[1]MODULE 7: SECONDARY PRODUCTION OF MACROINVERTEBRATES

Introduction

Secondary production is the formation of heterotrophic biomass through time. Secondary production of heterotrophic organisms is a measure that is similar in concept to primary production of autotrophic organisms. The magnitude and dynamics of secondary production of an organism or a population are functions of bioenergetics. Bioenergetics deals with the capture and flow (or fate) of energy. Since bioenergetics involves energy flows, it is a dynamic property, and is an aspect of ecological function rather than structure (e.g., population density, community composition). In studies of invertebrate assemblages, organisms often have different life cycle patterns, some have only one generation per year, whereas others can have many generations per year. Thus, comparisons of two populations using estimates of population density and secondary production can give us very different pictures about those populations when organisms differ markedly in the number of generations that they produce during a year.

The relationship between production and other bioenergetic parameters can be represented by the equations

$$I = A + F$$

and

$$A = P + R + U,$$

where I represents ingestion; A, assimilation; F, food that is defecated (egestion); P, production; R, respiration; and U, excretion. In practice U is often ignored. Each of these terms are fluxes (i.e., flows) of energy or carbon, with units of energy $area^{-1}$ $time^{-1}$. For the individual organism P represents growth, whereas for populations P represents the collective growth of all individuals.

How much an organism grows in a time interval depends on how efficiently food is converted to new tissue. Two characteristics of an organism's bioenergetics determine this efficiency: assimilation efficiency (A/I) and net production efficiency (P/A). Among stream macroinvertebrates, A/I can be highly variable (5 to 90%), whereas P/A is often close to 50%. [Note that the % of food an individual converts to production is A/I times P/A or P/I.] Historically, studies on the production of different types of organisms have used varying units

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to represent secondary production. In macroinvertebrate studies, units of dry mass or ash-free dry mass area^{-1} time^{-1} are typically used and these can be converted to other units such as energetic units (e.g., kcal m^{-2} year^{-1} or kJ m^{-2} year^{-1}).

To appreciate the concept of secondary production, it is important to understand the relationship between production and biomass. Biomass (B) is a measurement of how much living tissue mass (for an individual or a population) is present at one point in time (or averaged over several periods of time) and its units are mass (or energy) per unit area (e.g., g m^{-2}). Production (P), on the other hand, is a flow, the amount of biomass per unit area produced in a time period (e.g., g m^{-2} year^{-1}). Consequently, P/B is a rate, with units of inverse time (e.g., year^{-1}). [Take a minute to verify this yourself.] Production can be calculated for any time unit of interest, thus, weekly, monthly or yearly estimates can be made. Production takes into account the development time of an organism (or population) and, all else being equal, the shorter the development time the higher the P/B ratio.

In this laboratory we will calculate production of macroinvertebrates using two techniques. We will use existing data to do these calculations. This laboratory has been modified from Benke (1996) and data has been taken from Ross and Wallace (1981) and Marchant (1986).

Methods

The measurement of secondary production of stream macroinvertebrates often does not require much more information than is taken during a basic study of populations (e.g., quantitative samples taken at regular time intervals). The methods for estimating production can be divided into two basic categories: cohort and noncohort. Cohort techniques are often employed when it is possible to follow a cohort (i.e., individuals that hatch from eggs within a reasonably short time span and grow at about the same rate) through time. When this is not possible an noncohort technique must be used.

Exercise 1: Cohort technique

If one follows an individual cohort through time one can recognize a general decrease in density (N) due to mortality and increase in individual mass (W) due to growth (Figure 1). In this situation, the production between two sampling dates (i.e., the interval production) can be easily calculated directly from the field data as the product of the mean density between two sampling dates (Mean N) and the increase in individual mass (ΔW) or Mean N times ΔW. If we assume (or we know) that there is only one generation per year then annual production is most easily calculated as the sum of all the interval estimates:

$$P = \sum \text{Mean } N\Delta W$$

which is called the *increment summation method*. We can also examine production patterns throughout the year by determining mean daily production for each interval by dividing Mean $N\Delta W$ by the days in the interval.

There are other methods of examining cohort production (Benke 1996); however, we will use only the *increment summation method*. The data for this part of the laboratory are from a study of the caddisfly *Brachycentrus spinae* (Ross and Wallace 1981). Data Table 1 includes the date collections were made, the density of organisms (N = No. m^{-2}) and mass of individuals
(W; mg).

