FOOD OF THE YELLOW PERCH, *PERCA FLAVESCENS*, FOLLOWING A DECLINE OF THE BURROWING MAYFLY, *HEXAGENIA LIMBATA*[1, 2]

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Abstract. Changes in consumption of benthic invertebrates by yellow perch, *Perca flavescens*, in Oneida Lake during 1958–1973 were similar to changes in the bottom fauna of the lake from 1956 to 1974. The burrowing mayfly, *Hexagenia limbata*, which declined to extinction following severe oxygen depletions, was replaced in the diet by chironomids and amphipods and, to a lesser extent, by isopods and trichopterans. A slight decline in the growth rate of older perch occurred in recent years, which may be related to the disappearance of the mayfly. No obvious change in abundance of perch was evident.

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The burrowing mayfly, *Hexagenia*, is often an important food of yellow perch, *Perca flavescens*, and other freshwater fish (Hunt, 1953; Laarman and Schneider, 1972; Hudson and Swanson, 1972). In recent years, declines in *Hexagenia* populations have occurred in Lake Erie (Carr and Hiltunen, 1965; Britt, *et al*, 1973), Green Bay, Lake Michigan (Beeton, 1969), and Saginaw Bay, Lake Huron (Schneider *et al*, 1969). Britt (1955a) suggested that fish populations might be affected by the decline of *Hexagenia* in Lake Erie and Price (1961) subsequently reported that chironomids had replaced mayflies in the diet of several species. Extensive long-term studies concerning the response of fish populations to declining *Hexagenia* populations are lacking.

Oneida Lake is a large (207 km^2), shallow (mean depth = 6.8 m) eutrophic lake in central New York. Limnological features have been described by Greeson (1971). The burrowing mayfly, *Hexagenia limbata*, was abundant in Oneida Lake and an important food of yellow perch (Baker, 1918; Adams and Hankinson, 1928). From 1956 to 1964, however, the population of *Hexagenia* nymphs underwent a severe decline, apparently precipitated by oxygen depletions in the deeper areas of the lake which began in 1959 (Jacobsen, 1966). The present paper describes the consumption of benthic invertebrates by yellow perch during 1958–1973 and compares changes in the diet to changes in the bottom fauna from 1956 to 1974.

MATERIALS AND METHODS

Each year (1956 to 1974) bottom samples were taken periodically with an Ekman dredge (225 cm^2) during April-October at three sites between 4.3 and 12.2 m deep (fig. 1). Samples were washed through a screen (0.55 mm mesh), the organisms removed and preserved and identified later. Volumes were determined by water displacement. Since size of chironomids and *Hexagenia* varied considerably, data were expressed as volume per sample for these organisms, but as numbers per sample for other more uniformly sized species. Complete descriptions of the sampling sites and sorting techniques are included in Jacobsen (1966) and Tarby (1974). All samples from 1956–1974 were examined, although values for chironomids and *Hexagenia* for 1956–1964 are taken largely from Jacobsen (1966).

Yellow perch were collected in two 91 m nylon gillnets with equal lengths of 3.8, 5.1, 6.4, 7.6, 8.9 and 10.2 cm stretch mesh. Overnight sets were made at weekly intervals from early June to mid-September at 15 selected sites from 1958 to 1973 (fig. 1). A representative sample of perch from all mesh sizes was taken from the total sample. Total length of perch was measured to the nearest mm and ages were determined from standard scales. Stomachs were removed and the occurrence of each food organism was noted. Numbers,

