THE FOOD AND FEEDING RELATIONSHIPS OF THE FRESH-WATER DRUM, *APLODINOTUS GRUNNIENS* RAFINESQUE IN WESTERN LAKE ERIE[1]

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There has been little specific and detailed work on the food habits and feeding relationships of the sheepshead, or freshwater drum, *Aplodinotus grunniens* Rafinesque. In most instances single individuals or a few specimens have been used for stomach analysis. As far as is known there is only one record of a seasonal analysis of the feeding habits of this fish (Forbes, 1880).

The first record of the feeding habits of *Aplodinotus grunniens* was by Rafinesque (1820) in which he states that the drum of the Ohio River system feeds on a number of species of fish including suckers, catfishes and sunfishes, but that the principal food item is mussels, and especially, species of *Unio*.

Ewers (1933) found that the drum under 25 mm ate no insects, feeding entirely on Entomostraca. Beyond this size Forbes (1888) found that the sheepshead has a very long stage of insect diet, in which Chironomid larvae are important, but the mayfly naiads make up the principal food of the half-grown fish. At a later date, Forbes (1888) reported that mollusks make up one-fourth of the food of the half-grown and adults, half-grown fish ate principally univalve mollusks, while the adults consumed bivalves primarily. In Norris Reservoir, instead of eating mollusks, the larger sheepshead had ingested an occasional fish. Practically all size groups had taken insects or microcrustaceans. The bulk of the insects consisted of larvae and pupae of chaoborines and chironomids, and the bulk of the zooplankton consisted of the entomostracan, *Leptodora kindtii* (Dendy, 1946). Berner (1951) found that sheepshead taken from the lower Missouri River had fed predominantly on insect, fish and plant debris, while Bajkov (1930) found the adult sheepshead to be a competitor of the whitefish in Lake Winnepeg consuming primarily insects and crayfish. Edmister and McLane (unpublished report 1938) found that sheepshead taken from Sandusky Bay, Lake Erie, had fed on yellow perch, young sheepshead, and midge larvae.

There is no known discussion pertaining to the role played by the sheepshead in the communities of which the fish is an integral part. Several workers (Dendy, 1946; Ewers, 1933; Forbes, 1880) have indicated the types of organisms utilized as food by the various sizes of sheepshead. The role of competitor (Kinney, 1950; Gray, 1942; Ewers, 1933) and of forage fish (Clemens, 1947; Doan, 1941) has been indicated.

The present paper is an attempt to portray the food habits of the sheepshead and how they affect the relationships with other organisms found in the communities visited, by summarizing some of the work done in the western sub-basin of Lake Erie. The present study was conducted from the summer of 1947 through 1948.

I should like to express my gratitude to the staff and students of Franz Theodore Stone Institute of Hydrobiology for making this study possible and helping in many other ways. In addition, I wish to acknowledge my indebtedness to Dr. David C. Chandler of Cornell University for allowing me to use some of his unpublished data, for his many suggestions, and for reading the manuscript.

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METHODS

Six hundred and one individuals were examined, ranging in size from 13 mm to 460 mm Standard Length (SL). The material was collected during August and November, 1947, and from the time of ice breakup in late March, 1948, through the first week in December, 1948. The fish were taken from the mouth of the Portage River, Sandusky Bay, along the shores of the island archipelago and from the open lake about the islands. The methods of capture included trapnets, gillnets, trawl, seines, and hook-and-line. The results of the examination of the digestive tracts are expressed in percent frequency of occurrence, i.e., the number of fish containing each organism over the total number of fish with food in the digestive tract.

The tabulation of food items by percent frequency of occurrence seems to be best suited to the present study. The trapnet fishermen were the principal source of the sub-adult and adult sheepshead. In most cases, the trapnets were lifted every third day. This means that for those fish in the nets for the greatest length of time the state of digestion was often so far advanced that the various items could be identified only in a general way. The trawl and hook-and-line collections provided the best material for specific identification. Counts of individual insects and crustacea were made by mandibular tusks, head capsules, or some other hard parts that would indicate numbers of individuals. In such cases volumes or weights were of little value. Each food item is treated separately when tabulating by percent frequency of occurrence. It does not indicate whether one species makes up the entire stomach contents of a fish or whether several different items are found in a single stomach. Because of this, the tabulation of the various items does not necessarily total 100 percent.

