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ABSTRACT

From June 2 to September 26, 1974, an average yearling yellow perch in the Ottawa River increased in total caloric content by 18.0 kcal and accumulated 1.038 x 10^{-6}g of organic mercury. Estimated rations over this period were 53.5 kcal at the level of metabolism predicted by Winberg 1 (Winberg, 1956) and 84.5 kcal at the level of metabolism predicted by Winberg 2. Both food and water could serve as significant sources of pollutant for the observed accumulation of organic mercury.

Growth in length of yearling perch was linear with day of year and given by the equation:

$$FL = 1.712 + 0.036 \text{ day}$$

where FL is fork length (cm) of the perch and "day", day of year from day 153 to 270, 1974 (June 2 - September 26).

The caloric content of the perch over this period was constant (4,754 cal/g dry wt.), as was the concentration of organic mercury (432.17 x 10^{-9}g dry wt.).

Feeding activities of the yearling yellow perch were diurnal. Benthic invertebrates were the major food resource of the perch throughout the summer but zooplankton were important diet items in June (38.4% volume) while fish were significant diet items in August (61.7% volume) and September (12.1% volume).

Significant seasonal variation was observed in the caloric content of several benthic invertebrates.

SOMMAIRE

A partir du 2 juin au 26 septembre 1974, une perche jaune (perchaude) moyenne d'un an (d'un an parmis la moyenne) de la rivière Ottawa augmenta en teneur calorique totale de 18.0 kcal et accumula 1.638 x 10^{-6}g de mercure organique. Les rations pour cette période étaient évaluées à 53.5 kcal au niveau de métabolisme prédit par Winberg 1 (Winberg 1956) et à 84.5 kcal au niveau de métabolisme prédit par Winberg 2. Et l'eau et la nourriture peuvent servir comme sources significatives de polluant pour l'accumulation de mercure organique notée.

La croissance en longueur d'une perche d'un an était linéaire avec la journée de l'année et est représenteé par l'équation:

$$FL = 1.712 + 0.036 \text{ jour}$$

FL signifie la longueur (cm) de la perche jusqu'à la fourche et "jour" signifie la journée de l'année à partir du jour 153 a 270, 1974 (le 2 juin au 26 septembre).

La teneur calorique de la perche durant cette période était constante (4,754 cal/g poids sec) ainsi que la concentration du mercure organique (432.17 x 10^{-9}g poids sec).

La perche jaune d'un an se nourrit le jour. Durant l'été, le benthos invertébré constitue la source principale de nourriture de la perche. Au mois de juin, le zooplancton représentait une source importante de

nourriture (38.4% du volume). Au mois d'août, les menus poissons représentaient 61.7% du volume de la diète de la perche alors qu'en septembre, ils ne constituaient que 12.1%.

On a noté une variation saisonnière significative dans la teneur calorique de trois à quatre types de benthos invertébrés.

CHAPTER 1 INTRODUCTION

Following seminal papers of Lindeman (1942) and Ivlev (1945), the use of a bioenergetic approach in the description of aquatic ecosystems has become increasingly prevalent. Over the past twenty years, a bioenergetic approach has been used in the analysis of growth and metabolism of a number of fish species both in laboratory experiments (Solomon and Braefield 1972; Nimii and Beamish 1974) and field investigations (Gerking 1962, 1971; Mann 1965; Healy 1972; Hoss 1974; Wissing 1974; Small 1975).

In a bioenergetic approach, the dynamics of interaction between and within components of an aquatic ecosystem (or some part thereof) are described in terms of transfer of energy. In an investigation of the bioenergetics of a fish population, the different functions of that population, (metabolism, growth, reproduction and feeding), are expressed in terms of a common unit of energy (calories). From these functions, a cumulative energy budget may be calculated for the population. The cumulative energy budget may then be employed to determine the efficiency of energy utilization within the population and the efficiency of energy transfer to and from other members of the food web (Klekowski *et al.* 1970). Information derived from bioenergetic investigations is of use both as a tool in understanding relations within natural environments and as it may be applied to practical considerations such as aquaculture. A bioenergetic approach has also formed the basis for recent models of the accumulation of pollutants such as methyl mercury by fish (Fagerstron *et al.* 1974; Norstrom *et al.* 1976).

The energetics of natural populations has been discussed by Winberg (1956) and may be expressed by the equation:

$$R = \frac{1}{e(f)} (M + G)$$

where R is the energy content of the food consumed (ration), M is the energy required for metabolism, G is the energy equivalent of growth and e(f) is the efficiency of assimilation of food.

Norstrom *et al.* (1976) have estimated ration by the equation:

$$R = \frac{1}{e(f)} (\alpha_{1r} W^{.81} + \beta G + G)$$

where α_{1r} is a temperature dependent term which gives low routine metabolic level of a perch at any temperature (0 - 25°C), W is the wet weight of the fish (g), β a constant relating growth to the energy associated with growth and other terms as given above. Uptake of a pollutant such as methyl mercury and uptake from both food and water sources may be related to metabolic rate and a bioenergetic approach employed to describe pollutant bioaccumulation by fish (Fageistrom *et al.* 1974, Norstrom *et al.* 1976).

Although the bioenergetic approach to the study of production in species and populations of fish may be simply expressed in the form of the above equations, the acquisition of meaningful and quantitative values for the components of this formulation is a difficult task. It was felt that existing data with regard to metabolic rate and assimilation efficiencies of perch were sufficient for the degree of precision required and accordingly this study has concentrated on the measurement of field parameters of the energetics and pollutant accumulation of yearling yellow perch, *Perca flavescens* (Mitchill), during a period of rapid summer growth.

The objectives of the present study were therefore:

1) to determine the caloric content of organisms common in the diet of yearling perch in the Ottawa River;

2) to determine the quantity and kind of food consumed by the yearling perch;

3) to define growth and changes in body composition and pollutant concentration of the yearling perch;

4) to use the above data and existing information on metabolic rate of yellow perch to construct an energy budget for the yearling perch;

5) and finally, to employ the above energy budget and observed pollutant accumulation to examine the process of pollutant accumulation in wild fish and in particular to define the potential contribution of food and water as sources of uptake of organic mercury.

The study was begun during the fall of 1973 and concluded in the summer of 1975. The bulk of field work was conducted from June through September, 1974.

The results of each aspect of this study are presented and discussed in Chapters 2 through 4. In Chapter 5 the results of the previous chapters are employed in the construction of an energy budget for the yearling yellow perch and this energy budget is then employed in an examination of pollutant accumulation by the fish.

Selection of Yearling Yellow Perch as the Experimental Species.

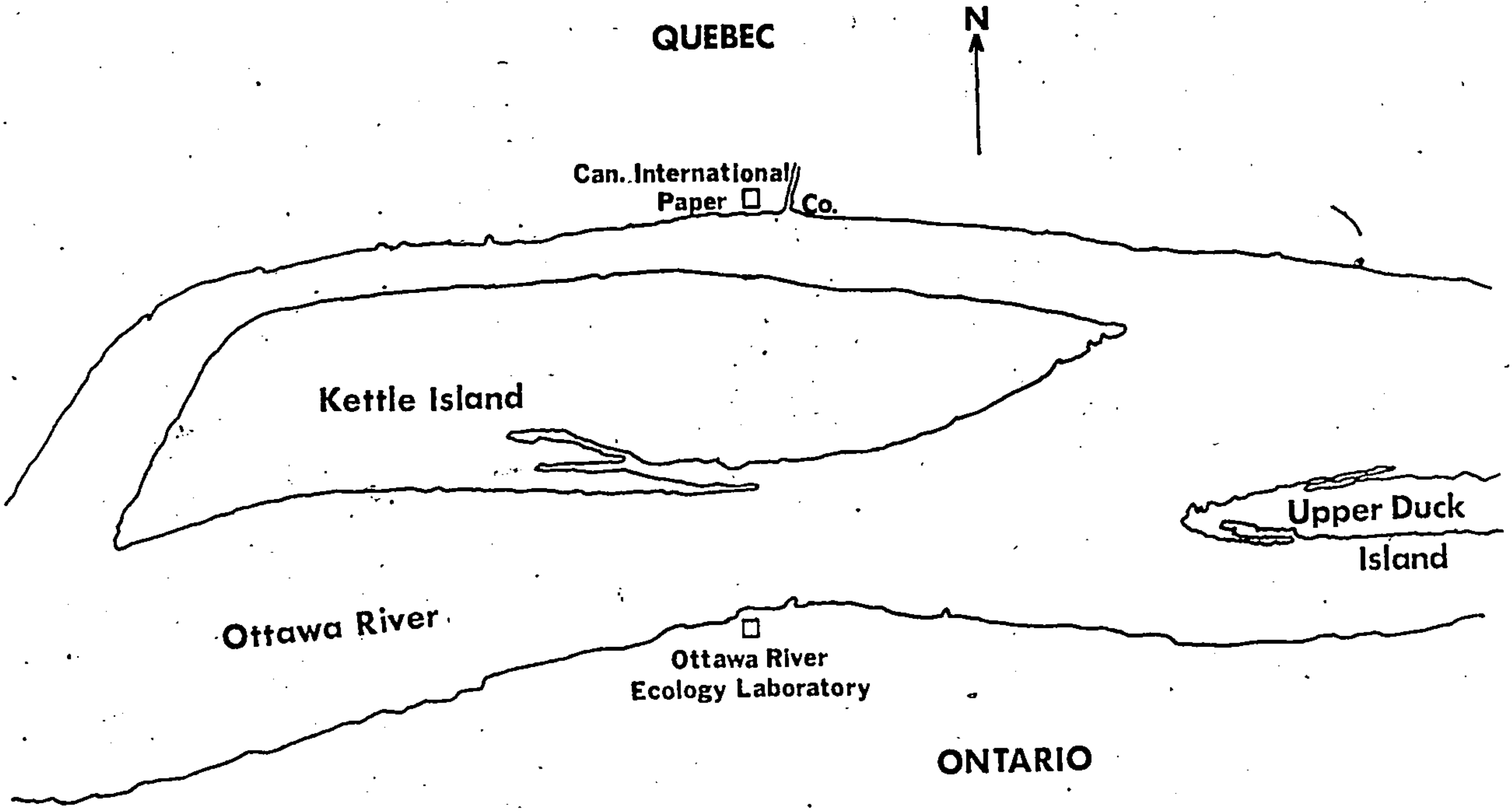
A previous study of Stobo (1971) had already defined many aspects of the life history of yellow perch in the Ottawa River. Thus it was known that yearling yellow perch were abundant in the study area throughout the summer and that they grew rapidly over this period. Additionally, the food habits of yearling perch in the study area had already been described and it was known that the perch did not spawn as yearlings, thus complications of gonadal production were avoided. The abundance and rapid growth rate of yearling perch and the availability of comparative data made yearling yellow perch the logical choice of experimental species for the present study.

The Ottawa River Study Area.

A three mile section of the Ottawa River below the cities of Ottawa and Hull had been selected as the site of investigation for The Ottawa River Project, a joint National Research Council - University of Ottawa project with the objectives of defining the transfer of pollutant chemicals, especially methyl mercury, through all compartments both biotic and abiotic of this section of the Ottawa River.

The Ottawa River in the study area (Figure 1-1) is a large, rapidly flowing temperate river with a reasonably high organic load (Stobo, 1970). Temperature of the river rises during the spring following break-up from 2-4°C to summer maxima in the order of 23-26°C (D. Mortimer, pers. comm.) then declines to 2-4°C with freeze-up, in winter. At no time is the main river stratified. Additional data concerning the physical-chemical composition of the Ottawa River in the study area are contained in the Ottawa River Program Interim Reports, 1972, 1973 and 1975. Due to the steep slope of banks and the strong current only limited areas of the study area could be effectively sampled by seine. These areas, principally the large shallow sand bars at the upstream ends of Kettle Island and Upper Duck Island, were the primary sites of collection of both fish and food items throughout the present study.

Figure 1-1 The Ottawa River Study Area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Upper Duck Island
Ottawa River
Ottawa River Ecology Laboratory
ONTARIO

CHAPTER 2 COLLECTION AND ANALYSIS OF FOOD ITEMS

Introduction

The analysis of energy flow through an aquatic ecosystem requires a knowledge of the caloric value of the system's biological components. To this end, numerous researchers have investigated the caloric values of a wide range of freshwater organisms (Slobodkin and Richman, 1961; Comita and Schindler, 1963; Wissing and Hassler, 1968; McCauley and Tsumura, 1974) with much of the existing data compiled in reviews by Prus (1970) and Cummins and Wuycheck (1971). In addition, the caloric content of a single species may vary considerably with season (Slobodkin, 1962; Schindler *et al.*, 1971; Wissing, 1969; Otto, 1974; Nilson, 1974). An accounting of the energy ingested by a predator such as a yellow perch must therefore include determinations of the caloric value of individual food items throughout the period investigated.

In this study, ash and caloric values of major items in the diet of yearling yellow perch (as indicated from the work of Stobo (1971))were determined at regular intervals throughout the period investigated, June through September, 1974. These values and coincident determinations of daily ration will be employed to give the caloric value of ingested ration.

Materials and Methods

Monthly collections of invertebrates-amphipods, isopods, chironomid larvae and damselfly nymphs were made with hand held dip nets from littoral vegetation and substrate within the Ottawa River Study area throughout the summer, 1974. Minnows were collected by beach seine from the littoral area at the upstream end of Upper Duck Island in August, 1975. The material was hand sorted to taxonomic group, washed and frozen (-20°C) for further analysis.

For analysis, the organisms were thawed and dried at 60°C for 24 hours (Crisp, 1971), ground to a homogenous powder with a mortar and pestle and stored in a dessicator. Minnows were freeze dried in a VerTis lyopholyzer, then treated as above. Pellets of sample material were pressed, weighted (10 to 20 mg) and caloric content determined using a Philipson non-adiabatic microbomb calorimeter (Philipson, 1964 - supplied by Gentry Wigget Instruments Ltd.). The calorimeter was calibrated with benzoic acid (6318 cal/g). Correction was made for heat input to the fuse wire but not for byproducts of combustion, sulphuric and nitric acids, as the error introduced is minimal (Paine, 1971). Three to six determinations of caloric content were made for each sample. Ash fraction was determined by combustion of sample material (10 - 20 mg) in a muffle furnace at 600°C to constant weight (Crisp, 1971).

Analysis of Data.

Data were compiled in a standard format on computer cards. Mean, standard deviation and a one way analysis of variance of the caloric content of each taxonomic group for all dates sampled was computed using the SPSS subprogram BREAKDOWN (Nie *et al.*, 1975) on the University of Ottawa's IBM 370 computer. Similarly individual date means were compared by t-test using the SPSS T-TEST subprogram (Nie *et al.*, 1975).

Results and Discussion

Amphipods, *Gammarus fasciatus* and *Hyalella azteca*, were collected in quantities large enough to permit analysis throughout the summer. Quantities of isopods sufficient for analysis were taken in July, August and September; adequate samples of chironomids were collected in July and August, while sufficient damselfly nymphs, *Enallagma signatum*, were collected in June and September. Minnows, *Hybognathus nuchalis*, an important late summer diet item, were collected in August, 1975. Although certain groups of organisms - *Ephemeroptera*, *Plecoptera* and *Trichoptera* were common in the diet of yearling perch, they were never collected in quantities sufficient for caloric analysis.

