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# THE STRUCTURE AND DYNAMICS OF CONE SPRING<sup>1</sup>

LAURENCE J. TILLY<sup>2</sup>

Zoology Department, University of Iowa, Iowa City

## TABLE OF CONTENTS

INTRODUCTION .....	169	<i>Pentaneura</i> sp. ....	180
MATERIALS AND PROCEDURES .....	170	Taxonomy and Life History .....	180
Physical and Chemical Factors .....	170	Trophic Position .....	180
Biotic Sampling .....	170	Physiological Data .....	180
Detritus .....	171	Net Production .....	180
Sampling Adequacy .....	171	Energy Flow .....	181
Energy Budget Formulation .....	171	<i>Phagocata velata</i> .....	181
Caloric Equivalents .....	171	Taxonomy and Life History .....	181
Respiration .....	171	Trophic Position .....	181
Community Respiration Measurement .....	172	Physiological Data .....	181
Net Primary Production Measurement .....	172	Net Production .....	182
Net Secondary Production Measurement .....	172	Energy Flow .....	182
Emergency Measurements .....	173	<i>Cardiocladius</i> sp. ....	182
PHYSICAL DESCRIPTION OF THE HABITAT,		Taxonomy and Life History .....	182
CONE SPRING .....	173	Trophic Position .....	182
BIOLOGY OF SPECIES POPULATIONS .....	173	Physiological Data .....	182
Flora .....	173	Net Production .....	182
Growth and Net Production in Major		Energy Flow .....	184
Producer Species .....	176	Community Energy Flow .....	184
<i>Bacopa rotundifolia</i> .....	176	Food web Approach .....	184
<i>Lemna minor</i> .....	176	Primary Production .....	184
<i>Impatiens capensis</i> .....	176	Detritus .....	184
Fauna .....	177	Allochthonous Import .....	184
<i>Gammarus pseudolimneus</i> .....	177	Primary Consumers .....	184
Taxonomy and Natural History .....	177	Secondary and Tertiary Consumers .....	185
Trophic Position .....	177	Decomposers .....	185
Physiological Data .....	177	Community Respiration .....	185
Net Production .....	177	Organic Export .....	186
Energy Flow .....	178	Energy Budget Summary .....	186
<i>Frenesia missa</i> .....	178	Efficiencies .....	187
Taxonomy and Natural History .....	178	Community Structure .....	188
Trophic Position .....	179	Spatial Distribution of Species .....	188
Physiological Data .....	179	Vertical Distribution .....	189
Net Production .....	179	Dispersion Pattern .....	189
Energy Flow .....	179	Species Diversity .....	189
<i>Physya integra</i> .....	179	Relative Species Abundance .....	190
Taxonomy and Life History .....	179	DISCUSSION AND CONCLUSIONS .....	192
Trophic Position .....	179	SUMMARY .....	194
Physiological Data .....	180	ACKNOWLEDGMENTS .....	195
Net Production .....	180	LITERATURE CITED .....	195
Energy Flow .....	180		

## INTRODUCTION

"Ecosystems" are unit ecological systems comprised of organisms interacting within their particular environments, cycling matter and transforming and

<sup>1</sup> Manuscript first received April 4, 1967. Accepted for publication December 21, 1967.

<sup>2</sup> Present Address: Department of Biological Sciences, The George Washington University, Washington, D. C. 20006.

degrading energy (Odum, 1959). Communities are the biotic components of ecosystems (Macfadyen, 1963) and are in turn comprised of ". . . populations coexisting in time and space, mutually regulative and interdependent, and depending ultimately upon some common energy source" (Engelmann, 1961).

The ecological analysis of ecosystems has recently occupied the attention of a number of workers (Hirston & Byers, 1954; Odum, 1957; Teal, 1957, 1962; Englemann, 1961; MacArthur, 1957). Most of these studies may be categorized as being either "structural" or "functional" in their approach.

Traditionally and practically, the two approaches to community study have remained separate, but gradually a body of theory has emerged which permits and demands unification of the two points of view. For example, Hirston, Smith & Slobodkin (1960) and Hirston (1964) have advanced a series of generalizations relating community organization to energy flow and competition. They propose that most if not all aspects of (terrestrial) community organization are a consequence of the fundamental energy limitation of the biosphere and, further, deduce from available evidence that the abundance levels maintained among the member species of terrestrial communities are determined largely by food chain considerations in which herbivores are predator limited.

MacArthur (1957) has suggested a series of biologically based mathematical models describing the organization of the community in terms of possible arrangements of niches (Hutchinson, 1957). MacArthur's models require that all the species of a community be included in an analysis.

Structural approaches in general require that as much as possible be known about the relationship between numbers of species, numbers of individuals and patterns of dispersion. Functional studies require metabolic information. It is essential, therefore, in order to test or formulate hypothesis about the functional and structural organization of communities to collect a body of data including both kinds of information about all the species found in one community. Hirston (1959), in stressing the importance of measuring relative species abundance in studies of community structure, remarks ". . . there is no justification other than convenience for omitting any species from an analysis of a community."

The purpose of the present study, therefore, was to keep sight of species while combining features of both the structural and functional approaches to secure data for use in the analysis of a simple community.

The suitability of springs as objects of ecological study has been discussed by Teal (1957) and Odum (1957), both of whom worked with relatively constant temperature systems to develop pictures of community metabolism.

Because of its small size, discrete character and promise of providing relatively constant physical and chemical conditions, an isolated and unnamed

cold spring near Conesville, Iowa, was selected as the site for study during the interval from July, 1961 through December, 1964 and named for purposes of this study "Cone Spring." A description of the conditions characteristic of this ecosystem follows in a later section.

## MATERIALS AND PROCEDURES

### PHYSICAL AND CHEMICAL FACTORS

Bimonthly or weekly measurements were made of dissolved oxygen, pH, CO<sub>2</sub>, total alkalinity, water and air temperatures, rate of discharge and export of particulate organic matter. Measurements of other chemical factors, (notably ortho-phosphate and nitrate nitrogen) were made with sufficient frequency to estimate seasonal levels.

Except for measurements of discharge and particulate organic matter all procedures were conventional ones as outlined by Welch (1948) or "Standard Methods" (APHA, 1960). All determinations were made in the field when practicable or completed at the laboratory within several hours of the time of collection.

The rate of discharge was measured directly by collecting the entire outflow of the spring in a calibrated pan and determining the time necessary to secure ten liters. The outflow could be collected because a plywood and aluminum flume had been constructed at the point where the spring basin narrowed to become a brook. The flume did not alter the flow gradient within the spring basin since it was placed at the original grade level and only the stream bed immediately downstream was excavated to permit insertion of the collecting pan below the flume.

Particulate organic matter in the outflow collected was measured by the method of Pennak (1949) using a Sharples Model T1 continuous flow centrifuge at 35-50,000 rpm. No correction was necessary for loss of carbonates since none were present.

### BIOTIC SAMPLING

Starting in October, 1962, and continuing at about 5-day intervals during the study period, core samples were removed from randomly-selected sites in the spring basin. The corer used was a rectangular sheet metal box having open square ends 5 cm on a side. Since the water was shallow and the substratum sandy, it was possible to enclose and remove a complete vertical section of the habitat with this device. The cores were usually 15 cm and never less than 5 cm long. Earlier tests had shown that none of the organisms with which this study is concerned were found at depths greater than 5 cm below the surface of the sand.

Cores were extruded into plastic boxes, covered with strained spring water and transported in insulated containers to the laboratory. In the laboratory sample boxes were held at spring temperature until within a day extraction procedures were begun.

Removal of macroscopic organisms from the sample units involved screening, elutriation and hand

sorting. The elutriated and decanted water was passed finally through a number 40 (U.S. Sieve Series) screen to remove quantitatively all organisms whose minimum body dimension in any direction was greater than about 0.5 mm. Animals so removed were sorted to species, counted, blotted with filter paper and weighed following procedures outlined by Teal (1956). In addition, length measurements to the nearest mm were made for most forms by means of a ruled plastic grid. The proportions of individuals of each length were recorded. For *Gammarus*, records were also kept of the relative proportions of males and females as well as gravid and precopular forms.

Plant parts, including roots, were separated according to species, placed in tared crucibles, dried in an oven at 106° C, allowed to equilibrate in a dessicator, weighed, incinerated in a muffle furnace at 650° C, returned to the dessicator to equilibrate once more and reweighed. Ash free dry weights (AFDW) were recorded for each species.

The abundances of microscopic plants and animals were estimated by means of Sedgewick-Rafter cell counts of subsamples from a strained residue.

Original sampling data for all species are recorded in an appendix of a Ph.D. thesis on file at the State University of Iowa Zoology Library.

#### DETRITUS

A large amount of organic debris was found in all sample cores. By the second month of the study, I began to estimate the quantity of this debris.

Screening removed the bulk of such debris but an important fraction of more finely-particulate material was finally recovered by a #12 plankton net. In this study "detritus" includes all of the organic materials exclusive of macroscopic organisms which could successfully be removed by the extraction procedures described above. After the plankton net concentrate was sub-sampled and allowed to settle, the supernatant was siphoned off. The remaining debris and the larger pieces picked out during hand-sorting were flushed into enameled pans and evaporated to dryness at 106° C. The dried remains were scraped into smaller evaporating dishes and crucibles. Ash free dry weights were then determined for detritus following the same procedures outlined above for live plant remains.

#### SAMPLING ADEQUACY

Application of the species-area curve (Cain, 1938) to the sampling data indicated that the critical point at which a 10% increase in area sampled produced an increase of 10% or less in species added was reached after only 3 sample units were counted. Monthly samples all included from 5 to 10 units and hence exceeded the conventional requirement for being "adequate".

Although sampling variance was found to be high in monthly samples of most species, this is to be expected in sampling from clumped distributions (DeBauche, 1962). The sample means in the present

study were assumed to be close approximations of the true population means.

#### ENERGY BUDGET FORMULATION

Slobodkin (1962) reviewed the theory of energy budgets and suggested the simplest steady-state budget to be  $I = R + Y$  where  $I$  is income or assimilation of energy;  $R$  is heat loss as a function of respiration and  $Y$  is yield, any energy-containing products leaving the population. These components of the budget are described below in reference to the methods used to estimate each of them for use with Cone Spring populations.

#### CALORIC EQUIVALENTS

The energy flow formulation demands that all budget items be expressed in comparable units. Calories or other energy units are most convenient because of their complete interchangeability.

A number of studies concerned with the determination of caloric values of animal and plant tissues (Golley, 1961; Slobodkin & Richman, 1961; Comita & Schindler, 1963) have shown that plants tend to have caloric values very close to 4 kcal/gm AFDW whereas animals tend quite uniformly toward values of 5-6 kcal/g AFDW (Golley, 1961; Slobodkin, 1962). It is probably justifiable to apply published values of caloric equivalents to biomass data as done in the present study (Golley, 1961).

Caloric equivalents used here were secured from: (1) Published values for the same or closely related species; (2) Average caloric values for a particular group of animals calculated from a series of published values; (3) The "physiological values" (Zoethout & Tuttle, 1952) of fats, carbohydrates and proteins applied to published or experimentally-secured values for the chemical composition of aquatic organisms; (4) Ivlev's (1934) wet oxidation technique for the determination of caloric values of organisms used to determine the caloric value of *Bacopa rotundifolia*. Ivlev (1934) found a nearly constant relationship of 3.38 kcal liberated per gram of O<sub>2</sub> consumed.

#### RESPIRATION

I estimated respiration from laboratory measurements of oxygen consumption, from published values for respiratory rates of closely-related forms and, in some cases, averages calculated from published values for a series of related organisms. I chose literature values secured from organisms living under conditions roughly comparable to those in Cone Spring.

Laboratory determinations of oxygen consumption were made for several of the Cone Spring forms using the method of Ewer (1941). Freshly-secured animals were placed in a 10 cc syringe filled with spring water, the initial dissolved oxygen content was determined by use of the micro-Winkler technique (Fox and Wingfield, 1938), and the syringe and contents allowed to remain at spring temperatures for 1 to 3 hours. Following this interval, which was sufficient to permit a measurable oxygen uptake to have occurred without seriously lowering oxygen

tensions, the oxygen content of the water was again determined. Such measurements could not be made in the field because of the difficulty of securing a large enough number of individuals without laboratory extraction procedures. All values for oxygen uptake were converted to a caloric equivalent using Ivlev's (1934) average oxyacalorific coefficient.

The caloric equivalents of respiratory rate/mg wet weight of organism were applied to the mean standing crop values for each organism to secure a population estimate of energy transformation per hour which was multiplied by the appropriate factors to give monthly values. Monthly values were summed to give an estimate of annual respiration. The respiration of the crop that died was estimated following the procedure used by Teal (1957).

#### COMMUNITY RESPIRATION MEASUREMENTS

Two approaches to the measurement of community respiration were made in the Cone Spring study. The first, an attempt to use Odum's (1956a) flow respirometry, was unsuccessful because emergent plants could exchange gases directly with the atmosphere, and also because in this small, very shallow, and rapidly flowing system, diffusion apparently masked any changes in dissolved oxygen concentration which may have been produced by the organisms present.

Dark bottle incubation of entire sample units was more successful. To use this method, freshly secured samples were placed in screw-cap jars of about 1500 cc capacity and covered with water secured from the outflow. A micro-Winkler sample (Fox & Wingfield, 1938) was withdrawn from the water within the jar to serve as a reference value for initial dissolved oxygen. The sampling syringe was equipped with a #20 mesh bolting cloth filter to prevent the accidental removal of organisms or debris. The 10 cc water sample was replaced with water from the same source, the jar was carefully capped to avoid introduction of any bubbles, wrapped in aluminum foil to prevent light from entering and allowed to remain for one hour in the water flow below the spillway. After 1 hour, the jar was carefully opened and several micro-Winkler samples quickly removed and fixed, or on other occasions one large sample was siphoned off for regular Winkler analysis.

Microorganism respiration was estimated by subtracting the appropriate values for the respiration of macroscopic species from total oxygen consumption. A possible source of error lies in the fact that the respiration of emergent plants under water may be poorly estimated by this technique.

#### NET PRIMARY PRODUCTION MEASUREMENT

A minimum estimate of net primary production may be secured from measurements of short interval changes in standing crop (Penfound, 1956). For the perennial macrophytes present in Cone Spring the regular sampling program described above provided the necessary data about standing crop. For

large annuals, growth was followed by making periodic measurements of height and at the end of the growing season mature plants were harvested to estimate their biomass contribution.

#### NET SECONDARY PRODUCTION MEASUREMENT

Net secondary production was estimated by the use of two different approaches depending upon the populations under consideration. For larger populations exhibiting relatively smooth growth curves, Teal's (1957) adaptation of Ricker's (1946) formulation for productivity was applied:  $P_t = P_0 e^{(k-i)t}$  where  $P_t$  and  $P_0$  are the populations (in weight or calories) present at the end and the beginning of a monthly interval respectively,  $k$  is the instantaneous growth rate,  $i$  is the instantaneous mortality rate and  $t$  is the time interval involved in one sampling period, in this case, one month. The value,  $k$  was estimated from field data using the greatest increase observed during one sampling interval as an estimate of growth in the absence of mortality. Once  $k$  was determined, it was substituted in Ricker's equation along with population values for successive months to derive the value,  $i$ , for each month. The instantaneous mortality value,  $i$ , was multiplied by the mean population present during the interval for which  $i$  was calculated to secure an estimate of the total mortality for that month. Successive month's values were summed to give a total annual mortality which was an estimate of the population's annual yield and, if no net change in standing crop occurred over the year, also represented net production.

The value used for the mean population present during an interval was  $\bar{P}$ , the geometric mean of  $P_0$  and  $P_t$  as suggested by Ricker and Foerster (1948).