Using columns 2 and 3 from Data Table 1, plot the mortality-individual mass graph. Construct it as in Figure 1; however, make sure to plot the x-axis with the exact number of days between each sampling interval instead of the constant value used in Figure 1. Finish the calculations on Data Table 1 using the instructions in the text and on Data Table 1.

Calculate Annual P by summing the "Interval P" column in Data Table 1. Annual B is estimated for you from monthly means since the sampling regime involved both monthly and bimonthly samples. Remember Annual B is just the average biomass estimated from the average of samples at a point in time.

Annual B = 39.9 mg/m^2

Annual P =

Annual P/B ratio =

Exercise 2: Noncohort technique

When a population cannot be followed as a cohort from field data (which might occur if the reproductive period is extended over a long time or for other reasons), it is necessary to use a noncohort technique to estimate secondary production. Noncohort methods are necessarily more complex than cohort methods. There are two different methods to estimate secondary production from noncohort data, but the *size-frequency method* has been used more than any other method and it is the method that we will use today. The *size-frequency method* requires an independent estimate of development time (the time required to take the organism from hatching to final size). **The *size-frequency method* is based on the assumption that a mean size-frequency distribution, which is determined from many samples collected throughout the year (average of the number of individuals or densities found in different size categories at different times throughout the year), can be used to approximate a mortality curve for an average cohort.** [Note: if you plot the size categories on the x-axis versus the frequency of each on the y-axis, then the frequencies should decline with size.]

We will use the data from Marchant (1986) on the stream mayfly (*Tasmanocoenis tonnoiri*). Plot a graph of the size-frequencies of Data Table 2. Use length as a class variable on the x-axis and make the height of the bars (frequencies) the height of the density of that size class. Using the following instructions complete Data Table 2. The decrease in density (ΔN) from one size (i.e., in this case length) category to the next is multiplied by the mean mass between size categories (MEAN W). Biomass is calculated as the sum of the biomass column. Note that in the last column, each value is multiplied by the total number of size classes (in this case 6). We do this because it is assumed that there is a total development time of one year and that there are the same number of cohorts during the year as size classes. Cohort production (P) is just the sum of the last column. [Note: disregard the negative value, see comment on Data Table 2.] Cohort P/B is equal to Cohort P divided by B. In this case where production assumes a 1 year life span.

B =

Cohort P =

Cohort P/B =

If development time is much different than 1 year, it is necessary to apply a correction factor to the sum of the last column. In this case this involves multiplication by YEARLY TIME INTERVAL/CPI where CPI (the cohort production interval) is the mean development time from hatching to final size. Units of the yearly time interval must match the units of CPI. In this example Marchant estimated the mean CPI to be 5 months, thus the Cohort P value must by multiplied by 12/5 to get annual production. CPI can be estimated from field data or experimentally determined.

Annual P =

Annual P/B =

Assignment:

Turn in your graphs and completed tables with all the above calculations on the bottom of each Data Table at the end of class (or during next laboratory period if indicated by instructor). Answer the following short answer questions and turn them in with your data.

1. Why might secondary production be a better response variable for comparative or experimental studies than density or biomass? [Hint: you can use your calculations from Data Table 2 to justify this.]

2. Under what conditions is it necessary to use a correction factor (CPI) in the size-frequency method if the development time is much less than 1 year? Should a correction factor be used for populations in which development time is greater than 1 year?

References

Benke, A.C. 1996. Secondary production of macroinvertebrates. Pp. 557-578, In, Hauer, F. R. and Lamberti, G.A. (Eds.) Methods in Stream Ecology, Academic Press, NY.

Marchant, R. 1986. Estimates of annual production for some aquatic insects from the La Trobe River, Victoria. Australian Journal of Marine and Freshwater Research 37: 113-120.

Ross, D.H. and Wallace, J.B. 1981. Production of *Brachycentrus spinae* Ross (Trichoptera: Brachycentridae) and its role in seston dynamics of a southern Appalachian stream (USA). Environmental Entomology 10: 240-246.

