

ECOLOGY OF ZOOPLANKTON OF THE CAPE THOMPSON AREA, ALASKA¹

JERRY C. TASH² AND KENNETH B. ARMITAGE

Department of Zoology, The University of Kansas, Lawrence, Kansas

(Accepted for publication March 20, 1966)

Abstract. In a survey of the physicochemical characteristics, primary productivity and occurrence of zooplankton in fresh and brackish waters at Cape Thompson, Alaska, between June 28, 1960 and August 7, 1961, 14 species of Cladocera and 38 species of Copepoda (13 Calanoida, 11 Cyclopoida and 14 Harpacticoida) were distinguished in collections from 10 lakes, 8 lagoons and 111 pools. Seventy-three per cent of all species were monocyclic; 13 per cent dicyclic; 9 per cent tricyclic; and 4 per cent tetracyclic.

The maximum of primary production was correlated with maximal numbers of zooplankton, maximal number of eggs per ovigerous female in the Cladocera, and maximal occurrence of copepodids. Many Copepoda produced eggs in late fall and early winter when primary production was low. Autumnal production of eggs by these species may be possible because of storage of energy as lipids during the period of high environmental energy, and use of the stored energy at the end of the developmental period to form eggs.

Analysis of community structure among zooplankton showed: 10 species with affinities and 7 interrelated recurrent groups occurred in the lakes; 3 species with affinities and 1 recurrent group occurred in the lagoons; 4 species with affinities and 3 interrelated recurrent groups occurred in the coastal pools; and no species with affinities occurred in the inland pools. One cladoceran, one cyclopoid and one or two calanoid copepods of different genera formed the major recurrent groups. The relationships between recurrent groups were the result of species within those related groups having similar distribution and overlapping developmental cycles.

Closely allied species occupied different aquatic habitats, but when congeneric species co-occurred, there were differences in size and life cycles.

The arctic is an especially favorable area in which to study the complex ecological interrelationships of zooplankton because the arctic aquatic ecosystems are more simple than their counterparts in temperate areas. Until recently (Edmondson 1955; Comita 1956), detailed studies of zooplankton in arctic Alaska had not been made. Most published works are short-term species surveys (Comita 1952; Johnson 1961; Juday and Muttkowski 1915; Marsh 1920; Reed 1962) or are taxonomic reports (e.g. Reed 1958; Wilson 1953).

The primary purpose of this paper is to examine some aspects of species associations of crustacean zooplankton from a series of lagoons, coastal and inland pools, and lakes.

METHODS AND MATERIALS

On 60 dates from June 28, 1960 to August 7, 1961, quantitative and qualitative collections of plankton and water samples for chemical analyses were taken and rates of C^{14} assimilation were measured in one freshwater lake and two coastal lagoons. Thirty-three collections of plankton and

eight water samples for chemical analyses were obtained from one coastal pool and from another freshwater lake. One hundred and eleven qualitative samples of zooplankton were collected from various temporary and permanent pools.

Temperature was measured with a Whitney thermometer calibrated with a glass thermometer to a precision of $\pm 0.5^\circ\text{C}$. Amounts of dissolved oxygen were measured by the azide modification of the Winkler method; pH with a Beckman G pH meter; alkalinity titrimetrically with phenolphthalein and methyl-orange indicators and 0.02 sulfuric acid. Carbon dioxide was estimated from total alkalinity, pH, and the dissociation constants as given by Rainwater and Thatcher (1960). Concentrations of calcium, magnesium, silica, sodium, chloride, total hardness, salinity and total solids were estimated by the Arctic Health Research Center, Anchorage, Alaska, in 1960, and by the U.S. Geological Survey, Palmer, Alaska, 1961 (detailed physicochemical analyses recorded in Tash 1964).

The C^{14} method of Steemann Nielsen (1952) and Steemann Nielsen and Aabye-Jensen (1957) was used to estimate primary production. Glass-stoppered light and dark bottles of 125-ml capacity were filled with water that was collected using a 3000-ml Kemmerer bottle coated with plastic to prevent contact between water and the metal. These bottles were inoculated with 8 ml

¹ Financial support of the U.S. Atomic Energy Commission (Project Chariot) for field work in 1960-61 is acknowledged. The authors wish to thank Douglas K. Hilliard of the Arctic Health Research Center for helpful advice and assistance throughout the project.

² Present address: Klamath Lake Investigations, USPHS, 2261 South Sixth Street, Klamath Falls, Oregon.

of $\text{NaHC}^{14}\text{O}_3$ having an activity of .004 mc. Usually two sets of bottles, each set consisting of one light and one dark bottle, were anchored at 0.3 m and 1.5 m depth during 1961 in another lagoon. The bottles were normally exposed from 20 to 24 hr, the exposure time varying because of weather conditions that affected travel to and from the sampling sites. Following exposure, each sample was filtered through a type HA Millipore membrane 24 mm in diameter. Counting and radiocarbon uptake readings were calculated in $\text{mg C/m}^3 \text{ hr}$ by the International agency for C^{14} determinations located at Charlottenlund Slot, Charlottenlund, Denmark, and the results were converted into $\text{mg C/m}^3 \text{ day}$.

Quantitative samples of zooplankton were obtained by two methods: 1) during ice-free periods, horizontal tows were made in the limnetic zone with an open uncalibrated Clarke-Bumpus plankton sampler using a #12-mesh plankton net; 2) during periods of ice cover, a Swedish ice auger was used to core the ice and whole samples of water were taken with a 3,000-ml Kemmerer bottle and were strained through a #12-mesh plankton net to concentrate the zooplankton. Qualitative samples were taken by these methods and also by stripping vegetation. Concentrated samples were fixed in 10% formalin and preserved in 80% ethanol.

Identification of zooplankton was made from preserved specimens using published keys and figures (Brooks 1959; Johnson 1961; Wilson 1959; Wilson and Yeatman 1959; Yeatman 1959). Mrs. Mildred S. Wilson identified most of the calanoid copepods and Harry C. Yeatman identified many of the cyclopoid copepods.

Quantitative data were calculated either from total counts of the numbers of individuals of a species present in a sample, or from three to six 1-ml Sedgewick-Rafter counts (the latter method used only when zooplankton were too abundant to warrant making a total count). One revolution of the Clarke-Bumpus sampler was assumed to represent 4 liters of water.