For the less abundant species and those for which the assumptions of steady growth and mortality were obviously not valid, Ricker's model was not used. Alternatively, a "cropping" or iterative method (Anderson & Hooper, 1956; Nelson & Scott, 1962), based on the summation of population losses between successive sampling intervals, was used.

It is clear that both of the above methods of estimation of yield will tend to give minimum values. Estimation of  $k$  from natural increases in the field is likely to be low because that method assumes zero mortality. The geometric mean, while having the useful attribute of dampening the aberrant effects of high sampling variance, may also obscure real population changes which then are assigned too little weight in yield estimation. The cropping method fails entirely to make any adjustment for biomass which appears, grows and dies between successive samples and hence gives the least useful estimate of mortality. Because iterative procedures tend to underestimate net production (Nelson & Scott, 1962), an attempt has been made to correct apparent net production by an appropriate factor. Neess & Dugdale, 1959, compared the estimate of tundipedid secondary production made using an iterative procedure

TABLE 1. Physiographic features of Cone Spring.

Total Area.....	141 m <sup>2</sup>
Study Area.....	116 m <sup>2</sup>
Upper Seep Area.....	25 m <sup>2</sup>
Slope of Seep Area.....	12 cm/m
Slope of Study Area.....	3.2 cm/m
Substratum.....	Fine to coarse sand; pebbles
Mean Water Depth.....	3 cm (Range 0.5-16.5 cm)

(Anderson & Hooper, 1956) with that made by the more exact method of planimetric integration. The integrative techniques gave an estimate which was 1.4 times as great as the iterative method. A comparison of the estimates by cropping (iterative method) with estimates from application of Ricker's model and the integrative technique of Neess & Dugdale indicates that the iterative method gives values which on the average are 30% of "actual". The empirically

TABLE 2. Physical and chemical features of Cone Spring.

	Seasonal Values				Seasonal Mean	Range
	Fall	Winter	Spring	Summer		
NO <sub>3</sub> -as N mg/l.....	10.2	10.5	7.0	8.9	9.15	7-12
PO <sub>4</sub> mg/l.....	.22	.26	0.25	—	0.24	0.15-0.35
pH.....	7.3	7.4	7.1	7.0	7.2	6.8-8.0
CO <sub>2</sub> mg/l.....	4.8	4.1	2.3	2.9	3.5	1.5-11.2
Methyl orange alk.*.....	43.2	38.2	40.1	36.8	39.8	31-62
D.O. mg/l.....	8.4	9.2	7.7	6.9	8.0	5.4-11.3
Temp. °C.....	11.0	9.7	14.7	14.8	12.6	5-18.5
Rate of flow l/sec.....	1.0	1.0	1.0	1.0	1.0	0.83-1.2

\*(as mg/liter CaCO<sub>3</sub>)

in an ESE-WNW direction, lies about 70 m northwest of the entrance to the gun club. It is the second of a series which arise from the slope forming the S.E. border of Cone Marsh within the gun club grounds.

The study area consisted of just the lower 116 m<sup>2</sup> along the main axis. The upper 25 m<sup>2</sup> area was found to be physically, chemically and biologically a different habitat characterized by superficial and intermittent flow and by the absence of any macroscopic organisms. The lower zone is the area occupied by a characteristic set of organisms and features more or less constant environmental conditions. It is within this region that most of the flow originates.

No one point in the spring area can be designated as the source; rather, the entire floor of this basin allows water to flow to the surface.

Tables 1 and 2 summarize the physiographic and physical-chemical features of Cone Spring. The outstanding characteristics of this habitat are: small size, shallowness, homogeneity and, especially, constancy of physical and chemical conditions. The water is rather soft, thermally stable and rich in nutrients (CO<sub>2</sub>, PO<sub>4</sub>, NO<sub>3</sub>, SiO<sub>4</sub>). The observed environmental characteristics render Cone Spring a favorable site for the study of community dynamics and structure.

derived correction factor of 3.2 times the iterative value was applied here.

#### EMERGENCE MEASUREMENTS

To quantify insect emergence, traps consisting of metal cylinders capped by plastic bags were set out randomly across the spring area. This device worked well for the caddis-fly, *Frenesia*, but was inadequate for any dipteran populations. Many of the dipterans in Cone Spring would not enter the trap upon emergence because they could crawl out of the water on the leaves of the emergent plant.

#### PHYSICAL DESCRIPTION OF THE HABITAT, CONE SPRING

Cone Spring is a small, shallow spring-brook located in Louisa County, Iowa (Oakland Twp., Sections 13, 14; T76NR5W), on the property known as Hill's Gun Club. This spring, with its main axis

#### BIOLOGY OF SPECIES POPULATIONS

All species populations encountered during the year of intensive sampling were evaluated as to their roles in Cone Spring according to the same general criteria involving natural history, metabolism and distribution. Table 2 lists all species encountered. Metabolic and distributional data will be included in a later section for minor as well as major species. Only those considered by virtue of their metabolic activity to be major species have been discussed here, but data on all member species are included in summary fashion in Table 4. Somewhat arbitrarily, the major species are designated as those responsible collectively for about 90% of the energy flow of the animal or plant community.

In several cases it has been necessary to designate a species by use of a letter rather than a scientific name because an exact determination has not yet been possible. This practice may be defended in cases in which the species are poorly known (Hairston & Byers, 1954; as in the case of their mites and the tendipedid larvae in this study).

#### FLORA

Within the spring basin 3 major primary producers are found: *Bacopa rotundifolia*, *Lemna minor* and *Impatiens capensis*. Populations of these 3 plants

TABLE 3. Aquatic species in Cone Spring, Iowa  
(1961-1964).

Algae
Chrysophyta
<i>Meridion circulare</i> (Grev.)
Higher Plants
Lemnaceae
<i>Lemna minor</i> L.
Scrophulariaceae
<i>Bacopa rotundifolia</i> Wettst.
Balsaminaceae
<i>Impatiens capensis</i> Mierb.
Protozoa
<i>Difflugia</i> sp.
<i>Centropyxis</i> sp.
<i>Astramoeba</i> sp.
<i>Tetrahymena</i> sp.
<i>Vorticella</i> sp.
<i>Trachelophyllum</i> sp.
Coelenterata
<i>Hydra oligactis</i> (?)
<i>Chlorhydra viridissima</i>
Platyhelminthes
<i>Phagocata velata</i> Stringer
Unidentified Rhabdocoels
Rotifera
Unidentified Branchionidae
Unidentified Bdelloida
Nematoda
Unidentified Mermithoid
Gordiida
<i>Gordionus</i> sp.
Annelida
Naididae
<i>Naidium breviseta</i> (Bourne)
Tubificidae
<i>Tubifex tubifex</i> (O. F. Müller)
Mollusca
Gastropoda
<i>Physa integra</i> Haldane
<i>Succinea retusa</i> Lea (-semi-aquatic)
<i>Deroceras laeve</i> (-semi-aquatic)
Pelecypoda
<i>Sphaerium</i> sp.
Crustacea
Ostracoda
<i>Cyclocypris</i> sp. (?)
Copepoda
<i>Bryocamptus zschokkei</i> (Schmeil)
<i>Atheyella nordenskioldii</i> (Lilljeborg)
Unidentified Cyclopoid
Amphipoda
<i>Gammarus pseudolimneus</i> Bousfield
Malacostraca
<i>Orconectes immunis</i> (Hagen)
Arachnoidea
Unidentified Limnocharidae
Unidentified Hydrachnidae
Insecta
Collembola
<i>Isotomurus palustris</i> (?) Börner
Megaloptera
<i>Chauliodes pectinicornis</i> L.
Trichoptera
<i>Frenesia missa</i> (Walker)
Coleoptera
<i>Rhantus</i> sp.
Odonata
<i>Agria</i> sp.
Hemiptera
<i>Nepa apiculata</i> L.
<i>Hebrus</i> sp.

Diptera
Tendipedidae
<i>Pentaneura</i> sp.
Unidentified member of Subfamily Pelopiinae,
Tendipedid "R.B."
<i>Corynoneura</i> sp.
<i>Cardiocladius</i> sp.
Unidentified <i>Hydrobaeninae</i>
Tendipedid "H"
Tendipedid "D.P."
Tendipedid scroll
Tendipedid "S" ( <i>Cricotopus junus</i> ?)
<i>Calopsectra</i> sp.
Heleidae
<i>Bezzia</i> sp. or <i>Palpomyia</i> sp. (Heleid "A")
Heleid "B" ( <i>Culicoides</i> sp.?)
Dixidae
<i>Dixa</i> sp.
Tipulidae
<i>Limnophila</i> sp.
Stratiomyidae
<i>Hermione</i> sp.
<i>Stratiomy</i> sp.
Psychodidae
<i>Psychoda</i> sp.
<i>Pericomia</i> sp.
Empedidae
<i>Chelijera</i>
Vertebrates
Amphibia
<i>Bufo americanus</i> Holbrook
<i>Acris gryllus</i> Baird
<i>Rana pipiens</i> Schreber
<i>Rana catesbeiana</i> Shaw

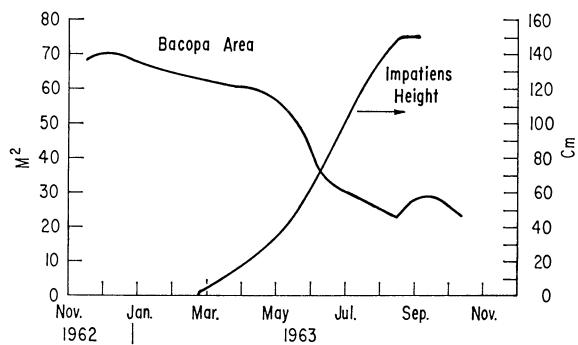
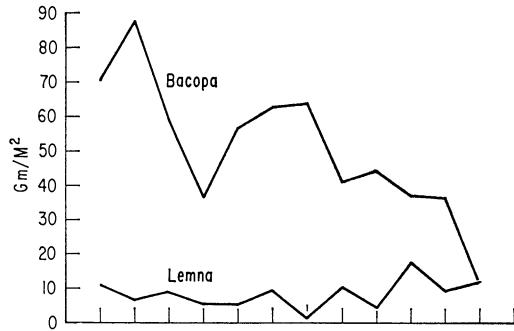
FIG. 1. Annual cycle of plant growth in Cone Spring showing changes in standing crop for *Bacopa* and *Lemna* in terms of ash per day weight/m<sup>2</sup> of the total study area and relationships between growth in height of *Impatiens* and the area occupied by *Bacopa*.

TABLE 4. Summary of population energy flow data in kcal/m<sup>2</sup>/yr.

Species	Mean Annual Standing Crop Kcal/m <sup>2</sup>	Respiration of Standing Crop	Apparent Yield	Actual Yield	Respiration of Net Production or Crop that Died	Total Respiration	Net Change in Standing Crop	Income
<i>Gammarus</i> .....	11.6	627.3	58.8	183.0	411.8	1039.1	0	1222.1
<i>Frenesia</i> .....	30.8	375.0	53.3	170.6	65.7	440.7	-	611.3
<i>Physa</i> .....	10.8	25.8	44.5	169.4	10.2	36.0	0	205.4
<i>Pentaneura</i> *.....	5.0	62.7	14.8	86.4	53.8	116.5	-0.4	202.9
<i>Phagocata</i> *.....	7.6	11.6	32.5	32.5;	2.2	13.8	+1.1	126.1
<i>Cardiocladius</i> .....	1.8	36.9	10.4	27.0	20.3	57.2	-	84.2
<i>Tubifex</i> .....	1.5	12.5	8.5	42.9	15.9	28.4	+0.2	71.5
Tendipedid "H".....	1.6	28.0	6.5	20.8	19.6	47.6	-	68.4
Heleid "A"**.....	0.15	26.6	1.9	9.2	17.0	43.6	0	52.8
<i>Chauliodes</i> *.....	3.6	14.8	-	2.8	3.3	18.1	-	20.9
Tendipedid "S".....	0.2	4.2	1.9	6.1	4.3	8.5	-	14.6
<i>Calopsectra</i> .....	0.2	5.1	2.0	6.4	2.2	7.3	-	13.7
<i>Limnophila</i> .....	0.3	6.0	1.1	3.5	3.2	9.2	-	12.7
Rhantus*.....	0.26	5.4	1.1	3.6	2.0	7.4	-	11.0
<i>Gordionus</i> .....	0.2	5.0	?	(4.8)	?	5.0	-	(9.8)
<i>Hermione</i> .....	0.4	6.1	0.7	2.2	1.5	7.6	-	9.8
<i>Dixa</i> .....	0.2	3.5	1.0	3.1	2.2	5.7	-	8.8
<i>Chelifera</i> .....	0.2	2.8	0.9	3.0	2.1	4.9	-	7.9
Tendipedid Scroll.....	0.08	1.1	0.5	1.6	1.1	2.2	-	3.8
Tendipedid D.P. ....	0.06	1.2	0.4	1.4	1	2.2	-	3.6
Tendipedid R.B.*....	0.07	1.1	0.5	1.5	0.9	2.0	-	3.5
<i>Naidium</i> .....	0.05	0.7	0.4	1.2	0.3	1.0	-	2.2
<i>Corynoneura</i> .....	0.03	0.6	0.3	0.9	0.6	1.2	-	2.1
Heleid "B"**.....	0.02	1.0	0.2	0.5	0.2	1.2	-	1.9
<i>Pericoma</i> .....	0.02	0.4	0.2	0.7	0.5	0.9	-	1.6
<i>Stratiomys</i> .....	0.1 (.28)	1	-	0.3	-	1	-	1.3
<i>Sphaerium</i> .....	0.02	0.2	0.2	0.6	0.2	0.4	0	1.0
<i>Psychoda</i> .....	0.002	0.06	0.02	0.06	0.03	0.09	-	0.15
<i>Nematode</i> .....	0.004	0.02	0.04	0.1	0.02	0.04	-	0.14
<i>Agria</i> *.....	?	?	?	?	?	?	-	?
All Primary Consumers.....	60.08			643.1		1805.33		2346.25
All Carnivores.....	16.7			136.5		202.6		419.1
Total Consumers.....	76.78			218.5 779.6 to 861.6		2007.93		2765.4

\*Carnivores

vary annually in relation to one another as a consequence of interactions in shading and low temperature.

The growth pattern of *Bacopa* shifts with the seasons seemingly in response to the annual growth of *Impatiens*, changes in light intensity, and the incidence of freezing temperatures. Graphs of change in area and standing crops of *Bacopa* and heights of *Impatiens* are given in Fig. 1. Whereas *Bacopa* is an emergent perennial plant growing after the fashion of watercress, *Impatiens* is a vigorously growing annual which reaches heights of two meters. In Cone Spring, *Impatiens* grew in clumps whose tops merged into a sort of canopy, shading large areas of the spring. Measurements with a Weston Model 603 light meter above and below full grown clumps showed that the *Impatiens* canopy reduced light intensity at the basin surface to values only  $\frac{1}{3}$  as high as in unshaded areas. During the period of *Impatiens* domination, *Bacopa* became greatly reduced in areal extent as well as in local density and hence in total

crop. Since *Bacopa* plants beneath the canopy showed the typical signs of elongation and etiolation usually associated with lack of adequate light, I inferred that diminished light intensity was responsible for the high mortality in *Bacopa* observed in these regions.

During the winter, although the spring itself did not freeze, emergent parts of plants did. *Impatiens* plants, of course, were destroyed completely with the first heavy frost; *Bacopa* plants lost only their tips. By mid-winter *Bacopa* was reduced to submerged, or just barely emergent, rosettes which, by vigorous lateral vegetative growth, partially re-invaded the areas from which they were earlier eliminated by *Impatiens*.