The results of caloric and ash analysis of the food organisms are presented in Table 2-1. In the amphipod, *Gammarus fasciatus*, caloric value (cal/g dry wt.) was similar in June and July but significantly lower ($p \leq 0.05$) in August. This may be related to the fact that *G. fasciatus* reproduces in June - July and animals with eggs and broods

Table 2-1

Ash and Caloric Value of Food Items
(mean, standard error of the mean and number (n) of samples given)

Gammarus fasciatus	June 24(1)	July 15	August 14	September 23	Total
Ash (% dry wt.)	22.99 ± .65 (5)	19.30 ± .73** (5)	22.33 ± 56* (5)	19.81 ± .25** (5)	21.09 ± .44** (20)
cal/g (dry wt.)	4205 ± 57 (4)	4258 ± 18 (5)	3934 ± 122* (5)	4125 ± 53 (5)	4129 ± 43* (19)
cal/g (ash free dry wt.)	5455 ± 74 (4)	5278 ± 22* (5)	5077 ± 144 (5)	5144 ± 66 (5)	5227 ± 53 (19)

Hyalella azteca	June 24	July 15	August 14	September 24	Total
Ash (% dry wt.)	23.62 ± 1.25 (5)	18.91 ± .54** (5)	17.10 ± .02* (4)	22.76 ± .23** (5)	20.78 ± .70**
cal/g (dry wt.)	3611 ± 53 (5)	3669 ± 67 (6)	4301 ± 45** (5)	4315 ± 61 (5)	3959 ± 79** (21)
cal/g (ash free dry wt. dry wt.)	4704 ± 68 (5)	4510 ± 79 (6)	5171 ± 54** (5)	5580 ± 80** (5)	4968 ± 100** (21)

Asellus spp.	July 10	August 14	September 23	Total
Ash (% dry wt.)	32.71 ± 1.10 (7)	19.61 ± .74** (5)	27.13 ± .25** (5)	27.22 ± 1.44** (17)
cal/g (dry wt.)	3252 ± 150 (3)	3981 ± 122** (5)	3795 ± 29 (5)	3741 ± 97** (13)
cal/g (ash free dry wt.)	4750 ± 320 (3)	4952 ± 152 (5)	5208 ± 40 (5)	5004 ± 97 (13)

Table 2-1 (Cont'd.)

Chironimidae spp.	July 15	August 14	Total
Ash (% dry wt.)	21.44 ± .45	13.97 ± .21**	16.11 ± 1.39
	(2)	(5)	(7)
cal/g (dry wt.)	4176 ± 30	4737 ± 47**	4527 ± 107
	(3)	(5)	(8)
cal/g (ash free dry wt.)	5315 ± 40	5507 ± 55**	5435 ± 50
	(3)	(5)	(8)

Enallagma signatum	July 10	September 23	Total
Ash (% dry wt.)	4.04 ± .50	25.52 ± .87**	13.59 ± 3.8
	(5)	(4)	(9)
cal/g (dry wt.)	5102 ± 107	5273 ± 41	5187 ± 61
	(5)	(5)	(10)
cal/g (ash free dry wt.)	5317 ± 112	7093 ± 54**	6205 ± 302
	(5)	(5)	(10)

Hybognathus nuchalis	Ash (% dry wt.)	cal/g (dry wt.)	cal/g (ash free dry wt.)
August 22, 1975	12.79 ± .37	5858 ± 19	6717 ± 22
	(5)	(5)	(5)

---

(1) Collections made in 1974 unless otherwise noted.

* $p \leq 0.05$ using t-Test between species, category date means ie *G. fasciatus*, ash %, July 15 with *G. fascialus*, ash %, June 24, or one way analysis of variance (3 or more groups).

**$p \leq 0.01$ using t-Test or one way analysis of variance.

were common in the sample, while the animals were not in reproductive condition in August. Otto (1974) noted a similar late summer drop in caloric content of *Gammarus pulex* in the Stampen stream in Sweden. Overall seasonal variation in caloric content (cal/g dry wt.) of *G. fasciatus* was significant ($p \leq 0.05$) and amounted to 8.0% of the minimum caloric value observed. Overall variation in ash fraction was highly significant ($p \leq 0.01$) but the caloric value of the organic fraction (cal/g ash free dry wt.) remained constant. Variation in the caloric content of *G. fasciatus* was thus effected through changes in the relative size of the ash fraction while the caloric content of the organic fraction remained stable. Cummins and Wuycheck (1974) reported caloric values of 4,050 cal/g dry wt. and 5,362 cal/g ash free dry wt. for *Gammaridae*, and the values determined in the present study lie within the range given.

In the amphipod, *Hyalella azteca*, caloric content (cal/g dry wt.) was similar in June and July (3,600 cal/g dry wt.) then rose to highly significantly different ($p \leq 0.01$) August - September values (4,300 cal/g dry wt.). Overall variation in caloric content (cal/g dry wt.) was highly significant ($p \leq 0.01$) and amounted to 19.5% of the minimum caloric value observed. Total variance in both ash percentage and the caloric value of the organic fraction (cal/g ash free dry wt.) was highly significant ($p \leq 0.01$). Thus changes in caloric content of *H. azteca* were effected through changes in relative size of the ash fraction and changes in the caloric value of the organic fraction. The values determined in the present study lie within the range of values presented by Cummins and Wuycheck (1971) for *H. azteca* with mean values of 4,033 cal/g dry wt. and 5,307 cal/g ash free dry wt.

With the isopods, *Asellus spp.*, caloric value differed highly significantly ($p \leq 0.01$) between July (3,252 cal/g dry wt.) and August (3,981 cal/g dry wt.) samples while August and September values were similar. Overall variation in both ash fraction and caloric content (cal/g dry wt.) was highly significant ($p \leq 0.01$) while the caloric content of the organic fraction remained constant. Seasonal variation amounted to 22.4% of the minimum observed caloric value (cal/g dry wt.). As in *G. fasciatus*, changes in the relative size of the ash fraction effected changes in caloric content while little change was observed in the caloric content of the organic fraction. Cummins and Wuychech (1971) reported a caloric value of 4,325 cal/g ash free dry wt. for *Asellidae*, their figure is however based on only two samples.

Highly significant differences were found in both ash fraction and caloric content of chironimid larvae ($p \leq 0.01$) between July (4,176 cal/g dry wt.) and August (4,737 cal/g dry wt.) samples, while a significant ($p \leq 0.05$) change occurred in the caloric value of the organic fraction (cal/g ash free dry wt.). The observed values lie within the range of values reported by McCauley and Tsumura (1974) for chironomid larvae.

In the damselfly nymph, *Enallagma signatum*, highly significant differences were observed in both percent ash fraction and in the caloric value of the organic fraction (cal/g ash free dry wt.) ($p \leq 0.01$) between June and September samples. Caloric content (cal/g dry wt.) did not change significantly between samples. A decrease in caloric content due to increased ash content is opposed by an increase in the caloric value of the organic fraction (cal/g dry wt.) presumably due to an increase in lipid content of the organic fraction. The mean caloric content (5,188 cal/g dry wt.) is similar to that reported by Cummins and Wuycheck (1974) of 5,350 cal/g dry wt. and very close to that reported by Lawton (1971) for *Pyrrhosoma nymphula* of 5,124 cal/g dry wt.

The caloric content of the silvery minnow, *Hybognathus nuchalis*, in August was 5,858 cal/g dry wt. Cummins and Wuycheck (1971) reported a caloric value for cyphrinids of 5,761 cal/g dry wt.

In summary, significant changes were observed in the caloric content of items in the diet of yearling perch with changes in time. In *G. fasciatus* these differences were 8.0% of the minimum observed caloric content, in *H. azteca*, 19.5% of the minimum observed caloric content, in *Asellus spp.*, 22.4% of the minimum observed caloric content and in chironomid larvae 12.1%

of the minimum observed caloric value. These changes are of considerable importance in determining the caloric value of ration ingested by the yearling perch. These values will be employed with coincident determination of the quantity and kind of food consumed by the perch (Chapter 3) to determine the energy equivalent of the ration (Chapter 5) in accounting the energy budget of the fish.

Changes in caloric content (cal/g dry wt.) were effected through two mechanisms. In the first of these, that exhibited by *G. fasciatus* and *Asellus spp.*, changes in caloric content were effected through changes in the relative size of the ash fraction alone with the caloric value of the organic fraction remaining constant. The second mechanism, as seen in *H. azteca* and chironomid larvae, effected changes in caloric content through changes in both relative size of the ash fraction and the caloric value of the organic fraction. The changes in the caloric value of the organic fraction are likely indicative of changes in the amount of storage lipid (Gerking, 1955). The observed differences between the species of amphipod may be related to habitat differences, with *H. azteca* associated with *Elodea canadensis* and *Myriophylum spp.* and quiet waters while *G. fasciatus* was associated with *Potamogeton spp.* and open flowing water (Mackie, 1971).

CHAPTER 3 FOOD HABITS AND ESTIMATION OF RATION

Introduction

A knowledge of the kind and quantity of food consumed by a wild fish is essential to an analysis of energy transformation by the population. Conversion of these estimates or ingested ration to their caloric equivalents (Chapter 2) allows their inclusion in an energy budget (Chapter 5).

Food Habits.

There exists a tremendous volume of literature concerning the food habits of fishes. The food habits of the yellow perch, both in Europe, *Perca fluviatilis*, and in North America, *Perca flavescens*, have been the subject of investigations by numerous researchers (Allen, 1935; Smyly, 1952; Alm, 1954; McCormack, 1970; Stobo, 1971; Noble, 1972b; Cannon, 1973; Clady, 1974; Tarby, 1974). These studies have established that the food preferences of the yellow perch change in a defined manner with growth. In general this ontogenetic process may be divided into three major stages characterized by the kind of food consumed; a planktiverous stanza, a benthophagus stanza and a pisciverous stanza (Il'ina, 1970).

Young perch normally consume large quantities of zooplankton, largely entomostraca (Smyly, 1952; Noble, 1972b). As the perch grows older and larger the diet changes and benthic invertebrates (chironomid larvae and pupae, amphipods, isopods, ephemeroptera nymphs, trichoptera larvae, etc.) become the major diet component, while the largest and oldest fish feed mainly on fish although some benthic invertebrates may be consumed (Allen, 1935; Alm, 1954; McCormack, 1970; Stobo, 1971; Clady, 1974; Tarby, 1974).

This process in which larger food items are consumed as the perch grows larger is in accord with theoretical models relating energy expended in predation, energy derived from prey and the body size of the predator (Kerr 1971a - c; Schoner, 1971; Werner and Hall, 1974). As the fish grows it is energetically advantageous to select larger food items. Yellow perch are, however, extremely plastic with respect to both food habits and growth rates in response to local environmental factors (Alm, 1954; Le Cren, 1958; Jerierska, 1974). Il'ina (1973) noted the occurrence of all three feeding stanzas within a population of underyearling yellow perch derived from a single spawning pair. In general, the transition from planktiverous to benthophageous feeding occurs in late underyearling to early yearling fish while the transition to a diet consisting largely of fish occurs from late yearling onward depending on food availability (Stobo, 1971; Jezierska, 1974).

In studies of movements and feeding periodicity of yellow perch, several authors have reported that perch are diurnal (active and feeding during the day; quiessent at night) in their activities (Carlander and Cleary, 1949;

Parsons, 1950; Scott, 1955; Hergenrader and Hassler, 1966). Tibbles (1956) however, found that a population of yellow perch in Lake Mendota was active throughout the whole day, similarly Tarby (1974) found no marked periodicity in the feeding of adult perch in Oneida Lake, New York. Keast and Welsh (1968) found feeding of yearling yellow perch to be diurnal with distinct morning and evening peaks of feeding activity. Noble (1972b) reported that dimersal underyearling perch fed diurnally with stomach contents reaching a peak in the early morning and remaining constant till evening. It can thus be surmised that feeding in yellow perch is largely diurnal but may be altered likely in response to food availability.

Enumeration of Stomach Contents.

A number of methods of enumeration of fish stomach contents have been employed by different authors. These methods as reviewed by Hynes (1950) and Windell (1968) may be summarized as follows:

(1) Frequency of occurrence method; stomach contents are examined with individual organisms sorted and identified. The number of stomachs in which each organism occurs is recorded and expressed as a percentage of the total number of stomachs examined. This method while demonstrating which organisms are consumed gives no indication of the quantities or numbers of these organisms in the overall diet of the fish.

(2) Numerical method; stomach contents are examined and sorted to taxonomic grouping. The numbers of individuals of each group are summed to give total numbers of each food item in the whole sample. These are usually expressed as a percentage of the total number of organisms found in all fish examined. Criticisms of this method are that it is often extremely difficult to count total numbers of small organisms which may be consumed in very large numbers by fish, or to obtain counts of fragmented organisms and that in the case of fish consuming plant material such counts are meaningless.

(3) Volume or weight method; stomachs of fish are examined and sorted to taxonomic grouping. The volume or weight of each food type in the stomach is determined, totaled for all stomachs and expressed as a percentage of the total volume of food in all stomachs examined. Difficulties with this method are encountered in the determination of accurate weights or volumes of very small food items.

(4) Dominance method; the number of fish in which each item occurs as the chief item, both numerically and volumetrically is recorded, totaled for all stomachs examined and expressed as a percentage of the total number of stomachs examined.

(5) Relative fullness of stomach-points method; each stomach is examined and assigned points on the basis of fullness (0 pts = empty; 5 pts = 1/4 full stomach;

10 pts = 1/2 full stomach; 20 pts = full stomach; 30-40 pts = distended stomach). Stomach contents are examined and sorted to taxonomic grouping. Each grouping is assigned a portion of the total points assigned to stomach on the basis of size and abundance. Points gained by each grouping are summed and expressed as a percentage of the total number of points assigned all stomachs. The limitation of this procedure is the subjectivity to the investigator.

In the present study, stomach contents were defined by weight, frequency of occurrence and relative fullness of stomach.

Food Consumption.

Estimates of food consumption of fish in nature have been made through the use of four general methods (Davis and Warren, 1968);

(1) Nitrogen balance method; fish are removed from the wild population and held in confinement for a short period of time. The rates of nitrogen loss from gills, kidneys and feces are determined. The sum of these losses are added to the nitrogen equivalent of observed growth and the total is taken as the equivalent of the nitrogen content of the food. This technique has been employed by Brikett (1969) and Fisher (1972).

(2) Comparison with growth at known rations; fish are taken from the wild and growth at specified levels of ration is determined. Food consumption is estimated from

a comparison of food consumption level and growth rate under experimental conditions with the observed rates of growth in natural situations. This method has been used by Allen (1951), Gerking (1962) and Windell (1966).

(3) Estimation of ration from metabolism and growth; this method as proposed by Winberg (1956) assumes that assimilated food energy (80% of food consumed) may be estimated as the sum of the caloric equivalents of observed growth in nature and twice the level of routine metabolism as determined by laboratory respirometry. This technique has been employed by Mann (1965) and Blackiel (1971) in their estimation of production of fish species in the Thames and Vistula Rivers, respectively. This method is used in this work in comparison with the estimated ration based on examination of stomach contents (see Chapter 5).

(4) Estimation of ration from stomach contents of wild fish; a large group of fish from the wild are caught and held in captivity. At the time of capture and regular intervals thereafter samples of fish are killed and the quantity of food in the stomach of each fish determined. From the rate of disappearance of food from the stomachs and from the quantity of food originally present an estimate is made of daily ration. This method as proposed by Bajkov (1935) has been used by Darnell and Meierotto (1962) and Wissing (1969).

Keast and Welsh (1968) present a modification of this method. Groups of wild fish are captured at regular intervals (3 hour) throughout a 24 hour period. The fish are killed and preserved on capture and the weight of stomach contents per gram of fish determined. From the mean weight of stomach contents per gram of fish weight at each interval throughout the 24 hour period minimum daily ration is estimated.

