^6 J/yr.

Significantly more amphipods (*Hyaella montezuma*) were collected by the 50-cm tow than the 100-cm tow (Table 6) and adult amphipods (≥ 4 mm) occurred at a significantly higher density than juveniles (≤ 3 mm).

The average (± 1 SE) density of *Belostoma bakeri*, pooled over the three collection methods, was 50 ± 2.6 animals m⁻² yr⁻¹ ($n = 648$) and ranged seasonally from 3 to 165 animals/m². The densities of *B. bakeri* differed significantly among collection methods for areal ($p < 0.001$)

TABLE 5. Annual secondary production for *Telebasis salva* in Montezuma Well, Arizona, during 1990, as estimated by the size-frequency method.

Size class (mm)	N_j (No./m ²)	ΔN_j	Geo-metric mean weight ($M_j \times M_{j+1}$) ^{0.5}	Production (mg m ⁻² yr ⁻¹)
1-2	44,273.2			
		12,292.7	0.05	563.3
2-3	31,980.5			
		22,597.7	0.10	2155.7
3-4	9382.8			
		3056.6	0.20	613.6
4-5	6326.2			
		3475.1	0.41	1421.8
5-6	2851.1			
		2003.0	0.68	1357.0
6-7	848.1			
		325.2	0.99	324.3
7-8	522.9			
		205.4	1.47	301.4
8-9	317.5			
		165.3	2.15	355.9
9-10	152.2			
		8.4	3.00	25.1
10-11	143.8			
		38.1	4.15	158.1
11-12	105.7			
		15.4	5.41	83.3
12-13	90.3			
		90.3	6.04*	545.4
Total				7904.9
			v(P) =	354,700.8
			95% C.I. = ± 2 SE = $\pm 2[v(P)^{0.5}] =$	± 1191.1

$N_j = n_j \times (P_c/P_a) \times (362/270.1) \times c$; CPI = 270.1
d, c = number of size classes = 12, n_j = number of larvae of size class j /m² from field collections.

$$\Delta N_j = N_j - N_{j+1}$$

Geometric mean weight (mg) = $(M_j \times M_{j+1})^{0.5}$; M_j = individual dry weight (dw) biomass (mg) of size-class j .

$$\text{Production} = \sum_{j=1}^{c-1} [(N_j - N_{j+1}) \times (M_j \times M_{j+1})^{0.5}] + (N_c \times M_c)$$

* = mean individual dry weight biomass (mg) of 12-13-mm larvae.

and volumetric ($p < 0.001$) estimates. The pattern of significance was the same for both areal and volumetric estimates, with the stove pipe collecting more animals than the 50-cm tow, which was greater than the 100-cm tow (SNK MR test).

Discussion

The annual productivity (7.9 g dw m⁻² yr⁻¹) of *Telebasis salva* in Montezuma Well is an order of magnitude higher than any previous estimate of production for damselflies and is comparable to that reported for multi-species assemblages of larval dragonflies (Table 7). Estimates of production for damselflies have ranged from 0.03 to 0.7 g dw m⁻² yr⁻¹ and from 0.42 to 8 g dw m⁻² yr⁻¹ for dragonflies. High production can result from either high standing stock biomass, rapid rate of biomass turnover, or a combination of both factors (Benke 1984). *Telebasis salva* displayed both high standing stock biomass and rapid biomass turnover rate.

The standing stock biomass ($\bar{B} = 0.783$ g dw/m²) of *T. salva* was substantially higher ($\geq 3 \times$) than has been reported for other damselfly species (Table 7), which range from 0.0018 to 0.28 g dw/m². As with production, standing stock biomass of *T. salva* is comparable to that reported for dragonflies, 0.115 to 2 g dw/m² (Table 7). Standing stock biomass was generally higher for smaller size classes ($\leq 5-6$ mm), but was fairly evenly distributed among all size classes.

The density of *T. salva* nymphs in Montezuma Well is higher than any estimate reported for odonate assemblages. The average density of *T. salva* nymphs was 4264 larvae m⁻² yr⁻¹ and ranged from 209 nymphs/m² in mid-April to 12,301 nymphs/m² in mid-August. Previously, McPeck (1990a) reported 1502 *Enallagma aspersum* nymphs/m² and total damselfly density (6 species) of 2100 nymphs/m² for a fishless Michigan reservoir during August. Benke and Benke (1975) reported over 1300 *Celithemis fasciata* nymphs/m² and total larvae dragonfly density (8 species) of over 1700/m² during July through September for a South Carolina pond that contained fish.