*Lemna minor* (duckweed) was found throughout the year occupying the interstices among the leaves of *Bacopa* as well as in mats in zones of weak flow where *Bacopa* was temporarily or permanently absent (Fig. 1). Duckweed may play a role as a "reserve" producer organism which helps to maintain

primary production at a more or less constant level. Aside from the qualitative observation that *Lemna* seems to be able to rapidly expand into many zones vacated by *Bacopa*, some indirect evidence of a possible stabilizing role is available from standing crop measurements of the two species. Coefficients of variation were calculated for the 1962-1963 series of monthly mean standing crops of *Bacopa* and *Lemna* and for a series of sums of these monthly means. The coefficient of variation, V, of the monthly means for *Lemna* was 52.12; for *Bacopa*, 34.59; but for the combined values, V was only 4.30. Thus the variability of the combined producer crop was only  $\frac{1}{2}$  to  $\frac{1}{6}$  of that of the crops considered separately.

#### GROWTH AND NET PRODUCTION IN MAJOR PRODUCER SPECIES

##### *Bacopa rotundifolia*

###### Annual cycle of growth

The annual cycle of standing crop of *Bacopa* is summarized graphically in Fig. 1. Unless otherwise stated, all plant biomass is ash-free-dry weight. The caloric equivalent of the *Bacopa* crop was 4.3 kcal/g.

Samples in the regular sampling program were taken only from the areas covered by *Bacopa*. Since the area occupied by *Bacopa* shifted in location and magnitude with the seasons some regions which were actually part of the Cone Spring ecosystem were bare of *Bacopa* each month. Therefore, the sample values were multiplied by the area of the *Bacopa* zone for the month in question and divided by 116 m<sup>2</sup>, the total area of the study zone.

The sum of all negative changes in standing crop through the year represents losses from *Bacopa* to the rest of the ecosystem. In Cone Spring during 1962-63 such losses were 107.4 g/m<sup>2</sup> or 461.8 kcal/m<sup>2</sup>/yr. Since gains in *Bacopa* crop during the year totaled only 47.5 g/m<sup>2</sup>, there was a net loss of standing crop of 59.9 g/m<sup>2</sup> or 257.4 kcal/m<sup>2</sup>/yr. The diminution in mean standing crop involved the loss of area occupied by *Bacopa* rather than a general thinning of the crop throughout the spring. The loss in area occupied by *Bacopa* was due to frost destruction of *Bacopa* during the winter of 1962 and more importantly to the shading of *Bacopa* during the summer.

A minimum estimate of net primary production is the crop lost to other trophic levels, 257.4 kcal/m<sup>2</sup>/yr. Of this total lost, 12.3 g/m<sup>2</sup> or 53 kcal/m<sup>2</sup> came from standing crop accumulated in some previous year, hence the net production which, by this method of calculation, can legitimately be credited to the system during the year of study was 47.5 g/m<sup>2</sup>/yr. or 204.4 kcal/m<sup>2</sup>/yr.

##### *Lemna minor*

*Lemna* was present in all areas of the spring basin throughout the entire year. The mean standing crop for 1962-63 was 8.2 g/m<sup>2</sup>. Although *Lemna*, like *Bacopa*, was not eaten by any herbivore, dead fronds were continuously being incorporated into the detritus which formed the food base for Cone Spring.

Changes in standing crop were used in estimating net production of *Lemna*. The average standing crop of *Lemna* increased by about 1 g/m<sup>2</sup> during the year of study. A summation of short-term losses for the year gives a total of about 31 g/m<sup>2</sup>/yr. Together these represent a net production of about 32 g/m<sup>2</sup>/yr. Assuming the same caloric equivalent of weight as calculated for *Bacopa*, a minimum estimate of net production would be 134 kcal/m<sup>2</sup>/yr.

##### *Impatiens capensis* Mierb.

Except during the interval March through May, *Impatiens* could not be adequately sampled by the methods employed for routine estimation of standing crops of other animals and plants. Seedlings appearing in the beginning of March were so large and reduced in number by June that they could not be included in samples. By this time many *Impatiens* plants were greater than 60 cm tall and had bases about 15 cm in diameter formed by clusters of adventitious roots. Removal of whole individual plants according to a separate sampling regimen was infeasible because of the marked changes which would have resulted from the absence of such plants in the community. The microenvironmental effects of the shading and shelter afforded by mature *Impatiens* plants have already been mentioned.

The annual growth of *Impatiens* is plotted in Fig. 1 as changes in average height per clump. Use was made of the fact that *Impatiens*, living under what seemed to be comparable conditions in a similar habitat adjacent to Cone Spring grew in height, at least, at rates similar to those measured for the Cone Spring *Impatiens* population. Toward the end of the growing season, plants were selected at random by means of a line transect (Dice, 1952) for removal from the experimental spring. These had a mean height of 138 cm and a mean weight of 44 g. The mean height of study zone *Impatiens* was 119 cm. The mean weight per plant was used as a crude factor for estimating the magnitude of the final crop of *Impatiens* in Cone Spring. The density of *Impatiens* in the study zone was about 0.6 plants/m<sup>2</sup>. Thus the total weight of the *Impatiens* crop at maturity was about 26 g/m<sup>2</sup>.

The fraction of this final crop which was produced during each month of the growing season was not successfully measured nor was the mortality associated with the final harvest accurately estimated. The maximum biomass of *Impatiens* per area was reached very early in the season and then declined to the final value. At first, the growth investment was in large numbers of small seedlings (2400/m<sup>2</sup> estimated present in April-May). Heavy mortality reduced the population to smaller numbers of larger individuals. By July the bulk of the mortality in terms of individual losses was over for the season.

The problem of estimating net production in an annual crop such as *Impatiens* becomes the problem of estimating the weight of the final crop plus the weight lost through mortality and seed shed. The final crop was about 26 g/m<sup>2</sup>. The total losses in

### ANNUAL CYCLES OF DETRITUS FEEDERS

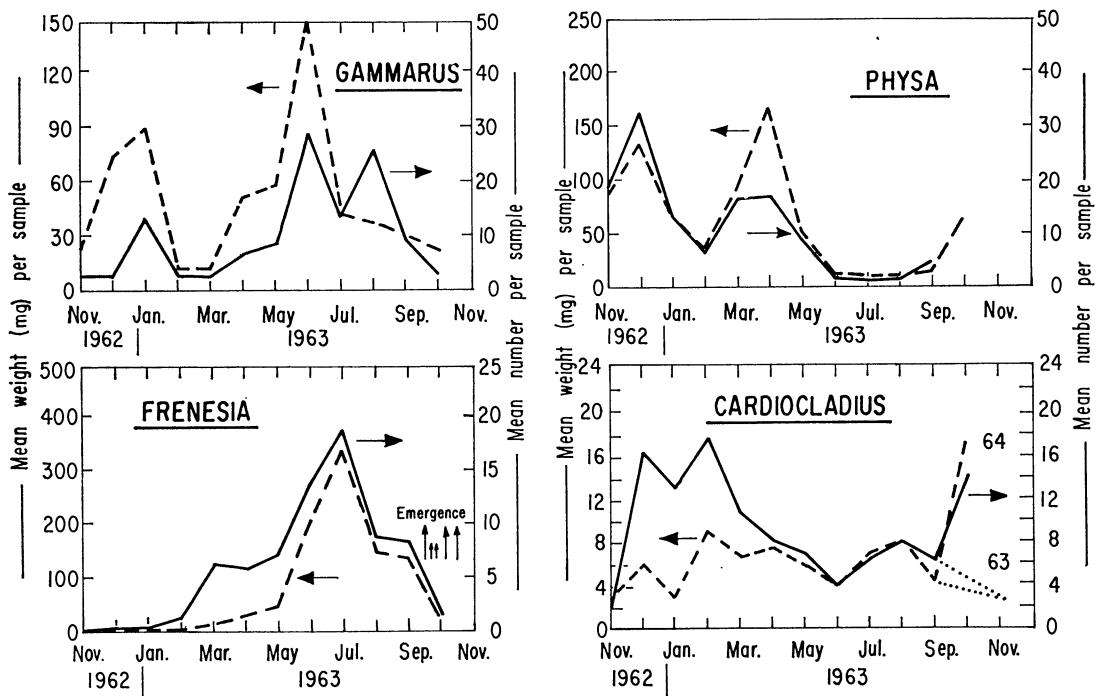


FIG. 2. Annual cycles of major detritus feeders. Changes in mean standing crops of numbers (solid lines) and biomass (dashed lines) blotted wet weight per 0.025 m<sup>2</sup> sample.

mortality are unknown but must have been at least 38 g/m<sup>2</sup> since a high of 64 g/m<sup>2</sup> was measured in May. The estimated seed deposit of 72 g/m<sup>2</sup> had a calorific equivalent of 461 kcal/m<sup>2</sup>/yr.

Annual net production for *Impatiens* must have been at least 64 g/m<sup>2</sup>/yr × 4.2 kcal/g = 269 kcal/m<sup>2</sup>/yr plus seed shed equivalent to 461 kcal/m<sup>2</sup>/yr or a total of 730 kcal/m<sup>2</sup>/yr.

#### FAUNA OF CONE SPRING

The annual cycles of Cone Spring consumers are summarized in Figs 2 & 3; energy flow data are summarized in Table 4.

#### *Gammarus pseudolimneus* Bousfield

##### Taxonomy and Natural History

The most important single consumer species found in Cone Spring during the 1962-63 sampling year was the amphipod *Gammarus pseudolimneus*, (Amphipoda, Gammaridae). Peak densities and biomass levels of *Gammarus* were reached in January and June. Mean densities for August were high but biomass was low, many young being included in these samples. The mean weight per individual gammarid reached a peak in December and a low in August. Gravid females and young were found in all months and in almost all samples indicating that the population was reproducing continuously.

##### Trophic Position and Feeding Relations

*Gammarus* is a scavenger which must be ranked in Cone Spring as the dominant consumer organism present during the period of study. Extremely catholic in its food habits, as are most amphipods (Penak, 1952; Embdy, 1911), I saw *Gammarus* feed on virtually all types of detritus available.

Predators observed to feed upon *Gammarus* at one time or another were *Phagocata*, *Pentaneura*, *Chauliodes* and *Rhantus*.

##### Physiological Data

The respiratory rate for this species was found from 4 measurements to be 1.25 mg of oxygen per gram fresh weight per hour or 4.22 cal/g/hr. The caloric value for this animal was taken as 0.67 cal/mg fresh weight. Calculations were based on Ivlev's (1934) determinations of caloric value and chemical composition of *Gammarus* adjusting for differences in crude protein and wet weight measured for Cone Spring organisms. Cone Spring forms contained an average of 8.37% nitrogen on a lyophilized dry weight basis.

##### Net Production

Net production was estimated by the method of Ricker (1946) using  $k = 1.466$  from the period of maximum natural increase observed in field populations between March and April samples. The greatest

## ANNUAL CYCLES OF CARNIVORES

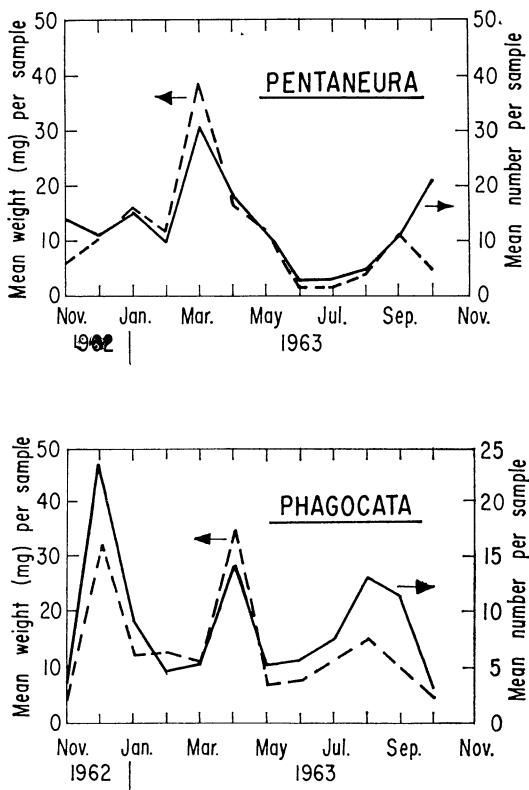


FIG. 3. Annual cycles of major carnivores. Changes in mean standing crops of numbers (solid lines) and biomass (dashed lines) blotted wet weights per 0.025 m<sup>2</sup> sample.

loss was observed in the interval June through July when large adults were eliminated from the population. Death of these adults represented a loss of about 58 kcal/m<sup>2</sup>. Total mortality for the year gave a yield of 183 kcal/m<sup>2</sup>.

## Energy Flow

Total respiratory expenditure by the *Gammarus* population over the year amounted to 1039 kcal/m<sup>2</sup>. Total annual assimilation of energy was estimated at about 1222 kcal/m<sup>2</sup>.

*Frenesia missa* (Milne)

## Taxonomy and Natural History

*Frenesia missa*, (Trichoptera, Limnephilidae), is the only trichopteran observed in the spring area. The life cycle of this species has been described by Flint (1956), and in most respects my observations generally confirm what Flint has reported. The population annual cycle is summarized in Fig. 2. Emergence of adults occurred from October through December. After copulating, females laid eggs at the spring edges and died in a few days. Larvae hatched and appeared in samples in increasing numbers until, in Cone Spring, they reached mean densities of 7480

individuals/m<sup>2</sup> in July. From this time through the end of the period of emergence, numbers declined. Prepupae were found in Cone Spring as early as August; true pupae developed by September.

Dynamic and energetic analysis of this population cycle in Cone Spring was complicated by the fact that hatching was spread over a long interval of time and egg laying was at the edges outside the defined zone of study. The changes in numbers observed are the composite result of interactions between development, immigration, growth and mortality. Flint's (1956) observations indicate that hatching rate is a function of ambient temperature. Probably, some eggs are laid in zones kept relatively warm by the continuous flow of spring water and hence hatch early (in November, December and January). Eggs laid in areas away from the the protecting influence of the flow would be delayed in hatching until air and soil temperatures began to rise again in March and April.

After hatching, larvae may feed and grow in regions at the edges of the spring. Later they may immigrate into the sampling zone and then be included in counts. The emergence data suggest some upstream movement by the caddis larvae. Emergence from the downstream half of the spring was only 2/3 that from the upstream half based on equal sampling effort. Observations of individuals in regions of flow indicate that *Frenesia* tends to show a positive rheotropism. Margalef (1960) notes that such upstream orientation has survival value for forms requiring rapid flow and low temperature or some concomitants of these. It is notable that far more *Frenesia* were found in the spring basin than in the spring brook downstream.

Egg laying probably occurred from October 15 through December, the interval during which adult caddis flies were seen to be active around the spring. About 94% of the total emergence had occurred by November 15 so most of the egg deposit had been made by this time. As a means of estimating the limits of potential larval densities, counts of eggs per virgin female were made giving values of 138, 130 and 122 for a mean of about 130 eggs per female. The sex ratio was determined by examination of emergence samples to be about 1:1. Total emergence was about 1974 adults/m<sup>2</sup>. Most of these adults remained in the spring area. *Frenesia* is not a strong flier and behaviorally resists dislodgement from an area by clinging tightly to perches in wind and creeping and hiding rather than flying when disturbed. My observations during periods of highest emergence suggest that between 75 and 90% of the emerged adults remained in the spring region to mate and lay eggs. On this basis the potential larval population entering the spring zone can be calculated as between 96,230 and 115,480 individuals/m<sup>2</sup>. The maximum number of individuals observed during any sampling interval was a mean of about 7600/m<sup>2</sup> in July. Mortality to this stage (5th instar) would amount to 92 to 93% of the September population.

About 3200 prepupae and larvae/m<sup>2</sup> gave rise to the 1974 adults/m<sup>2</sup> which emerged between October and December. Mortality in the transition from prepupae to adult amounted to about 37% of the prepupal numbers.