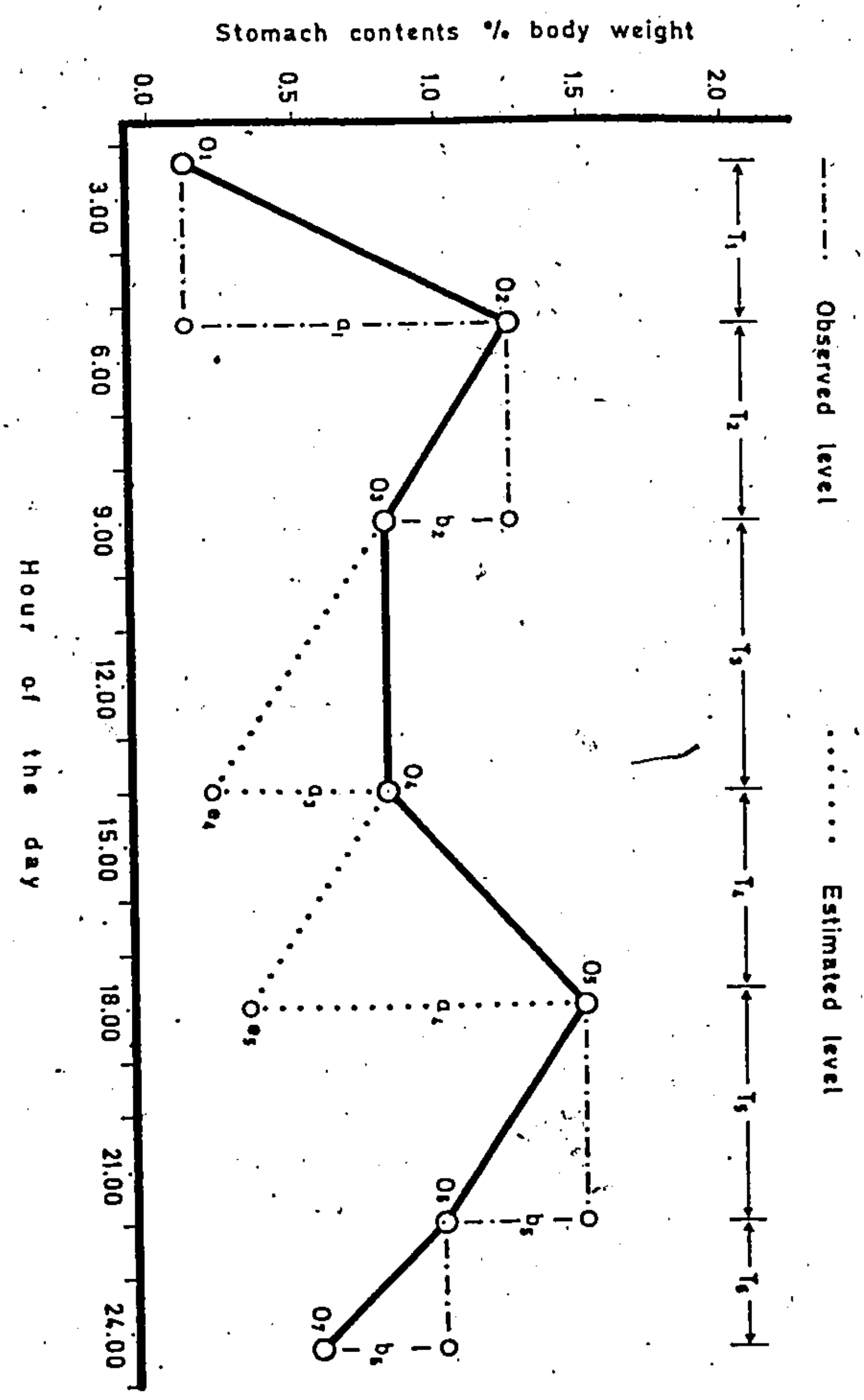
Noble (1972a) and Swenson and Smith (1973) in another modification of this technique first obtain estimates of digestion rates of natural food items by fish of the species and size range being investigated under laboratory conditions. This rate is then used in conjunction with observed levels of fullness of stomachs of fish from the field to estimate ration.

In the present study daily ration was estimated following the procedure of Tarverdiyeva (1972) in which both consumption and digestion are estimated from levels of food in the stomachs of wild fish at the time of capture. This method is shown diagrammatically in Figure 3-1. Mean levels of stomach contents as a percentage of body weight are shown for intervals sampled (o_1, o_2, ... o_n for intervals t_1, t_2, ... t_n respectively).

From those intervals in which a consistent decline in stomach contents is seen (t_2, t_5, t_6) it is assumed that only digestion is occurring. Interval digestion is estimated as the difference between initial and final observed levels of stomach contents.

$$b_2 \text{ (interval digestion)} = o_2 - o_3$$

Figure 3-1 Diagramatic representation of stomach content level with time of day plot as used in determining daily ration. Detailed explanation given in text.


Stomach contents % body weight
0.0
0.5
1.0
1.5
2.0
Hour of the day
3.00
6.00
9.00
12.00
15.00
18.00
21.00
24.00
Observed level
Estimated level
T1
T2
T3
T4
T5
T6
O1
O2
O3
O4
O5
O6
O7
a1
b2
a3
a4
b5
b6
e4
e5

Field digestion rate (FDR) is estimated as the sum of all interval digestions (b_i) divided by the total time over which these interval are applicable (t_i).

$$\text{Field digestion rate (FDR)} = \frac{(b_2 + b_5 + b_6)}{(t_2 + t_5 + t_6)}$$

For those intervals in which original stomach contents are minimal ($\leq$ 0.2% body weight) and stomach contents increase, interval ration is estimated as the difference between original and final levels of stomach fullness.

$$a_1 \text{ (interval ration)} = o_2 - o_1$$

If stomach contents are appreciable at the start of the interval (> 0.2% body weight), but a change in stomach content levels other than the consistent decline of those intervals for which interval digestion was estimated is observed, it is assumed that digestion of the contents at the start of the interval occurs at the field digestion rate and an expected level of stomach contents is determined. This expected level is calculated as the level of stomach contents at the beginning of the interval minus the product of field digestive rate and the length of the interval.

$$e_3 \text{ (expected level)} = o_3 - (\text{FDR} \times t_3)$$

Interval ration is then estimated as the difference of the observed stomach level at the end of the interval and the expected level.

a_3 (interval ration) = $o_4 - e_3$

Estimated daily ration is the sum of interval rations over the 24 hour period.

Estimated Daily Ration (EDR) = $a_1 + a_3 + a_4$

This method assumes that a representative portion of a resident population is sampled throughout the day; that the population feeds synchronously; that all food items are digested at the same rate and that the rate of digestion may be adequately described by a linear function.

Mark - recapture methods may give an indication of the validity of first assumptions. Windell (1966) found that there was no marked difference in the rate of passage of food items of several types through the stomachs of bluegill sunfish in both single and mixed meal feeding experiments. Similarly, it has been shown in a number of studies that the size of meal has relatively little effect upon rate of digestion (Hunt, 1960; Windell, 1966; Kitchell and Windell, 1968; Magnuson, 1969).

Rates of digestion have been found to be linear in the bluegill sunfish (Windell, 1966), bass, warmouth and gar (Hunt, 1960) and with sauger and walleye (Swenson and Smith, 1973). Magnuson (1969) determined that a polynomial regression with a relatively small second order component accounted for digestion by the skipjack tuna. Brett (1970), with sockeye salmon, Tyler (1970) with cod and Elliot (1972) with brown trout; all found that digestion was best described by an exponential function. However, even if the 'real' nature of gastric digestion is exponential, approximation of this rate by a linear function may not introduce a large error. In the present case, field digestive rate is estimated from data in which stomach contents are always relatively high ($\geq$ 0.2% body weight). In this portion of digestion function, the exponential function describing digestion is steep (Brett, 1970) and error introduced by a linear approximation of this portion of the exponential function should be minimal. Accordingly, in the present study, the field digestive rate was considered linear and daily ration will be estimated by the procedure of Tarverdiyeva (1972) as given above.

Materials and Methods.

Collection and Handling of Fish;

On each sample date (June 11, July 23, August 20 and September 18, 1974) fish were collected at 3-4 hour intervals from 3:00 hours to just after 24:00 hours. Collections were made on the littoral areas at the upstream ends of either Kettle (August) or Upper Duck (June, July, September) Islands. Yellow perch of the appropriate size range were collected with a nylon bag seine (100 ft. x 6 ft., 3/16 in stretched mesh) with 1-5 beach hauls made per interval. If possible 10 or more fish were collected in each sample interval but in some intervals fewer than 10 fish were collected. Fish were killed immediately by a blow to the hand and preserved in formalin (4%) solution.

Analysis of Stomach Contents;

Preserved fish were damped dry on a paper towel, weighed and fork and total lengths (Hubbs and Lagler, 1964) measured. The intact stomach was removed from the fish and assigned points on the basis of fullness. The stomach was then damped dry and weighed. The stomach was then opened; the contents removed and the empty stomach damped dry and weighed. The weight of stomach contents was the difference between these weighings and was expressed as a percent of the fish weight.

The contents of each stomach were examined under a binocular disecting microscope and the organisms sorted to taxonomic groupings. Each grouping was then assigned a proportion of the total points assigned to the stomach on the basis of the size and abundance of each group.

Data Analysis;

Data for each individual fish (date of capture, fish weight, fish length, weight of stomach contents, assigned points for the stomach and assigned points for each taxonomic grouping) was compiled on computer cards and analyzed using SPSS subprograms (Nie *et al.*, 1975). Weight of stomach contents was correlated to assigned stomach points using the Pearson correlation coefficient, SPSS subprogram PEARSON COR. Mean weight of stomach contents for each time interval for each sample date was calculated using the SPSS subprogram BREAKDOWN while the

CROSSTABS subprogram was used in calculating frequencies of taxonomic groupings of food items for each sample date.

Results and Discussion.

Residency of the Population;

In August and September a considerable number of yearling perch had been tagged. Tagged fish caught in early hauls and released again were recaptured later on the same day in the August sample (some individual fish were recaptured twice); while in the September sample fewer fish were captured and no tagged fish released in the first samples were recaptured in later hauls. This indicates that in the August sample, at least, the population was resident in the sample area throughout the day.

Relationship of Weight of Stomach Contents to Assigned Stomach Points;

Pearson correlation coefficients of .92 to .95 ($p < 0.001$) were obtained in relating assigned stomach points to the weight of stomach contents for each sample date. The overall correlation for all months between assigned stomach points and stomach content weight was .89 ($p < 0.001$). This indicates that stomach fullness may be adequately estimated by the points method and that further partitioning of these points is valid. Noble (1972a) obtained similarly high correlations between estimated fullness of stomachs (points) and weight of stomach contents.

Food Habits.

Percent volume and percent frequency of individual food item groupings in the diet of yearling perch for all sample dates are presented in Table 3-1. Relative volume composition of food items (over 2% volume) in the diet of the perch on each sample date is illustrated in Figure 3-2. The diet of yearling perch changes considerably over the study period and from these changes the following trends in diet are revealed:

(1) Zooplankton (cladocera and copepods) were a major food resource for yearling perch in June (38% volume of diet) but in subsequent months were either not consumed or were consumed in minimal quantitites only.

(2) Benthic invertebrates as a group were the major food resource for the yearling yellow perch population throughout the study period. Amphipods (*Gammarus fasciatus* and *Hyalella azteca*) were found in high frequencies in the diet for each sample interval and comprised a relatively constant proportion of the diet in all months (9 to 14% volume of diet in any one interval; 10.5% volume of the overall diet for all samples). The frequency of occurrence of chironomid larvae in the diet of yellow perch was high in all months; in two months, July and September chironomid larvae comprised the major constituent of the diet (44-46% volume) while in July and September were present in the diet in significant proportions (10-11%

Table 3-1

Volume Composition (%) and Frequency of Occurrence (%) of Food Items in the Diet of Yearling Yellow Perch

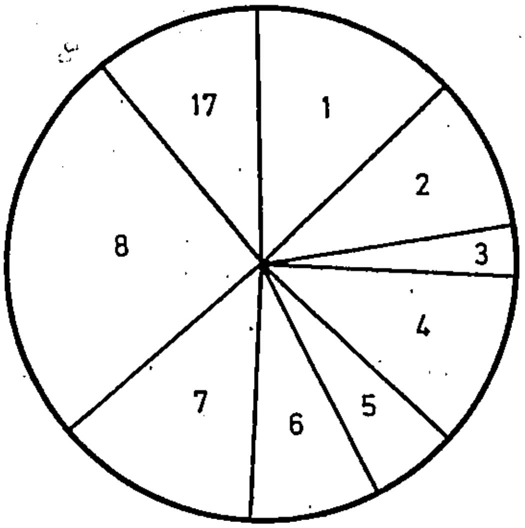
	June 11, 1974		July 23, 1974		August 20, 1974		September 18, 1974		Total	
	% Volume	% Frequency	% Volume	% Frequency	% Volume	% Frequency	% Volume	% Frequency	% Volume	% Frequency
Nematoda and *Oligochaeta*	-	-	1.9	5.9	.5	2.5	.3	3.1	0.5	3.3
Mollusca	-	-	-	-	.4	3.7	.1	1.6	0.2	1.6
Copepoda	25.3	47.6	-	-	.1	1.3	-	-	4.9	8.2
Cladocera	13.1	39.4	-	-	-	-	.7	4.7	2.6	6.5
Amphipoda	13.0	33.3	8.9	29.4	9.1	35.0	14.0	46.9	10.5	36.3
Isopoda	-	-	-	-	1.1	1.3	1.5	7.8	0.7	2.4
Hydracarina	-	-	2.2	10.3	.2	2.5	3.4	12.5	1.0	6.9
Ephemeroptera Nymphs	11.3	27.3	26.2	47.1	6.4	31.2	6.6	21.9	11.2	32.7
Odonata Nymphs	.9	3.0	.6	2.9	-	-	-	-	0.3	1.2
Plecoptera Nymphs	8.1	15.2	1.1	5.9	.4	2.5	-	-	2.0	4.5
Trichoptera Larvae	5.5	9.1	3.6	10.3	.8	5.0	9.5	34.4	3.6	14.7
Hemiptera	-	-	.2	1.5	.4	3.7	-	-	0.2	1.6
Chironomidae Larvae	9.8	33.3	43.6	67.4	11.0	48.7	45.8	68.7	22.3	54.3
Chironomidae Pupae	3.0	9.1	2.3	13.2	1.5	20.0	2.7	20.3	2.1	16.7
Adult *Diptera*	1.7	12.1	1.9	10.3	3.9	12.5	1.5	15.6	2.7	12.7
Fish	-	-	-	-	61.7	30	12.1	3.1	30.4	10.6
Miscellaneous	8.4	63.6	7.0	35.3	2.6	28.7	1.7	10.9	4.4	30.6

Figure 3-2

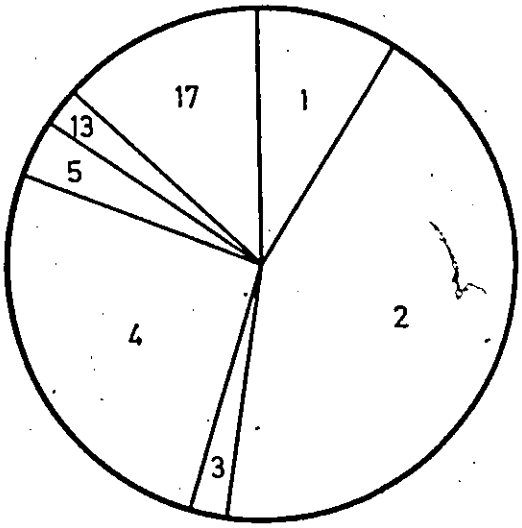
Relative Volume Composition of Diet of Yearling Perch on Dates Shown, 1974*

1. *Amphipoda*
2. *Chironomidae* Larvae
3. *Chironomidae* Pupae
4. *Ephemeroptera* Nymphs
5. *Trichoptera* Larvae
6. *Plecoptera* Nymphs
7. *Cladocera*
8. *Copepoda*
9. Fish
10. Adult *Diptera*
11. *Odonata* Nymphs
12. *Hemiptera*
13. *Isopoda*
14. *Hydracarina*
15. *Nematoda* and *Oligochetae*
16. *Mollusca*
17. Miscellaneous

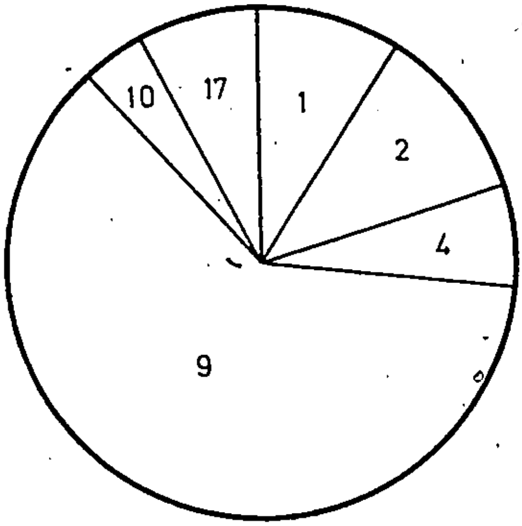
*Only items ≥ 2% volume of diet shown, all others are grouped in Miscellaneous.