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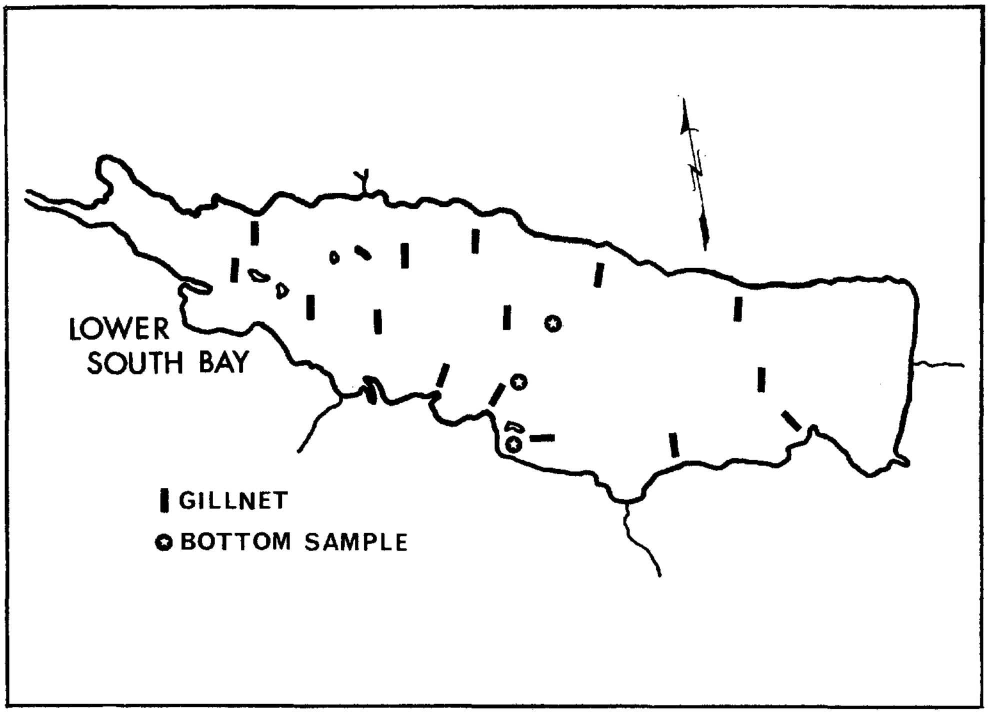

FIGURE 1. Location of 15 gillnet sites and 3 bottom sampling stations on Oneida Lake.

weights, and volumes of different food organisms were not determined.

RESULTS

BOTTOM FAUNA. A total of 1383 bottom samples were examined (table 1). Tubificidae, Ceratopogonidae, and Hirundinea were common in the samples but are not examined further because they were not identified in perch stomachs. The decline of *Hexagenia limbata* noted by Jacobsen (1966) has continued at all three sites, and the species is now essentially extinct in Oneida Lake. The last nymph was seen in 1968. The upward trend in chironomids from 1956 to 1964 (Jacobsen, 1966) has not continued beyond 1964, when chironomids were extremely large and abundant, but the population has remained stable. Jacobsen (1966) stated that relative volumes of organisms other than chironomids and *Hexagenia* were insignificant before 1965, and other organisms still average less than 15% of the benthos volumetrically (table 1). The abundance of amphipods (*Gammarus*) and isopods (*Asellus*), however, increased dramatically after 1962. Before that year amphipods were abundant only in 1956 and only a single tiny isopod was taken in 1960. In 1964, a year of extreme abundance of chironomids, the population of isopods increased 15-fold for all sites combined but their numbers subsequently declined and leveled off. During the period of study there has been a significant upward trend in the abundance of amphipods (Spearman rank correlation $r_s = 0.71$; $p < .01$). Despite a peak in 1965, numbers of trichopterans have remained low and in many years none were taken in bottom samples (table 1).

FOOD HABITS OF YELLOW PERCH. In general, food habits of yellow perch have reflected the changes in abundance of the benthic invertebrates (table 2). Occurrence of *Hexagenia* in perch stomachs declined following the oxygen depletion in 1959, especially after 1963. None have been seen in stomachs since 1969, as compared with 1968 in the bottom samples (fig. 2). Occurrence of chironomids in

TABLE 1

Mean volume of Hexagenia *nymphs and chironomid larvae and mean number of Amphipoda, Isopoda, and Trichopteran larvae per dredge sample at 3 sites in Oneida Lake, 1956–1974.*