#### Trophic Position

*Frenesia* is a scavenger feeding upon dead vegetation, twigs and debris (Lloyd, 1921; Ross, 1944; Flint, 1956); this was confirmed by observations at Cone Spring.

*Chauliodes* and *Rhantus* preyed upon *Frenesia*, under laboratory conditions. It is difficult to conceive of any of the other Cone Spring predators being able to effectively overcome *Frenesia* individuals except possibly when the latter are very young.

#### Physiological Data

The respiratory rate for *Frenesia* was estimated as 0.45 gm O<sub>2</sub>/g wet wt/hr by extrapolation from the data of Fox and Baldes (1935) for *Limnophilus* using the surface law (Zeuthen, 1953). (Metabolism is proportional to the weight to some power, here taken to be 0.73). The caloric value for *Frenesia* was taken as 0.98 kcal/mg wet weight using Teal's (1957) determination, which he reported agreed with an analysis from the data of Birge and Juday (1922).

#### Net Production

Attempts to estimate losses representing net production by Ricker's (1946) method were unsuccessful because of the complications introduced by immigration. Values secured using this method were in many instances negative, indicating that immigration changes were masking those due to mortality. The simplest approach remaining was to use the iterative (or "cropping") method. The biomass (or caloric) increases in standing crop per sample were the sum of increases due to growth of the initial population plus increases due to immigration of individuals grown "outside" the system. To determine the portion of increase legitimately creditable to the study zone, the initial energetic value of immigrants was subtracted from any growth of immigrants after arrival. Import through immigration was estimated by comparing mean numbers of individuals appearing in successive samples from April through July. By the beginning of this period, no additions to the population through reproduction were occurring. Increases in numbers were attributed to immigration in the following amounts:

1 larva increase in May was	
equivalent to 6.3 mg	= 2.4 kcal/m <sup>2</sup>
7 larvae in June equivalent to	41.2 kcal/m <sup>2</sup>
5 larvae in July equivalent to	35.2 kcal/m <sup>2</sup>
Total immigration	78.8 kcal/m <sup>2</sup>

Total increases determined by summing monthly increases in caloric standing crop were 132.1 kcal/m<sup>2</sup>/yr. Subtracting the portion of this increase due to immigration as estimated above, 78.8 kcal/m<sup>2</sup>/yr, leaves 53.3 kcal/m<sup>2</sup>/yr apparent increase due to net

production. Apparent increases in populations underestimated actual increases (measured by Ricker's method) among other Cone Spring populations by an average factor of 3.2. Assuming that the same underestimate is true of these methods when applied to *Frenesia* populations, actual net production is estimated to be about 170.6 kcal/m<sup>2</sup>/yr.

About 37% of the prepupal crop failed to emerge. Assuming that deaths all occurred at the time of emergence, this 37% would be equivalent to 19.7 kcal/m<sup>2</sup>/yr (37% of 53.3 kcal/m<sup>2</sup>/yr apparent increase). Of the remaining apparent increase (33.6% kcal/m<sup>2</sup>/yr) representing the successfully emerging crop, 70 to 90% were believed to remain in the spring area to deposit eggs and die, hence from 23.5 to 30.2 kcal/m<sup>2</sup>/yr were returned to Cone Spring as production available for other consumers in Cone Spring. On this basis from 2 to 6% of *Frenesia* net production was lost from Cone Spring through emergence and adult emigration.

#### Energy Flow

Respiration energy expenditures are estimated as 440.7 kcal/m<sup>2</sup>/yr. Energy assimilation was about 611 kcal/m<sup>2</sup>/yr.

#### *Physa integra* Haldeman

##### Taxonomy and Life History

One of the larger and more conspicuous animals found in Cone Spring is the pulmonate snail, *Physa integra*. Active populations of this species were present during the entire period of study. Annual curves of density and biomass for Cone Spring *Physa* populations are bimodal with peaks in December and April (Fig. 2). Lowest values for density and biomass were found in summer and fall. The mean weight/individual varied during the year from a low of 3.2 mg in September, 1963, to a high of 9.8 mg in April, 1963. Increases in biomass appeared to be a function of increases in numbers of individuals as well as individual growth. Reproduction occurred in all seasons but was reduced from December through March. Young individuals were found in most samples throughout the year. Mortality, growth and reproduction tend to be much more constant throughout the year for this species in Cone Spring than in other aquatic systems where it has been studied (see Jenner, 1951; Clampitt, 1963).

#### Trophic Position and Feeding Relations

This species is a detritus feeder or scavenger. Although individuals may occasionally feed upon live plant material, direct observations and gut analysis indicate that the bulk of the food devoured by *Physa* is dead organic debris. When found on *Bacopa* plants in Cone Spring, it appears preferentially to crop off the dead and dying portions rather than the fresh living tissues. Aside from its scavenger role *Physa* seems to be important as a sort of biological comminutor, making debris available to smaller forms such as Tendipedid "H" which requires smaller particle size for feeding. As was also noted by Clampitt

(1963), this species seems to pass a great deal of organic material through its digestive tract without any obvious change except in particle size.

#### Physiological Data

The respiratory rate of *Physa integra* was from 4 determinations calculated to be 0.17 cal/g wet weight (shellless)/hr. This rate is low in comparison with the other animals present but compares favorably with published values, Winberg and Balazkaya (1959), Berg *et al.* (1958) and Berg and Oekelman (1959). The low rate may represent an adaptation to high mucus production similar to that postulated by Teal (1957) for *Phagocata*.

The caloric content of *Physa* was assumed to be equal to that measured by Slobodkin and Richman (1961) for the semi-aquatic pulmonate snail *Succinea ovalis*. Since their values were given on an ash free dry weight basis, an adjustment had to be made relating wet weight of *Physa* to ash free dry weight. Ash free dry weight in *Physa* was found to be 24% of total wet weight (excluding shell). On this basis, 1 mg wet weight is equivalent to 1.0 geal. The nitrogen content of whole *Physa* including shell was found to be 1.98% on a lyophilized dry weight basis. The live tissue weight of this gastropod averaged 44% of the total wet weight (10 determinations). Throughout this paper the "wet weights" referred to for *Physa* are values corrected for shell weight according to this proportion.

#### Net production

Net production was estimated for *P. integra* by the method of Ricker (1946). The greatest biomass increase observed in field populations occurred between September and October (1963) samples. From this increase, k was estimated as 1.433. Using this value for k, i was calculated for each monthly interval. The greatest mortality for any of these monthly intervals occurred between April and May during which time about 25% of the total loss was suffered. The graphs of number, biomass and individual weight changes suggest that this mortality involved loss of over-wintering adults. Mortality totalled 169 kcal/m<sup>2</sup>/yr. None of the other invertebrates present in Cone Spring fed upon *Physa*. Robins, redwing blackbirds and killdeer have all been observed apparently feeding in the area and could have removed *Physa*. The magnitude of losses to such visiting predators is unknown but is probably small relative to the total production of the prey populations involved.

#### Energy Flow

*Physa* populations in Cone Spring had a mean standing crop of 4600 animals/m<sup>2</sup>, having a caloric value of 10.8 kcal/m<sup>2</sup>/yr and experienced mortality providing energy to other trophic levels at a rate of 169 kcal/m<sup>2</sup>/yr.

#### *Pentaneura* sp.

##### Taxonomy and Natural History

*Pentaneura* (Diptera, Tendipedidae, Pelopiinae) is

an active tendipedid found in larval stages in Cone Spring throughout the entire year. The mean annual density for the *Pentaneura* population was 5120 larvae/m<sup>2</sup>. The annual biomass mean was 4.8 g/m<sup>2</sup>.

The annual population cycle (Fig. 3) includes a peak of biomass and number in March followed by a low in June and July. The mean weight per individual showed no seasonal trend but varied around a value of about 1 mg. Young and old larvae were found in samples throughout the entire year and emergence was detected in all seasons for this species. I assumed that some approximation of a stable age distribution existed in this population.

#### Trophic Position

The trophic position of this species was difficult to determine. In the laboratory it was predaceous and occasionally cannibalistic, but in the absence of potential prey survived to emergence with nothing but detritus as food. Stomach analyses which were performed in large number did not resolve the problem because *Pentaneura* feeds upon large herbivorous tendipedids by sucking out the guts and leaving behind the hard parts of the exoskeleton which would permit identification of the prey. Leathers (1922) reported similar behavior for *Pentaneura carnae*.

#### Physiological Data

The respiratory rate assumed for *Pentaneura* was 1.8 cal from *Anatopynia dyari*, a closely related and behaviorally similar form abundant in Root Spring, Massachusetts. The caloric value assumed for *Pentaneura* in Cone Spring is 0.88 geal/mg wet weight and is also taken from Teal's (1957) analysis for *A. dyari*.

#### Net Production

In *Pentaneura* net production includes molting losses and emergence as well as mortality per se. Ricker's (1946) formula was applied in the calculation of net production for this species. From the natural increase occurring in the population biomass between May and June, k was estimated to be 1.792. "Net annual losses" for *Pentaneura* amounted to 96.3 kcal/m<sup>2</sup>/yr. The term "net production" cannot legitimately be applied to this value. Since cannibalism is known to occur in this species, to calculate net production, mortality losses must be adjusted by an amount equal to the energy withdrawn from within the population itself. This in turn requires that the fraction of net loss which is due to mortality be known.

Teal's (1956) data for 2 tendipedid populations reveals that losses through emigration and molting deposit amounted to values 1.2 and 1.1 times the mean standing crop for *Calopsectra dives* and *Anatopynia dyari* respectively. Assuming that a similar relation between mean standing crop and emigration and pupation losses holds for *Pentaneura* populations in Cone Spring, *Pentaneura* mortality may be calculated. Mean standing crop for *Pentaneura* throughout the year was 5 kcal/m<sup>2</sup>. Losses

from emigration and molting could be expected to be (1.1) (5 kcal/m<sup>2</sup>/yr) or about 6 kcal/m<sup>2</sup>/yr. Subtracting this amount from the estimated net loss (96.3 kcal/m<sup>2</sup>/yr — 6 kcal/m<sup>2</sup>/yr) leaves a total mortality of 90.3 kcal/m<sup>2</sup>/yr. It is this mortality value which must be adjusted for cannibalism.

The proportion of mortality to be charged to cannibalism is difficult to estimate because other predators present will also kill *Pentaneura*. It may be possible to estimate the proportion of *Pentaneura* mortality due to cannibalism by assuming that each predator's toll on *Pentaneura* is proportional to the fraction of total carnivore assimilation for which the organism is responsible. *Pentaneura* assimilation amounts to about 35% of total carnivore assimilation. Therefore, 35% of total *Pentaneura* mortality has been charged to cannibalism on the implicit premise that predation is a function of random contacts with potential prey (Lotka, 1925). Analysis of sampling data to be discussed later indicate that most of the predators tend to be randomly (or even uniformly) distributed. This would mean that a *Pentaneura* individual would have no greater chance of encountering and killing another *Pentaneura* than would a different predator. Teal (1957) estimated for *Anatopynia* that this predator ingested about 30% of what is killed. As this would also appear to be a reasonable estimate for the efficiency of *Pentaneura* feeding, the amount of energy actually channeled back into the *Pentaneura* population is calculated as 30% of the losses due to cannibalism.

Using the foregoing data and assumptions, the energy budget for *Pentaneura* may be calculated. Total mortality was found to be 90.3 kcal/m<sup>2</sup>/yr. The energetic value of the crop killed by cannibalism was estimated to be 35% of total mortality of (0.35) (90.3) = 31.6 kcal/m<sup>2</sup>/yr. Only 30% of the crop killed was actually ingested. The remainder, therefore, was passed on to other trophic levels as a part of net production. The amount of energy taken from *Pentaneura* by cannibalism and returned through ingestion was (0.30) (31.6 kcal/m<sup>2</sup>/yr) or 9.5 kcal/m<sup>2</sup>/yr.

Since the standing crop of *Pentaneura* diminished by the net amount 0.4 kcal/m<sup>2</sup> during the year of study, this amount of energy assimilated in a previous year was expended by the population and appeared in the net loss figure. Taking this loss and the losses involved in cannibalism into account, the formula for net production calculation becomes: Net production = Net loss — (ingested energy from cannibalism + loss in standing crop). So calculated, net production for *Pentaneura* was 96.3 kcal/m<sup>2</sup>/yr — (9.5 kcal/m<sup>2</sup>/yr + 0.4 kcal/m<sup>2</sup>/yr) = 86.4 kcal/m<sup>2</sup>/yr.

#### Energy Flow

The energy transformed by the *Pentaneura* population during the year as estimated by respiration was 116.5 kcal/m<sup>2</sup>/yr. Assimilation totalled 202.9 kcal/m<sup>2</sup>/yr.

#### *Phagocata velata* Stringer

##### Taxonomy and Life History

A large population of the planarian *Phagocata velata* (?) (Planariidae) was found in Cone Spring during the entire year of study. The annual population cycle (Fig. 3) seems to consist of 3, 4 month sub-cycles giving population and biomass peaks in December, April and August.

The mean weight per individual worm increased fairly evenly from the beginning of sampling in October to a peak of 2.7 mg (wet weight) in February and declined thereafter to a low of 0.9 mg in September. In general, mean biomass per sample changed in proportion to the number of individuals present but the change in biomass per sample is no simple function of individual size. Although the February peak of individual weight is associated with a low in number of individuals and biomass per sample, no comparable trend can be seen in the May, June and July samples.

Comparison of the population curves with the annual cycle of water temperature suggests that falling temperature may have had a directly inhibitory effect upon the frequency of fragmentation, the means of asexual reproduction in these forms (Hyman, 1951). Members of the Planariidae are known to experience a decrease in ovary and testis size and maturity as a consequence of lowered environmental temperatures (Reynoldson *et al.*, 1965).

Even if the above explanation acceptably accounts for the changes in individual weight, density and biomass fluctuations remain unexplained. Perhaps vagaries of this sort also noted by Teal (1957) for *Phagocata* are related to the abilities of flatworms to regenerate, to resorb tissues readily in the absence of suitable food and to reproduce by asexual as well as by sexual means.

Annual standing crop means for biomass and numbers were 6.4 g/m<sup>2</sup> and 3600 worms /m<sup>2</sup> respectively.

##### Trophic Position

*Phagocata* is one of the top carnivores in Cone Spring. Although it is a small form (approximately 1-2 mg wet weight), it is able to handle a large size range of prey because of its habit of feeding in groups upon invertebrates ensnared in the mucus trails secreted by traveling worms.

##### Physiological Data

Metabolic values measured by Teal (1956) for Root Spring *Phagocata gracilis* were applied to Cone Spring flatworms. The respiratory rate was calculated to be 0.25 cal/g wet weight/hr. The caloric equivalent of mucus production was assumed to be the same as for Teal's (1957) animals, 0.94 cal mucus/cal body weight/month or 1.25 cal/mg/mo. The caloric value was given as 1.33 cal/mg wet weight. It was not clear from Teal's data whether percentages were expressed in terms of dry or wet weights of organisms. The low values for respiratory rate are interpreted by Teal (1956) to be an adapta-

tion which may help to compensate for the relatively high loss of energy involved in mucus production by this form. Another conservative adaptation is the tendency of these animals to aggregate in clusters and remain quiescent for long periods of time. The animals move actively when they have been stimulated by mechanical disturbance or the presence of food. Inactive groups of animals were often seen clustered on rocks and under leaves.

#### Net Production

Since growth does not appear to be constant and age structure is unknown, it was not possible to make use of Ricker's (1946) mortality formulation. Net losses were estimated by summing negative changes in standing crop for the season. Apparent losses for the year were estimated as 31.4 kcal/m<sup>2</sup> for this population. The standing crop experienced a gain of 1.1 kcal/m<sup>2</sup>/yr. No adjustment was made for the underestimation of net production involved in the iterative method used. Planarians are not subject to the same kinds of losses as most insects and crustaceans, therefore no upward correction could be justified for *Phagocata*. Net production including mucus expenditure was 114.5 kcal/m<sup>2</sup>/yr.