DISCUSSION

The mayfly, *Hexagenia*, and the amphipod, *Gammarus*, are the two important items in the sheepshead's diet for all ages. The fish up to 30 mm consume only entomostracans and beyond this size insects become important. The larger sheepshead take an occasional fish and crayfish. In its search for food the sheepshead visits three habitats. For the young-of-the-year fish the benthic and limnetic communities are important while the deep water mud bottoms and the shoals are the most important communities for the sub-adult and adult fish.

Food Consumed

Table 1 gives the make-up of the diet of 218 young-of-the-year fish ranging in size from 13 to 108 mm SL. These fish were taken during August 1947 and from the 26th of July to December 7th, 1948. The young-of-the-year sheepshead have been divided into size groups for the three areas from which they were taken because of differences in diet. The results are summarized in table 2.

Copepods (*Cyclops* and *Diaptomus*) made up 95.6% of the diet for the 12 to 30 mm sheepshead taken from the open lake. *Gammarus* was found in 40.3% of these same size fishes. The remaining food items were taken in approximately equal amounts. The three forms of Daphnia (8.9%) were preyed upon but not in the quantities in which they were apparently available. The mayfly *Hexagenia* (1.5%) was not utilized by these small sheepshead apparently because of the large size of the naiads.

For the size group 31–75 mm, 72.3% of the fish fed on *Hexagenia*. This is a marked increase over the 1.5% of the smaller fish. As with the *Gammarus* taken by the 10–30 mm fish, the smaller sizes of *Hexagenia* were utilized. It was with this size group of sheepshead that *Hexagenia* appeared most frequently in the stomachs and continued in similar quantities for all larger size groups. *Gammarus* was the second most frequent stomach content constituent with 53.8%. There were no striking differences between the percent occurrences of *Leptodora, Daphnia*

TABLE 1

Food of the young-of-the-year sheepshead for 1947 and 1948. Percent is the frequency of occurrence of an item in the total number of stomachs containing food.

Organism	Number of Fish	Percent
Copepoda	119	54.6
Hexagenia naiad	98	45.0
Gammarus	88	40.4
Chironomidae Larva and pupae	72	33.0
Ostracoda	41	18.8
Leptodora	34	15.6
Daphnia	26	11.9
Round worm	17	7.8
Trichoptera Larvae	4	1.8
Leech	3	1.4
Coleoptera larvae	2	0.9
Heptageniidae naiad	2	0.9
Fish	1	0.5
Stenomena naiad	1	0.5
Culicidae Larvae	1	0.5
Corixidae	1	0.5
Caenis naiad	1	0.5
Plant Parts	7	3.2
Unidentified	4	1.8
Total	218	

TABLE 2

Food of the young-of-the-year sheepshead according to size distribution and areas sampled.

	Sandusky Bay		Portage River				Open Lake					
SL in mm	31 — 75		10 — 30		31 — 75		10 — 30		31 — 75		76 — 108	
Total Number	5	%	4	%	39	%	67	%	65	%	27	%
Copepoda	4	80	...	...	...	...	64	95.6	28	43.1	...	...
Gammarus	...	...	...	...	1	2.6	27	40.3	35	53.8	15	55.6
Leptodora	...	...	...	...	3	7.7	17	25.4	12	18.5	...	...
Ostracoda	...	...	...	...	...	...	17	25.4	26	40.0	1	3.7
Round Worms	...	...	...	...	...	...	13	19.4	5	7.7	...	...
Chironomidae (Larvae and Pupa)	5	100	4	100	37	94.9	11	16.4	13	19.9	...	...
Daphnia	...	...	1	20	1	2.6	6	8.9	16	24.6	1	3.7
Hexagenia (Naiad)	...	...	...	...	7	17.9	1	1.5	47	72.3	19	70.4
Leeches	...	...	...	...	...	...	...	...	1	1.5	2	7.4
Corixidae	...	...	...	...	...	...	...	...	1	1.5	...	...
Trichoptera (Larvae)	...	...	...	...	...	...	...	...	...	...	1	3.7
Haeptogeniidae (Naiad)	...	...	...	...	2	5.1	...	...	...	...	...	...
Ephemeridae (Naiad)	...	...	...	...	2	5.1	...	...	...	...	...	...
Coleoptera (Larvae)	...	...	...	...	1	2.6	...	...	...	...	...	...
Caenis Naiad	...	...	...	...	1	2.6	...	...	...	...	...	...
Culicidae Larvae	...	...	...	...	1	2.6	...	...	...	...	...	...
Plant Material	3	60	...	...	4	10.3	...	...	...	...	...	...
Unidentified	...	...	...	...	...	...	3	4.5	1	1.5	...	...

and Ostracoda in the 10–30 and 31–75 mm classes, but these items were conspicuously scarce in the larger fish. The copepods formed only 43.1% of the contents of the 30–75 mm fish and were not consumed by the 76–108 mm group of sheepshead. *Hexagenia* and *Gammarus* are the most frequent food items for the fish 76 mm, and longer, taken from the open lake over silt and clay bottom.