The density of animals, and presumably biomass and production, were higher in the top 50 cm of the littoral water column in Montezuma Well than in the 50-100 cm stratum. The 50-cm tow and stove pipe collected significantly more *T. salva* nymphs, *Belostoma bakeri*, and *Hyalella montezuma* (not counted for the stove pipe) on a volumetric basis than the 100-cm tow. The density of another major invertebrate predator, *Ranatra montezuma* (Heteroptera:Nepidae), was

TABLE 6. Comparison of the average (\pm SE) density of *Hyalella montezuma* estimated from the 50-cm and the 100-cm net tows. All data are based on 12 samples per method for 17 dates.

Method	<i>n</i>	Animals m ⁻³ yr ⁻¹					
		Adult and juvenile		Adult		Juvenile	
		\bar{x}	± 1 SE	\bar{x}	± 1 SE	\bar{x}	± 1 SE
50-cm net tow	204	5326 ^A	± 444	5698 ^a	± 506	4955 ^a	± 729
100-cm net tow	204	2849 ^B	± 183	3861 ^a	± 250	1836 ^b	± 248

Adult amphipods: body length ≥ 4 mm. Juvenile amphipods: body length ≤ 3 mm.

Method: $F_{1,782} = 34,716$, $p < 0.001$. Superscripts A and B indicate results of Student-Newman-Keuls Multiple Range test for total amphipods ($\alpha = 0.05$). Superscripts a and b indicate results of the Mann-Whitney *U*-test within a method, between ages of amphipods. Significant differences among means are indicated by different letters.

also significantly higher in the 0–20 cm stratum of the littoral zone than for the 20–100 cm stratum (Runck and Blinn 1990). Runck (1989) observed that the standing crop of *Potamogeton* in Montezuma Well was greater ($p < 0.001$) in the upper 50 cm of the littoral water column than in the 50–100 cm stratum. This difference is due to the absence of foliage on *Potamogeton* stems below 50 cm deep. The dense foliage in the top 50 cm of the littoral zone provides an abundant substratum for *T. salva*, *R. montezuma*, *B. bakeri*, and *H. montezuma*.

Overall community macroinvertebrate production is high in the fishless, constantly warm ($21 \pm 4^\circ\text{C}$) environment of Montezuma Well (Fig. 2). Annual production for the primary prey,

H. montezuma, in the Well was 215 g dw m⁻² yr⁻¹ (3.1×10^6 J m⁻² yr⁻¹, Dehdashti and Blinn 1991). *Ranatra montezuma* and *B. bakeri* also display high productivity. Annual production of *R. montezuma* averaged 1.0 g dw m⁻² yr⁻¹ for 1989 and 1990 (Runck and Blinn 1990) and 2.8 g dw m⁻² yr⁻¹ in 1990 for *B. bakeri* (unpublished data). Together, *T. salva*, *H. montezuma*, *R. montezuma*, and *B. bakeri* have a combined mean annual biomass of 12.3 g dw/m² and make up at least 85% of the total macroinvertebrate mean annual biomass in Montezuma Well.

The amphipod *H. montezuma* is the primary prey of *T. salva*, *R. montezuma*, and *B. bakeri* (Blinn and Runck unpublished data). *Telebasis salva* is also preyed on by *R. montezuma* and *B. bakeri*,

TABLE 7. Comparison of annual production (g dw m⁻² yr⁻¹) and mean biomass (g dw/m²) for larval odonates in aquatic ecosystems. Ranges represent more than one site or more than one year.