Year	Number of samples	Mean volume/sample (ml)		Mean number/sample		
		Hexagenia	Chironomidae	Isopoda*	Amphipoda*	Trichoptera
1956	29	0.41	0.10	0.00	2.21	0.00
1957	65	0.16	0.16	0.00	0.66	0.00
1958	60	0.37	0.16	0.00	0.48	0.02
1959	25	0.06	0.32	0.00	0.08	0.04
1960	106	0.05	0.19	0.01	0.33	0.00
1961	74	0.01	0.25	0.00	0.08	0.00
1962	80	0.02	0.49	0.03	0.55	0.00
1963	74	0.01	0.22	0.15	0.96	0.14
1964	92	0.01	0.91	2.26	1.00	0.01
1965	120		0.31	2.23	1.34	0.31
1966	135	0.01	0.19	0.67	2.19	0.04
1967	85		0.42	1.27	4.13	0.01
1968	67		0.34	1.19	2.97	0.00
1969	105	0.00	0.30	0.35	2.24	0.08
1970	42	0.00	0.40	0.33	2.98	0.00
1971	48	0.00	0.20	0.60	0.92	0.08
1972	62	0.00	0.32	0.13	3.63	0.24
1973	54	0.00	0.16	1.31	2.78	0.00
1974	60	0.00	0.27	1.90	3.70	0.03
		Unweighted Average of Yearly Means				
1956–1961		0.18	0.20	0.00	0.64	0.01
1962–1967		0.01	0.42	1.10	1.70	0.09
1968–1974		0.00	0.28	0.83	2.75	0.06

*The mean volume of a single isopod or amphipod is about 0.01 ml.
**less than .005 ml.

TABLE 2

Frequency of occurrence of food organisms in stomachs of yellow perch taken in gillnets in Oneida Lake, 1958–1973.

Year	Number* caught	Number examined	Percent							
			With food	*Hexagenia*	Chironomidae	Isopoda	Amphipoda	Trichoptera	Zoo-plankton	Fish
1958	921	468	52.8	63.2	8.5	0.0	5.3	1.2	9.3	25.9
1959	1363	713	38.8	52.3	5.4	0.0	5.1	0.7	31.4	18.4
1960	1479	809	23.4	18.0	7.9	0.0	6.3	0.5	27.5	39.7
1961	1390	659	38.8	42.6	3.5	0.0	7.0	1.2	12.9	37.1
1962	1443	651	48.8	18.6	4.4	0.0	18.9	2.2	7.2	50.3
1963	1496	585	48.5	39.4	3.2	0.0	16.5	0.4	18.7	25.4
1964	1367	675	37.8	14.5	30.2	0.0	30.2	0.4	16.1	27.1
1965	1568	638	50.9	1.8	47.4	0.0	6.2	0.3	3.4	42.5
1966	1448	594	44.9	6.7	45.3	1.5	28.5	1.5	9.4	7.9
1967	1585	632	39.4	6.0	47.4	5.2	18.5	0.0	12.0	13.7
1968	1746	661	57.0	0.0	14.3	0.8	20.2	0.3	24.4	34.2
1969	1598	590	67.6	0.3	22.8	2.0	26.6	2.5	11.5	22.6
1970	1998	586	67.2	0.0	32.5	0.5	10.7	2.8	41.6	14.0
1971	826	479	67.0	0.0	10.9	0.9	9.0	5.0	46.7	36.8
1972	925	561	65.6	0.0	26.9	3.0	14.1	6.3	45.4	21.2
1973	1541	611	72.5	0.0	27.3	10.6	42.2	4.1	31.4	1.4
			Weighted Average of Yearly Means							
1958–65	11,027	5198	41.4	30.6	14.6	0.0	12.1	0.9	15.0	33.7
1966–73	11,667	4714	59.8	1.2	27.2	3.2	21.8	2.9	28.9	18.8

*Standardized yearly catch at 15 sites; individual site catches were standardized with regard to length of net used, gillnet color, and time in water. Data based on stomachs containing food.

perch stomachs increased rapidly in 1964, paralleling a similar increase in the botton samples. Consumption of chironomids has remained fairly high since 1964 (11–47%). Although isopods became abundant in bottom samples in 1964, they first appeared in perch stomachs in 1966 (fig. 2). Isopods