Chironomid larvae make up an important part of the diet of the small sheepshead living in the rivers and bays, as evidenced by the work of Forbes (1880), Dendy (1946), and the present writer. The young sheepshead from Sandusky Bay, up to 75 mm, fed on midge larvae while from the Portage River 100% of those individuals up to 30 mm, and 94.9% of the fish between 31–75 mm had consumed chironomid larvae. Of the sheepshead taken from the open lake, only 16.4% of them up to 30 mm and 19.9% up to 75 mm had utilized the midges for food. Whether or not availability plays a part is not clear. The sample from Sandusky

TABLE 3

Food habits of sheepshead except young-of-the-year. Nov. 1947, 27th April – 22nd November, 1948.

Organism	Number of Fish	Percent
Hexagenia Naiads	304	79.4
Gammarus	123	32.1
Cambarus	53	13.8
Fish	30	7.8
Trichoptera Larvae	27	7.1
Chironomidae Larvae and Pupae	15	3.9
Leptodora	7	1.8
Leech	7	1.8
Psephenus Larvae	4	1.0
Daphnia	3	0.8
Sialis infumata Larvae	1	0.3
Asellus	1	0.3
Stenonema Naiad	1	0.3
Total	383	

Bay is not large enough to make a definite statement but the material from the Portage River clearly indicates that insects make up a very important part of the food in this type of habitat. Because of different ecological habitats the composition of the diet of these fish is different from that of the fish taken from the open lake. The writer cannot explain the complete absence of copepods from the Portage River collections, for these forms were collected at the three different times the fish were taken. The collections taken from these two areas were the only ones in which plant material was found in the stomach contents.

When the studies of the young-of-the-year sheepshead for the three areas are summarized, the Copepoda (54.6%), *Hexagenia* (45.0%), *Gammarus* (40.4%), and Chironomidae (33.0%) are the four items most frequently found. The Ostracoda (18.8%), *Leptodora* (15.6%) and *Daphnia* (11.9%) make up a secondary, yet significant part of the diet of these fish. The remaining food items (table 1) are probably incidental.

The sheepshead continues to utilize insects to a very large extent beyond the first year. This is apparent in table 3 where 92.0% of the fish had taken some forms of insects, 79.4% of these having fed on *Hexagenia*. *Gammarus* was the second most frequently found item while crayfish and fish ranked third and fourth. There are indications that crayfish appear more frequently with the increase in size of the sheepshead. Fish appear to be well distributed throughout the diet of the larger size classes and are primarily those bottom dwelling forms living in the shoal areas such as *Percina caprodes*, *Poecilicthys f. flabellaris*, *Etheostoma b. blennoides*. The only other one recognized is the cyprinid, *Notropis a. atherinoides*, which occurs over shoal areas as well as in the open lake. The Trichoptera found in 7.5% of the stomachs were mainly of the family Leptoceridae. The Dipteran family Chironomidae were represented in 3.9% of the stomachs. The remaining items in table 3 can be classed as incidental.

The author has received the impression, from the results of others observations, that the river-inhabiting sheepshead feed primarily on mollusks while those individuals living in lakes do not. This observation is substantiated in part by the material collected in Lake Erie. It is reported that there are insufficient numbers of mollusks in some lentic habitats (Norris Reservoir, Dendy, 1946), but so far as Western Lake Erie is concerned, this is not true. At times, windrows of clam shells are found upon its beaches and during the course of collecting operations as many as 300 clams have been taken during one drag of the trawl. Most of these were no longer available to the sheepshead as the twine size was such that only the larger clams were retained yet enough of the smaller-sized clams were taken to show a supply exists which could be utilized as food by the sheepshead. Richardson (1836) and Dickerman (1948) reported mollusk shells in the stomachs of the Lake Erie sheepshead. At no time during the present study was there any evidence of clams or snails being taken. The stomach contents, particularly of the trawl collections, were in such a condition that there was no question as to the identity of the food items.