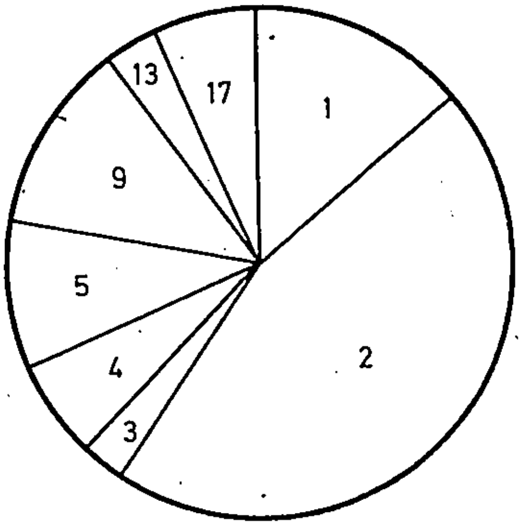
June 11



July 23



August 20



September 18

volume). Ephemeroptera nymphs were important diet items in June (11% volume) and July (26% volume), and were significant in August and September (6.5% volume). Trichoptera larvae were relatively important in the diet of yearling perch in June (5.5% volume) and September (9.5% volume) while plecoptera nymphs were significant diet items in June (8.1% volume).

(3) Fish, largely silvery minnows, *Hybognathus nuchalis*, comprised the major diet item in August (62% volume) and were significant in the September diet (12% volume) of the yearling yellow perch.

These results clearly show the opportunistic nature of feeding by yellow perch yearlings and indicates that the population may be considered as facultative benthophages in the classification of Il'ina (1970). Benthic invertebrates remained the primary food resource of the yearling yellow perch throughout the summer but other organisms, zooplankton and fish were consumed when the opportunity availed itself.

The virtual disappearance of zooplankton from the diet of yearling perch after June may in part be attributed to a change in food preference by the fish with larger food items being preferentially consumed. However, the observed decline in the consumption of zooplankton by the perch must also be related to dramatic decreases in the standing crop of zooplankton observed in open river sections of the Ottawa River Study Area between June and July (Croskery, 1972; Trudel, 1973). Galbraith (1970), McCormack (1970), Stobo (1971) all have noted that zooplankton were significant in the diet of yellow perch larger and older than those of the present study. Thus, the observed decline in the abundance of zooplankton from the diet of the yearling perch after June is likely related to changes in the abundance of zooplankton more than changing food preferences.

Similarly the high incidence and proportion of fish in the diet of the yearling perch in August reflects the opportunistic nature of their feeding. All of the identifiable remains of fish in the diet of the August sample were silvery minnows, *Hybognathus nuchalis*. These minnows were present in very large numbers in the sampling area during the August collections. Several hundred silvery minnows were often collected in seine hauls which collected fewer than 10 yearling perch. Qadri and Code (1973) noted similar aggregations of silvery minnows at the upstream ends of Kettle and Upper Duck Islands in August, 1973. McCormack (1970) noted a similar August increase in the proportion of fish in the diet of perch of all ages in Lake Windermere and Tarby (1974) found that predation of older perch on underyearling perch was most intense in August. The increased consumption of fish in August is thus effected by an increase in the availability of fish as food to the yearling perch combined with the increased capacity of the rapidly growing perch to consume much larger food items in August than was possible for these same fish to consume in June.

The food habits of the yearling perch over the study period were such that the perch best fit the category of facultative benthophages in the classification scheme of Il'ina (1970). Benthic invertebrates were the main food resource of the perch over the whole summer. Zooplankton and fish, largely mid-water organisms, were consumed when they were abundant and the opportunity availed itself. In the absence of significant amounts of mid-water organisms, predation pressure upon the benthos increased, and chironimid larvae in particular became the major diet item.

Feeding upon benthos was also opportunistic to a large degree. The peak levels of individual insect taxons in different months were undoubtedly related to changes in abundance and availability of these organisms to the perch population which is in turn related to the life history of individual insect species. The constant proportion of amphipods in the diet of the yearling perch indicates that the abundance and availability of these organisms to the perch remained constant throughout the summer. The small but constant proportion of adult diptera in the diet indicates that some surface feeding occurred and that the entire water column of the littoral zone was employed in the feeding of the yearling perch.

Comparison of the diet of yearling perch in the

Ottawa River Study Area, 1974, with that noted by Stobo (1971) for yearling perch from Kettle Island, 1967-1968, reveals several differences. Principal among these is the large contribution of debris (32.5% volume of diet) and gastropods (9.5% volume of diet) to the ration of yearling perch in Stobo's study as compared to the present study (miscellaneous 4.4% volume of diet; molluscs .2% volume of diet). Stobo (1971) noted that much of this debris consisted of wood chips, other plant material, pieces of mollusc shells and remains of unidentifiable organisms, in that order of importance. In the present study, the miscellaneous category consisted of unidentifiable remains of organisms, identified organisms which occurred in only one or two samples (*Colleoptera, Formicidae,* other *Hymenoptera, Hiuridinea,* etc.) and plant material in that order of importance, wood fibre was not noted. The contributions of chironomid larvae, ephemeroptera nymphs and amphipods to the diet of yearling perch was far greater in the present study, while the contributions of isopods, odonata nymphs and trichoptera larvae were less in the present study than in that of Stobo. Fish were not noted in the diet of yearling yellow perch at the Kettle Island station in 1967-68 (Stobo, 1971) while in the present study fish comprised a major diet item in August and were significant in the September diet. Stobo (1971) gives neither the time of day or the time of year his fish were collected and his sample is based on only

14 fish, but a comparison of the diets of yearling perch in 1967-68 with that of 1974 would indicate that feeding conditions have improved for the perch. Improved feeding conditions allow the perch to be more selective in their feeding and the proportion of detritus in the diet would be expected to decrease as was seen in the present study.

Feeding Periodicity and Daily Ration.

The frequency of occurrence of diet items over 5% volume of monthly diet and of empty stomachs (assigned 0 points) for the time of day on each sample date is given in Tables 3-2 to 3-5.

The diurnal nature of feeding by yearling perch is clearly evident from the Tables 3-2 to 3-5. Highest frequencies of empty stomachs were found in the pre-dawn period in all months although there was no interval in which all stomachs were empty. The frequency of empty stomachs decreases after dawn, often decreasing to zero, and the frequency of empty stomachs remains low throughout the day. After dusk, the frequency of empty stomachs increased, and high frequencies were again found in the final sampling interval. No distinct pattern is apparent in the relationship of the frequency of any individual food item to time of day.

The mean weight of stomach contents (% body weight) by time of day for each of the dates sampled is given in Figures 3-3 to 3-6. The diurnal nature of feeding

Table 3-2

Frequency of Occurrence of Food Items by Hour of Day - June 11, 1974

(only items ≥ 5% volume of diet included)

Time	04:30	07:30	11:00	15:30	20:30	24:30	Total
Amphipoda	20	0	37.5	100	25	100	33.3
Chironomidae Larvae	0	20	37.5	100	25	100	33.3
Ephemeroptera Nymphs	40	40	25	0	0	25	27.3
Trichoptera Larvae	20	0	12.5	0	0	25	9.1
Plecoptera Nymphs	0	0	37.5	50	25	0	15.2
Cladocera	0	70	59	0	50	0	39.4
Copepods	20	100	12.5	50	75	75	47.6
Miscellaneous	40	80	75	50	75	25	63.6
Empty Stomachs	40	0	0	0	0	0	6.1

Table 3-3

Frequency of Occurrence of Food Items by
Hour of Day - July 23, 1974

(only items ≥ 5% volume of diet included)

Time	03:30	07:30	10:30	13:15	16:30	20:30	24:15	Total
Amphipoda	10	50	40	20	30	30	25	29.4
Chironomidae Larvae	0	100	20	90	70	90	25	67.4
Ephemeroptera Nymphs	0	50	30	90	70	70	12.5	47.1
Miscellaneous	10	30	50	70	40	20	25	35.3
Empty Stomachs	90	0	40	10	10	10	62.5	30.9

Table 3-4

Frequency of Occurrence of Food Items by Hour of Day - August 20, 1974

(only items ≥ 5% volume of diet included)

Time	03:00	06:30	09:30	12:30	16:00	19:00	21:45	24:45	Total
Amphipoda	10	30	50	60	40	40	30	10	35.0
Chironomidae Larvae	10	60	50	70	90	60	20	30	48.7
Ephemeroptera Nymphs	0	40	20	40	70	50	30	0	31.2
Fish	20	20	30	40	10	50	40	30	30
Empty Stomachs	70	20	20	0	0	0	30	40	22.5

Table 3-5

Frequency of Occurrence of Food Items by Hour of Day - September 18, 1975

(only items ≥ 5% volume of diet included)

Time	03:45	06:40	09:45	13:00	15:45	18:30	21:45	24:45	Total
Amphipoda	33.3	10	50	50	60	70	50	50	46.9
Chironomidae Larvae	33.3	10	90	100	90	100	25	50	68.7
Ephemeroptera Nymphs	0	0	30	30	10	40	50	25	21.9
Trichoptera Larvae	0	0	20	70	50	60	25	25	34.4
Fish	0	0	0	0	0	10	25	0	3.1
Empty Stomachs	66.7	90	10	0	10	0	25	50	28.1

by the yearling perch is again evident; in all months mean stomach content weights in the sample subsequent to sunrise and mean weights of stomach contents in the sample prior to sunset were greater than those of the interval after sunset. Thus yearling perch in the Ottawa River Study Area were distinctly diurnal in their feeding habits. A similar diurnal nature in the activities and feeding of yellow perch has been reported by a number of authors (Carlander and Cleary, 1949; Parsons, 1950; Scott, 1955; Hergenrader and Hassler, 1966; Keast and Welsh, 1968; Noble, 1972b). It would thus appear this is a general pattern for yellow perch although different feeding patterns have been noted for perch in some instances (Tibbles, 1956; Tarby, 1974).

Feeding periodicity from sunrise to sunset varied considerably among sample dates. In June (Figure 3-3), feeding periodicity was distinctly bimodal with a first peak in stomach fullness observed in the early morning (07:30 hr.), followed by a decline in stomach contents towards noon; a second peak in stomach contents was observed in the afternoon (15:30 hr.) with a subsequent decline in stomach fullness. Keast and Welsh (1968) described a similar bimodal feeding periodicity with distinct morning and evening peaks in stomach fullness for yearling yellow perch in June in Lake Opinicon, Ontario.

In July (Figure 3-4), three peaks in stomach fullness were observed, the first in the early morning

Figure 3-3. Mean stomach content levels of Yearling Perch by time of day for June 11, 1974. Mean stomach contents (as percent body weight), standard error of the mean and sample size (n) shown. (*Mean, range and (n) shown.)

↓ Sunrise, ↓ Sunset

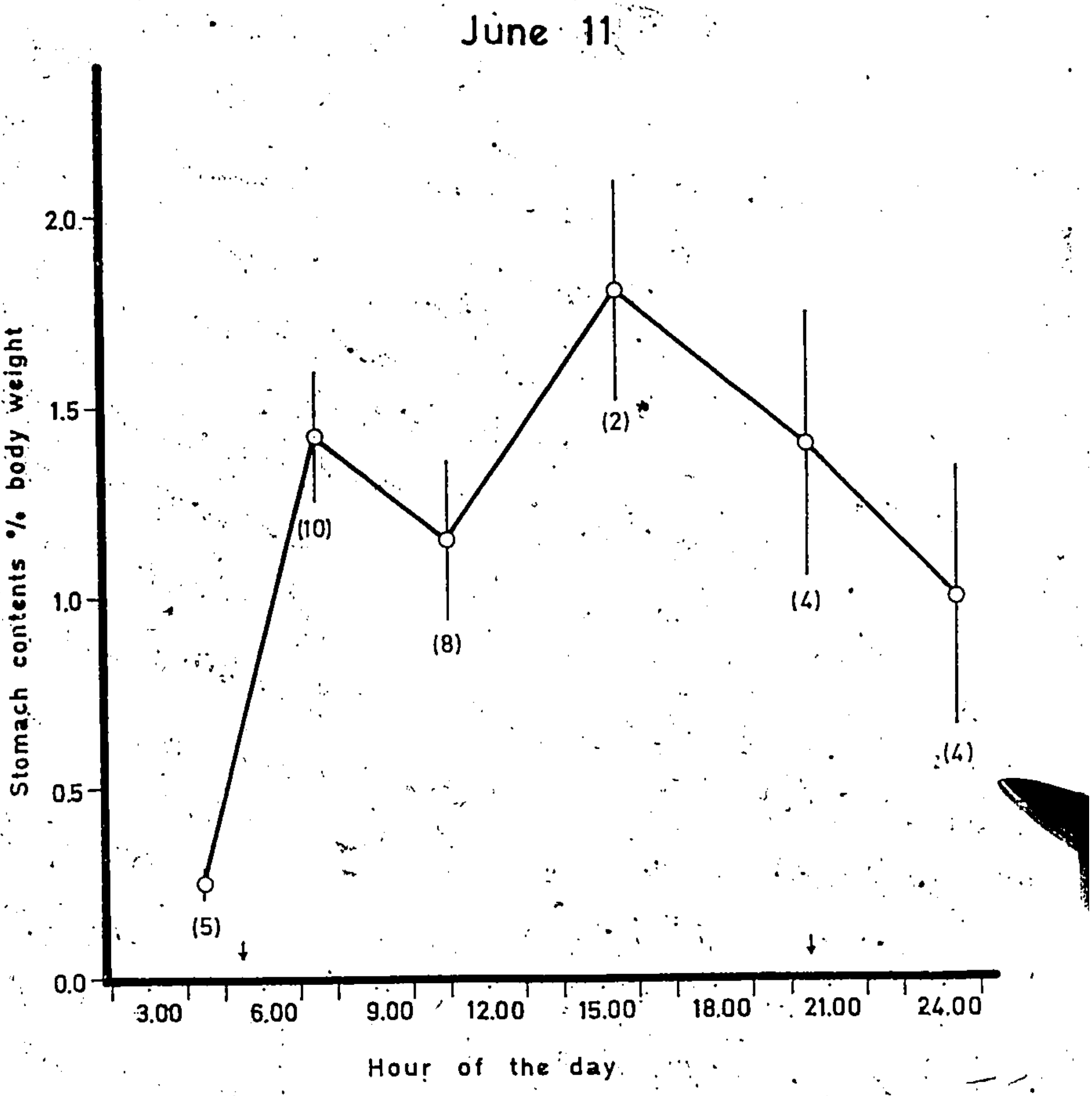
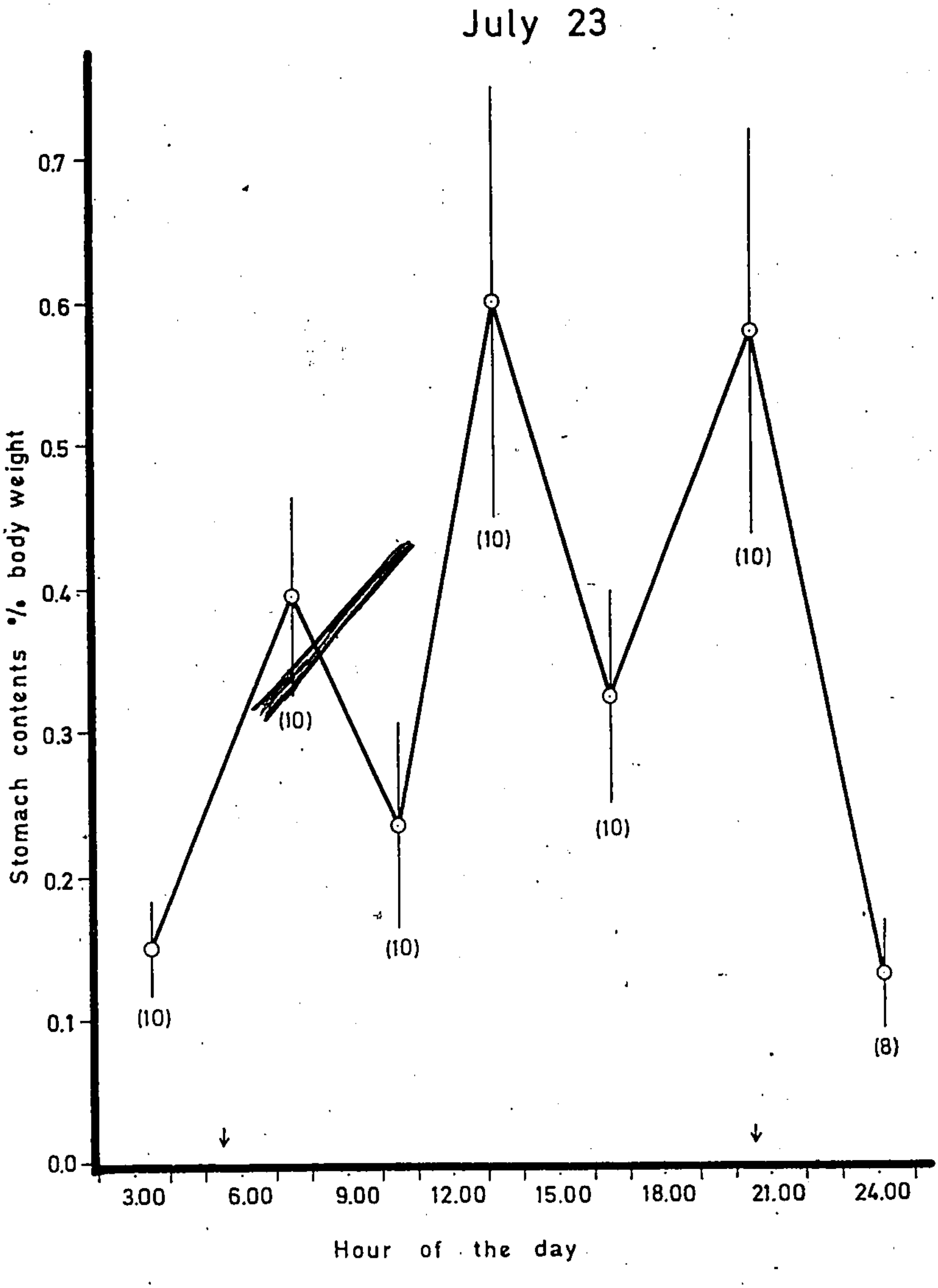