All mortality was attributed to non-predatory causes. Hyman (1951) declares that no other macroscopic forms will eat planarians. Cannibalism reported by Teal (1957) for *P. gracilis* and by Armstrong (1960) for *Dugesia* and by Hyman (1919) for other species was never observed either in the laboratory or the field for Cone Spring animals. Teal (1957) believed that most of the "cannibalism" he observed in Root Spring was really *P. morgani* feeding upon *P. gracilis*. Since *P. velata* was the only planarian present in Cone Spring, such predation was not a factor there.

It should be pointed out that "mortality" as defined here includes all losses in mean standing crop and may occur without the loss of any individuals as individual weight decreases. Studies of tricladids by Root (1960) and Armstrong (1964) indicate that mortality in terms of loss of numbers of individuals is not a usual event in planarian populations except as a result of cannibalism. Reynoldson (1960, 1961) however, believes that starvation is an important cause of loss of numbers in the population of pond planarians he studied. In Cone Spring, food supply for planarians never appears to be limiting. Environmental conditions in Cone Spring in general appear to be much more stable than for most ecosystems, yet populations do fluctuate in both numbers and biomass. If small (or large) individuals were swept over the dam by the flow, they would be counted as dead in subsequent censuses. No worms were ever collected in outflow water except immediately after violent disturbance had upset the vegetation immediately upstream from the dam. Causes of mortality, therefore, remain unidentified.

#### Energy Flow

Two alternative energy flow calculations have been tabulated for *Phagocata* populations. The first assumes that mucus production is an expense akin to respiration, the second considers mucus production to be a part of net production. Total assimilation is the same for each.

Respiration was estimated to be 13.8 kcal/m<sup>2</sup>/yr for *Phagocata*. Mucus "loss" (or "production," depending upon the point of view) was 82 kcal/m<sup>2</sup>/yr. Assimilation totalled 126 kcal/m<sup>2</sup>/yr for Cone Spring *Phagocata*.

#### *Cardiocladius* sp.

##### Taxonomy and Life History

Members of the genus *Cardiocladius* are widely distributed throughout North America and are known as inhabitants of flowing water systems (Pennak, 1952; Wirth & Stone, 1956). In Cone Spring they are found primarily in the upper layers of the substratum or in association with the submerged portions of *Bacopa*.

The annual cycle for *Cardiocladius* in Cone Spring is summarized in Fig. 2. Mean density throughout the year was 3840 individuals per m<sup>2</sup> equivalent to 2.2 kcal. No obvious peaks occurred in density or biomass but numbers were generally higher in fall. The curve of individual weight compared with that for numbers shows that young larvae were abundant during December and January. The curves look deceptively as though one cohort population hatching from eggs sometime in the fall grows and emerges sometime in late summer. The sampling data belie this supposition since adults, young and mature larvae were observed in all sampling intervals.

##### Trophic Position

*Cardiocladius* is a robust form having anteriorly a sturdy pair of rasping prolegs which it uses to grind up medium to large (5-30 mm diam. particles) pieces of debris. When offered a choice, this tendipodid selected dead rather than fresh *Bacopa* leaves as food. Gut examinations made for these forms support their placement as strict detritus feeders.

##### Physiological Data

The respiratory rate applied in these calculations for *Cardiocladius* populations is 1.61 cal/mg wet weight/hr. This was the value determined by Teal (1956) for a detritus-feeding tendipodid, *Calopsectra dives*, and it agrees closely with an average tendipodid respiratory rate calculation from literature values. The caloric equivalent of weight applied was the average tendipodid value of 0.78 geal/mg wet weight.

##### Net Production

Net production for *Cardiocladius* was estimated by means of Ricker's (1946) model. A minimum estimate of the instantaneous rate of increase ( $k = 1.222$ ), was calculated using figures for the population biomass increase between January and February,

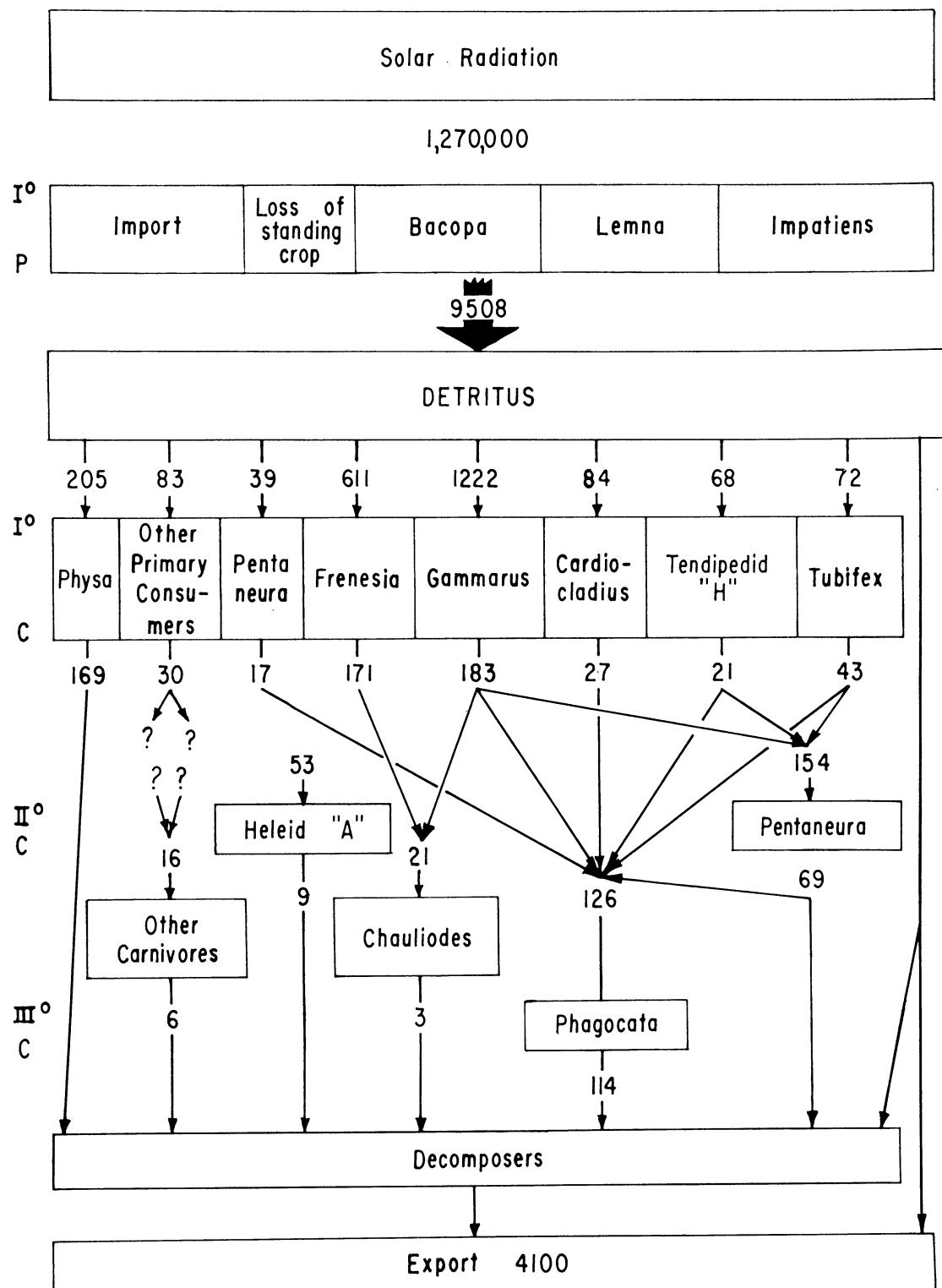


FIG. 4. Quantitative food web indicating relations of major species in Cone Spring simplified and quantified in terms of income and yield estimated as described in the text. Boxes represent component units recognized; numbers above boxes are income estimate, numbers below are yield estimates. Trophic levels are symbolized as follows: I° P = primary producers, I° C = primary consumers, II° C = secondary consumers and III° C = tertiary consumers. Only the main directions of energy flow in kcal/m<sup>2</sup>/yr have been indicated by arrows; minor species have been lumped.

1963. As for *Pentaneura* net production includes not only mortality but also emergence and molting. Since no net change in standing crop occurred in the year, net production is equal to yield in this case. The total net production by *Cardiocladus* for the year of study was 27.0 kcal/m<sup>2</sup>/yr. Sources of predatory mortality were not clearly identified. Predation was never observed in the field. In the laboratory, however, *Rhantus* would eat *Cardiocladus* and when the midge larva was purposely injured, *Phagocata* did also.

#### Energy Flow

The total respiratory expense for this population was 57.2 kcal/m<sup>2</sup>/yr. Total assimilation was 84.2 kcal/m<sup>2</sup>/yr.

#### COMMUNITY ENERGY FLOW

##### FOOD WEB APPROACH

Using the foregoing data, a functional picture of the community in terms of energy flow was constructed. The approach used involves quantification of the food web after the manner described by Macfadyen (1963). The term "trophic level" is used to simplify discussion, but quantification of energy flow through trophic levels has been accomplished by dealing separately with the species populations which collectively comprise each level. Such a treatment makes it possible to distinguish the relative importances of different species in directing the energy flow of the Cone Spring community. This approach also makes possible a reasonable treatment of the energy flow of species which may operate simultaneously at more than one trophic level. No such adjustment for a division of energy flow is possible using a strict trophic level analysis (Ivlev, 1945).

The energy flow data for species populations discussed previously and summarized in Table 3 have been used in constructing the food web diagrammed in Fig. 4. Some of the data used in assembling the portions of the web relating to energy flow from plant populations, import and export are introduced and discussed below.

The outstanding feature of the Cone Spring food web is that it centers about detritus rather than about primary producers. The general pattern of energy flow in this food web is: primary producers—detritus—primary consumers—secondary and tertiary consumers—decomposers—export via outflow water. Each of these links will be considered in some detail below.

Only about a dozen animal species have been referred to separately in this simplified food web. The species included are responsible for over 95% of the faunal net production and more than 96% of the animal assimilation. It seems justifiable, therefore, to restrict discussion of food web relations largely to these major species recalling, however, that the minor species were treated individually in making the original calculations.

#### PRIMARY PRODUCTION

Net primary production for Cone Spring may be estimated as the sum of such production for *Bacopa*, *Lemna* and *Impatiens*. Estimates, which are considered to be low in each case, were for these species; 204 kcal/m<sup>2</sup>/yr, 134 kcal/m<sup>2</sup>/yr and 730 kcal/m<sup>2</sup>/yr respectively. Total autochthonous production available to consumer populations was 1068 kcal/m<sup>2</sup>/yr.

#### DETRITUS

An enormous quantity of potential energy is on hand in the Cone Spring system in the form of the standing crop of detritus. The mean annual standing crop was about 880 g/m<sup>2</sup>; the lowest mean monthly crop was 760 g/m<sup>2</sup>. Expressed in terms of potential energy, the mean annual crop was about 3696 kcal/m<sup>2</sup> assuming the applicability of the caloric equivalent of 4.2 kcal/g AFDW calculated from Golley's (1961) data for plants.

By contrast, the mean standing crop of all consumers was estimated as about 77 kcal/m<sup>2</sup>. Fig. 5 summarizes the annual cycle of detritus standing crop. Quantitative data on detritus crop were not collected during the first month of the study nor in October, 1963.

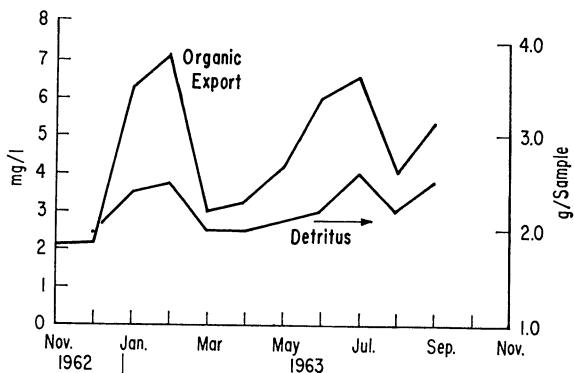


FIG. 5. Annual cycles of detritus and organic export showing monthly changes in standing crop of detritus per 0.025 m<sup>2</sup> in relation to the quantity of centrifugible organic matter exported. Measures are ash-free-dry weights.

#### ALLOCHTHONOUS IMPORT

Import of leaves, twigs, fruit and other organic debris was estimated to be about 149 g/m<sup>2</sup> in 1962, equivalent to about 626 kcal/m<sup>2</sup>/yr. Most of this deposit entered the spring area between August and November from deciduous trees and shrubs surrounding the spring. Since the dominant shrub surrounding the spring was the low growing blackberry (*Rubus*), deposits to the spring basin probably occurred without being adequately measured by debris traps. Import was probably underestimated.

#### PRIMARY CONSUMERS

The primary consumers which were most important in terms of energy flow in the Cone Spring community were *Gammarus*, *Frenesia*, *Physa*, *Cardio-*

*cladius*, *Tubifex* and Tendipedid "H". Collectively these 6 species assimilated an estimated 2262.9 kcal/m<sup>2</sup>/yr and passed on to succeeding trophic levels about 614 kcal/m<sup>2</sup>/yr in net secondary production. Other macroscopic primary consumers assimilated only about 83 kcal/m<sup>2</sup>/yr. As the food web diagram attempts to show, however, even the major species are not equally important in their role in transferring energy to secondary consumers. *Gammarus* was by far the most important secondary producer and consumer organism in Cone Spring. This amphipod's importance is accentuated when one considers that the 2 species next in rank in terms of assimilation have only very attenuated relations with secondary consumers in the food web.

As has been noted, Physids were not eaten by Cone Spring carnivores and *Frenesia* larvae do not seem to be preyed upon by any major consumer except *Chauliodes*. It must be concluded, therefore, that *Gammarus* populations were supplying the bulk of energy to higher trophic levels.

A second conclusion which is suggested by these data is that a large amount of primary consumer net production flowed back into the detritus crop and to decomposer levels. This quantity can be estimated to have been of the order of 300 kcal/m<sup>2</sup>/yr considering non-predatory losses from *Physa* and *Frenesia* alone. Adding molting losses from *Gammarus*, *Cardiocladius* and Tendipedid "H" as a portion of net production unavailable to a strict carnivore, the proportion returned to the detritus standing crop must have been almost one-half of the total primary consumer net production.

#### SECONDARY AND TERTIARY CONSUMERS

Four species were recognized as major carnivores in Cone Spring. These were *Phagocata*, *Chauliodes*, Heleid "A" and *Pentaneura*. Of these, *Phagocata* and *Chauliodes* were considered to be strict predators and, in fact, top carnivores. Reasons were given earlier for classifying *Pentaneura* as both predator and detritus feeder. Heleid "A" was classified tentatively as a predator.

The only population known to obtain a significant amount of assimilated energy at the tertiary consumer level was *Phagocata* which probably accounted for the 49 kcal/m<sup>2</sup>/yr predatory mortality suffered by *Pentaneura* populations. Since *Phagocata* required an estimated total of about 126 kcal/m<sup>2</sup>/yr for support of its population, the origin of more than 77 kcal/m<sup>2</sup>/yr *Phagocata* assimilation remains to be accounted for. Most if not all of this energy had to arise from net production by detritus feeders. *Phagocata* is a secondary and tertiary consumer.