A number of food items appear to be incidental. The presence of such items may be explained on the basis of the feeding process of the sheepshead, whereby the fish captures its food by a sucking action. Such forms as Trichoptera, Chironomidae, and *Asellus* that are not as abundant as *Hexagenia* or *Gammarus* are taken in as the fish sucks up the latter forms.

Food Web in Western Lake Erie

The tabulated summary of items consumed as food by the sheepshead (tables 1, 3) indicates a diversity of organisms, yet 43.4% or 10 of the 23 items were so seldom found that they probably can be classed as insignificant. Of these 10 items two were found only in the adults or sub-adults and both, *Sialis* and *Asellus*, were found in one fish. Mayflies of the genus *Stenonema* were found in both the young-of-the-year and the larger fish, while seven of the items were consumed only by the young-of-the-year fish.

The sheepshead normally ranges over a wide territory for, when all of the items of tables 1 and 3 are taken into consideration, it is evident that three different habitats are normally visited, i.e., the soft mud bottoms of the lake and bays, the shoal areas, and the open waters. Of the three, the soft mud bottom of the open lake is the most important, the limnetic habitat is the least so for the sub-adult and adult fishes, while the mud bottoms and limnetic habitats appear to be equally important for the young-of-the-year sheepshead.

The stomach contents of the small sheepshead (10–20 mm SL) indicate this size range to be primarily pelagic feeders, consuming almost exclusively copepods and cladocerans. Approximately 95% of the 10–30 mm fish consume copepods, while 34% had taken some form of cladoceran. Two genera, *Cyclops* and *Diaptomus*, dominate the copepod part of the stomach contents with the major item being *Cyclops*. These data are related to Jahoda's (1948, pp. 84–87) findings as he reported the diaptomids to make up approximately 5% of the entomostracan fauna during June and July, with an increase to 20% in September. This small percentage during June and July is reportedly due, not to a decrease in the numbers of *Diaptomus*, but to a tremendous increase in the numbers of the other entomostraca (*Daphnia retrocurva*, *D. longispina*, *Cyclops vernalis* and *C. bicuspidatus*).

As the season progressed the fish began feeding on larger organisms than entomostracans, however, within the latter group the copepods continued to appear more frequently in the fishes diet than the cladocerans. Availability of the copepods no doubt played a part in determining the entomostracans consumed by the young sheepshead. Chandler (1940) indicated that the cladocerans never make up a large portion of the zooplankton of the lake. Since *Cyclops* was found in a greater number of stomachs than *Diaptomus* and since the former is more abundant during the summer season (Chandler, 1940, p. 325) it is apparent that *Cyclops* is an important source of energy for the young-of-the-year sheepshead. The daphnids and *Leptodora* appeared in the stomachs in approximately equal numbers, although Chandler (1940, p. 324) indicated *Leptodora* to be less abundant than the daphnids. Andrews (1948, p. 20) reported the *Leptodora* population to be at a low level during late July and to remain so until late in August at which time there is a secondary pulse of low intensity. Correspondingly, *Leptodora* apparently plays a secondary role as a food item since approximately 15% of the fish had consumed this cladoceran.

It would be interesting to ascertain to what extent the young sheepshead is a pelagic organism, particularly at that stage when it is feeding solely on entomostracans. Are these young fish independent of the bottom at that time as suggested by the pelagic entomostracans or do they feed on the copepods and cladocerans that might be located in the water-mud interface? The latter is supported, in part, by the numbers of ostracods that are consumed by these small sheepshead (table 2).

As the young sheepshead surpasses 20 mm in length, the composition of the diet begins to change from pelagic organisms to benthic animals located in the mud of the quiet water areas of the lake. *Hexagenia*, *Gammarus*, and the chironomids make up the principal items taken by the young-of-the-year sheepshead from the benthic zone. Associated with this qualitative change in the diet it becomes apparent that particle size is an important factor because there is an increase in the size of the organisms consumed as the size of the fishes increase. At first, the small one year old *Hexagenia*, small immature *Gammarus* and the chironomids are ingested but by the end of the first growing season the sheepshead is taking only the larger *Hexagenia* and *Gammarus*. The midges begin to decrease in importance by that time since 33% of the young-of-the-year sheepshead had taken chironomids while only 3.9% of the larger fish had done so.