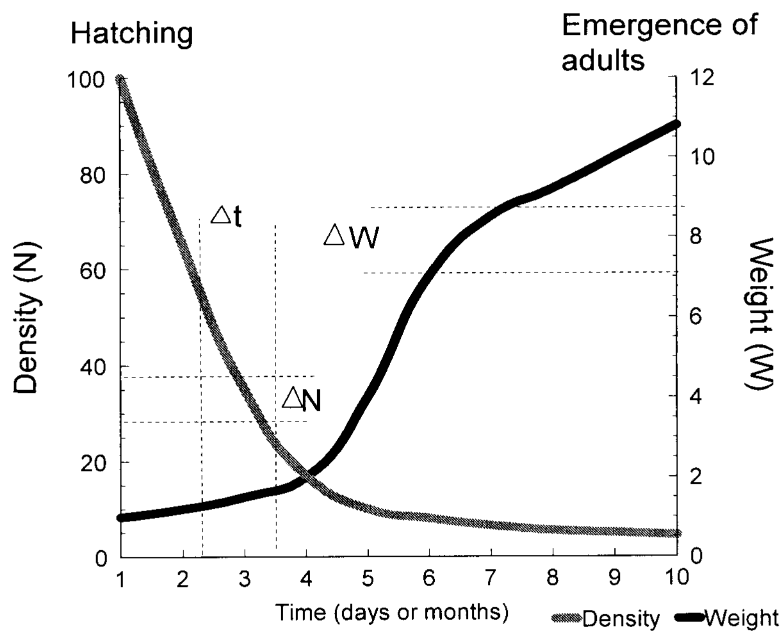

Figure 1. Hypothetical cohort of a stream insect showing curves of individual growth in mass (W) and population mortality (N) (modified after Benke 1984).

DATA TABLE 1

DATE	DENSITY (No/m^2) N	INDIVIDUAL MASS (mg) W	BIOMASS (mg/m^2) N X W	INDIVIDUAL GROWTH $\Delta W = W_I - W_{I-1}$	MEAN N (No./m^2) $(N_I + N_{I-1})/2$	INTERVAL P (mg/m^2) (MEANNΔW)	TIME INTERVAL (Days) Δt	DAILY P (mg m^{-2} day^{-1}) (MEAN N$\Delta W/\Delta t$)
18 May*	282.9	0.021	5.9	XXXXXXXX	XXXXXXXX	XXXXXXX	XXXXXXX	XXXXXX
1 Jun*	226.8	0.057	12.9	0.036	254.9	9.17	14	0.66
13 Jun	181.9	0.088					12	
29 Jun	138.5	0.173					16	
13 Jul	109.2	0.352						
26 Jul	87.5	0.940						
17 Aug	60.2	1.206						
30 Aug	48.3	1.796						
15 Sep	36.8	1.821						
3 Oct	27.1	3.199						
14 Nov	13.0	3.557						
7 Dec	8.8	4.631						
27 Jan	3.8	6.853						
17 Feb	2.6	8.477						
13 Mar	1.7	11.548						
27 Apr	0.0	14.800						
XXXX	XXXXX	XXXXXX	XXXXXXX	XXXXXXXX	XXXXXXX	Annual P = $\sum$	XXXXXXX	XXXXXX

*Some numbers in these rows may be slightly different from what you calculate due to rounding errors.

Annual B = 39.9 mg m^{-2} Annual P = Annual P/B =

DATA TABLE 2

LENGTH (mm)	DENSITY ($No./m^2$) N	INDIVIDUAL MASS (mg) W	NO. LOST ($No./m^2$) ΔN	BIOMASS (mg/m^2) N X W	MASS AT LOSS (mg) MEAN W = $(W_I + W_{I-1})/2$	BIOMASS LOST (mg/m^2) MEAN WΔN	TIMES NO. SIZE CLASSES 6(MEAN WΔN)
0.5	706.0	0.001	XXXXXXX	0.71	XXXXXXX	XXXXXXX	XXXXXXX
1.5*	848.0	0.02	-142.0	17.0	0.011	-1.49	(-8.95)a[#]
2.5*	118.0	0.08	730.0				
3.5	46.0	0.18					
4.5	4.0	0.35					
5.5	0.3	0.52					
XXXXXXX	0	0		XXXXXXX			
XXXXXXX	XXXXXXX	XXXXXXX	XXXXXXX	B = $\sum$	XXXXXXX	XXXXXXX	Cohort P = $\sum$

*Some numbers in these rows may be slightly different from what you calculate due to rounding errors.

[#] Negative value at top of table (far column) disregard since it is probably an artifact caused by inefficient sampling of the smallest size class or rapid growth through size interval.

B =

Annual P = 12/5 (Cohort P) =

Cohort P =

Annual P/B =

Cohort P/B =