The total net production available to the remaining carnivores was about 227 kcal/m<sup>2</sup>/yr. The *Chauliodes* population was assumed to have secured its assimilated energy from *Frenesia* larvae. *Pentaneura*, Heleid "A" and the minor carnivores collectively required about 262 kcal/m<sup>2</sup> for their support during the year, about 35 kcal/m<sup>2</sup>/yr more than ap-

peared to be available from suitable prey populations.

The imbalance found between energy available to carnivores and energy required by carnivores in this segment of the food web may be regarded as further evidence that *Pentaneura* feeds at 2 trophic levels. It is not inconsistent with field and laboratory observations to consider that *Pentaneura* assimilates at least 35 kcal/m<sup>2</sup>/yr from the detritus standing crop. This amount would be about 18% of this midges' total estimated assimilation. In the food web diagram (Fig. 4), the proportion of *Pentaneura* assimilation and net production credited to the primary consumer level was 20% as a reasonable estimate giving a crude sort of balance to the energy flow picture.

#### DECOMPOSERS

The bacteria and other decomposers were not adequately sampled in Cone Spring. The rate at which plant decomposition occurred, however, suggests that large populations were present among the detritus of the substratum. Standard plate counts made for outflow water at several intervals during the winter and spring of 1963 gave an estimate of average density of about 100 organisms/cc. If one considers that these bacteria were associated with the detritus being exported and that the export was a representative sample of populations in the substratum detritus, one may secure an order of magnitude estimate of bacterial density. On the average each cc of discharge water contained about 4 mg AFDW particulate organic during the year of study. The mean annual standing crop of detritus was about 880 g/m<sup>2</sup>. Using the above figures to make the necessary calculations bacterial populations of at least  $22 \times 10^9$  individuals/m<sup>2</sup> are suggested. These figures do not seem unreasonable since Odum (1957) by plate counts of mud samples from the upper cm of substratum in Silver Springs, Florida, found densities of about  $40 \times 10^9$  bacteria/m<sup>2</sup>. According to these calculations, organisms eating detritus would be consuming a significant number of bacteria. Decomposers may thus be an important intermediate in their nutrition.

#### COMMUNITY RESPIRATION

An attempt was made during the study of Cone Spring to estimate respiratory rates of the community as a whole. The incubation of whole core samples in darkened screw-top vessels gave results measurable by the standard (APHA, 1960) or micro-winkler test (Fox & Wingfield, 1938) within an hour. The mean for a series of 6 community respiration measurements taken during the interval from July through September, 1963, was 0.65 mg/sample/hr. The caloric equivalent of the mean value (Ivlev, 1934) was 2.20 geal/sample/hr or 880 geal/m<sup>2</sup>/hr. Based on this mean rate, community respiration was about 7710 kcal/m<sup>2</sup>/yr. Subtracting the annual macrofauna respiration, 2008 kcal/m<sup>2</sup>/yr, leaves 5702 kcal/m<sup>2</sup>/yr to be divided between microorganisms and producer populations.

From static dark bottle incubation of *Bacopa*,

several estimates of respiratory rate were secured. The mean value of these rates was 1.3 mg O<sub>2</sub>/g/hr. Using mean annual values for *Bacopa* standing crop, (50.4 g/m<sup>2</sup>) and Iylev's (1934) oxycalorific coefficient, *Bacopa* respiration amounted to about 2000 kcal/m<sup>2</sup>/yr in Cone Spring. Applying the same rate and extrapolating similarly, *Lemna* respiration about 320 kcal/m<sup>2</sup>/yr.

Subtracting macroflora respiration from the total unaccounted for, 5702 kcal/m<sup>2</sup>/yr, leaves about 3400 kcal/m<sup>2</sup>/yr or 0.39 kcal/m<sup>2</sup>/hr to be charged to microorganism respiration in Cone Spring. This compares with a bacterial metabolism estimated by Odum in Silver Spring, Florida (1957), as 0.079 g O<sub>2</sub>/m<sup>2</sup>/hr or 0.267 kcal/m<sup>2</sup>/hr. Although not specifically discussed, Odum (1957) implied that the bacterial ooze sampled was free from any significant number of other microorganism populations. Since this was not true in Cone Spring, the difference between Odum's Silver Springs estimates and those in the present study of Cone Spring could in part be due to inclusion of the metabolism of protozoa, copepods and microorganisms other than bacteria in the respiration measurements of the latter. Teal (1962) estimated bacterial activity in a spartina marsh to be about 3890 kcal/m<sup>2</sup>/yr.

#### ORGANIC EXPORT

Energy bound in particulate organic matter placed in suspension by the continuously flowing water of Cone Spring leaves this ecosystem for Cone Marsh at a high rate throughout the year. The magnitude of these losses was estimated for the interval March through September, 1963. Fig. 5 compares the rate of organic export with the mean monthly standing crop of detritus.

The mean rate of export of organic matter was found to be dependent upon the mean monthly standing crop of detritus according to the relation Y = 8.2X - 13.4. The slope of the line so defined was significantly different from zero at the 98% confidence level.

From this relation, it was possible to estimate the magnitude of exported organic matter for months in which detritus samples were taken. This was necessary for the first part of the year of study when the centrifuge used to remove particulate organic matter from outflow water was inoperable.

The value of the total annual export was estimated by multiplying the mean rates per month times the number of liters calculated to have left Cone Spring during each interval. The total export was about 145 kgm AFDW of organic debris per year. Converting this figure to its approximate caloric equivalent, 4 kcal/g AFDW from wet oxidation of debris, it was estimated that Cone Marsh, below the spring, gained about 58 x 10<sup>4</sup> kcal/yr through the action of Cone Spring. Expressed as a contribution from the entire 141 m<sup>2</sup> basin export from Cone Spring was about 4100 kcal/m<sup>2</sup>/yr.

TABLE 5. Ecosystem energy budget items kcal/m<sup>2</sup>/yr.

Energy Budget Items.....	Kcal/m <sup>2</sup> /yr
Macrofauna Respiration.....	2008
Microorganism Respiration.....	3400
Total Consumer Respiration.....	5408
Exported Organic Matter.....	4100
Change in Standing Crop	
<i>Bacopa</i> .....	-259
<i>Lemna</i> .....	+5
Consumers.....	+7
Total (Net).....	-247
Net Primary Production	
<i>Bacopa</i> .....	204
<i>Lemna</i> .....	134
<i>Impatiens</i> .....	730
Total.....	806
Import.....	626

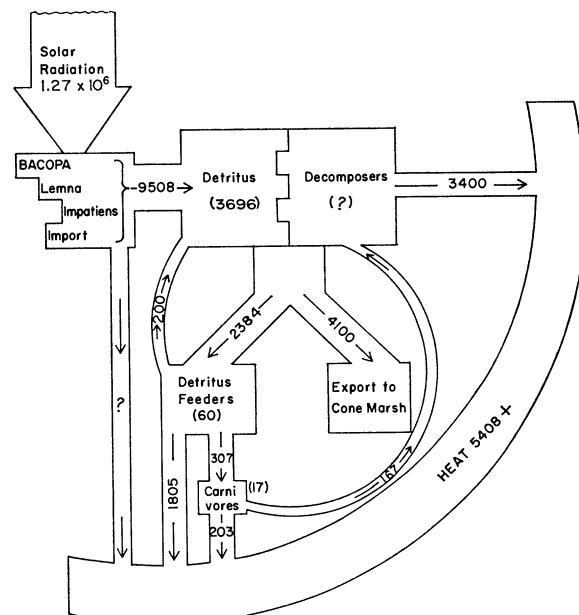


FIG. 6. Energy flow diagram summarizing the major pathways through the Cone Spring ecosystem. Numbers in parentheses represent mean monthly standing crops. All values are kcal/m<sup>2</sup>. Flow rates per year are indicated by arrows.

#### ENERGY BUDGET SUMMARY

The energy budget of the Cone Spring community is summarized for convenient reference in Table 5. Some of these data have been used in constructing the energy flow diagram, Fig. 6, and are referred to in the discussion to follow.

Examination of the estimates of income and expenditures of energy reveals a rather gross disparity indicating either an overestimate of energy expenditures or an underestimate of energy income. Energy income was probably underestimated. The respiratory rate estimates for macrofauna, if in error, are believed to be too low rather than too high. The estimate of microorganism respiration does not seem

to be inordinately high compared to that found in other systems and I believe the export measurements to be reasonably accurate.

The cropping and harvest methods for measuring net primary production are subject to large scale errors due to their inability to account for all forms of mortality. The debris traps used to measure allochthonous input are also believed to have given an underestimate.

Considering measure of annual community expenditures to be correct, Cone Spring energy income must have been at least 9508 kcal/m<sup>2</sup> during 1962-63 since income must equal expense. Changes in standing crop indicate that approximately 247 kcal/m<sup>2</sup> of this total came from reserves stored in previous years. About 9261 kcal/m<sup>2</sup>/yr must have been produced in or around Cone Spring.

#### EFFICIENCIES

The ratio, yield of a higher trophic unit to the yield of the immediately lower trophic unit, was calculated for primary consumers and for secondary consumers. This efficiency named by Wiegert's (1964) method, "gross efficiency of primary consumer yield/primary producer yield," was estimated as 862 kcal/m<sup>2</sup>/yr/9508 kcal/m<sup>2</sup>/yr or 9% for Cone Spring populations.

The gross efficiency of secondary consumer yield/primary consumer yield lies in the range 12-25% depending upon what corrections are made for *Phagocata* data. *Phagocata*'s behavior as both secondary and tertiary consumer tends to increase its apparent efficiency and consequently the trophic level efficiency. Efficiencies are elevated also if mucus from *Phagocata* is counted as yield rather than expense. Slobodkin (1962) reviewed the problem implicit here, pointing out the fact that the magnitude of efficiencies measured may depend upon what the investigator is willing and able to measure as "yield".

A ratio describing the efficiency of a trophic level in utilizing available food was discussed by Odum (1959). This ratio, the gross efficiency of higher trophic level income/lower trophic level yield was calculated for Cone Spring populations and listed in Table 6 for comparison with values calculated by Teal (1957) for Root Spring, Massachusetts and Silver Springs, Florida, (Odum, 1957).

The 3 communities do not agree with respect to their trophic level efficiencies. Cone Spring data seem to offer support for Lindemann's (1942) hypothesis that higher trophic levels are more efficient in utilizing available energy; data from Silver Springs and more emphatically Root Spring show the opposite relation. Teal (1957) interpreted the extremely high (76%) efficiency recorded for primary consumers as a consequence of the favorability of the environment in Root Spring.

Probably the real difference lies in the inequivalence of the trophic levels being examined. Teal (1957) pointed out that in a steady-state community showing no export or accumulation of energy the

TABLE 6. Comparisons of trophic level efficiencies in percent.

Trophic Level Efficiency	Cone Spring	Root Spring	Silver Springs
Gross efficiency of primary consumer income/primary net production.....	24	76	38
Gross efficiency of secondary consumer income/primary consumer net production.....	58	36	26

TABLE 7. Gross efficiencies of yield/income.

Species	Gross Efficiency of Yield/Income	Species	Gross Efficiency of Yield/Income
<i>Gammarus</i> .....	15.0	Tendipedid Scroll	42.1
<i>Frenesia</i> .....	27.9	Tendipedid D.P.	38.9
<i>Physa</i> .....	82.5	Tendipedid R.B.	42.9
<i>Pentaneura</i> .....	42.6	<i>Naidium</i>	54.5
<i>Phagocata</i> .....	25.7; 90.8	<i>Corynoneura</i>	42.9
<i>Cardiocladius</i> .....	32.1	<i>Heleid</i> "B"	26.3
<i>Tubifex</i> .....	60.0	<i>Pericoma</i>	43.8
Tendipedid "H".....	30.4	<i>Stratiomys</i>	23.1
Heleid "A".....	17.4	<i>Sphaerium</i>	60.0
<i>Chauliodes</i> .....	14.4	<i>Psychoda</i>	40.0
Tendipedid "S".....	41.8	<i>Nematode</i>	71.4
<i>Calopsetra</i> .....	46.7	<i>Agria</i>	?
<i>Limnephila</i> .....	27.6		
<i>Rhantus</i> .....	32.7		
<i>Gordionus</i> .....	49.0		
<i>Hermione</i> .....	22.4		
<i>Dixa</i> .....	35.2		
<i>Chelifera</i> .....	38.0		

primary consumer efficiency must be 100%. The low efficiency measured for primary consumers in Cone Spring is therefore a result in part of the export activity of the spring as well as an indication that microscopic forms usually considered as decomposers should be included as primary consumers. If one considers net income minus export to be available energy the efficiency of utilization for Cone Spring primary consumers recognized would be 58%. This means in turn that about 42% of primary consumption is accomplished by organisms included as decomposers. Making the same sort of calculation for Silver Springs data, primary consumer utilization efficiency would be 53% instead of 38%. Evidently microorganisms were less important as primary consumers in Root Spring than in the other two systems considered.

Irrespective of the validity of Lindemann's hypothesis concerning trophic level utilization efficiencies, it is still worth considering whether consistent trophic level differences exist between populations in their efficiencies of converting intake into yield. The gross efficiencies of yield/income were calculated for all species populations and are summarized in Table 7. This is an approximation of the efficiency described by Slobodkin (1960) as "ecological efficiency" and considered by him to be among the more useful efficiencies for describing population interactions. It

is an approximation because yield values calculated for Cone Spring populations include all kinds of production passed to other consumers and do not measure what is actually ingested by consumers as required by Slobodkin's definition. Net production by members of one trophic level must be greater than ingestion by members of higher trophic levels. In general, the gross efficiencies of yield/income were similar to those recorded by Teal for populations in Root Spring, Massachusetts. Teal's values ranged from 13 to 87% in comparison to a range of 15-83% for Cone Spring populations with no obvious tendency for carnivores to have higher efficiencies.

The gross efficiency of yield/intake for the whole community was found to be 31%, a figure very close to the 29% found by Teal (1957) for the Root Spring, Massachusetts, community.

Slobodkin (1960, 1962) has given reasons why "ecological efficiency" would probably not exceed the range 5-20%. For several of the major species populations, some comment upon measured efficiencies is therefore in order. *Frenesia* populations were calculated to have a gross efficiency of yield/income of about 28%. It was observed that the *Frenesia* population was maintained to some extent by immigration from unsampled edge regions. Wiegert (1964) has shown that populations importing energy by immigration will be calculated to have higher ecological efficiency than populations not profiting from gains charged outside the studied ecosystem. Tendipedid "H" and *Cardiocladius* may also have profited from the import of energy in young larvae which immigrated from unsampled edge zones.

*Physa* was calculated to have the enormously high efficiency of 82%. This high value is undoubtedly due in part to the very low respiratory rate calculated for this species. Mucus production was not measured for this species but is likely to have been sizeable. If charged as a maintenance cost equivalent to respiration, and not as yield, a lowered efficiency would result.

Immigration may be a factor in the *Physa* population since this is one of the few species which, by crawling over the dam could successfully enter Cone Spring from the brook below. Even allowing reasonable revisions of costs and net production for such items, however, it appears that efficiencies for this species would still be higher than levels generally predicted by Slobodkin (1962).

For the *Pentaneura* population, the gross efficiency of yield/income has been calculated to be about 43%. When the *Pentaneura* population is viewed only as a source of food for *Phagocata*, this efficiency is estimated at about 21% (assuming about 10% of *Pentaneura* weight to be unavailable to *Phagocata*).

The gross efficiency of *Phagocata* yield/income was calculated as about 26% excluding mucus as yield and 91% including mucus as yield.

The gross efficiency of primary consumer income/secondary consumer income may be considered to be a closer approximation of Slobodkin's (1960) eco-

logical efficiency. Calculated for Cone Spring trophic levels, this efficiency was 370/2346 or 13%. The 49 kcal/m<sup>2</sup> estimated to be passed on from *Pentaneura* to *Phagocata* was subtracted from the total for predator assimilation to get the numerator used.