The mayfly genus *Hexagenia* is the prime source of energy for the sheepshead in Western Lake Erie. It makes up a food link (Allee, *et al.*, 1949) in one of the shortest food chains available to the sheepshead. When the community is taken into consideration, *Hexagenia* is an integral part (food mesh, Allee, *et al.*, 1949) of the entire food web of which the sheepshead is an essential unit. This is emphasized by the fact that 67.3% of the sheepshead examined had fed on *Hexagenia*. This high percentage can be explained by the large numbers of the mayfly present in the bottom muds as compared to the other benthic organisms. Table 4 is taken from Chandler (unpublished data). The non mayfly fauna (exclusive of clams) consisted of chironomid larvae, *Gammarus*, Trichoptera, Gastropods and Oligochaetes. The nine stations extend from west to east over a distance of about 35 miles through the island archipeligo. The results of station 9 can be explained in part by the fact that the water is 60 feet and over in depth while the other stations have a depth of 40 feet or less. Table 4 suggests that there is a tremendous population of mayflies superimposed on typical concentrations of benthic organisms. By sheer numbers the mayflies would be most readily available to the sheepshead, thus accounting for the high percentage of *Hexagenia* in the diet of the fish.

As indicated in that section pertaining to food items consumed *Hexagenia* begins to play an important role after the sheepshead exceed 30 mm. This average length is reached about mid-August. The new crop of *Hexagenia* is just becoming apparent in the bottom ooze but has not been found in the stomachs of the sheepshead. The one year old *Hexagenia* naiads average about 15 mm at this time (Chandler, unpublished data); this figure varying somewhat from year to year. It is this age group that is found in the fishes stomachs and in a number of instances these small sheepshead were gorged with a single mayfly, suggesting that the fishes took the largest individuals that they could ingest. Prior to mid-August the mayfly naiads were not utilized by the very small sheepshead because of size or because the fish had not as yet become a benthic feeder. In as much as there are two year groups of *Hexagenia* present in the bottom muds, the sheepshead has a continuous source of energy derived from this mayfly genus. The standing crop of mayflies varies from one year to the next, i.e., there is an alternation of low concentrations with high concentrations. Apparently even during the years of low productivity the numbers of *Hexagenia* are sufficient to meet the needs of those animals that feed on them.

TABLE 4

Numbers and weights of bottom fauna / m^2 from Western Lake Erie on June 17 and 18, 1943. (From Chandler unpublished data.)

	Station	Number/m^2	Weight/m^2(grams)
Mayflies	1	174	21.85
non-Mayflies			2.16
Mayflies	2	225	33.37
non-Mayflies			1.58
Mayflies	3	256	32.05
non-Mayflies			0.98
Mayflies	4	235	30.63
non-Mayflies			1.05
Mayflies	5	365	33.80
non-Mayflies			1.55
Mayflies	6	345	28.18
non-Mayflies			0.76
Mayflies	7	930	31.53
non-Mayflies			1.17
Mayflies	8	870	27.09
non-Mayflies			1.05
Mayflies	9	none	0.00
non-Mayflies			4.11

The sheepshead acts as a competitor and as a prey in several instances. During the early stages it is in competition with the young of such fish species as *Perca flavescens*, *Lepibema crysops* (Ewers, 1933) and *Percopsis omiscomaycus* (Ewers, 1933; Kinney, 1950) and the various sizes of *Notropis a. atherinoides* (Ewers, 1933; Gray, 1942). As adults, the sheepshead are in competition in the deep water with such forms as *Perca flavescens* and *Hybopsis storerianus*. In the shoal areas, the sheepshead feeds on *Cambarus* and darters, as does the black bass, *Micropterus d. dolimieu* (Doan, 1940; personal observation of the author). During the first year of its life, the sheepshead serves as a forage fish. On several occasions the author has found the young in the stomachs of *Stizostedion v. vitreum*. The sheepshead made up a substantial portion of the diet of *Stizostedion v. vitreum*, *S. c. canadense* and *Micropterus d. dolimieu* (Doan, 1940, 1941). Clemens (1947) found the young sheepshead to make up a major part of the diet of *Lota lota maculosa*. Beyond the first year the sheepshead does not appear to be preyed upon by animals other than man.

Figure 1 is a graphic representation of a tentative food web of which the sheepshead is the climax organism. This presentation suggests that such a food web is a self-contained unit, i.e., a closed system. Actually it is an open system, energy being derived from other food webs and other communities. It is portrayed here as a closed system simply for convenience and because of lack of detailed information. The three communities visited by the sheepshead are represented. The direction of the arrows indicate the source of energy from one link to another: for example, the sheepshead feeds on *Etheostoma b. blennoides*, therefore this darter is a source of energy for the sheepshead.