STUDY AREA

The Cape Thompson study area is about 161 km north of the Arctic Circle, 201 km northwest of Kotzebue, and forms a semicircle approximately 32 km to the north, to the south and inland of the mouth of Ogotoruk Creek at $68^\circ 06' \text{ N}$, $165^\circ 46' \text{ W}$ (Fig. 1). The aquatic habitats in the study area are located in a predominately tundra drainage area and range from small ephemeral pools to large perennial lakes and lagoons. Based on proximity to the Chukchi Sea, the aquatic habitats

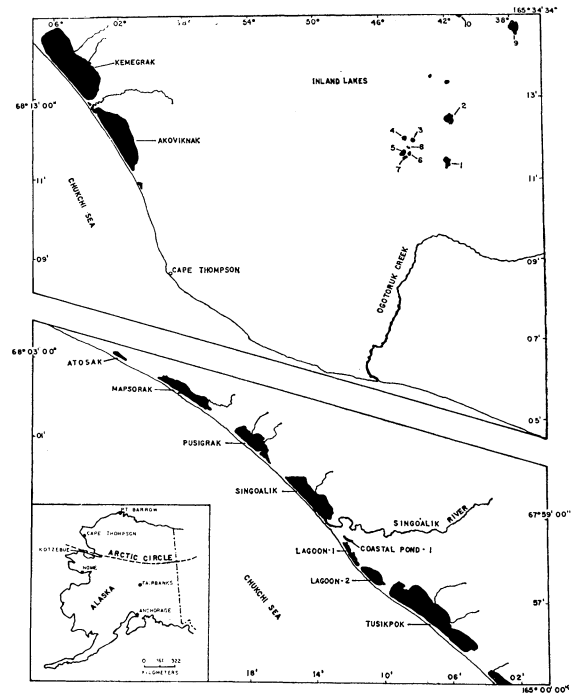


FIG. 1. Named and numbered lagoons and inland lakes sampled in the Cape Thompson area. Based on U.S. Coast and Geodetic Survey Topographic Map T-9425 Alaska.

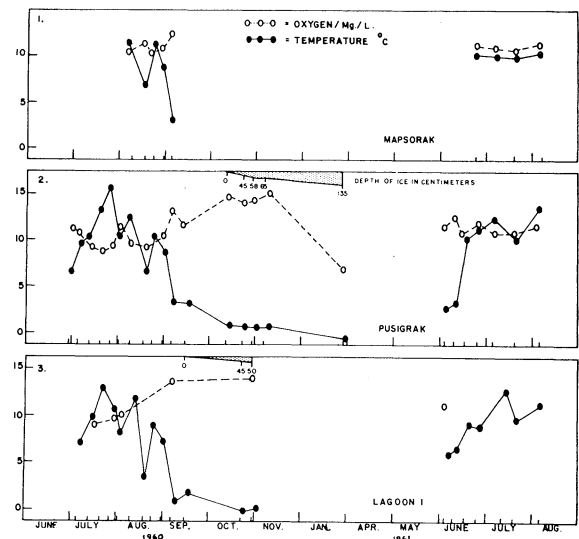


FIG. 2. Oxygen in mg/L , temperature of water in $^\circ\text{C}$, and thickness of ice in centimeters for Mapsorak, Pusigrak and lagoon 1 during 1960-61.

of the area were arbitrarily divided into lake, lagoon, inland pool, or coastal pool categories. Lakes and inland pools are considered perennially freshwater, lagoons and coastal pools are considered as brackish in degrees varying through-

out the year. All aquatic habitats are shallow, from 3 to 4 m in depth.

Temperatures above freezing occur usually on fewer than 100 days per year. Water temperatures rose rapidly in spring and usually reached a peak near 15°C in June or July, then declined gradually until September when a rapid decline occurred (Fig. 2, 3). Ice cover usually began to

creased from 10 to 100 times as the ice froze during late 1960 and early 1961. In this same period, hydrogen ion concentrations shifted from slightly basic to slightly acid.

Carbon assimilation (mg C/m³ day) was higher in lake 4 than in Pusigrak (Fig. 4). Annual car-

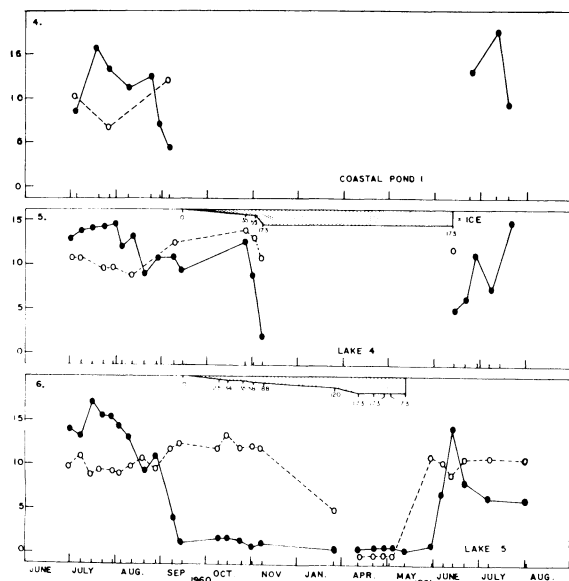


FIG. 3. Oxygen in mg/l, temperature of water in °C, and thickness of ice in centimeters for coastal pond 1, lake 4 and lake 5 during 1960-61.

form in mid-September and typically lasted until mid-May or early June.

RESULTS

During ice-free periods, physicochemical values found in aquatic habitats at Cape Thompson were similar to those recorded for other areas of Alaska (Conita and Edmondson 1953; Edmondson 1956; Hobbie 1960; Livingstone, Bryan, and Leahy 1958). The pH ranged from 6.6 in winter to 7.6 in summer in all aquatic habitats. Lagoons at Cape Thompson usually had higher values of calcium, magnesium, silica, sodium, chloride, total hardness and total solids than the lakes. Manganese and phosphate were more abundant in the lakes. Since steady winds tend to disrupt stratification in the aquatic habitats of the Arctic (Edmondson 1956), oxygen concentration was about 10 mg/liter at all depths throughout most of the growing season. However, oxygen concentration decreased to 0.0 mg/liter during the winter under ice cover (Fig. 2, 3). Ionic concentrations were highest under 1.50 to 1.75 m of ice. Cations, anions, salinity, carbon dioxide and alkalinity in-