The gross efficiency of net primary production/total insolation was calculated to be 9508 kcal/m<sup>2</sup>/yr/1.27 x 10<sup>6</sup> kcal/m<sup>2</sup>/yr or about 0.8% using climatological data available for Iowa in 1962-1963 (U.S. Department of Commerce, 1962; 1963) as an estimate of solar radiation probably available to Cone Spring. The comparable efficiency for gross primary production was calculated as about 1% assuming gross production to be 4/3 net (Odum, 1959).

Gross production efficiencies calculated for some other ecosystems are: 0.2% for Root Spring in April (Teal, 1957); 5.8% for Eniwetok Reef (Odum and Odum, 1955); 1.6% for an Ohio cornfield in summer (Transeau, 1926); 8.0% for Silver Springs, Florida (Odum, 1957); and 0.3% for George's Bank, Newfoundland (Clark, 1946). Cone Spring, by comparison, may be considered to be rather high in efficiency. This, of course, is because of the role of the Cone Spring basin in concentrating energy fixed by vegetation in the area surrounding the spring. The area supplying energy-laden products to the spring basin can be reasonably estimated to be at least several times that of the basin itself. Efficiencies based on the greater area would be in line with usual estimates from such latitudes.

Considering the community as a producer unit yielding energy to Cone Marsh, the gross efficiency of net ecosystem yield/net primary production was 4100 kcal/m<sup>2</sup>/yr/9508 kcal/m<sup>2</sup>/yr, about 43%.

#### COMMUNITY STRUCTURE

A second method of community analysis, complementary to the metabolic approach, is the study of structure. The aspects of community structure considered in the present study were dispersion, species diversity and the distribution of abundance.

#### SPATIAL DISTRIBUTION OF SPECIES

Although separate plots of spatial distribution were not made for all species, evidence of several kinds indicates that most of the inhabitant species abundant enough to be sampled with any frequency have a rather uniform horizontal distribution throughout Cone Spring.

A frequency plot of the numbers of species occurring in 89 randomly selected samples revealed that the 7 most frequently occurring species were found in more than 75% of all samples; 3 species were found in about 50% of all samples and 28 species were found in fewer than 30% of all samples.

If one examines samples for the incidence of "failure of occurrence" of the most frequent species following the procedure outlined by Hairston and Byers (1954), it is possible to check the departure from randomness of the distribution of these forms among the samples randomly selected for study. If

89 random samples from the regular sampling series are examined, one finds only 64 failures of occurrence of the 7 indicator species. Comparing the distribution of absences with the binomial expectations for the distribution of such absences, one finds many more samples having no absences than expected by chance alone. For example, according to the binomial probabilities 22.37 samples of the 89 would be expected to have no absences. Actually 37 samples were found to contain all 7 indicator species. For the remaining classes, fewer than the expected number of absences were observed. Checking the departure from binomial expectations using the chi-square test gave  $\chi^2 = 13.916$  which with two degrees of freedom indicates a highly significant departure from random expectations ( $p < 0.005$  for larger values).

This means that these indicator species are present in the whole set of samples much more constantly than would be expected by chance and, in view of the observed general distribution of samples, would support the contention that these major species, at least, are very uniformly distributed throughout Cone Spring.

#### VERTICAL DISTRIBUTION

It has already been remarked that the vertical dimension of the Cone Spring ecosystem is very restricted.

Examination of 10 of the first core samples taken revealed that normally no macroscopic forms (down to the size of harpacticoid copepods) were found below 5 cm of substratum depth; most of the Cone Spring community members live in the detritus constituting the upper 2-3 cm of the substratum.

#### DISPERSION PATTERN

The patterns in which organisms are usually dispersed may be categorized as regular, random or clumped (Macfadyen, 1963). The pattern revealed by sampling has been shown to be influenced by the size of the sample and the size of the sample unit used (Cole, 1946; Comita, 1957; Curtis & McIntosh, 1950; Kershaw, 1964; Evans, 1952; Healy, 1964).

The relationship between observed variances and means of sampling data from Cone Spring populations indicated that most species there were not normally distributed. Most forms appeared to exhibit some degree of clumping. The index of aggregation of Lexis was measured for different populations and tested for significance at the 95% confidence level following the methods of Debauche (1962). Populations were also ranked according to degree of aggregation as estimated by the use of  $k$  from the negative binomial distribution (Healy, 1964; Debauche, 1962; Bliss & Fisher, 1953). The value of  $k$  increases with decreasing aggregation, equaling zero for data fitting a logarithmic distribution pattern. Unfortunately,  $k$  cannot be efficiently estimated for populations represented by very low numbers of individuals (Hairston and Byers, 1954).

Table 8 summarizes the results of both series of calculations. Most of the Cone Spring predators are

found among those species listed as showing no significant departure from randomness in their dispersion. An actively predaceous form which may cannibalize would be expected to be more regularly spaced than a detritus feeder. *Phagocata* is an exception to this generalization. In contrast to other Cone Spring predators, *Phagocata* "hunts" and feeds communally.

In contrast to the findings of Hairston and Byers (1954) for soil arthropods, the rarer species do not seem to be more clumped than the abundant in Cone Spring. Spearman's Rank Correlation technique was applied in the comparison of the rank assigned by the annual mean of the mean number per sample per month with the rank according to the magnitude of  $k$ . The Spearman Rank Correlation Coefficient,  $C$ , was 0.38256, not significantly different from zero at the 95% confidence level indicating that no significant relation exists between clumping and numerical abundance of species in Cone Spring.

On the Michigan old field (Hairston and Byers, 1954) the clumping more evident for rare forms was interpreted as meaning that only very locally were conditions suitable for these species.

The lack of relationship between clumping and abundance for Cone Spring species may simply be an indication that the spring system is relatively more homogeneous than the old field habitat. However, the possible influence of sample unit size upon the old field data cannot be ignored. Sample units which are too large will be able to reveal clumping only for the rarer forms which allowed a sufficient number of zero samples to be taken for a pattern to be revealed (Curtis & McIntosh, 1950; Evans, 1952).

#### SPECIES DIVERSITY

In any community a complete census would reveal a certain total number of individuals,  $N$ , in which were represented a lesser number of species,  $S$ .  $S$  would be an unbiased measure of the number of occupied niches in the community. The ratio  $N/S$  is useful for comparing communities of different sizes and in practice it is the relationship between  $N$  and  $S$  which is used in community analyses as an objective measure of the structural property known as species diversity (Williams, 1964).

Since complete censuses are seldom possible, attempts have been made to estimate the actual species diversity from the results of sampling and, for this purpose, a series of species diversity indices have been devised which take into consideration the general tendency of sampling to give biased estimates of the diversity of a community. Macfadyen (1963) and, especially, Williams (1964) have provided useful reviews of the concept of species diversity.

In Cone Spring 89 samples contained a total of 8209 individuals of 37 species of macroscopic aquatic organisms. Grouped by months the annual mean number of individuals per sample was 90; the mean number of species recovered was 12. The mean numbers of individuals and mean numbers of species per

TABLE 8. Clumping and abundance ranks.

Species	Est. k	Rank by k	Rank by #/ sample	Index of Lexis	Rank by Lexis Index	Significantly Clumped?
<i>Gammarus</i>	0.830	16	3	5.151	4	yes
<i>Frenesia</i>	2.950	23	7	2.545	11	yes
<i>Physa</i>	1.315	20	2	3.984	6	yes
<i>Pentaneura</i>	60.338	25	1	1.184	24	no
<i>Phagocata</i>	0.594	15	5	4.774	5	yes
<i>Cardiocladius</i>	0.498	11	4	5.686	3	yes
<i>Tubifex</i>	0.338	7	8	5.932	2	yes
Tendipedid "H"	2.12	21	9	2.435	13	yes
Heleid "A"	2.988	24	6	2.447	12	yes
<i>Chauliodes</i>	—	26	20	0.931	27	no
Tendipedid "S"	0.304	5	10	6.095	1	yes
<i>Calopsectra</i>	0.402	8	12	3.154	9	yes
<i>Limnophila</i>	0.870	17	21	1.229	22	no
<i>Rhantus</i>	2.667	22	23	1.073	26	no
<i>Gordionus</i>	0.562	12	18	1.745	19	yes
<i>Hermione</i>	0.583	14	13	2.064	17	yes
<i>Dixa</i>	1.032	18	11	2.141	16	yes
<i>Chelifera</i>	0.465	10	19	1.805	18	yes
Tendipedid Scroll	1.278	19	24	1.228	23	no
Tendipedid "D.P."	0.567	13	14	3.217	8	yes
Tendipedid "R.B."	0.176	3	17	3.830	7	yes
<i>Naidium</i>	0.348	6	25	0.931	28	no
<i>Corynoneura</i>	0.144	2	22	2.555	10	yes
Heleid "B"	0.133	1	15	2.345	14	yes
<i>Pericomia</i>	0.196	4	26	2.253	15	yes
<i>Stratiomys</i>	0.459	9	16	1.406	21	yes
<i>Sphaerum</i>	—	—	—	1.162	25	no
<i>Psychoda</i>	—	—	—	—	—	—
<i>Nematode</i>	—	—	—	1.419	20	—
<i>Agria</i>	—	—	—	—	—	—

sample changed little throughout the year. A plot of Menhinick's (1964) species diversity index,  $d = S/\sqrt{N}$  for all samples (Fig. 7) showed an apparent increase in diversity from December 1962 to June 1963. This trend could not be correlated with any measured environmental variables. The diversity indices calculated ranged in value from a low of 1.11 in December 1962 to a high of 1.62 in May 1963. Mean species diversity for the year was 1.35 calculated as an average of the monthly means. The low value found in April 1963 is probably an artifact. Only about half the usual number of samples could be taken that month. Individual numbers were similar but species number declined. Menhinick's index was affected despite the fact that the number of samples taken exceeded the conventional requirements for sampling adequacy according to Cain's (1938) species-area standard.

When Margalef's (1957) diversity index,  $d = (S-1)/\ln N$ , was applied to the Cone Spring data a curve similar to that generated by the use of Menhinick's index was produced. Williams (1964) has shown that Margalef's index correlates with the information theory measure of diversity, H.

There are few species diversity data available for useful comparison with figures based on Cone Spring. Calculations of Menhinick's diversity index using data from a variety of aquatic and terrestrial systems (e.g. Hairston, 1959; Menhinick, 1964; Williams, 1964) produced values for d which ranged

from 0.94 to 26.46. Species diversity in Cone Spring seems relatively low.

#### RELATIVE SPECIES ABUNDANCE

The relative abundance of species is of theoretical importance in regard to community organization so long as the species in question are of similar size and taxonomy (MacArthur, 1960; Hairston, 1964) and have generation times which are short relative to the periods of environmental variation (Hutchinson, 1957).

In an environment as stable and homogeneous as Cone Spring one would expect the selective forces of non-biotic environmental factors to remain fairly constant over periods of time which are long compared to the generation time of the species in competition. The Cone Spring community includes 18 species of dipterans for which relative abundance distribution was considered.

One of the most interesting theoretical models for abundance distribution is that of MacArthur (1957). Starting from biological considerations, MacArthur proposed 3 models which might relate to the manner in which individual communities were organized. All models were based on the assumption that the community is divisible into niches (Hutchinson, 1957). The relative abundances of component species are presumed to be a measurable manifestation of the apportionment of available niches within the community.

The first model assumes that the niches are con-

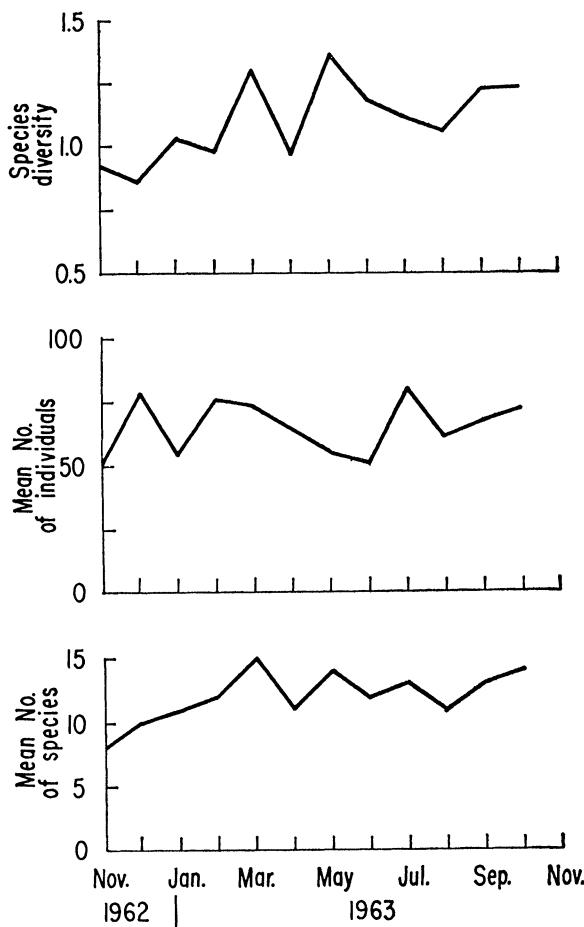


FIG. 7. Annual cycle of species diversity calculated using Menhinick's (1964) index and based on average numbers of individuals and numbers of aquatic species found in each month's sample.

tiguous and non-overlapping, implying that they are determined by the quantity of some resource which when used by one species becomes unavailable to all others.

Of the 3 proposed models only the first has found any support in data from field studies and it is this model that is intended when "MacArthur's model" is mentioned.

According to MacArthur's (1957) formulation, the abundance of the  $r^{\text{th}}$  rarest species can be represented

$$\text{as } \frac{m}{n} \sum_{i=1}^r \frac{1}{n-i+1} \text{ where } m \text{ is the total number}$$

of individuals,  $n$  is the number of species and  $i$  is the interval between successively ranked species and the rarest species.

When plotted with abundance of each species as ordinate and rank ( $r$ ) in rareness on a log scale as abscissa, a convex curve results if the community is actually randomly divided into niches (and if the other necessary conditions discussed above are met).

An objective test of departure from expectations was described by Hairston (1959) based on ratios

of observed to expected variances. No probability levels could be assigned, but a perfect fit would result in a variance ratio of 1. Since, as Hairston (1959) proposed, food is the most likely factor to qualify as an unshared resource, metabolic expressions will be better than numbers of individuals in describing the distribution of abundance. A further partitioning of species according to trophic levels was suggested by Slobodkin (1960) for similar reasons. Therefore, the dipteran associations tested for fit to the MacArthur model were detritus feeders and carnivores with abundance expressed in terms of assimilation, kcal/m<sup>2</sup>/yr.

For 14 detritus feeding dipterans having a total assimilation of 233 kcal/m<sup>2</sup>/yr the ratio of variances was 3.17, a relatively poor fit. For 4 carnivorous dipteran species having a total assimilation of 261 kcal/m<sup>2</sup>/yr the ratio of variances was 1.78, a closer but not unequivocal fit to the MacArthur model.

Hairston (1964) asserts that animal communities, in general, do not fit the MacArthur models and accedes to the view of Preston (1948; 1962) that the lognormal distribution is the one which best describes the relative abundance of associated species.

Hairston (1964) suggests the use of the variance ratio (observed variance/MacArthur expected) as a measure of organization. According to this view "an increased variance reflects an increased degree of organization of the community. Where the observed variance is no greater than expected in MacArthur's random distribution model organization may be considered as virtually lacking."

On this basis the community of Cone Spring dipterans is relatively low in organization. Detritus feeding forms, however, apparently show a greater degree of organization than do carnivores. Such a situation is contrary to that predicted for terrestrial forms by Hairston *et al.* (1960) and Hairston (1964). Food limited carnivores are expected to be regulated in abundance by competition while herbivores (and detritus feeders?) are expected to be regulated more randomly by their respective intrinsic rates of increase (Hairston, 1964).