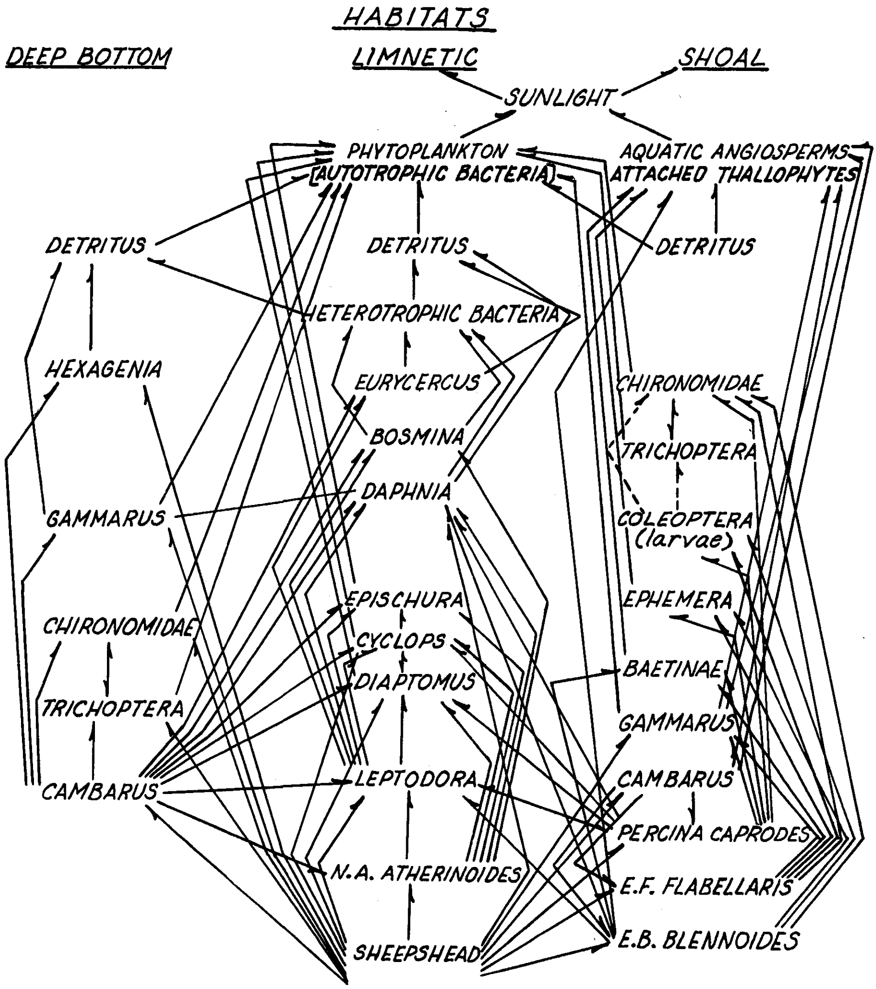

FIGURE 1. A tentative food web in Western Lake Erie using the sheepshead as the climax organism.

The most striking group making up figure 1 are the secondary consumers (after Lindeman, 1942). Within this category there are several subdivisions dependant on energy level requirements. The primary carnivore is the sheepshead; the secondary, the three darters from the shoal habitat and the lake emerald shiner from the limnetic community; the tertiary group is made up of insects and some crustaceans but they are not so readily discernable since most of them apparently play a dual role, that is, they are omnivorous in feeding habits.

In keeping with most communities, the nearer a particular trophic level is to the ultimate energy source the greater the diversity of organisms found within that level. The majority of the organisms within each food niche not only act as consumers at that particular level but also serve as a source of energy for organisms belonging to a higher food niche or consumer level. Those organisms having omnivorous food habits, reach across two trophic levels within a food web and such food habits produce food chains of varying lengths. This is the case with the crayfishes (Turner, 1926; Tack, 1941; Norton, 1942) where they act as scavengers or even show preferences for plant material. The omnivorous habits of *Gammarus fasciatus* are indicated by its feeding on various species of the submerged higher aquatic plants and on zooplankters (Clemens, 1950). Dr. M. W. Boesel (personal communication) indicated the chironomids to be both herbivorous and carnivorous. He believes that both types of feeding habits are present within phylogenetic groups of chironomids. The larval stages of the aquatic Coleoptera and Trichoptera are represented in both types of feeding habits. Ross (1944, p. 4) indicated the caddis flies to be omnivorous, taking whatever is available. Such forms as the Hydropsychidae and Limnophilidae feed on plankton, on insect larvae, and on each other. The caddis fly genus *Oecetis* that is found in the deep water habitat of the lake is, according to Ross, primarily a predacious form. Slack (1936) indicated that most caddis flies are primarily phytophagous, but only three entirely so. The remaining caddis flies displayed varying degrees of omnivorous habits, with only one being predominantly carnivorous.