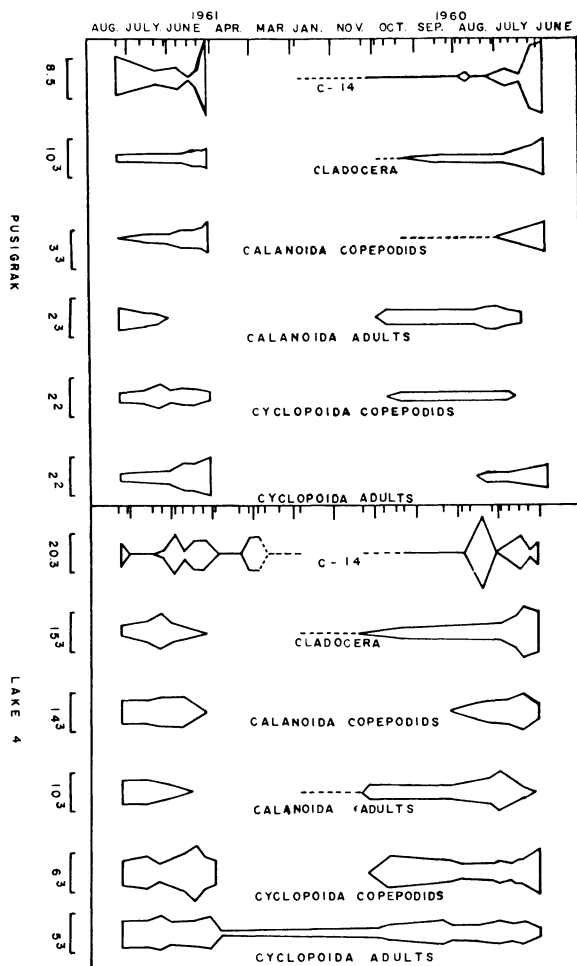


FIG. 4. C¹⁴ assimilation in mg C/m³/day and total numbers of Cladocera and of Cyclopoida and Calanoida adults and copepodids per m³ in Pusigrak and lake 4 in 1960-61. The dotted lines represent numbers too small to plot as numbers.

bon assimilation at Cape Thompson was low. This low value supports Livingstone's observations (1963, p. 571) that annual primary production in arctic and subarctic habitats is relatively low in comparison with that of temperate aquatic habitats.

Fourteen species of Cladocera and 38 species of Copepoda (13 Calanoida, 11 Cyclopoida and 14 Harpacticoida) were distinguished and their distributions in the various habitats recorded (Table I). Of the total number of species, 16 were collected over 50% of the time from lakes, 10 from lagoons, 18 from inland pools, 4 from coastal pools

TABLE I. Habitat preference of Cladocera and Copepoda at Cape Thompson, Alaska. A habitat preference was assumed when at least 50% of the total occurrences of a species were in any one of four habitats. Four species were ubiquitous and are included under a separate heading

LAKES	LAGOONS	INLAND POOLS
<i>Holopedium gibberum</i>	<i>Ilyocryptus acutifrons</i>	<i>Polyphemus pediculus</i>
<i>Macrothrix laticornis</i>	<i>Eurytemora composita</i>	<i>Daphnia pulex</i>
<i>Eurycerus glacialis</i>	<i>E. foveola</i>	<i>Bosmina coregoni</i>
<i>Alona guttata</i>	<i>E. raboti</i>	<i>Eurycerus lamellatus</i>
<i>A. affinis</i>	<i>Limnocalanus johanseni</i>	<i>Alona costata</i>
<i>A. rectangula</i>	<i>Halicyclops</i> sp.	<i>Diaptomus alaskaensis</i>
<i>Heterocope septentrionalis</i>	<i>Microarthridion littorale</i>	<i>Cyclops vicinus</i>
<i>Eurytemora</i> sp. nov.	<i>Tachidius discipes</i>	<i>C. strenuus</i>
<i>Diaptomus arcticus</i>	<i>Nitroca spinipes</i>	<i>C. magnus</i>
<i>D. gracilis</i>	<i>Danielssenia stefanssoni</i>	<i>C. venustoides</i>
<i>D. glacialis</i>		<i>C. crassicaudis brachycercus</i>
<i>D. pribilofensis</i>		<i>C. languidoides</i>
<i>Eucyclops agilis</i>		<i>Paracamptus reggiae</i>
<i>Cyclops scutifer</i>		<i>Moraria affinis</i>
<i>Epactophanes richardi</i>		<i>M. mrazeki</i>
<i>Moraria duthiei</i>		<i>Canthocamptus staphylinoides</i>
		<i>Attheyella nordenskiöldii</i>
		<i>Bryocamptus tikchikensis</i>
COASTAL POOLS	UBIQUITOUS	
<i>Eurytemora canadensis</i>	<i>Daphnia middendorffiana</i>	
<i>E. gracilicauda</i>	<i>Chydorus sphaericus</i>	
<i>Onychocamptus mohammed</i>	<i>Cyclops vernalis</i>	
<i>Bryocamptus subarcticus</i>	<i>C. capillatus</i>	

TABLE II. The number of Cladocera and Copepoda in the Cape Thompson area that had monocyclic, dicyclic, tricyclic, or tetracyclic developmental cycles and the corresponding percentage of the total species in the group that had each (From Tash 1964)

Species group	No. species	Species that were							
		Monocyclic		Dicyclic		Tricyclic		Tetracyclic	
		No.	%	No.	%	No.	%	No.	%
Cladocera	14	5	50	3	21	3	21	1	9
Calanoida	13	10	77	2	15	1	7		
Cyclopoida	11	7	64	2	18	1	9	1	9
Harpacticoida	14	14	100						
Total	52	38	73	7	13	5	9	2	4

and 4 were ubiquitous. The number of generations in the annual life cycle of various species was analyzed by Tash (1964). Seventy-three per cent of all species of Cladocera and Copepoda at Cape Thompson were monocyclic; 13% dicyclic; 9% tricyclic; and 4% tetracyclic (Table II). Egg counts of most species of Harpacticoida were maximal in June or July; egg counts of most species of Cyclopoida and Cladocera were maximal from June to August inclusive and most Calanoida had maximal egg counts from July to October inclusive (Table III).

COEXISTENCE OF CONGENERIC SPECIES

Momentary samples of limnetic zooplankters usually contain only one species in a genus (Pennak 1957). This pattern also occurs in pond populations (Armitage 1961; Armitage and Davis

1966). When two or more species of the same genus coexist in the same body of water, competition (used in the sense of Milne 1961: p. 60) may be inferred. However, competition may be less than inferred because ecological displacement may be obscured by ordinary sampling methods, and, without careful study, character displacement and other intrinsic mechanisms that partition the habitat may be overlooked (Cole 1961).

One mechanism that appears to partition the environment is size displacement. Congeneric occurrences are characterized by marked differences in the sizes of the adults (Hutchinson 1951). The size and distribution of the species of Cladocera and Copepoda collected at Cape Thompson were examined for possible size displacement or other mechanisms that might reduce potential competition. The length of males of *Diaptomus* spp. were: *Diaptomus arcticus*, 2.0–3.0 mm; *D. glacialis*, 2.3–2.9 mm; *D. pribilofensis*, 1.0–1.5 mm; *D. alaskaensis*, 1.2–1.5 mm; *D. gracilis*, 1.2–1.3 mm.