June 11
Stomach contents % body weight
2.0
1.5
1.0
0.5
0.0
(5)
(10)
(8)
(2)
(4)
(4)
3.00
6.00
9.00
12.00
15.00
18.00
21.00
24.00
Hour of the day

Figure 3-4. Mean stomach content levels of Yearling Perch by time of day for July 23, 1974. Mean stomach contents (as percent body weight), standard error of the mean and sample size (n) shown.

↓ Sunrise, ↓ Sunset


July 23
Stomach contents % body weight
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
(10)
(10)
(10)
(10)
(10)
(10)
(8)
3.00
6.00
9.00
12.00
15.00
18.00
21.00
24.00
Hour of the day

(07:30 hr.), a second in the early afternoon (13:15 hr.) and the third near sunset (20:30 hr.). In August (Figure 3-5), a peak in stomach fullness was observed early in the morning (06:30 hr.) followed by a slight decrease to a mid-morning level (09:30 hr.) which remained constant until early afternoon (16:00 hr.) when stomach contents decreased with a subsequent lesser peak in stomach fullness observed in the evening (19:00 hr.). In September (Figure 3-6), stomach fullness increased throughout the morning, reached a relatively constant level from early afternoon to evening after which the level of stomach contents subsequently declined. Noble (1972b) observed plateaus in stomach fullness similar to those observed in August and September in the present study for demersal under-yearling perch feeding upon zooplankton, in Oneida Lake, New York. The observed changes in feeding periodicity result from changes in the availability of food items over the day and changes in digestion rate with different temperatures and fish body sizes for each sample date (Elliott,1975). It is also apparent that a sampling program beginning at dawn and ending at dusk would be sufficient to account for the daily ration of yearling perch in the Ottawa River Study Area.

Estimated daily ration for yearling perch on June 11 was 2.03% body weight with a field digestive rate of .088% body weight per hour, while estimated rations and digestion rates for the others dates were: July 23,

Figure 3-5. Mean stomach content levels of Yearling Perch by time of day for August 20, 1974. Mean stomach contents (as percent body weight), standard error of the mean and sample size (*n*) shown.

↓ Sunrise, ↓ Sunset

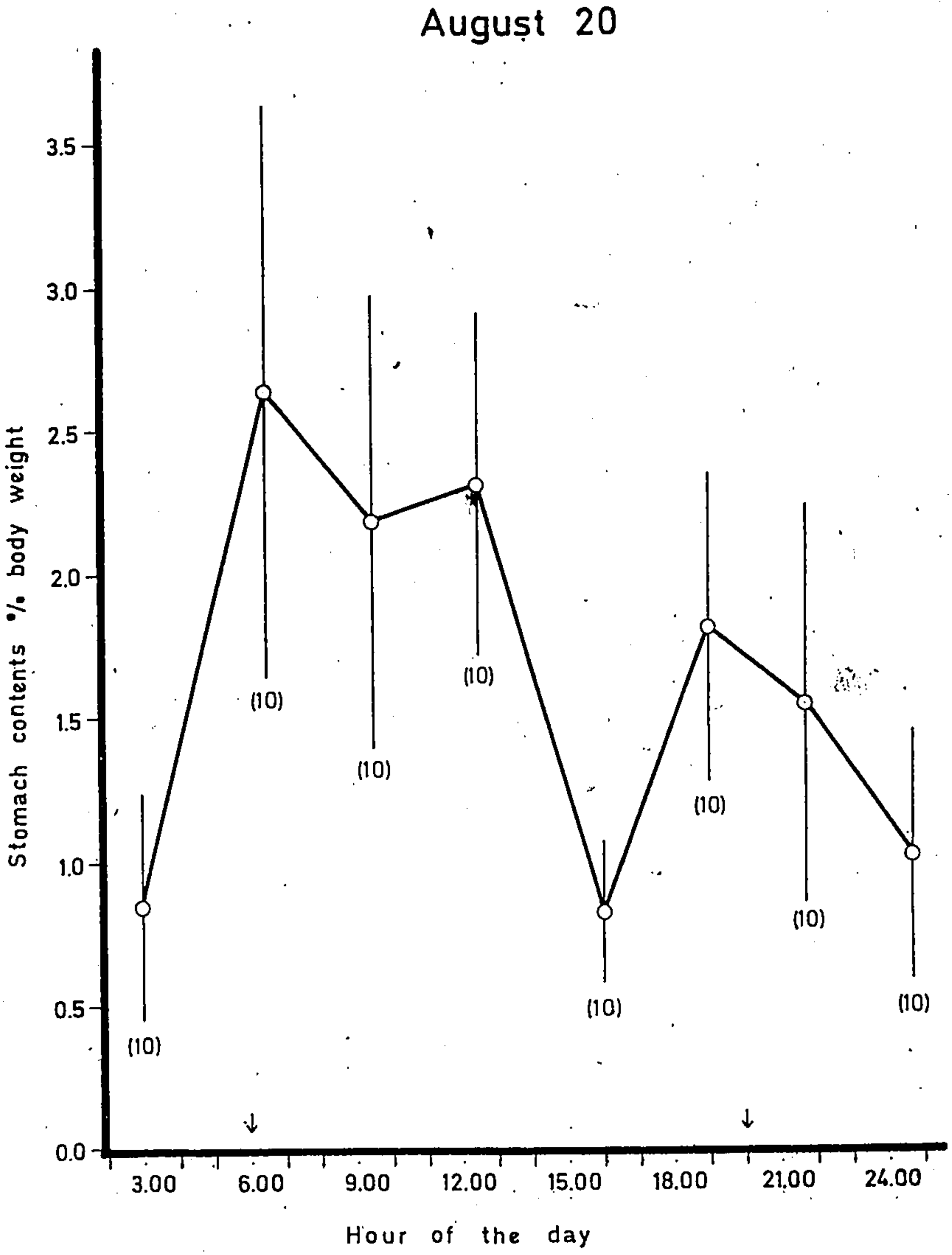
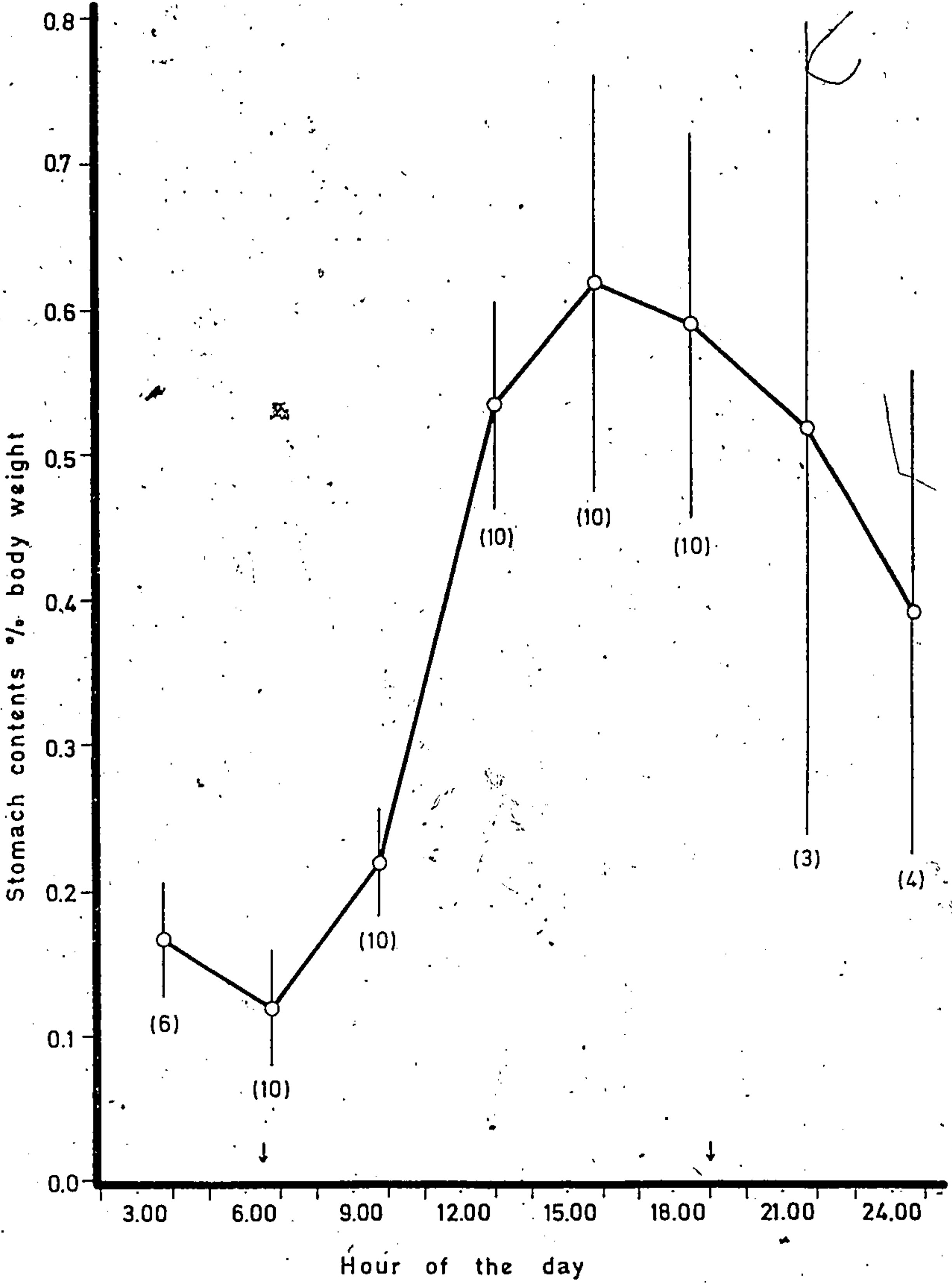

August 20
Stomach contents % body weight
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
(10)
(10)
(10)
(10)
(10)
(10)
(10)
(10)
3.00
6.00
9.00
12.00
15.00
18.00
21.00
24.00
Hour of the day

Figure 3-6. Mean stomach content levels of Yearling Perch by time of day for September 18, 1974. Mean stomach contents (as percent body weight), standard error of the mean and sample size (n) shown.

↓ Sunrise, ↓ Sunset

September 18



estimated ration 1.48% body weight, field digestion rate .089% body weight per hour; August 20, estimated ration 4.31% body weight, digestion rate .223% body weight per hour; September 18, estimated ration .93% body weight, digestion rate .044% body weight per hour.

Tarverdiyeva (1972) reported that the field digestive rate of georgian cod was 0.64% body weight per hour while that of the patagonian toothfish was 0.16% body weight per hour. Chikova (1970) estimated the rate of field digestion of a 4 year old perch to be 0.12% body weight per hour. Both changes in temperature and changes in size of fish influence digestion rate (Brett, 1970; Noble, 1973) and it is possible that a combination of both factors was largely responsible for the observed variation in field digestion rate. The extremely low estimates of field digestive rate for June 11, July 23, and September 18, could also be artifacts of unrepresentitive sampling of the feeding fish. If field digestive rate was underestimated, ration would also be underestimated. This problem will be commented on further in Chapter 5.

The observed daily rations are within the range of values reported for the rations of wild fish by a number of authors (1-4% body weight per day). Keast and Welsh (1968) estimated the daily ration of yearling perch in Lake Opinicon in June to be 2.0% body weight per day, a value similar to the estimated ration in June for yearling perch in the present study, while rations of other fishes in June were 4% body weight per day for rock bass, 2.6% body weight per day for pumpkinseed and 2.5% body weight per day for bluegill. Seaburg and Moyle (1964) estimated the rations of bluegill, pumpkinseed and crappie as 1-2% body weight per day averaged over the entire summer. Chikova (1970) noted high levels of food consumption by fourth year perch and estimated the daily ration for August as 3.1% body weight per day. Jerierska (1974) found that yearling perch would consume from 4 to 8% body weight per day and that both ration and growth were greater with fish fed fish rather than invertebrates.

The estimated rations of this Chapter when converted to their caloric equivalents are utilized in an overall energy budget in Chapter 5.

CHAPTER 4 GROWTH AND BODY COMPOSITION OF THE YEARLING PERCH

Introduction

Growth may be measured in terms of change in length, weight, nitrogen content or energy level depending upon the objectives of the study in question. Ricker (1975) demonstrated that the instantaneous rate of change in length may be equated to the instantaneous rate of change in weight through the use of a constant 'b' derived from the length - weight relationships of the fish. Analysis of growth by changes in length or weight alone, although relatively simple, is limited in that it gives no insight into changes in the composition of the fish.

Gerking (1962, 1971) and others (Pandian 1967a, 1967b; Birkett, 1969) have considered that deposition of nitrogen in tissue, which is equated to increase in body protein, is the best index of growth. Protein level within a species of fish, expressed as % wet weight, remains relatively constant although variations of 15-18% may occur between species (Hamoir, 1955). Lipids on the other hand may be considered as only temporary energy reserves and are subject to large seasonal variation (Gerking, 1955).

In the bioenergetic scheme of Davis and Warren (1968), growth represents the deposition by the fish of that energy which is in excess of energy required for metabolism and energy which is unavailable to the fish (fecal loss and nitrogenous excretion). Energy or caloric content has been employed by Mann (1965) and Warren and Davis (1968) to assess growth and metabolism. Nimii and Beamish (1974) in an examination of growth of the large-mouth bass found that the bioenergetic or energy based approach was most useful in describing growth.

Throughout this study, lengths of yearling perch were measured. In addition, monthly samples of fish were taken for determination of body composition and pollutant concentration. These results provide the basis for an analysis of the growth of yearling yellow perch over the study period and its relation to pollutant accumulation.

Materials and Methods.

Collection of Fish;

From June through September, fish were collected by beach seine from the beaches at the upstream ends of Kettle and Upper Duck Islands for both tagging and analysis. An additional sample of yearling perch were collected by gill net from Kettle Island Bay in May, 1975. Fork and total length of the fish (Hubbs and Lagler, 1964) were measured and the fish tagged with a Floy fingerling tag. Scale samples were taken from the perch during the tagging program, pressed between acetate slides and aged (Jobes, 1952).