Number of species	Annual production (g dw m ⁻² yr ⁻¹)	Mean biomass	System	References
Damselfly				
1 species	7.9	0.78	Lentic	This study
1 species	0.7	0.18–0.28	Lentic	Lawton (1971)
1 species	0.2	0.03–0.03	Lotic	Dudgeon (1989a)
1 species	0.4	0.01–0.07	Lotic	Gaines (1992)
3 species	0.03	0.001–0.005	Lotic	Benke et al. (1984)
Dragonfly				
3 species	6.0	2.0	Lentic	Benke (1976)
10 species	5.5	0.53–0.58	Lotic	Benke et al. (1984)
1 species	0.01	0.19–0.21	Lotic	Wallace et al. (1987)
1 species	0.2	0.18	Lotic	Dudgeon 1989b
1 species	0.2	0.36	Lotic	Dudgeon 1989b

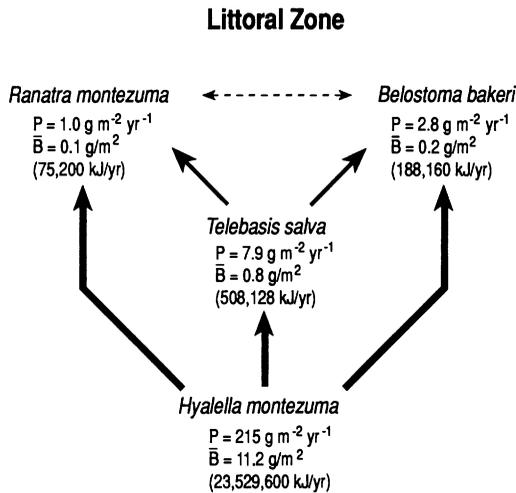


FIG. 2. Proposed trophic structure and energy flow in the littoral zone in Montezuma Well, Arizona. Thickness of arrows indicates the relative amount of energy transferred between organisms. P = annual production; \bar{B} = mean annual biomass; numbers in parentheses are energy values (kJ) derived from production estimates and the area of the littoral zone (0.32 ha)

but the active, swimming behavior of *H. montezuma* is more conspicuous to sit-and-wait predators such as *R. montezuma* and *B. bakeri* than the sit-and-wait behavior adopted by *T. salva* nymphs. Therefore, energy flow from *H. montezuma* to *R. montezuma* and *B. bakeri* may be greater than from *T. salva*.

The estimated prey production required to support the production of *T. salva* in Montezuma Well was $18.6 \text{ g dw m}^{-2} \text{ yr}^{-1}$. This quantity was estimated by dividing the annual production of *T. salva* ($7.9 \text{ g dw m}^{-2} \text{ yr}^{-1}$) by the product of assimilation and net production efficiencies of the damselfly nymph *Pyrhosoma nymphula*, because these parameters were not estimated for *T. salva*. Lawton (1970) reported assimilation and net production efficiencies for *P. nymphula* larvae of 85% and 50%, respectively, giving a gross production efficiency of 42.5%. We have already (Runck and Blinn 1990) estimated that $4.0 \text{ g dw m}^{-2} \text{ yr}^{-1}$ of prey production was necessary to support production of *R. montezuma*. Using the same assimilation (50%) and net production (50%) efficiencies for *B. bakeri* that we used for *R. montezuma*, we estimate $11.3 \text{ g dw m}^{-2} \text{ yr}^{-1}$ of prey production would be necessary to support production of *B. bakeri*. Based on the above calculations, production of

H. montezuma alone ($215 \text{ g dw m}^{-2} \text{ yr}^{-1}$) provides enough energy to support production of *T. salva*, *R. montezuma*, and *B. bakeri* ($33.8 \text{ g dw m}^{-2} \text{ yr}^{-1}$).

In Montezuma Well, mortality was higher for smaller size-classes of *T. salva* nymphs than larger size-classes (Table 4). In fishless systems, invertebrate predation would be expected to be greater on smaller size classes, whereas in systems containing fish, predation by fish would be greater on larger size classes. A 99.6% reduction in the density of *T. salva* nymphs occurred between the 1–2-mm and 12–13-mm size classes. Odonates typically have a larval mortality of 78 to 99.5% (Macan 1964, 1966, Lawton 1970, Benke and Benke 1975, Benke 1976).