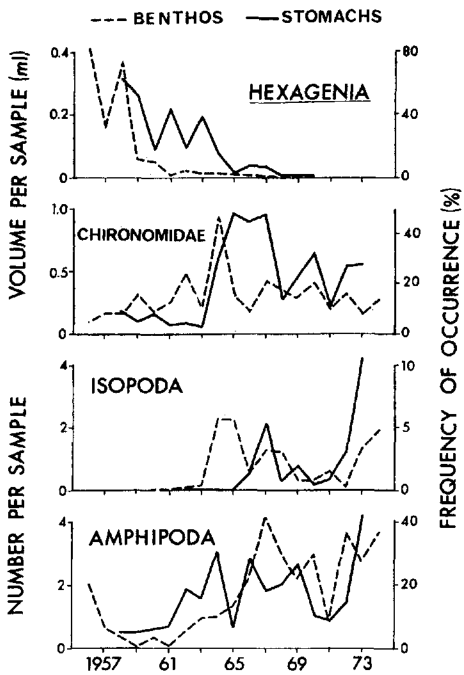

FIGURE 2. Mean volume of *Hexagenia* nymphs and chironomid larvae and mean number of Amphipoda, Isopoda, number of Amphipoda and Isopoda per dredge sample compared with frequency of occurrence of these organisms in stomachs of yellow perch, 1956 to 1974.

have been eaten by perch each year since, although frequency has remained relatively low (1–11%). As with abundance in bottom samples, frequency of occurrence of amphipods in perch stomachs has increased significantly throughout the study ($r_s = .54$; $p < .05$). Consumption of Trichoptera has increased slightly during the period of study, but these organisms still represent only a small part of the total diet (table 2).

Decapoda, Gastropoda, Pelecypoda, Odonata, Hemiptera, Coleoptera and Hirudinea were occasionally found in perch stomachs but were never abundant. Since these organisms were not enumerated in bottom samples in all years, they are not examined in detail. Organisms other than benthos (primarily crustacean zooplankton and fish) are often major components in the diet of yellow perch in Oneida Lake (table 2).

DISCUSSION

Changes in bottom fauna in Oneida Lake were similar to those which occurred in portions of the Great Lakes. Although Britt (1955b) described a temporary recovery of *Hexagenia* in western Lake Erie in 1954, followed by a rapid population decline to near extinction by 1965 (*Britt et al*, 1973), no such recovery has occurred in Oneida Lake (table 1). *Hexagenia* nymphs have also disappeared from Lower South Bay (fig. 1; Clady, 1975), which indicates that the extinction was lakewide. Forney (1973) suggested that burrowing by the large *Hexagenia* population prior to 1959 contributed to the aeration of sediments, and that worsening oxygen conditions in the deeper waters of Oneida Lake in recent years may be due partly to the absence of this burrowing activity. Thus, it is possible that the initial catastrophic dieoff of *Hexagenia* in 1959 also contributed to the eventual extinction and failure of re-establishment of the species in Oneida Lake. In the absence of a large breeding population nearby, it is doubtful that *Hexagenia* can make a rapid recovery even if suitable conditions occur.

Substantial increases in chironomids have occurred in Lake Erie (Carr and Hiltunen, 1965) and in Green Bay, Lake Michigan (Beeton, 1969) in conjunction with mayfly declines in these lakes. Schneider and co-workers (1969) found no such increase in chironomids in Saginaw Bay, Lake Huron, but they did find a substantial increase in amphipods. In Oneida Lake both isopods and amphipods increased dramatically after 1962 and peaked in the mid-to-late 1960s (table 1). Jacobsen's (1966) conclusion that the niche occupied by *Hexagenia* was being filled by chironomids should be modified to include isopods and amphipods.

Consumption of benthic organisms is

not determined solely by their abundance. Size, distribution, activity and exposure of prey have also been found to influence the selection of food organisms by fish (Ivlev, 1961; Tarby, 1974; Ware, 1973). The large size of *Hexagenia* may partly explain its high frequency of occurrence in perch stomachs through 1964.