Since small body size should be equitable roughly to high intrinsic rate of natural increase (Smith, 1954) one should find a negative relationship between body size and abundance for herbivores but no relationship for carnivores (Hairston, 1964). For Cone Spring dipterans, species were ranked according to the caloric equivalent of body size and abundance rank was assigned according to assimilation calories. Both carnivores and detritus feeders showed a positive trend but neither correlation was significant. Spearman Rank Correlation coefficients were 0.0923 and 0.2000 for detritus feeders and carnivores respectively. The hypothesis is not supported. Either the control mechanism or the trophic units being compared could account for the lack of agreement. The possibility that detritus-feeders are trophically more equivalent to carnivores than to herbivores will be discussed later.

## DISCUSSION AND CONCLUSIONS

Ecosystem communities are usually too large and complex to be studied in one piece. Cone Spring, although relatively small and discrete, is no exception. Species populations and trophic levels constitute the 2 most logical subunits into which a community may be divided for study. Population studies are tedious and cumbersome, but trophic level studies tend to oversimplify and obscure important biological information.

For example, in Cone Spring, it was found that an Eltonian pyramid of classic dimensions could be constructed using trophic level energy assimilation values secured by analyses of separate populations. The impression from such a trophic pyramid is that a large amount of surplus food exists in the form of primary consumers available to carnivores. A closer look, considering population interactions reveals that the energy budget is much tighter than would be supposed by trophic level analysis. The second most productive primary consumer, *Frenesia*, was eaten in quantity only by *Chauliodes* populations which did not assimilate a large amount of energy. The *Physa* population which ranked third in primary consumer net production among species was apparently not preyed upon by Cone Spring inhabitants at all. Budgetary considerations force one to consider that Cone Spring predators may be food limited. Such a consideration would not have been suggested by strictly trophic level analysis.

As already mentioned *Pentaneura* populations had interactions on 2 trophic levels and *Phagocata* was both secondary and tertiary consumer at one time.

Strict laboratory approaches such as those very usefully applied by Slobodkin (1954; 1959; 1962) and Richman (1958) to single species populations would not have revealed what important interactions occur at the community level. What was actually treated as the unit of community organization in the Cone Spring study was neither the trophic level nor the population, but the food web segment, an energy flow pathway including a set of primary consumers which feed alike and the particular set of predators which prey upon them.

Margalef (1960; 1963) has discussed extensively a series of generalizations which he proposes as "unifying principles" for the study of communities. Foremost among these generalizations is the idea that community structure and function are most meaningfully understood in terms of the history of the community. Evolution within communities, Margalef maintains, leads to stabilization of structure-function relationship at a certain level of maturity dependent upon interactions possible between sets of organisms and environmental factors. He considers that maturity can be measured, therefore, in terms of observable structural and metabolic relationships which can be sampled in communities. Connell and Orias (1964) present a model which seemingly would account for the evolution of such structural (and presumably

functional) relationships as are described by Margalef.

One of the most appealing aspects of Margalef's (1963) approach is that it seeks to account for both structural and functional relationships as complements of one another. For instance, biomass is one tangible aspect of structure which is measurable and requires a constant flow of energy for its maintenance.

Margalef (1963) offers the generalization that "more mature ecosystems, with a richer structure, have a lower primary production per unit biomass." Total productivity does not decline, but actually increases. More organization is maintained per unit expenditure of energy, however.

Both Odum (1956 b) and Margalef (1963) have made use of the ratio of primary production to total biomass as an expression of this principle, Odum calling the ratio "community turnover," Margalef referring to it as the P/B ratio. In Cone Spring a ratio of this sort may be calculated for comparison with those from other ecosystems. It is convenient, however, to substitute caloric equivalents for biomass for the Cone Spring data. Such a substitution should not change the relationship involved and in fact should result in some degree of standardization since all components can be expressed in terms of the same (caloric) units. Table 9 compares several aquatic ecosystems with respect to standing crop and energy flow. The P/B ratios presented are understandable in terms of Margalef's generalization. The value found for the unstable and presumably less "mature" Mid Oconee community is about 10 times as high as those secured for Cone Spring and Root Spring. Why the very stable Silver Springs should appear to be less mature than Cone Spring is not clear, but it appears reasonable that Lake Mendota which is not exporting its "organization" (Margalef 1960; 1963) should rank as the most mature in comparison with a set of flowing systems.

Cone Spring may usefully be considered as an ecosystem maintained in immaturity by the deformational influence of flow, the restrictions of small size and the limits placed upon reproduction by low temperature. Physical conditions play an obvious role in influencing the organization and structure of the Cone Spring community.

A number of features exhibited by members of the Cone Spring community may be interpreted as adaptation to flowing water. The preponderance of flying insects among the fauna may be the result of selection for forms which can close the colonization cycle more readily than can the strictly aquatic forms (Margalef, 1960). *Physa*, *Phagocata* and *Gammarus* in Cone Spring have all been observed to exhibit positive rheotaxis. *Pentaneura* and *Cardiocladus* have been seen to use their clawed anal prolegs as anchors against the flow in an artificial spring system in the laboratory. *Frenesia* builds heavy cases of sand grains.

Avoidance of the effects of flow seems to be another

TABLE 9. Comparison of aquatic ecosystems.

Ecosystem	Mean Standing Crop Consumers			Net Income	Export	Consumer Yield		Consumer Respiration		Yield/mean consumer crop (P/B)
	Primary	Secondary	Total			Primary	Secondary	Primary	Secondary	
Cone Spring	60	17	77	9508	4100	643 7%	136-218 17-2%	1805 19%	203 2%	14
Root Spring (Teal, 1957)	67	15	72	3105	868	554 18%	119 4%	1746 56%	89 3%	18
Silver Springs (Odum, 1957)	184	54;8*	246	9319	2500	1478 16%	67;6* 1%	1890 20%	316 4%	38
Mid Oconee River (Nelson & Scott 1962)	20	3	23	4340	—	710 16%	36 1%	—	—	189
Georgia Salt Marsh (Teal, 1962)	—	—	—	8205	3671	209 2.5%	17 0.2%	596 7%	48 1%	—
Lake Mendota (Judson, 1940)			294	3730	—	—	—	—	—	13

Income, export, yield and respiration are rates in Kcal/m<sup>2</sup>/yr; standing crops are Kcal/m<sup>2</sup>; P/B ratios are dimensionless. Blanks have been left where information was lacking. Where necessary published data were converted to Kcal equivalents following the original author's suggestions or applying average equivalents from the literature. Percentages shown are based on net income. Asterisks (\*) refer to tertiary consumers.

adaptive pathway favored by Cone Spring fauna. Many of the animals in Cone Spring live among the detritus particles in the layer described by Schwoerbel (1962) as the hyporheal, where flow is greatly diminished. *Dixa*, a filter feeder, avoids being displaced in the flow by clinging with most of its body attached to emergent vegetation or pebbles. The habit practiced by a number of Cone Spring insects of laying eggs in the moist edges of the spring out of the flow is a behavioral adaptation which would enable the least vagile stages to avoid the problems of displacement to which they, especially, would be subject.

A second physical factor which may be important in influencing the Cone Spring community is temperature. As was discussed earlier, water temperatures in Cone Spring were generally lower and more constant than temperatures in most temperate zone communities. This may have allowed psychrophilic organisms such as *Phagocata velata* and *Gammarus pseudolimneus* to become and remain members of the community. Some degree of regulation, however, may result from the influence of temperature upon the reproduction of some of the Cone Spring forms. The abundance of *Phagocata* may be related to water temperature. In emergent organisms such as *Cardiocladus* marked shifts in densities could be expected to occur as a result of random fluctuations in the air temperature and weather. Populations of adults which happen to emerge at a favorable time may leave more progeny than those emerging under unfavorable conditions.

Biotic feedback mechanisms which condition the direct effects of the environment upon organisms must develop if communities are to mature (Connell and Orias, 1964). Giving evidence that Cone Spring has achieved a degree of maturity beyond that of a pioneer community is the occurrence of a series of biotic interactions largely centering about the effects

of the emergent *Bacopa* upon this ecosystem. *Bacopa* grew over the entire flow area in Cone Spring and always formed a dense mat in the downstream area where outflow occurred. Its presence there and elsewhere in the flow permitted the accumulation of detritus and organisms which would otherwise have been swept downstream. This "strainer" effect is conjectured to have had at least two significant results on the history of Cone Spring. The accumulation of detritus permitted the support of larger and more varied populations of detritus feeders and predators of detritus feeders. *Bacopa*, through its action in retarding flow and in providing physical support for other organisms, diminished the energy expenditure required for maintenance of position and enabled this to be channeled into reproduction. Probably more than any other single component, *Bacopa* is responsible for whatever degree of complexity and organization beyond the pioneer stage the Cone Spring community has achieved. Although no statistical difference in species composition or diversity was found between *Bacopa* regions and non-*Bacopa* zones above the dam, the continuous presence of the *Bacopa* mat in the region of the outflow from the spring basin may be important to the maintenance of community organization. The springbrook community a short distance below the *Bacopa* area was found in qualitative sampling to be much less diverse than the Cone Spring community above. Conditions in the two communities were, superficially at least, very similar and, although most of the springbrook forms were also inhabitants of Cone Spring, the converse was not true. The presence of *Bacopa* as a structural element is probably responsible for the observed differences.

A major weakness of Margalef's (1963) model is its failure to provide any mechanism for the regulation of abundance in ecosystems. He implies that regulation operates through the food chain in a

classically density-dependent fashion as described by Hairston *et al.* (1960).

However, in Cone Spring the abundance of dipterans (the most abundant single taxon) does not conform to theoretical expectations. The expected patterns of abundance were set on the unproved assumption that aquatic detritus feeders are trophically equivalent to herbivores. Newell (1965) discovered that certain marine molluscs he studied were eating detritus but assimilating mostly bacterial aufwuchs protein. Ivlev (1945) found he could rear tendipedids on filter paper if bacteria were present as intermediaries. If aquatic detritus-feeders as a group are eating bacteria, they are actually predators and therefore may be expected to be controlled by available food and competition rather than by carnivores.

Snails studied by Hairston (1964) (and classically thought of as detritus-feeders or herbivores) were regulated in abundance by competition rather than by predators. Ratio of variance tests suggested that the abundances of detritus-feeding dipterans in Cone Spring are not related to individual body size (and intrinsic rates of increase) as would be theoretically expected for herbivores or their equivalents. Thus in their statistical attributes these detritus feeders resemble carnivores.

The instances cited above of reduction of abundance and enhancement of reproduction by the action of temperature and other physical factors would appear to be cases of density-independent action. The existence of relationships between physical factors and abundance does not necessarily imply that abundance is regulated only by physical factors, however. Huffaker (1965), for example, has described a predator-prey system in which density independent stresses set the level at which density-dependent equilibrium was established. Higher stresses result in a lower (in abundance) equilibrium. Density-independent factors such as temperature extremes may be acting in Cone Spring to set the abundance levels at which density-dependent regulation occurs.

I am proposing an admittedly conjectural scheme to account for the organization and regulation of the Cone Spring community. This scheme involves the assumption, only partially supported, that detritus feeders act in Cone Spring as predators rather than herbivores. I suggest that energy flows from (autochthonous and allochthonous) primary producers to the detritus standing crop which serves as food for primary consumers. (Both community metabolism measurements and primary consumer efficiency estimates suggest the existence of large populations of microscopic primary consumers in Cone Spring.) It is possible that most of the primary consumers are microscopic organisms which, in turn, are utilized as the real limiting source of food by detritus feeders. Detritus feeders, then are primary carnivores available as food to secondary and tertiary carnivores.

Feces and egested materials re-enter the detritus pool where they become the substrate for growth of

primary consumer-decomposer populations once again. As just suggested, bacterial populations may be functioning as both primary consumers and decomposers. To what extent any given species may function simultaneously in both of these roles is a total guess.

According to the scheme envisioned, bacterial populations are likely to be either predator limited or food limited or both depending upon how much trophic specialization occurs. Primary producers would be expected to be limited by light and space. Almost all the macroscopic forms would be limited by available food.

The above model, based essentially upon Hairston *et al.* (1960) and Hairston (1964) is compatible with the facts of abundance distribution and metabolism observed in Cone Spring. What are needed for confirmation or negation are information about trophic classification, metabolism and standing crops of microorganisms and results from the experimental manipulation of well-described ecosystems. Since numerous systems appear to be detritus centered a generalized version can and should be tested.

#### SUMMARY

- During the interval July 1961 to June 1964, Cone Spring was studied for the purpose of securing data for combined structural and functional community analysis.

- The ecosystem was characterized as shallow, cold, homogeneous, nutrient rich and generally environmentally stable.

- Data on numbers of individuals, weights, caloric equivalents, respiratory rates, distribution and natural history for all 32 macroscopic species native to the system were collected for more than one complete annual cycle.

- Measurements were made of import and export of organic matter.

- Ricker's model or cropping methods were used to estimate natural losses suffered by each consumer population.

- The 3 major plants present interacted to share the biotope in space and time. *Impatiens* by shading the others in summer, *Lemna* by occupying the interstices among the strands of *Bacopa* which when unshaded in winter grew laterally underwater to occupy areas vacated by *Impatiens*.

- Detritus apparently formed the base of the food web in the Cone Spring community; no major species was found to ingest fresh, growing plant material.

- The major consumer species accounting for more than 90% of the heterotroph energy flow were, in order of declining importance, *Gammarus pseudolimneus*, *Frenesia missa*, *Physa integra*, *Pentaneura* sp., *Phagocata velata*, and *Cardiocladus* sp.

- The *Gammarus* population alone was responsible for almost one half of the primary consumer energy flow.

- Frenesia* and *Physa*, the species second and third in total flow requirements were not important links in the food web of macroscopic organisms. The

energy available to predators was therefore less than a single trophic level analysis suggested and primary consumer non-predatory mortality was relatively high at 35%.

11. *Pentaneura* fed as both secondary and primary consumer and *Phagocata* evidently served as simultaneously secondary and tertiary consumer.

12. The community energy budget showed that about 56% of the net income was transformed to heat and about 43% exported in the outflow. About 60% of the available income was utilized by primary consumers in Cone Spring.

13. The ratio (net income/available solar energy) for Cone Spring was about 0.0075, a high value for a temperate community. The calculated efficiency was relatively high because a considerable portion of the Cone Spring net income came from adjacent terrestrial systems.

14. The gross efficiencies of yield/income for species populations in Cone Spring ranged from 13 to 83% with no trophic level differences observable. For the community as a whole the same efficiency was 31%, a figure close to the 29% found by Teal (1957) for Root Spring.

15. Data are presented suggesting that clumps of most species were rather uniformly distributed throughout the Cone Spring basin so that they were included in samples at a frequency greater than chance would predict.

16. Correlation failed to reveal any clearcut relationship between clumping and abundance, possibly because of the interactions occurring between sample unit size and the clumping indices used, but there was a suggestion that carnivores were less clumped than detritus feeders.

17. Species diversity in Cone Spring appears to be relatively low and seasonally rather stable.

18. MacArthur's (1957) model failed as a description of the pattern in which abundance was distributed among Cone Spring dipterans even when trophic grouping and metabolic abundance expressions were used in the calculations. According to Hairston's (1964) view of the Cone Spring dipteran community is low in organization although detritus feeding forms show more organization than do carnivores.

19. Some recent hypotheses concerning the organization and regulation of communities were tested with Cone Spring data for comparison with those of Hairston (1964). A model which may account for Cone Spring organization is proposed and discussed.

20. Data reviewed suggest that Cone Spring may reasonably be classified as a steady-state ecosystem maintained in a permanently immature condition by the deformational forces of flow and low temperature, abetted by the spatial restrictions of small area and shallowness.

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