The entomostracan, *Leptodora kindtii*, can be included in this group belonging to the secondary consumer level since it feeds primarily on other zooplankters (Andrews, 1948). Andrews believes availability to be the factor that determines the composition of the diet of *Leptodora* in that the less active forms of prey are taken more readily than faster forms. The other entomostracans still are enigmatic. (Welch 1935, p. 250) has divided the cladocera into predators, such as *Leptodora*, and those that filter their food from the water. Virtually all particulate matter is consumed but only very minute organisms, such as bacteria, as well as debris are utilized as food, the algae passing through the intestine unchanged. Welch indicates that *Cyclops* exercises some selectivity and is primarily a predator, feeding on other entomostraca and rotifers while *Diaptomus* appears to take anything larger than one micron that can be gotten into the feeding apparatus.

The mayflies probably best represent Lindeman's (1942) primary consumers. *Hexagenia* is a saprophagous feeder (Shelford and Boesel, 1942), consuming the detritus from the higher aquatic plants, the phytoplankton of which the diatoms make up the major portion and various animal structures. The other mayflies, such as the Baetinae and Ephemera, are probably herbivorous. Dr. N. W. Britt (personal communication) has seen *Stenonema* clean the filamentous algae from the rocks placed in an aquarium.

The sheepshead and the darters occupy the same food niches, as plankton and insect feeders. Both groups of fishes feed on plankton at a certain size, and they feed on insects in a particular habitat; the sheepshead feeds primarily on those insects in the deep water areas, and the darters feed on those in the shoal habitat. There are indications that the Chironomidae and Trichoptera occupy the same food niches in the shoal habitat, and in the benthic region. The predacious caddis flies and midges feed on the same organisms, the same applying to the herbivorous members of both groups. It is possible that the mayflies, such as *Stenonema*, occupy the same food niche in the shoal habitat as do the herbivorous midges and caddis flies. *Gammarus* is coexistant with *Hexagenia* in the benthic food niche. The entomostraca all occupy the same niche as plankton organisms.

Weeks (1943) has demonstrated that there are about 2.5 times as many heterotrophic bacteria present in the mobile water-mud interface as in the sediments below this layer. The numbers of aerobic bacteria fluctuate, and this is believed to be the result of their dying off and their number being replenished by influxes from the rivers. The anaerobic bacteria remained at a constant level of abundance during the course of Week's investigation, indicating that these bacteria maintained themselves by reproducing within the aquatic soils of the lake. The aerobic bacteria far exceeded the anaerobic forms, with mean values of 10,330,000 and 137,000, respectively, per gram of oven dry sediments taken from the mobile layer.

The balance in the nitrate cycle of the subaquatic soils in Western Lake Erie seems to be in favor of nitrate reduction (Beaver, 1942). There were only moderate numbers of ammonia oxidizing organisms present while the numbers of nitrate oxidizing bacteria seemed to be the limiting factor in the production of nitrates. Those organisms involved in cellulose break-down were present only in certain areas, whereas the starch hydrolyzing micro-organisms were present in all areas examined. It is not clear just how extensive the numbers of autotrophic bacteria are in the lake. The work done by Beaver (1942) suggests that they are not as abundant as the heterotrophic forms and, that they are an insignificant food source in the economy of the lake.

In an aquatic habitat it is possible that the zooplankton, photosynthetic plants in the form of the phytoplankton, and the heterotrophic bacteria occupy different trophic levels than those depicted by Lindeman (1942). According to Lindeman, the zooplankters, acting as consumers, obtain their energy from the plants, and the heterotrophic bacteria utilize both the plants and animals as a source of energy. It is conceivable that the heterotrophic bacteria may frequently act as primary consumers and that many of the smaller herbivorous zooplankters feed on them (Clarke and Gellis, 1935).