D. arcticus and *D. pribilofensis* were abundant in most of the lakes and some of the pools. Adult *arcticus* are about twice as large as adult *pribilofensis*. Presumably, the difference in size permits partitioning of the environment, especially of food. The size of late copepodid stages of *pribilofensis* overlaps early stages of *arcticus*, but *pribilofensis* developed later in the season and more slowly than *arcticus*; therefore, size displacement was accentuated by the time displacement of population development.

TABLE III. The average number of subitaneous eggs per ovigerous female of the species of Cladocera and Copepoda in the Cape Thompson area in 1960-61. P, pools; L, lakes; Lg, lagoons; C, composite from several habitats

Species	Habitat	Months								
		June	July	Aug.	Sept.	Oct.	Nov.	June	July	Aug.
MONOCYCLIC										
Cladocera										
<i>Polyphemus pediculus</i>	P			2.7						
<i>Bosmina coregoni</i>	P			2						
<i>Alona guttata</i>	L			2						
<i>A. affinis</i>	L		2							
<i>Holopedium gibberum</i>	Lg		3.0	4.1	8.1					
Calanoida										
<i>Eurytemora foveola</i>	Lg	3.9								
<i>Eurytemora</i> sp. nov.	L			14						
<i>Diaptomus alaskaensis</i>	P							17		
<i>D. gracilis</i>	L			25.9						
<i>D. pribilofensis</i>	L			13.5	12.3	12.0				
<i>D. arcticus</i>	C			24.4	34.0					
Cyclopoida										
<i>Eucyclops agilis</i>	L	28.9	21.0	23.5				29.2		
<i>Cyclops scutifer</i>	L	55.9	35.6							
<i>C. magnus</i>	P		126							
<i>C. capillatus</i>	P		40							
<i>C. venustoides</i>	P						30			
Harpacticoida										
<i>Epactophanes richardi</i>	L	8.5								
<i>Moraria duthiei</i>	L	16.2								
<i>M. mrazeki</i>	P	11.8								
<i>Attheyella nordenskiöldii</i>	P		23.9							
<i>Tachidius discipes</i>	Lg	42								
DICYCLIC										
Cladocera										
<i>Daphnia pulex</i>	Lg		3.1	9.4				21.7	6.0	
<i>Holopedium gibberum</i>	L		29.0	19.1	12.0				26.0	15.1
Calanoida										
<i>Eurytemora canadensis</i>	P		48.5	49.0	51.0	49.0			52.7	
<i>E. gracilicauda</i>	P		15.5					54.5	23.0	
Cyclopoida										
<i>Cyclops strenuus</i>	P	48.0	74.3	85.4			50.3	60.2	84.0	
<i>C. crassicaudis brachycerus</i>	P						36.0	31.0		
<i>C. languidoides</i>	C						16.5	23.4	35.0	
TRICYCLIC										
Cyclopoida										
<i>Cyclops vernalis</i>	P		95.4	48.0				65.8	46.9	
	L	29.3	21.0	24.5				36.9	19.0	26.5
POLYCYCLIC										
Cladocera										
<i>Daphnia middendorffiana</i>	P		4.0	2.7				21.9	6.2	
	L		4.8	1.7				8.8	5.5	
<i>Eurycercus lamellatus</i>	P		9.4	57.3	2.0			8.7	6.0	2.0
<i>E. glacialis</i>	L			9.5					4	
<i>Alona costata</i>	P		1	2	2				2	
<i>A. rectangula</i>	P		2	2	2					
<i>Chydorus sphaericus</i>	C	2	2	2	2			2	2	2

D. arcticus, *D. glacialis*, *D. pribilofensis*, and *D. gracilis* coexisted in lake 7, and *D. arcticus*, *D. glacialis* and *D. pribilofensis* in lake 6. Only a few individuals of *glacialis* and *gracilis* were present and they were not found in any other samples. Both species have been reported from lakes and ponds (Wilson 1959) and hence may be able to

coexist with their numerically more successful counterparts because of repeated invasions of the lakes or because the short Alaskan summer does not permit sufficient time for the potentially dominant species to "drive out" the numerically subordinate species. Also, the various species may belong to different communities in the lakes.

In this connection it is interesting to note that neither *glacialis* nor *gracilis* formed affinities with other species (Table IV) nor was a member of any recurrent group (Fig. 5).

Diaptomus alaskaensis avoided interaction with most species in an extraordinary fashion. Atypical for diaptomids, it occurred only in small ephemeral pools where it had a greatly accelerated life cycle that was completed during the period of maximal primary production when other species that might interact with it were just starting their developmental cycles.

Cyclops scutifer and *C. strenuus* have so many morphological characteristics in common that many workers consider *C. scutifer* the same or a subspecies of *C. strenuus* (Yeatman 1944). However, at Cape Thompson the two species occupied different habitats at different times of the year, *C. strenuus* primarily dwelling in pools during the summer and *C. scutifer* exclusively dwelling in lakes from early winter to late spring. These differences eliminate interaction between the two species and also provide isolation that might eventually result in a more distinct morphological separation.

Eurycerus lamellatus and *E. glacialis* had similar life cycles, but avoided interaction by occupying different aquatic habitats, the former species dwelling mostly in pools and the latter in lakes.

Although *Daphnia middendorffiana* and *D. pulex* occurred at Cape Thompson, *D. middendorffiana* was the dominant species, occurring abundantly in many lakes, lagoons and pools, whereas *D. pulex* was present in small numbers in only a few pools, one lake and two lagoons.

Interactions between other species of Cladocera or Copepoda were not distinguished. Cyclopoida contains predatory species, but none of the species found at Cape Thompson was observed taking prey.

AFFINITIES BETWEEN SPECIES AND RECURRENT GROUPS

The grouping of animals on the basis of vegetation or of various physical or chemical factors in the environment generally has been unsatisfactory (Fager 1957; Gisin 1947; Sørensen 1948). Physicochemical data from Cape Thompson were inadequate for detailed comparisons with zooplankton. The increase in carbon dioxide, the decrease in oxygen and the concentration of chemicals and organic constituents in the water below the ice probably eliminated species that might otherwise have overwintered. Concentrated chemical and organic constituents were released into the water

after spring thaw and resulted in a high rate of primary productivity that provided energy for the maximal numbers of zooplankters.

Often species were associated on the basis of habitat preferences (McKee and Coker 1940; Reed 1962). An analysis of the distribution of species of Cladocera and Copepoda showed that 15 species preferred lakes; 10 preferred lagoons; 18, inland pools; 4, coastal pools and 4 were ubiquitous (Table III). This method provides a general indication of species associations but does not accurately indicate affinities between species.