A sample of 10 fish was taken from June through September, 1974, for body composition analysis. The perch were held for 24 hours in food free tanks (supplied with Ottawa River water) before being killed by a blow to the head. The fish were blotted dry, total and fork lengths measured, scales removed for aging, and weighed. The fish were then individually tagged and frozen (-20°C) for subsequent analysis.

Body Analysis;

Frozen fish were placed in preweighed plastic trays and freeze-dried for 48 hours in a VerTis lyopholyzer. Fish were then weighed and dry weight and moisture content determined. The fish were then ground to a homogenous powder in a micro-mill (Tekmar Company, Model A-10), the powder was then freeze dried for an additional 24 hours, placed in air tight vials and frozen (-20°C).

Frozen samples were allowed to equilibrate to room temperature in a dessicator. Three determinations were made of ash and caloric content of each fish tissue sample using the methods given in Chapter 2.

Lipid was estimated gravimetrically after extraction of fish tissue samples with chloroform-methanol-water following the procedures of Bligh and Dyer (1959). The chloroform (lipid) extract was dried under nitrogen, allowed to equilibrate to laboratory conditions and weighed. The lipid sample was redissolved in hexane for pesticide analysis (Norstrom and Peter, 1972).

Remaining tissue was analyzed for total and inorganic mercury, (if sufficient tissue was present) by a modified Magos method (Norstrom and Peter, 1972).

Condition factor was calculated by the formula (Weatherly, 1972);

$$K = 100 \times \text{wet weight (g)} / \text{total length (cm)}^3$$

Total calories per fish were determined by the formula;

$$TCAL = \text{dry weight (g)} \times \text{cal/g (dry wt.) (of the individual fish)}$$

Statistical Analysis;

All data were compiled on computer cards and analyzed using the SPSS subprograms BREAKDOWN, T-TEST, ONEWAY (oneway analysis of variance) and REGRESSION (both simple and multiple regressions) (Nye *et al.*, 1975). Analysis of covariance of length-weight relationships of the yearling perch was performed using the program FP88A at the National Research Council.

Results and Discussion.

The lengths of a total of 494 yearling perch were recorded from June through September, 1974. Thirty-eight of these were in the monthly samples for body composition analysis. (Two of the ten fish taken in the September body composition sample proved to be 2+ fish, rather than yearlings. They were excluded from analysis.) In the tagging program, a total of 408 fish were captured, tagged and measured; 48 fish were recaptured at least once: (As above fish found to be older than yearlings were not included in analysis.) No significant difference was found in the mean lengths of yearling perch caught on the same day at the upstream ends of Kettle and Upper Duck Islands ($p \leq 0.01$; Student's t) and the samples were combined in subsequent analysis. Table 4-1 gives the mean lengths of all yearling perch caught from June 1974 to May 1975 (tag recaptures excluded).

No interchange was observed between yearling perch on the upstream end of Kettle Island and those on the upstream end of Upper Duck Island. One hundred and forty-six perch were tagged at Kettle Island and all fish recaptured at this site (15) were tagged at the same site; similarly 262 fish were tagged at the head of Upper Duck Island and all fish recaptured (33) at this site had been tagged there.

Length - Weight Relationships;

Fork length of yearling perch was related to total length of the perch by the following expression:

$$TL\ (cm) = 0.381 + 1.104\ FL\ (cm)$$

$$\text{Standard Error } (b) = 0.003;\ r = .998;\ n = 454 \qquad (4\text{-}1)$$

where TL is total length of fish, FL is fork length of fish. In all expressions relating length and other variables, fork length shall be used as it had a consistently better correlation to other variables than did total length.

The relation of length of fish to fish weight, both dry and wet weights respectively, of yearling perch used in body analysis was:

$$\log WW\ (g) = -2.018 + 3.084 \log FL\ (cm)$$

$$\text{standard error } (b) = 0.062;\ r = 0.992;\ n = 38 \qquad (4\text{-}2)$$

where WW is wet weight of fish, FL as above.

Table 4-1

Lengths of Yearling Perch, 1974-1975

Date	Day of 1974	N	Mean Fork Length (cm)	S. E. of Mean
June 3, 1974	154	13	7.469	.191
June 4, 1974	155	4	7.375	.240
June 14, 1975	165	15	7.660	.117
June 28, 1975	179	10	8.180	.223
June 29, 1975	210	10	9.280	.200
August 1, 1975	212	28	9.332	.154
August 2, 1975	213	14	9.121	.222
August 13, 1975	224	12	9.975	.194
August 19, 1975	231	58	10.115	.090
August 22, 1975	234	10	10.030	.169
August 28, 1975	240	54	10.596	.087
September 5, 1975	247	140	10.655	.061
September 12, 1975	254	52	10.844	.090
September 13, 1975	255	16	11.025	.209
September 26, 1975	270	8	11.487	.201
May 15, 1975	501	16	10.569	.099

$$\log DW\ (g) = -2.958 + 3.438 \log FL\ (cm)$$

$$\text{standard error } (b) = 0.084;\ r = 0.987;\ n = 38 \qquad (4\text{-}3)$$

where DW is dry weight of fish, FL as above. Comparison of length-weight regressions based on individual monthly samples with the overall length-weight regression based on the combined data for all months by an analysis of covariance (Snedecor, 1956), revealed no significant difference between regressions ($p \leq 0.01$). Thus the overall regression equations, 4-2 and 4-3, are used subsequently in describing all yearling perch from June through September.

The coefficient 'b' of equation, 4-2, is nearly 3.0. This indicates that throughout the observed growth stanza the yearling perch were growing isometrically (Tesch, 1968).

Changes in Body Composition;

Table 4-2 presents the results of ash, moisture, lipid, caloric and mercury analysis of yearling yellow perch from June through September, 1974. While significant differences were found between samples in those criteria which reflect growth of the fish over the season, length, weight and total calories per fish, the body composition and mercury contamination of the yearling perch remained relatively constant.

Significant differences in moisture content were observed between the June 28 sample (76.75% moisture) and the July 29 sample (74.86% moisture) ($p \leq 0.01$) and the

Table 4-2

Body Composition of Yearling Yellow Perch for 1974

Day (killed)	N	Fork Length (cm)	Total Length (cm)	Wet Weight (g)	Dry Weight (g)	Moisture Content (% Dry Wt)	Ash Content (% Dry Wt)	Lipid Content (% Dry Wt)	Condition Factor+	Cal/g (Dry Wt)	Cal/g (Ash-Free) (Dry Wt)	Total Cal/Fish	Total Mercury 1x10^{-9} g/g (Dry Wt)	Inorganic Mercury 1x10^{-9} g/g (Dry Wt)	Organic Mercury 1x10^{-9} g/g (Dry Wt)
June 28 1974 (179)	10	8.81(1) ± .22	8.65 ± .24	6.40 ± .54	1.508 ±.145	76.75 ± .46	18.24 ± .33	10.73 ± .96	.970 ± .019	4,679 ± 73	5,727 ± 89	7,106 ± 747	590.84 ± 30.34	187.68 ± 6.86	415.35 ± 57.49
July 29 1974 (210)	10	9.28** ±.20	9.80** ±.19	9.59** ±.52	2.416** ±.145	74.86** ± .31	17.92 ± .47	12.42 ± .77	1.010 ± .017	4,688 ± 68	5,710 ± 82	11,367** ± 764	596.59 ± 23.20	161.64 ± 13.61	435.00 ± 16.95
August 22 1974 (234)	10	10.03** ± .17	10.58** ± .18	12.01** ± .66	3.169** ±.197	73.69* ± .33	18.63 ± .37	14.12 ± .90	1.005 ±.012	4,890* ± 66	6,007* ± 69	15,489** ± 968	650.29 ± 44.67	172.83 ± 9.39	477.46 ± 44.04
September 26 1974 (270)	8	11.49** ± .23	12.03** ± .23	18.34** ±1.23	4.807** ±.362	73.88 ± .29	18.65 ± .44	13.21 ± .83	1.044 ±.015	4,714 ± 80	5,855 ± 114	23,038** ±2,002	502.86* ±36.93	119.01** ± 11.31	382.55 ± 30.67
Total	38	9.65** ±.22	10.17** ± .22	11.23** ± .78	2.879** ±.217	74.84** ± .27	18.34 ± .20	12.59* ± .47	1.085* ±.009	4,754 ± 37	5,823 ± 47	13,787** ±1,077	589.48 ±18.57	158.64** ± 6.99	432.17 ± 18.49

+ Condition Factor = Wet Weight (g) x 100/(Total Length (cm))^3

(1) - Mean and standard error of mean given.

** $p \leq .01$ in either one way analysis of variance or t-test between category value for time interval and category value for preceding time interval.

* $p \leq .05$ " " "

July sample and the August 22 sample (73.69% moisture) ($p \leq 0.05$). Although overall variation in moisture content for all dates was statistically significant ($p \leq 0.05$), actual changes in moisture content were small (73.69 - 76.75% wet weight) and the biological significance of these differences may be minimal.

The ash fraction of the yearling perch was constant throughout the study period (18.34% dry weight) with no significant variation observed between samples.

No significant difference was observed between sample dates with respect to either lipid content or condition factor. The overall variation in both lipid content and condition factor was significant ($p \leq 0.05$), with lowest mean lipid content (10.73% dry wt.) seen in June and highest mean lipid content (14.12% dry wt.) seen in August.

Caloric content of the yearling perch remained constant. Although a significant difference was observed in caloric content between July and August samples, overall variation was not significant. The mean caloric content of the yearling perch was 4,754 cal/g (dry wt.) and 5,823 cal/g (ash free dry wt.) respectively.

While there was no significant variation in the concentration of total mercury in the yearling perch over all sample dates, a significant decrease ($p \leq 0.05$) in the concentration of total mercury was observed between August (650.29 ppb) and September (502.86 ppb). This decrease was largely effected by a highly significant decrease in the concentration of inorganic mercury in the yearling perch observed between August (172.83 ppb) and September (119.01 ppb). Overall variation in concentration of inorganic mercury was significant ($p \leq 0.01$) but no significant variation in the concentration of organic mercury was observed. The ratio of organic mercury to inorganic mercury in the yearling perch thus increased from 2.21:1.0 in June to 3.21:1.0 in September. The change in the concentration of inorganic mercury from August to September would appear to correlate with the observed increase in the contribution of fish to the diet of yearling perch over this period (Chapter 3).

A high correlation (negative) was observed between lipid content and moisture content ($r = -0.708$; $p \leq 0.01$). Similarly, a high correlation was observed between caloric content (cal/g dry wt.) and lipid content ($r = 0.779$; $p \leq 0.01$). Thus changes in caloric content were effected principally through changes in lipid content. These findings are in accord with reports of Gerking (1955), Love (1970) and Nimii and Beamish (1975).

Pearse (1925) reported a considerable variation in the fat content of yellow perch with season, with low values observed in the spring, (1-2% fat on a wet weight basis), highest levels seen in late summer (4-5% fat wet weight) and intermediate levels in the fall (2-3% fat wet weight). Newsome and Leduc (1975) reported a similar trend in the seasonal variation in fat content of immature yellow perch in stunted populations in two Laurentian lakes. Jerierska (1974) found that yellow perch caught in March had a lower caloric value than perch caught in September (5.35 kcal/g ash free versus 6.27 kcal/g ash free) and considered this indicative of a lower lipid content in the March fish. Wissing (1969) reported changes in the caloric content of underyearling white bass in Lake Mendota of 500 cal/g dry wt. (11% original value) between August and September. Kelso (1973) noted an increase in the energy content with season of walleye in Blue Lake, Manitoba, of about 12% of the total energy, which coincided with seasonal growth patterns. Gerking (1955) found little difference in the fat content of summer and fall bluegill. The consistency of the body composition and caloric content of yearling perch observed in the present study is thus contrary to the general observation that in wild fish, caloric and lipid content reach maximum values in late summer, presumably in preparation for overwintering. Many of the previously mentioned studies however were conducted on older, mature fish where complications of lipid deposition in relation to reproductive cycles could mask purely seasonal trends. Those studies of immature fish have been of either warm-water fish, white bass (Wissing, 1969), which may not feed overwinter or of perch which were stunted and thus likely food limited (Newsome and Leduc, 1975). The perch population investigated in the present study showed good growth relative to perch of other areas (Stobo, 1971) and yellow perch do feed considerably overwinter (Moffet and Hunt, 1945). The yearling perch of the present study had relatively high lipid content (>10% dry wt.) at all times whereas those of Newsome and Leduc (1975) had a relatively low lipid content (5-6% dry wt.) in June which increased with season. Thus Ottawa River yearling perch may not exhibit marked seasonal variation in lipid content, caloric content or condition factor because they maintain a relatively high lipid and caloric content and a high condition factor throughout the year.

Growth;

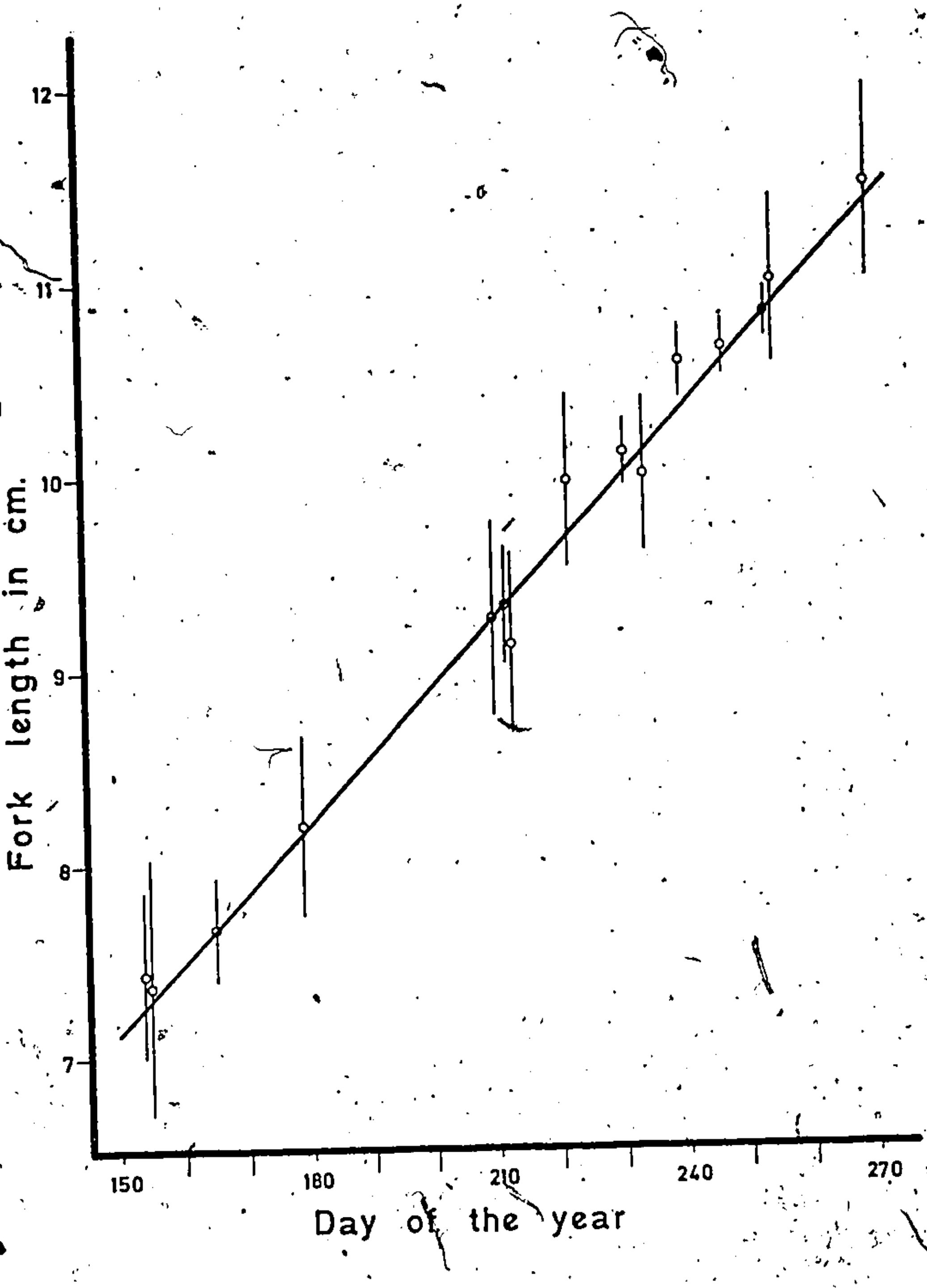
The relationship between length of the yearling perch and day of year from day 153 (June 3) to day 270 (September 26) 1974 is shown in Figure 5-1 (tag recaptures were excluded as tagging may affect the growth of the fish (Tesch, 1968)). As the sample of yearling perch caught May 15, 1975 were of similar size to those caught in late September it is assumed that growth beyond day 270 was negligible. The relation between change in length of the perch and day of year was linear (Test of lineararity, Nye, *et al.*, 1975; F = 0.81, df 1:14; ns.), with the yearling perch growing at a rate of 0.036 cm per day. The relation of growth in length to day of year was thus:

$$\text{Fork length (cm)} = 1.712 + 0.036\ \text{day}$$

$$(153 \le \text{day} \ge 270)\quad SE(b) = 0.001;\ r = .806;\ n = 434 \qquad (4\text{-}4)$$