Furthermore, mortality was higher for 2–3 mm *T. salva* nymphs (62.2%) than for 1–2 mm nymphs (52.2%) and may reflect the oviposition behavior of this species. *Telebasis* species commonly oviposit eggs in dense algal mats (Smith and Pritchard 1956), areas not generally inhabited by large predators (personal observations). Algal mats are abundant in the littoral zone of Montezuma Well during the summer and provide a physical refuge from larger predaceous insects for newly eclosed (1–2 mm) *T. salva* nymphs. Preliminary data showed the average (± 1 SE) size of *T. salva* nymphs in algal mats was $1.9 \pm 0.1 \text{ mm}$ ($n = 6$). As nymphs grow, they leave the algal mats to forage on larger prey (e.g., *H. montezuma*) not found in the mats and thereby experience higher predation mortality.

Components of mortality for *T. salva* nymphs could include lack of sufficient food, predation, and cannibalism of smaller individuals by larger size classes. The high production of *H. montezuma* suggests sufficient food is available for *T. salva*. The high density of *T. salva* nymphs may lead to a higher occurrence of intraspecific interactions between nymphs. These interactions may result in nymphs walking or swimming more often. Odonate larvae from fishless systems are generally more active (walking, swimming, behavioral displays) and thus more conspicuous than larvae from systems with fish (McPeck 1990b). Predation by *R. montezuma* and *B. bakeri* may be significant in the fishless Montezuma Well ecosystem if *T. salva* behaves in the pattern proposed by McPeck (1990b).

Cannibalism can be a major source of larval mortality for odonates (Johnson 1991). Al-

though we have no data on the incidence of cannibalism for *T. salva*, the asynchronous emergence and long flight season for *T. salva* resulted in considerable size overlap among co-occurring larvae (Table 2) and cannibalism could be expected to be important under these conditions (D.M. Johnson, East Tennessee State University, personal communication).

The annual P/\bar{B} ratio of 10.0 for *T. salva* was 2 to 4 times that reported for other odonate larvae. Annual P/\bar{B} ratios reported for damselfly larvae range from 2.5 to 5.1 (Lawton 1971, Benke et al. 1984, Dudgeon 1989a) and 2.7 to 5.0 for dragonfly larvae (Benke and Benke 1975, Benke et al. 1984, Wallace et al. 1987, Dudgeon 1989b). Annual P/\bar{B} is approximately equivalent to the biomass turnover rate, or turnover ratio, which is the amount of time to replace the biomass of the population. For *T. salva* the biomass turnover rate was 36.5 d based on an annual P/\bar{B} of 10.0.

Annual P/\bar{B} is dependent on the cohort production interval, CPI (Benke 1984). A short CPI results in a high annual P/\bar{B} and biomass turnover rate. A high annual P/\bar{B} could result from overestimation of production, underestimation of mean annual biomass, a combination of the two, or error in the CPI. The lab-derived CPI and P_a for *T. salva* may not be the same as for the field. However, the constant warm temperature of Montezuma Well probably reduces any error associated with rearing *T. salva* at a constant temperature in the laboratory. One possible source of error for the lab-derived CPI is the ad libitum feeding of the nymphs. Feeding rates were probably maximal in the rearing chambers because competitors and predators were absent and the escape space for prey was limited. However, rapid development of *T. salva* larvae in the field would not be surprising given the warm water temperature and abundant prey in Montezuma Well.

The cohort P/\bar{B} ratio for *T. salva* (7.5) was also high compared with other odonates. Cohort P/\bar{B} ratios for aquatic insects that emerge as adults from aquatic habitats are typically between 2 and 5 (Waters 1987). The amount of mortality incurred by a population has the greatest effect on the cohort P/\bar{B} ratio, with higher mortality resulting in higher P/\bar{B} ratios (Waters 1969, Allen 1971, Rigler and Downing 1984). Cohort P/\bar{B} can be overestimated by the same errors described for annual P/\bar{B} and if the P_e/P_a cor-

rection is not used with the size-frequency method (Waters 1987).

Our data suggest that high larval mortality (99.6%) contributes to the high cohort P/\bar{B} ratio for *T. salva*. Waters (1969) proposed that the ratio of final to initial population size, i.e., mortality, had the greatest effect on cohort P/\bar{B} and suggested that the expected ratio of final to initial population size for aquatic insects that emerge from the aquatic habitat might be approximately 10%. Using the annual density of 1–2 mm nymphs as the initial population size and the density of 12–13 mm nymphs as the final population size from Table 4, the ratio of final to initial population size is 0.4%, substantially lower than the 10% proposed by Waters (1969).

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