Recently workers have applied statistical techniques to associate species (Cassie 1961; Cole 1949; Fager 1957). Statistical analysis of species associations offers the advantage of repeatability without subjective elements altering the results. Fager (1957) devised an index of affinity between species based on their presence and absence in samples and provided a table from which the significance of an observed number of joint occurrences could be estimated. From tables derived by Fager's formulae, recurrent groups can be determined and their relationships established. This procedure was applied to the species of Cladocera and Copepoda found at Cape Thompson.

Affinities at 0.05 level of significance were determined between species of Cladocera and Copepoda (Table IV) and the relationships between recurrent groups established (Fig. 5). When 52 species were considered, only 6 showed affinities (Table IV, 1). *Daphnia middendorffiana*, *Chydorus sphaericus* and *Cyclops vernalis* belonged to the ubiquitous group determined by habitat preference (Table I). The other three species were common and abundant in collections from inland pools and lakes. The foregoing analysis yielded little more information than the grouping by habitat. Only the most common and/or widespread species were associated.

Since analysis of all samples yielded unsatisfactory results, the affinities between 30 species from 10 lakes, 33 species from 71 inland pools, 22 species from 27 coastal pools and 23 species from 8 lagoons were determined and recurrent groups established. No affinities were found among species from the inland pools.

Ten species showed affinity in the lakes (Table IV, 2) and seven interrelated recurrent groups were established (Fig. 5, II). The relationships between recurrent groups can be explained mostly by consideration of the distribution and developmental cycles of the species involved. The largest group, ABCD, contained species that had overlapping cycles and that were present in all of the lakes. Groups F, H, and I occurred together in

TABLE IV. Affinities at .05 level of significance between species of Cladocera and Copepoda collected at Cape Thompson. The letters preceding species names in the vertical column represent the same species in the horizontal columns. (+ = affinity; - = no affinity)

Species by Areas	Species										Affinity
1 All habitats	A	B	C	D	E	F					
A. <i>Heterocope septentrionalis</i>	.	+	+	+	-	-					3
B. <i>Diaptomus arcticus</i>	+	.	+	-	-	-					2
C. <i>D. pribilofensis</i>	+	+	.	-	-	-					2
D. <i>Daphnia middendorffiana</i>	+	-	-	.	-	-					1
E. <i>Cyclops vernalis</i>	-	-	-	-	.	+					1
F. <i>Chydorus sphaericus</i>	-	-	-	-	+	.					1
2 Lakes	A	B	C	D	E	F	G	H	I	J	
A. <i>Daphnia middendorffiana</i>	.	+	+	+	+	+	+	+	+	+	9
B. <i>Heterocope septentrionalis</i>	+	.	+	+	+	+	+	+	+	+	9
C. <i>Diaptomus pribilofensis</i>	+	+	.	+	+	+	+	+	+	+	9
D. <i>Eucyclops agilis</i>	+	+	+	.	+	+	+	+	+	+	9
E. <i>Cyclops scutifer</i>	+	+	+	+	.	+	+	+	+	+	8
F. <i>Diaptomus arcticus</i>	+	+	+	+	+	.	-	+	+	-	7
G. <i>Moraria duthiei</i>	+	+	+	+	+	+	.	+	+	-	7
H. <i>Holopedium gibberum</i>	+	+	+	+	+	+	+	.	-	-	7
I. <i>Cyclops vernalis</i>	+	+	+	+	+	+	+	+	.	-	7
J. <i>Chydorus sphaericus</i>	+	+	+	+	-	-	-	-	-	.	4
3 Lagoons	A	B	C								
A. <i>Daphnia middendorffiana</i>	.	+	+								2
B. <i>Limnocalanus johanseni</i>	+	.	+								2
C. <i>Cyclops vernalis</i>	+	+	.								2
4 Coastal pools	A	B	C	D							
A. <i>Cyclops vernalis</i>	.	+	+	+							3
B. <i>Chydorus sphaericus</i>	+	.	+	+							3
C. <i>Eurytemora gracilicauda</i>	+	+	.	-							2
D. <i>E. canadensis</i>	+	+	-	.							2

some of the lakes and had overlapping cycles, but no one group was present in all of the same lakes with any other group. For similar reasons, groups G, H, and I formed distinct units. Because of its rarity in the limnetic zones of lakes, group J was separated from all other groups except ABCD. Because its cycle overlapped the cycles of all other species, either in early spring, early winter, or during both periods, group E showed relationship with all groups except J. All species in the recurrent groups except group E had developmental cycles during the summer.

Four species showed affinity in the coastal pools (Table IV, 4) and three interrelated recurrent groups were established (Fig. 5, IV). Group AB contained ubiquitous species with overlapping cycles. Groups C and D showed relationship with group AB, but not with one another. The species in C and D belong to the same genus and may be mutually exclusive because they had cycles during the same time sequence. Usually the species of either group C or D was collected with the species of group AB.

Three species showed affinity in the lagoons (Table IV, 3); and formed one recurrent group

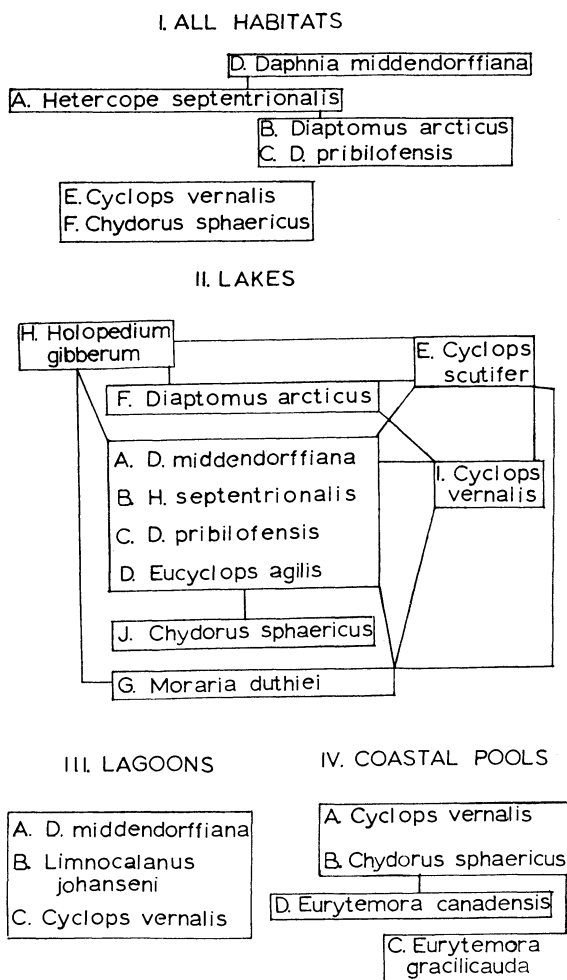


FIG. 5. Relationship between recurrent groups of species determined from the affinities of Table IV. A recurrent "group" may consist of a single species. Related recurrent groups are joined by a straight line.