Figure 4-1. Fork Length of Yearling Perch by day of year from day 154 (June 2) to day 270 (September 27), 1974.
Mean and 95% confidence limits of mean Fork Length shown for individual lines.
Calculated regression of Fork Length versus day given by Equation 4-4 in text.

$$\text{Fork Length (cm)} = 1.712 + 0.36 \text{ day}$$


Fork length in cm.
12
11
10
9
8
7
150
180
210
240
270
Day of the year

Through equations 4-2, 4-3 and 4-4, the weight and growth rate (g per day) of an average yearling yellow perch for any day during this period may be estimated in terms of dry or wet weight by the equations given below:

$$\mathrm{WW}\ (\mathrm{g}) = 9.6 \times 10^{-3}(1.712 + 0.036\ \mathrm{day})^{3.084} \quad (4\text{-}5)$$

$$\frac{d\ \mathrm{WW}}{dt}\ (\mathrm{g/day}) = 1.07 \times 10^{-3}(1{,}712 + 0.036\ \mathrm{day})^{2.084} \quad (4\text{-}5a)$$

$$\mathrm{DW}\ (\mathrm{g}) = 1.10 \times 10^{-3}(1{,}712 + 0.036\ \mathrm{day})^{3.438} \quad (4\text{-}6)$$

$$\frac{d\ \mathrm{DW}}{dt}\ (\mathrm{g/day}) = 1.36 \times 10^{-4}(1{,}712 + 0.036\ \mathrm{day})^{2.438} \quad (4\text{-}6a)$$

Ney and Smith (1975) have reported a similar linear relationship between growth in length and day of year (during the growth period) for underyearling yellow perch in the Red Lakes, Minnesota.

The growth of yearling yellow perch in the Ottawa River Study Area, 1974, was very similar to that reported by Stobo (1971) for the growth of yearling yellow perch at Kettle Island, 1968. Stobo reports growth of 42 mm for yearling perch, from 72.5 to 114.5 mm fork length; present data using a growth season of from day 154 to day 270 gives growth of 41 mm fork length, from 73 to 114 mm fork length. The close agreement of growth of yearling yellow perch between years indicates a consistent rate of growth of Ottawa River perch and suggests that present results may be generalized to years other than that studied.

Growth of perch in the Ottawa River is similar to that of other lakes and streams in North America (Stobo, 1971).

The data on growth of yearling perch in this Chapter is employed in the calculation of an energy budget (Chapter 5).

CHAPTER 5 ENERGY TRANSFORMATION AND POLLUTANT BIOACCUMULATION

In the present study, detailed information has been compiled on feeding, growth, energy content and pollutant levels in yearling perch during a period of rapid summer growth. Seasonal variation in the caloric content of food items common in the diet of perch, has been determined throughout the study period. Similarly, growth, body composition and pollutant levels of the yearling perch have been determined throughout the summer.

From these data, estimates of daily ration (consumption) have been derived, the first based on the conversion of estimated daily ration from stomach contents (Chapter 3), to its caloric equivalents (Chapter 2); the second based on the utilization of expressions relating growth and metabolism of fish to consumption (Winberg, 1956; Norstrom *et al.*, 1976) in conjunction with the observed growth (Chapter 4). An energy budget has then been constructed from this data to give the limits of total ration of an average yearling yellow perch over the study period. From this energy budget, and the observed accumulation of organic mercury in the perch (Chapter 4), the process of bioaccumulation of organic mercury is examined using the model of Norstrom *et al.*,(1976), especially with regard to distinguishing the potential contribution of both food and water as sources for uptake of organic mercury.

Caloric Value of Daily Ration Estimated from Stomach Contents.

Estimated daily ration, expressed as percent body weight of the yearling perch on each sample date (Chapter 3; June 11, 2.03% body weight; July 23, 1.45% body weight; August 20, 4.31% body weight; September 18, .93% body weight) was multiplied by the dry weight of a yearling yellow perch on that date as predicted by equation 4-6 (Chapter 4) to give the estimated daily ration (g dry weight/day).

The estimated daily ration for that date was then allocated proportionally to individual food items on the basis of their contribution to the overall diet of that day (Chapter 3, Table 3-1). Only items over 5% volume of the diet on an individual day were used in individual calculation of caloric contribution; all items less than 5% volume of the diet and miscellaneous items were lumped in the category 'other'. The weights of individual food items multiplied by the caloric value of that item gave the number of calories contributed to the daily ration. Whenever possible caloric values were assigned to individual food items of the basis of the data compiled in Chapter 2 (*Amphipoda* represent the mean of monthly values of *Gammarus* and *Hyalella;* the July *Chironomidae* value was used for June-July rations, the August value for August-September rations). If the caloric value of the diet item was not included in Chapter 2, caloric values were taken from literature sources (Cummins and Wuycheck, 1971; Schindler *et al.*, 1971; Caspers, 1975). The 'other' category was assigned a caloric value of 4,754 cal/g dry wt., the mean value of the yellow perch over the study period. Summation of the caloric contribution of all individual food items gave the total number of calories in the daily ration as estimated from stomach contents. Table 5-1 gives the caloric equivalents of estimated daily ration for each sample date.

Caloric Value of Ration as Estimated from Metabolism and Observed Growth.

Ration may also be estimated from predicted metabolism and observed growth (Chapter 3). In the present study, ration has been estimated from metabolism and observed growth utilizing the equations of Norstrom *et al.*, (1976) and Winberg (1956).

In the bioenergetic formulations of Norstrom *et al.*, (1976), ration is predicted by the following equation:

$$R = \frac{1}{e(f)} \left(\alpha_{1r} W^{.81} + \beta G + G\right) \qquad (5\text{-}1)$$

where R is the energy equivalent of the ingested ration (cal), e(f) is the assimilation efficiency coefficient, W is the wet weight of the fish (g), α_{1r} a temperature dependent term which gives low routine metabolic level at any given temperature (kcal/wk x $g^{-.81}$), β a constant relating growth to the energy associated with growth and G is growth (cal). Using a β value of 1.0 (Norstrom *et al.*,

Table 5-1a

Caloric Value of Ration as Estimated from Stomach Contents on June 11, 1974 (162)+

Dry Weight of Perch = 1.002 g

Estimated Ration, 2.03% DW = 20.24 mg

	Volume Proportion of Diet (%)	Weight of Ration (mg)	Caloric Value of Item (cal/mg dry wt.)	Ingested Calories
Amphipoda	13.0	2.63	3.908	10.28
Chironomidae	12.8	2.59	4.176	10.82
Ephemeroptera	11.3	2.29	5.469(1)	12.52
Trichoptera	5.5	1.11	4.999(1)	5.55
Plecoptera	8.1	1.64	5.263(3)	8.63
Cladocera	13.1	2.65	4.805(2)	12.73
Copepoda	25.3	5.12	5.550(2)	28.42
Other	10.9	2.21	4.754	10.51
Total		20.24		99.45

Table 5-1b

Caloric Value of Ration as Estimated from Stomach Contents on July 23, 1974 (204)$^+$

Dry Weight of Perch = 2.1445 g

Estimated Ration, 1.48% DW = 31.74 mg

	Volume Proportion of Diet (%)	Weight of Ration (mg)	Caloric Value of Item (cal/mg dry wt.)	Ingested Calories
Amphipoda	8.9	2.82	3.964	11.18
Chironomidae	45.9	14.57	4.176	60.84
Ephemeroptera	26.2	8.32	5.469	45.50
Other	19.0	6.03	4.754	28.67
Total		31.74		146.19

Table 5-1c

Caloric Value of Ration as Estimated from Stomach Contents on August 20, 1974 (232)+

Dry Weight of Perch = 3.0826 g

Estimated Ration, 4.31% DW = 132.70 mg

	Volume Proportion of Diet (%)	Weight of Ration (mg)	Caloric Value of Item (cal/mg dry wt.)	Ingested Calories
Amphipoda	9.1	12.08	4.122	49.79
Chironomidae	12.5	16.59	4.737	78.59
Ephemeroptera	6.4	8.49	5.469(1)	46.43
Fish	61.7	81.88	5.858	479.65
Other	10.3	13.66	4.754	64.94
Total		132.70		719.40

Table 5-1d

Caloric Value of Ration as Estimated from Stomach Contents on September 16, 1974 (261)$^{+}$

Dry Weight of Perch = 4.328 g

Estimated Ration, .929% DW = 40.21 mg

	Volume Proportion of Diet (%)	Weight of Ration (mg)	Caloric Value of Item (cal/mg dry wt.)	Ingested Calories
Amphipoda	14.0	5.63	4.220	23.76
Chironomidae	48.5	19.50	4.737	92.37
Ephemeroptera	6.6	2.65	5.469$^{(1)}$	14.49
Trichoptera	9.5	3.82	4.999$^{(1)}$	19.10
Fish	12.1	4.87	5.858	28.53
Other	9.3	3.74	4.754	17.78
Total				

Mean Caloric Value of Food Items for All Months is 5.163 cal/mg

[+] Day of 375 of 1974

(1) Cummins and Wuycheck (1971)

(2) Schindler *et al.*, (1971)

(3) Caspers (1975)

1976) ie., the energy cost of deposition of tissue is equivalent to the energy content of the tissue deposited, and an assimilation efficiency coefficient of 0.8 (Winberg, 1956), the expression 5-1 reduces to:

$$R = 1.25 \left({}_{1r} W^{.81} + 2G \right) \qquad (5\text{-}1a)$$

In the bioenergetic formulations of Winberg (1956), routine metabolic rate, Winberg 1, and active metabolism, Winberg 2, are estimated by the following equations:

$$R = \frac{1}{e(f)} (M + G) \qquad \text{Winberg 1} \qquad (5\text{-}2)$$

$$R = \frac{1}{e(f)} (2M + G) \qquad \text{Winberg 2} \qquad (5\text{-}2a)$$

where R is the energy equivalent of the ingested ration (cal), e(f) the assimilation efficiency coefficient, G is growth (cal) and M is the routine metabolic level of the fish (cal). Routine metabolism, M, of the fish is given by the equation:

$$M = Q \times q_{ox} \times t \qquad (5\text{-}2b)$$

with Q the oxygen consumption of the fish (ml O_2/hr), q_{ox} a coefficient for conversion of oxygen consumption (ml/hr) to calories and t the duration of the interval in question (hr). A q_{ox} of 5.0 cal/ml O_2 (Winberg, 1956) is used in present calculations. Q is determined by the equation:

$$Q = 0.3W^{0.8}/q_T \qquad (5\text{-}2c)$$

with W the wet weight of the fish (g) and q_T, a temperature normalization coefficient to correct estimated oxygen consumption at the interval temperature to estimated consumption at 20^0C (Winberg, 1956). Using an e(f) of 0.8 (Winberg, 1956) the term $\frac{1}{e(f)}$ is equal to 1.25.

If ration is estimated on a daily basis, W is taken as the weight of the fish on that day as predicted by equation 4-5; while if ration is estimated over a longer period, W was taken as the weight predicted by equation 4-5 for the middle of that interval. Similarly if growth, G, is estimated on a daily basis, it is calculated as the product of daily growth in dry weight as predicted by equation 4-6a and the mean caloric value of the yearling perch over the study period (4,754 cal/g dry wt.). Over a longer interval, G is estimated as the difference between predicted dry weights of an average yearling perch at the beginning and end of the interval (equation 4-6), multiplied by the mean caloric value of the perch.

Temperature data used in the present study were supplied by Dr. D. Mortimer (National Research Council, Ottawa) and represent a composite of temperature records taken by a number of personnel from the Ottawa River Study Area over the summer of 1974.

Table 5-2 compares ration as estimated from stomach contents (Tables 5-1) with ration as estimated from the equations of Winberg (1956) and those of Norstrom *et al.*, (1976). It is apparent that only for the

2

Table 5-2

Comparison of Estimates of Ration of Yearling Yellow Perch on Four Dates of 1974(1)

Day	Water Temp. (°C)	Wet Weight of Perch (g)	Growth (day) (cal)	Daily Ration Estimated by			
				Winberg 1 (cal)	Winberg 2 (cal)	Norstrom *et al.* 1976 (cal)	Stomach Contents (cal)
June 11	14	4.8842	89.14	203.40	295.38	313.19	99.45
July 23	20	8.5795	139.15	425.11	676.28	551.55	146.19
August 20	24	11.8799	179.99	679.50	1,134.01	781.38	719.40
September 18	16	16.1069	229.01	576.99	867.71	843.93	196.03

(1) Details of calculation of ration given in text.

August 20 sample is ration as estimated from stomach contents within the limits of Winberg 1 and Winberg 2. On all other dates, ration as estimated from stomach contents is far below that predicted by any of the metabolic estimations; in fact, assimilation efficiencies of 0.90, 0.95 and 1.17 are required to account for growth alone on days June 11, July 23 and September 18 respectively.

It is obvious that ration as estimated from stomach contents on these dates must underestimate actual consumption by a considerable amount. The basis of these underestimates was likely unrepresentitive sampling of the yearling perch. Yellow perch tend to feed in the littoral zone than move to deeper water when satiated (Hassler and Bardach, 1949), similar behavior has been observed for brown bullheads, walleye and sauger in the Ottawa River (P. Rubec, personal communication). Beach seining would thus tend to sample feeding fish with less than full stomachs while fish which were satiated would not be vulnerable to sampling and daily ration would consequently be underestimated. Additionally, this non-random sampling of the feeding yearling perch could lead to an underestimation of field digestive rate which would further depress estimated daily ration. The net result of these factors is that in the present study, ration as estimated from stomach contents underestimated ration.

Estimates of daily ration based on stomach contents of wild fish have varied from estimates of 1% to more than 4% body weight per day (Seaburg and Moyle, 1964; Keast and Welsh, 1968; Brio, 1969; Chikova, 1970; Tarverdiyeva, 1972), thus any individual estimate may be 'reasonable'. In relatively few of the published accounts of the field energetics of aquatic species has ration been estimated from gut contents of field organisms. In those studies in which ration has been estimated from gut contents, Wissing (1969) with underyearling white bass found that his estimated ration was sufficient to account for all aspects of the energy budget while Healy (1972) found that his estimates of ration of sand gobbies based on stomach contents were inadequate to account for growth and metabolism during periods of rapid somatic growth during the summer. Healy (1972) suggested that these imbalances at low rations are general and that fish on restricted rations are able to shunt more energy into growth than would be predicted on the basis of metabolism as predicted from studies of standard oxygen consumption. Solomon and Braefield (1972) in a detailed long term laboratory study of the energetics of yellow perch concluded that total metabolism of perch on restricted rations above maintenance was between the limits predicted by Winberg 1 and Winberg 2. Yearling perch in the Ottawa River may be considered to be on a restricted ration above maintenance and Winberg 1 and Winberg 2 have thus been considered the limits of ration for yellow perch in the present study.