The presence of the large numbers of aerobic bacteria indicate a rapid and efficient break-down of organic material which would not be possible under anaerobic conditions. This rapid decomposition of detritus provides a source of essential elements readily available to the producer level in the form of dissolved nutrients. In fresh water lakes the greatest portion of this decomposition takes place in the benthic regions. These dissolved nutrients become available by water circulation in the limnetic regions. The importance of the dissolved organic matter has been demonstrated by Juday (1942).

The detritus found in the various habitats is derived from two principal sources, the lake itself and the tributary rivers. The lake-derived detritus is obtained from several different sources. In the bay areas the higher aquatic plants and attached algae contribute a major portion along with the bodies of fish and other animals. This material apparently is carried into the benthic region by the lake currents (Shelford and Boesel, 1942, after Krecker, 1931). In the limnetic community the dead bodies of the zooplankters and phytoplankters settle quickly to the bottom where decomposition occurs.

Photosynthesis is largely the work of the phytoplankton in the lake community made up mostly of diatoms. The higher aquatic plants and attached algae play a minor role except in the shallow bay areas (Allee, *et al.*, 1949, p. 503). The value of these plants probably is in the form of detritus that settles to the bottom.

The photosynthetic process is the only process in the community which results in a net gain of organic matter, the effect of the other trophic levels being a net loss in organic matter. In the lake, photosynthesis can take place only in the shoal and limnetic habitats. It is limited in its output by such factors as light intensity, turbidity, amount of carbon dioxide and temperature (Allee, *et al.*, 1949). The total surface of chlorophyll bearing organisms exposed to these factors affects the output. Annual variations in lake level affect the abundance of the cattail beds and lily pads. High-water level years cause extensive destruction to such beds by drowning out the plants. Turbidity retards the growth of the submerged aquatics and controls the magnitude of the phytoplankton blooms. These physical factors have a profound effect on the growth and productivity of the plants and in turn the economy of the lake will be influenced by the magnitude of this productivity.

SUMMARY AND CONCLUSIONS

The mayfly, *Hexagenia*, and the amphipod, *Gammarus*, are the two important items in the sheepshead's diet for all ages. The items consumed by the youngest fish studied are entomostracans, taken until the fish is approximately 30 mm long. Beyond this size the diet is primarily one of insects with a gradual decrease in entomostracans. As the sheepshead becomes larger a few fish are consumed as well as some crayfish.

The sheepshead in Western Lake Erie visits three habitats during its life. The benthic and limnetic communities are most important for the young-of-the-year individuals, while the deep water mud bottoms and shoal habitats are the most important for the sub-adult and adult fishes. The 10-20 mm fish feed primarily on limnetic organisms. Beyond this size they consume benthic fauna. After the first season they move back and forth between the shoal areas and the deep water benthic community. During its early stages, the sheepshead is in competition for food with several other deep water and pelagic fishes. The young-of-the-year sheepshead serve as food for several species of piscivorous fishes.

The food web of which the sheepshead is the climax organism is interpreted in the sense of Lindeman's trophic levels. The sheepshead, darters, lake emerald shiner, some of the insects and some of the crustaceans belong to the second consumer level; *Hexagenia* belongs to the primary consumer level. The position of the bacteria, detritus, and the photosynthetic organisms are discussed and the role they play in the exchange of energy within the food web.

It becomes apparent from the present discussion that there are several parts of this food web in which specific information is lacking or data are scanty. These weak areas probably can be grouped under three headings: (1) the feeding habits of the zooplankters and bottom fauna, (2) the position of the heterotrophic bacteria, and (3) the relative importance of the detritus from the phytoplankton, higher aquatic plants, and river contributions.

There is disagreement as to what constitutes food for the zooplankters. In many instances the nannoplankton serves as food while in other cases smaller zooplankters serve as a source of energy. In those forms with a filtering apparatus availability is the determining factor, there being no clear-cut distinction between carnivore or herbivore.

Detailed life history studies are lacking for the majority of organisms that comprise the bottom fauna. General statements about the feeding habits are not entirely justified, since all types are found within a family group or some other taxonomic category. A knowledge of seasonal variations in food consumption is needed before any kind of a comprehensive food web can be set up.

Little is known about the origin or fluctuating numbers of the heterotrophic bacteria in the subaquatic soils, nor about the physiologic processes by which these bacteria break down the detritus. Data are scanty pertaining to the energy expended by these bacteria in this breakdown.

Further information is needed about the relative importance of the detritus derived from the various kinds of plant and animal tissues. Nothing is known about the quantities of organic material produced each year and how it influences the general community metabolism.

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