(Fig. 5, III). All species of group ABC occurred together in several lagoons.

The above application of Fager's index of affinity illustrates the necessity of using samples from similar habitats. The greater the variance between habitats, the fewer were the number of affinities between species of microcrustacea found in those habitats. The lakes were the most uniform group of habitats in the Cape Thompson area and species collected from them showed the greatest number of affinities. The coastal pools were the second most uniform group. They were somewhat removed from the coastline and less subject to wind and storm-swept waves from the Chukchi Sea than the lagoons; most coastal pools are in low swampy areas and are less apt to dry out than many inland pools. The constant flux between marine and freshwater conditions in the

lagoons may account for the failure of more species to invade and maintain populations there. The inland pools were the most varied group of aquatic habitats and there was no affinity between any pair of species collected from them.

In each of the habitats the major recurrent group consisted of species from different genera. In the lagoons (Fig. 5, III), this group consisted of one cladoceran, one calanoid and one cyclopoid copepod. The same pattern occurred in the coastal pools (Fig. 5, IV). Two Calanoida were in the major recurrent group in the lakes (Fig. 5, II). These two species were in different genera and were markedly different in size, *H. septentrionalis* males being about two to three times larger than males of *D. pribilofensis*. Thus separate "niches" in the community are suggested for these Calanoida.

Each of the major recurrent groups in each habitat may be considered as a community or as forming the major component of the limnetic community. The major component is similar to the community structure described for small Colorado lakes (Pennak 1957). In his paper, Pennak emphasized that a limnetic population usually consisted of one calanoid and one cyclopoid, or, if more than one species of either of these groups was present, the species were in different genera. The application of Fager's technique to populations collected from similar habitats strongly supports the pattern of community structure derived from the examination of momentary samples.

The affinities between species in the samples collected from the lakes further support the concept of the basic limnetic community. Recurrent groups E, G, H, I and J all belonged to genera different from those of group ABCD. Only group F, *Diaptomus arcticus*, was generically identical to a member of the major group. The size difference between these two species, which implies niche separation, was described previously. Groups E and I, both *Cyclops*, showed affinity. There was no size distinction between these species, but their life cycles only partially overlapped. An understanding of the relationships between the major component of the limnetic community and other recurrent groups or species that had no affinities requires an analysis of the physiological characteristics and ecological requirements of the species involved. Such information is not available for any species of zooplankton.

DISCUSSION

The relationship between the number of generations that can be produced by many species of plankton has been directly related to temperature

and length of the growing season (Green 1961). Only species that are physiologically adapted for having high rates of metabolism in relatively cool waters can produce more than one generation during a short period. Therefore, the high percentage of monocyclism is not unexpected for species subjected to the cool waters and short growing season at Cape Thompson.

All calanoids except two species of *Eurytemora* were monocyclic. *E. canadensis* and *E. gracilicauda* were dicyclic; there was some indication that the latter was tricyclic. Most cyclopoids were monocyclic; *Cyclops strenuus*, *C. crassicaudis brachycercus*, and *C. languidoides* were dicyclic and *C. vernalis* was tricyclic (perhaps tetracyclic). One generation of all species of Harpacticoida, except two, was collected only in the short prevernal/vernal season. *Moraria duthiei* and *Attheyella nordenskioldii* were collected throughout the summer, but no copepodids of a second generation were taken. Thus all species were monocyclic and monocyclism may be inherent in the Harpacticoida.

Fifty per cent of the species of Cladocera were monocyclic. Many species were restricted to small ephemeral pools that dried up before a second generation could form. For example, *Chydorus sphaericus* and *Eurycercus lamellatus* were polycyclic in perennial pools and lakes, but monocyclic in ephemeral pools. Perhaps most species of Cladocera are capable of forming more than one generation per year in the Arctic if they are in a suitable environment.

The reproductive cycles of the majority of Cladocera and Copepoda result in the vernal production of young when the maximal amount of environmental energy is available (Fig. 4). Enough young must be produced to provide so many adults that their eggs may allow the population to become reestablished the following growing season. The numbers of adults required to assure survival of the species population may differ considerably between Copepoda and Cladocera. A cladoceran ephippium typically contains one or two eggs; a single copepod may produce as many as 120 (Table III). Thus cladoceran populations must be 5 to 30 times larger than calanoid or cyclopoid populations in order to produce the same number of diapause eggs. In the Cape Thompson area, the Cladocera and Calanoida appeared to utilize environmental energy differently. Cladocera seemed to convert surplus energy directly and quickly into individuals; some Calanoida appeared to store surplus energy in the summer and convert it into eggs in the fall (Table III).

The few studies on the storage of energy by

freshwater microcrustacea seem to support the above observations. Richman (1958) found low caloric values for *Daphnia*. Comita and Schindler (1963) found caloric values for *D. pulex* similar to those found by Richman and these values were always less than those of several species of *Diaptomus*. The low caloric values, and observations that populations of most species of Cladocera grow rapidly in an energy-rich environment and decrease rapidly in an energy-poor environment (Slobodkin 1961), indicate that the group does not store much energy for later use.

The evidence for the storage of lipid in the Calanoida is more substantial. Work currently in progress has shown a high content of lipid in some freshwater calanoids. The high caloric values of *Diaptomus* (Comita and Schindler 1963) indicate large reservoirs of stored energy, probably lipids. Food storage has been studied more extensively in marine microcrustacea. Several species of *Calanus*, *Paracalanus* and *Pseudocalanus* store large amounts of lipid (Gunther 1934; Orr 1934; Nakai 1948; Blumer, Mullin, and Thomas 1963). In *Calanus finmarchicus* much of the lipid is utilized in egg formation (Marshall and Orr 1955).

Although analyses of food storage in species of Cladocera and Copepoda collected at Cape Thompson were not performed, some insight to the utilization of food by various species may be interpolated from the average number of eggs produced per female during 1960–61 (Table III). In most species of Cladocera, the maximal number of eggs per female occurred in the spring when primary production and the total number of zooplankton were high (Figure 4). Since Cladocera seem to be opportunistic species that respond quickly to changes in their environment, the survival of the group may depend on the abilities of the various species to produce large populations during optimal periods. The production of large populations increases the chance for larger numbers of individuals to produce ephippia (usually one or two eggs per ephippium) that overwinter to carry the species into the next year.

Most species of *Diaptomus* and *Eurytemora* that were monocyclic produced egg sacs in the fall and early winter when primary production and total number of zooplankton were low (Fig. 4). Females of *Heterocope septentrionalis* and *Limnocalanus johanseni*, which deposit eggs singly, had well-developed ovaries and were collected with spermathecae from August through mid-October. The eggs of Calanoida hatch in early spring and peak numbers of copepodids occur when primary production is maximal. Thus reproduction is

timed to increase the probability of survival of the young (in terms of energy). These species cannot take advantage of the early spring bloom to increase numerically, but must pass through 12 growth stages that require as long as 3 months. Therefore, the ability to store food could be a survival mechanism for such species, allowing them to accumulate energy and produce eggs later when environmental energy is minimal.