Despite a 10-fold decline in biomass after 1959, frequency of occurrence of *Hexagenia* declined only 3- or 4-fold in perch stomachs through 1964 (fig. 2). Strong selection for burrowing mayflies by yellow perch and perhaps other fishes may have contributed to the extinction of *Hexagenia*, particularly after the population was severely reduced by oxygen depletion. Selection for familiar organisms could also have contributed to the two-year lag between appearance of isopods in the benthos and in stomachs and the maintenance of apparently high levels of consumption of chironomids in 1965–1967 (fig. 2).

Unfortunately, precise electivity indices of perch for various benthic organisms could not be determined because organisms in the stomachs were not enumerated. Use of frequency of occurrence does not reflect the true intensity of predation, but could account partially for the apparent lags between changes in the benthos and changes in perch food habits. For example, although frequency of occurrence of *Hexagenia* in perch stomachs remained relatively high through 1964, the number of nymphs consumed per perch may have declined from 1959 through 1964. Differences between the "benthos" and "stomach" curves in figure 2 may also be due to differences in the benthos and gillnet sampling stations (fig. 1).

In general, food habits of yellow perch have reflected the changes which have occurred in the benthos. *Hexagenia* has been replaced in the diet by chironomids and amphipods and, to a lesser extent, by isopods and trichopterans. Crustacean zooplankton (primarily *Daphnia*) has also played a significant role in the diet in recent years (table 2). Price (1961) reported that chironomids replaced mayflies in the diet of yellow perch and other fish in Lake Erie, following a decline of *Hexagenia* in the 1950s. McCormack (1970) found that European perch, *Perca fluviatilis*, in Lake Windermere increased their intake of the isopod *Asellus* as this organism became more abundant in the bottom fauna.

Britt (1955a) suggested that populations of fish, particularly forage species such as trout-perch, *Percopsis omiscomaycus*, and silver chub, *Hybopsis storeriana*, might be adversely affected by the decline of *Hexagenia* in Lake Erie. Larkin (1956) and Keast (1965) on the other hand, maintained that flexibility and adaptability are the rule in freshwater fish, and that their elastic growth rates and ability to change their diet enable most fish to sustain populations under changing conditions. Total catches of yellow perch in gillnets have not changed appreciably during 1958–73 (table 2), indicating that the population of perch in Oneida Lake has remained stable since the decline of *Hexagenia*. A slight, but significant, decline in the

TABLE 3

Length of yellow perch collected in Oneida Lake during 1958–1960 and 1969–1973.

Years	Total length (mm) at Age						
	II†	III	IV	V	VI	VII	VIII
1958–1960	180	217	248	264	276	285	281
	(145)**	(487)	(473)	(525)	(308)	(56)	(22)
1969–1973	183	225	247	256	266	273	281
	(603)	(866)	(413)	(856)	(506)	(358)	(177)
Calculated t	−2.24	−8.11*	1.02	12.04*	9.05*	6.12*	0.07

*Significant at .01 level.
**Number of fish are in parentheses.
†Perch collected during the summer were slightly older than the ages (II, III, IV, etc.) listed.

size of older perch has occurred in recent years (table 3). Perhaps perch must now expend more energy capturing the smaller chironomids, amphipods, isopods and zooplankton, and the decline in growth rate is therefore related to the decline of *Hexagenia*. From 1958 through 1973, there was a highly significant increase with time ($r_s = 0.74$, $p < .01$) in the percentage of perch which contained food, suggesting that perch had to feed more continuously because of the smaller size of these organisms relative to *Hexagenia* nymphs.

A direct relationship between abundance of *Hexagenia* nymphs and growth of white crappie, *Pomoxis annularis*, and freshwater drum, *Aplodinotus grunniens*, was found in Lewis and Clark Lake (Swedberg, 1968; Siefert, 1969). Although parallel changes in size of yellow perch of age V to VII occurred in the present study, it appears that most perch in Oneida Lake are opportunistic feeders and have adapted to the extinction of the mayfly with little overall adverse effect.

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