The cyclopoids and harpacticoids seem to rely less on food storage than calanoids. Both groups encyst as various copepodid stages during periods of stress. Cyclopoids may store some food since they seem capable of producing eggs almost as soon as they come out of encystment in the spring. The carnivorous cyclopoid, *Euchaeta antarctica*, has high lipid content throughout the year, but the total lipids increase for the production of the large fat-laden eggs (Littlepage 1964). The cyclopoids may also be more euryphagic as they are known to be predatory as well as phytophagous. The ability to produce eggs throughout the growing season (Table III) and to form polycyclic developmental cycles indicate that the Cyclopoida may be better adapted for arctic conditions than either the Cladocera or Calanoida.

Hutchinson (1951) applies the term "fugitive" to species that seem able to "invade" a lake or pond with great rapidity in the early spring, but are later almost completely eliminated as the more slowly increasing zooplankton species intensify the demands on space and nutrients. Such species tend to survive by means of good dispersal mechanisms that enable them to invade new environments. A reservoir of such species may be maintained in temporary ponds, *Diaptomus clavipes* is such a species. It colonizes small bodies of water soon after formation, but disappears after other species become established. Such species should be capable of rapid reproduction. In the Cape Thompson area, inland pool species were primarily Cladocera, Cyclopoida and Harpacticoida (Table I). The Harpacticoida are all monocyclic and are capable of completing the reproductive cycle during the vernal season. The other two groups contained many species that were di-, tri-, or polycyclic (Table III). None of these species formed affinities with others, a further testimony to the ephemeral nature of their existence.

Fugitive species need not be limited to temporary pools. In any aquatic environment with marked seasonal environmental fluctuation there is opportunity for fugitive species to develop populations. Such species would occupy the environment at times when the "permanent" members of the community are at low points of their popula-

tion cycles. Some of the recurrent groups (E, J, H, etc.) of the lakes (Fig. 5) or those species showing no affinities may be fugitive species in the sense expressed here.

In varying environments that microcrustaceans inhabit, many factors may terminate or inhibit population growth. The factors that determine population growth in the arctic environment are simpler to study since growth must be completed by most species within the short summer growing season. In the broadest use of the idea of fugitive species, all species in the Cape Thompson area are fugitive as no species is present year-around. The interactions between species within a community, the magnitude of a population of an individual species, and, in the final analysis, species survival depend upon the efficiency of each species to utilize energy. Studies of the role of physiological mechanisms in simplified environments, as the arctic, will form a physiological basis for determining community structure and illuminate the ways that environmental energy is partitioned among the members of the community.

LITERATURE CITED

- Armitage, K. B. 1961. Species composition and seasonal distribution of limnetic crustacean zooplankton of northeastern Kansas. *Trans. Kan. Acad. Sci.* 64: 27-35.
- Armitage, K. B. and M. Davis. 1966. Population structure of some pond microcrustacea. *Hydrobiologia* (in press).
- Blumer, M., M. M. Mullin, and D. W. Thomas. 1963. Pristane in zooplankton. *Science* 140: 974.
- Brooks, J. L. 1959. Cladocera, p. 587-656. In W. T. Edmondson (ed.). *Fresh-water biology*. John Wiley and Sons, New York.
- Cassie, M. R. 1961. The correlation coefficient as an index of ecological affinities in plankton populations. *Mem. Inst. Ital. Idrobiol.* 13: 151-177.
- Cole, L. C. 1949. The measurement of interspecific association. *Ecology* 30: 411-424.
- Cole, G. A. 1961. Some calanoid copepods from Arizona with notes on congeneric occurrences of *Diaptomus* species. *Limnol. Oceanogr.* 6: 432-442.
- Comita, G. W. 1952. *Cyclops magnus* from Amchitka, Alaska. *Hydrobiologia* 4: 337-340.
- . 1956. A study of a calanoid copepod population in an arctic lake. *Ecology* 37: 576-591.
- Comita, G. W., and W. T. Edmondson. 1953. Some aspects of the limnology of an arctic lake. *Stanford Univ. Publ., Univ. Ser. Biol. Sci.* 11: 7-13.
- Comita, G. W., and D. W. Schindler. 1963. Caloric values of microcrustacea. *Science* 140: 1394-1396.
- Edmondson, W. T. 1955. Seasonal life history of *Daphnia* in an arctic lake. *Ecology* 36: 439-455.
- . 1956. The relation of photosynthesis by phytoplankton to light in lakes. *Ecology* 37: 161-174.
- Fager, E. W. 1957. Determination and analysis of recurrent groups. *Ecology* 38: 586-595.
- Gisin, H. 1947. Analyses et synthèses biocenotiques. *Arch. Sci. Phys. Natur.* 29: 42-75.
- Green, J. 1961. A biology of Crustacea. H. F. and G. Witherby, Gateshead on Tyne. 180 p.
- Gunther, E. R. 1934. Observation on the fatty constituents of marine plankton. 1. Biology of the plankton. *J. Exp. Biol.* 11: 173-197.
- Hobbie, J. E. 1960. Limnological studies on Lakes Peters and Schrader, Alaska. Rept. 5 to Geophys. Research Div., Air Force Cambridge Research Center, Contr. AF 19(604)-2959: 1-47.
- Hutchinson, G. E. 1951. Copepodology for the ornithologist. *Ecology* 32: 571-577.
- Johnson, M. W. 1961. On zooplankton of some arctic coastal lagoons of northwestern Alaska, with description of a new species of *Eurytemora*. *Pac. Science* 15: 311-323.
- Juday, C., and R. A. Muttkowski. 1915. Entomostraca from St. Paul Island, Alaska. *Bull. Wis. Natur. Hist. Soc., N. S.* 13: 23-31.
- Littlepage, J. L. 1964. Seasonal variation in lipid content of two antarctic marine Crustacea. *Biologie Antarctique* 1312: 463-470.
- Livingstone, D. A. 1963. Alaska, Yukon, Northwest Territories, and Greenland, p. 559-574. In D. G. Frey (ed.) *Limnology in North America*. Univ. of Wis. Press, Madison.
- Livingstone, D. A., K. Bryan, Jr., and R. G. Leahy. 1958. Effects of an arctic environment on the origin and development of freshwater lakes. *Limnol. Oceanogr.* 3: 192-214.
- Harsh, C. D. 1920. Freshwater Copepoda. *Can. Arctic Exped., 1913-18, J. Labroquerie Taché, Ottawa* 7: 1-24.
- Marshall, S. M., and A. P. Orr. 1955. On the biology of *Calanus finmarchicus*. VIII. Food uptake, assimilation, and excretion in adult and stage V *Calanus*. *J. Mar. Biol. Assoc. U. K.* 37: 459-472.
- McKee, P. W., and R. E. Coker. 1940. Notes on plankton Entomostraca of the Carolinas. *J. Elisha Mitchell Sci. Soc.* 56: 177-187.
- Milne, A. 1961. Definition of competition among animals, p. 40-61. In *Mechanisms in biological competition*. Symposia Soc. Exp. Biol., No. 15. Academic Press, New York.
- Nakai, Z. 1948. Estimation of oil content in copepods. A method and some results. *Contr. Central Fish Sta. Japan.* 1946. 8-11. *Chem. Abstr.* 1951 (26444), p. 253.
- Orr, A. P. 1934. On the biology of *Calanus finmarchicus* IV. Seasonal changes in the weight and chemical composition in Lock Fyne. *J. Mar. Biol. Assoc. U. K.* 20: 613-632.
- Pennak, R. W. 1957. Species composition of limnetic zooplankton communities. *Limnol. Oceanogr.* 2: 222-232.
- Rainwater, F. H. and L. L. Thatcher. 1960. Methods for collection and analysis of water samples. U.S. Geol. Surv., Water-supply paper 1454. 301 p.
- Reed, E. B. 1958. *Diaptomus (Mixodiatomus) theeli* Lilljeborg (Copepoda, Calanoida) from Arctic Alaska. *Can. Field Naturalist* 72: 152-155.
- . 1962. Freshwater plankton Crustacea of the Coville River Area, Northern Alaska. *Arctic* 15: 27-50.
- Richman, S. 1958. The transformation of energy by *Daphnia pulex*. *Ecol. Monogr.* 28: 273-291.
- Slobodkin, L. B. 1961. Growth and regulation of animal populations. Holt, Rinehart and Winston, New York. 184 p.
- Sørensen, J. 1948. A method of stabilizing groups of

- equivalent amplitude in plant sociology based on the similarity of species content and its application to analyses of the vegetation on Danish commons. *Biol. Skr.* 5: 1-34.
- Steedmann Nielsen, E.** 1952. The use of radioactive carbon (C-14) for measuring organic production in the sea. *J. Cons. Int. Explor. Mer.* 18: 117-140.
- Steedmann Nielsen, E., and E. Aabye-Jensen.** 1957. Primary oceanic production; the autotrophic production of organic matter in the oceans. *Galathea Rep.* 1: 47-135.
- Tash, Jerry C.** 1964. The zooplankton of fresh and brackish waters of the Cape Thompson area, Alaska. Ph.D. Thesis, The University of Kansas.
- Wilson, M. S.** 1953. New Alaskan records of *Eurytemora* (Crustacea, Copepoda). *Pac. Science* 7: 504-512.
- . 1959. Free-living Copepoda: Calanoida, p. 738-794. In W. T. Edmondson (ed.) *Fresh-water biology*. John Wiley and Sons, New York.
- Wilson, M. S. and H. C. Yeatman.** 1959. Free-living Copepoda: Harpacticoida, p. 815-861. In W. T. Edmondson (ed.) *Fresh-water biology*. John Wiley and Sons, New York.
- Yeatman, H. C.** 1944. American cyclopoid copepods of the *viridis-vernalis* group, (incl. a desc. of *Cyclops carolinianus* n. sp.) *Amer. Midland Naturalist* 32: 1-90.
- . 1959. Free-living Copepoda: Cyclopoida, p. 795-815. In W. T. Edmondson (ed.) *Fresh-water biology*. John Wiley and Sons, New York.

ROLE OF ALLOCHTHONOUS DETRITUS IN THE TROPHIC STRUCTURE OF A WOODLAND SPRINGBROOK COMMUNITY¹

G. WAYNE MINSHALL²

*Department of Biology and Potamological Institute,
University of Louisville, Louisville, Kentucky*

(Accepted for publication June 22, 1966.)

Abstract. The community trophic structure of Morgan's Creek, Meade County, Kentucky was analyzed through regular measurement of standing crops of the chief potential sources of plant materials available to the animals (suspended particulate, attached particulate, and allochthonous leaf materials) and an examination of their gut contents. The most important food was allochthonous leaf materials, which occurred as suspended material in the water, as a component of materials attached to the streambed, and as whole leaves and fragments. Diatoms were the only other important source of plant materials and constituted the greatest proportion of the attached organic fraction.

Mean standing crop measurements of potential foods for five sampling stations ranged from 0.6 to 1.0 kcal/m³ for suspended particulate organic matter; 12 to 19 kcal/m² for attached particulate organic matter; and 4.7 to 13 kcal/m² for allochthonous leaf materials. Comparison of standing crop data with previous findings indicates that the values generally are within the known ranges for flowing waters. Analysis of gut contents and determination of the principal pathways of energy flow in the stream indicate that imported organic matter in the form of allochthonous leaf materials provides the main source of energy for the primary consumers and, indirectly, for the entire benthic community of Morgan's Creek. Of the 37 taxa of animals studied, 24 were herbivores, 5 omnivores, and 8 carnivores. In general, detritus made up from 50 to 100% of all the materials ingested by both the herbivores and omnivores. The total number of benthic animals was comprised of 14% herbivores, 83% omnivores, and 3% carnivores. *Gammarus minus* was the single most important member of the fauna. It contributed 81% of the total number of invertebrates, and well over 90% of its diet consisted of allochthonous leaf detritus.

INTRODUCTION

It has been known for a number of years that dead organic matter may be ingested by aquatic invertebrates. However, only comparatively recently was it realized that allochthonous detritus can play an important role in the economy of aquatic ecosystems (Jones 1949, 1950; Dunn 1954; Elton 1956; Teal 1957; Odum and Smalley 1959; Brown 1961; Darnell 1961, 1964;

Hynes 1961, 1963; Nelson and Scott 1962; Chapman and Demory 1963; Minckley 1963; Egglishaw 1964). The present study provides further evidence of the importance of allochthonous detritus to the benthic communities of flowing waters, and explores the role of this food in the trophic economy of a relatively simple system, a woodland springbrook.

At present the only other study relating specifically to the role of detritus in stream productivity is that of Nelson and Scott (1962) on the Middle Oconee River, Georgia. Nelson and Scott measured standing crops of the major sources of primary food and of the bottom fauna over an entire

¹ Contribution No. 91 (New Series) from the Department of Biology, University of Louisville, Louisville, Kentucky 40208.

² Present address: Department of Biology, Idaho State University, Pocatello, Idaho.