Present methods of determination of feeding periodicity and daily ration of wild fish have changed little from those of Bajkov (1935). The large variation observed among individual fish caught at the same time (Jenkins and Green, 1974) and difficulties in collecting a random sample from the field are such that the data obtained using present techniques are often inadequate for the detailed analysis required in a bioenergetics approach. Two recent techniques do however show considerable promise in resolving this problem. Swenson and Smith (1973) with walleye and sauger determined the weight of food items at time of ingestion using condition of the food item and experimentally determined digestive rates. From the average amount of food ingested by a fish over the whole day, they estimated daily ration of an average fish. This method may however be limited in application to pisciverous fish which consume large discrete meals and meal components but may be of limited utility in determining rations of planktiverous or bethophageous fish which consume large numbers of small and varied prey items. A second approach is that of Kolehmainen (1974), in which daily values of intake of a trace contaminant (in this case ^{137}Cs, which is accumulated only through the food chain) by bluegill sunfish was determined. As the level of contamination of the food of the bluegill was known it was possible to estimate daily ration of the fish. It is suggested that a study of this type in which the transfer of both a trace contaminant and of energy (calories) were monitored in the same field population would be of considerable value.

Table 5-3 presents estimated rations of an average yearling yellow perch in the Ottawa River Study Area from day 154 to day 270, 1974. Growth over the period was 18.0 kcal; estimated rations were 53.5 kcal at the level of ration predicted by Winberg 1, 84.5 kcal at the level of ration predicted by Winberg 2 and 69.6 kcal at the level of ration predicted by Norstrom *et al.*, (1976). Estimated growth conversion efficiencies are 33.7% at the level of ration predicted by Winberg 1, 21.3% at the level of ration predicted by Winberg 2 and 25.9% at the level of ration predicted by Norstrom *et al.* Wissing (1969) reports growth conversion efficiencies of 27.9% and 37.3% for underyearling white bass in Lake Mendota in the summers of 1967 and 1968 respectively. Ivlev (1945) and Winberg (1956) indicate that food conversion efficiencies of this order (20 - 40%) may be expected in young rapidly growing fish.

As the concentration of organic mercury in the perch remained constant over the growth period (432.17 x 10^{-9} g/g dry wt. - Table 4-2) net accumulation of these substances is the product of growth (3.79 g dry wt.) and the above concentration. An average yearling perch thus accumulated 1.638 x 10^{-6} g of organic mercury, from day 154 to day 270.

The amount of organic mercury cleared from a yellow perch may be determined by the equation (Norstrom *et al.*, 1976):

$$\Delta P = -k_{cl}\ P\ W^{\zeta} \qquad (5\text{-}3)$$

where, ΔP, is the amount of pollutant eliminated, k_{cl} a coefficient of clearance, P, the amount of pollutant in the fish (body burden), W, the weight of the fish and ζ an exponent of body weight for clearance. Using a k_{cl} of .029 $g^{-\zeta}$ day^{-1} for organic mercury from fish (de Freitas *et al.*, 1975); determining P as the product of the dry weight of a yearling perch at the middle of each weekly interval (Table 5-3) as predicted by Equation 4-6 and the mean concentration of organic mercury in the perch (4.3217×10^{-7} g/g); employing W is the wet weight (g) of a yearling perch for each given for each interval in Table 5-3, and employing a ζ value of -0.58 (Sharpe *et al.*, 1975) the amount of organic mercury cleared from an average yearling perch from day 154 to day 270, 1974 was 0.832×10^{-6} g.

The total uptake of organic mercury by an average yearling perch in the Ottawa River is thus the sum of observed accumulation (1.638×10^{-6} g) and estimated clearance (0.832×10^{-6} g), or 2.470×10^{-6} g of organic mercury.

If it is assumed that uptake of organic mercury occurred solely from food contamination, the concentration of organic mercury in the diet required to effect the

Table 5-3

Estimated Ration of Yearling Perch (Day 154 - 270, 1974)

Period (days)	Mean Temperature (^{o}C)	Wet* Weight (g)	Growth (cal)	Ration as Estimated by: Winberg 1 (cal)	Winberg 2 (cal)	Norstrom *et al.*, (1976) (cal)
153-161	13^{o}C	4.5337	647.63	1,355.55	1,901.56	2,129.36
161-169	15^{o}C	5.0294	739.68	1,655.10	2,385.60	2,542.99
169-177	17^{o}C	5.7190	809.52	1,982.18	2,952.45	2,896.35
177-185	19^{o}C	6.3832	882.90	2,376.88	3,650.13	3,273.49
185-193	20^{o}C	7.0977	959.78	2,710.51	4,221.30	3,622.23
193-201	22^{o}C	7.8644	1,041.18	3,237.71	5,173.95	4,130.96
201-209	23^{o}C	8.5795	1,125.76	3,664.26	5,921.33	4,525.30
209-217	23^{o}C	9.5619	1,214.63	3,979.84	6,441.39	4,902.94
217-225	24^{o}C	10.4966	1,308.01	4,516.70	7,398.28	5,368.48
225-233	24^{o}C	11.4912	1,404.33	4,853.43	7,951.44	5,768.94
233-241	24^{o}C	12.5476	1,506.05	5,206.40	8,530.24	6,189.98
241-249	22^{o}C	13.6677	1,610.92	5,026.54	8,039.42	6,418.14
249-257	21^{o}C	14.8535	1,720.71	5,115.63	8,080.36	6,748.10
257-265	19^{o}C	16.1069	1,834.46	4,962.96	7,632.85	6,842.18
265-270	17^{o}C	17.2607	1,206.46	2,849.75	4,191.43	4,236.09
Total			18,012.02	53,493.44	84,471.73	69,595.53

*Wet weight in middle of period, i.e., in week 153 - 161 - wt. at day 157.

total uptake of organic mercury may be determined from estimated rations. The ration of an average yearling perch from day 154 to day 270, 1974, was 53.5 kcal at the level of metabolism predicted by Winberg 1, 84.5 kcal at the level of metabolism predicted bt Winberg 2 and 69.6 kcal at the level of metabolism predicted by Norstrom *et al.*, (1976) (Table 5-3). At a mean caloric value of 5.163 kcal/g (Table 5-1) the weight of these estimated rations are 10.36 g dry wt., 16.36 g dry wt. and 13.48 g dry wt. at the levels of metabolism predicted by Winberg 1, Winberg 2 and Norstrom *et al.*, (1976), respectively. The concentration of organic mercury required to effect the estimated total uptake may be calculated from the equation:

$$C_{pf} = \frac{\Delta P}{e_{pf}\ R} \qquad (5\text{-}4)$$

where C_{pf} is the concentration of pollutant in the diet, ΔP is the total uptake of pollutant, e_{pf} is the efficiency of assimilation of pollutant from the diet and R the ration ingested. In the present case, using a ΔP of 2.470×10^{-6} g of organic mercury, an e_{pf} for organic mercury of .8 (de Freitas *et al.*, 1974) and the weights of ration given above, the concentration of organic mercury in the diet required to effect the total uptake would be 298×10^{-9} g/g, 187×10^{-9} g/g and 229×10^{-9} g/g at the levels of ration predicted by Winberg 1, Winberg 2 and Norstrom *et al.*, (1976) respectively.

The required concentrations of $187 - 298 \times 10^{-9}$

g/g organic mercury in the diet are greater than the concentration of organic mercury in the diet (33 x 10^{-9} g/g wet weight - approximately 125 x 10^{-9} g/g dry weight) employed by Norstrom *et al.*, (1976) in their model of accumulation of organic mercury by yellow perch in the Ottawa River. Levels of total mercury (inorganic and organic) in benthic invertebrates in the Ottawa River Study (from 100 - 3000 x 10^{-9} g/g wet weight) varied considerably with time and location of collection. A large variation was also observed in the relative contribution of organic mercury to the total mercury in these benthic invertebrates, anywhere from 0 - 60% of total mercury was organic mercury (Ottawa River Project Report #3, 1975).

Conversely if it is assumed that the sole source for uptake of organic mercury was the water, the concentration of organic mercury in the water required for the total uptake may be determined from estimated metabolism and observed growth. Respiratory level (Q') may be determined from Table 5-3 by the equation:

$$Q' = .8R - G \qquad (5\text{-}2)$$

where R is estimated ration (kcal) and G observed growth (kcal) and .8 the assimilation efficiency. Respiratory level was thus 28.4 kcal at the level of metabolism predicted by Winberg 1, 53.2 kcal at the level of metabolism predicted by Winberg 2 and 41.3 kcal at the level of metabolism predicted by Norstrom *et al.* (1976). Respiratory level may be related to the volume of water passing over the gills of the fish, and this volume may then be related to the concentration of pollutant in the water required to effect the estimated total uptake by the equation (Norstrom *et al.*, 1976):

$$C_{pw} = \frac{\Delta P \times e_{ox} \times C_{ox} \times q_{ox}}{e_{pw} \times Q'} \qquad (5\text{-}5)$$

where C_{pw} is the concentration of pollutant in water, ΔP and Q' as defined above, e_{ox} the efficiency of assimilation of oxygen from water by the gills of the fish, e_{pw} is the efficiency of assimilation of pollutant from water by the gills of the fish, q_{ox} the caloric equivalent of oxygen and C_{ox} the concentration of oxygen in the water. Using e_{pw} of 0.12 and an e_{ox} of 0.75 (Norstrom *et al.*, 1976), a q_{ox} of 3.42 (Brodie 1945), a C_{ox} of 9.18×10^{-6} g/g (mean C_{ox} over the period; C_{ox} for given temperature from American Public Health Association 1971), Q' and ΔP as given above the concentrations of organic mercury in the water required to effect the estimated total uptake are 17.07×10^{-12} g/g, 9.267×10^{-12} g/g and 11.74×10^{-12} g/g at the levels of metabolism predicted by Winberg 1, Winberg 2 and Norstrom *et al.*, (1976) respectively. Norstrom *et al.*, (1976) employed a water concentration of organic mercury of 5×10^{-12} g/g in their bioaccumulation model. Norstrom and Brownstein (1973) reported levels of organic mercury in Ottawa River water from $10 - 50 \times 10^{-12}$ g/g in the summer of 1972, but in 1973 using improved analytical techniques were unable to detect organic mercury.

in Ottawa River water.

Thus if either food or water is considered to be the only source for uptake of organic mercury, the concentration of organic mercury in either food or water estimated to be required to account for the total uptake of organic mercury by an average yellow perch over the study period is in excess of apparent levels in the Ottawa River. This strongly suggests that both food and water are important as sources for uptake of organic mercury by the yearling perch.

Table 5-4 gives the amount of uptake of organic mercury from both food and water sources predicted by equations 5-4 and 5-5 respectively at the levels of metabolism predicted by Winberg 1, Winberg 2, and Norstrom *et al.*, (1976) using the same values for concentrations of organic mercury in food (125×10^{-9} g/g dry wt.) and water (5×10^{-12} g/g) as were employed in the model of Norstrom *et al.*, (1976). The close agreement between the estimated uptake of organic mercury derived from observed accumulation and estimated clearance (2.470×10^{-6} g organic mercury) and that uptake which is predicted using the model of Norstrom *et al.*, (1976) based on metabolism and observed growth (2.400×10^{-6} g organic mercury) indicates that the model is realistic and operationally useful in describing the process of pollutant bioaccumulation by perch in the Ottawa River.

Table 5-4

Estimated Uptake of Organic Mercury for an Average Yearling Yellow Perch in the Ottawa River from day 154 - 270, 1974

	Estimated Uptake of Organic Mercury (ΔP, at metabolic level predicted by):		
	Winberg 1	Winberg 2	Norstrom *et al.*, (1976)
Food(1)	1.036×10^{-6}g (58.9%)(3)	1.636×10^{-6}g ((54.7%)	1.348×10^{-6}g (56.2%)
Water(2)	0.724×10^{-6}g (41.1%)	1.356×10^{-6}g (45.3%)	1.052×10^{-6}g (43.8%)
Total	1.760×10^{-6}g	2.992×10^{-6}g	2.400×10^{-6}g

(1) $\Delta P = e_{pf} \times R \times C_{pf}$

$C_{pf} = 125 \times 10^{-9}$ g/g dry wt.

(Details in text) (5-4)

(2) $\Delta P = C_{pw}\ e_{pw}\ Q/e_{ox}\ C_{ox}\ q_{ox}$

$C_{pw} = 5 \times 10^{-12}$ g7g dry wt.

(Details in text) (5-5)

(3) Relative contribution (%) of uptake vector to total uptake of organic mercury at given metabolic level.

In the present study it has not been possible to define the relative contribution of either food or water as vectors for uptake of organic mercury beyond the observation that both routes of uptake in all likelihood contribute significantly to total uptake. Similarly in models of pollutant uptake the relative contribution of food and water as vectors to total uptake is dependent on the expressions employed in describing metabolism and growth (Table 5.4), on the values used as concentrations of pollutant in food and water, and the values of uptake and clearance parameters used in the model (Norstrom *et al.*, 1976). As the concentration of pollutant in both food and water is often relatively poorly defined, an experimental design which would define the relative contribution of food and water as vectors of uptake of pollutant without a precise definition of the concentration of pollutant in either food or water could be of considerable utility in a further elaboration of the process of pollutant accumulation by fish.

The present work and the pollutant bioaccumulation model of Norstrom *et al.*, (1976) does indicate that field studies, laboratory studies and modelling may be integrated to give a realistic description of the process of pollutant bioaccumulation by fish.

CHAPTER 6 SUMMARY

(1) Significant seasonal variation was observed in the caloric content of several invertebrate groups over the summer. These differences amounted to 8% of the minimum caloric value in *Gammarus fasciatus* (3,943 - 4,258 cal/g dry wt.), 19.5% of the minimum caloric value in the amphipod, *Hyalella azteca*, (3,611 - 4,315 cal/g dry wt.), 22.4% of the minimum caloric value in isopods, *Asellus spp* (3,252 - 3,981 cal/g dry wt.) and 12.1% of the minimum caloric value in chironomid larvae, *Chironomidae spp.* (4,176 - 4,737 cal/g dry wt.). In *G. fasciatus* and *Asellus spp.* changes in caloric content were effected through changes in the relative size of the ash fraction with the caloric value of the organic fraction remaining constant, while in *H. azteca* and larvae of *Chironomidae spp.* changes in caloric content were effected through changes both in the relative size of the ash fraction and in the caloric value of the organic fraction.

(2) The yearling perch were diurnal in their feeding activities with mean stomach content levels increasing after sunrise and decreasing after sunset. Benthic invertebrates (*Amphipodae, Chironomidae, Ephemeroptera, Trichoptera* and *Plecoptera*) were the major food resource of the yearling perch throughout the summer. Zooplankton (*Cladocera* and *Copepoda*) were important diet items in June (38.4% volume of the diet), however, while fish

(largely *Hybognathus nuchalis*) comprised the major diet item in August (61.7% volume) and were significant in the September diet (12.1% volume). The observed changes in diet likely reflect changes in both food selection and in food availability. Estimated daily rations, based on stomach content levels were 2.0% body weight/day on June 11, 1.5% body weight/day on July 23, 4.3% body weight/day on August 20 and 0.9% body weight/day on September 18, 1974.

(3) Growth in length of the yearling perch was linear with day of year from day 154 to day 270, 1974 (June 3 to September 26) and given by the equation:

$$FL = 1.712 + 0.036 \text{ day} \qquad (4\text{-}4)$$

in which FL is fork length of the perch (cm) and day, day of year from day 154 to day 270. Growth in weight was given by the equation:

$$WW = 9.6 \times 10^{-3}(1.712 + 0.036 \text{ day})^{3.084} \qquad (4\text{-}5)$$

where WW is the wet weight of the perch (g).

The caloric content of the yearling perch was constant over the summer (4,754 cal/g dry wt.) as was the concentration of organic mercury in the fish (432.17×10^{-9} g/g).

(4) Estimates of ration based on stomach content levels were below those estimates based on growth and predicted metabolism for June 11, July 23 and September 18 samples. This imbalance was likely due to unrepresentitive sampling of the perch population.

From day 154 to day 270, 1974, an average yearling yellow perch in the Ottawa River Study Area increased in caloric content by 18.0 kcal. Estimated total ration for this period is 53.5 kcal at the level of metabolism predicted by Winberg 1 (Winberg 1956), 84.5 kcal at the level of metabolism predicted by Winberg 2 and 69.6 kcal at the level of metabolism predicted by the expressions of Norstrom *et al.*, (1976).

(5) Over this same period total uptake of organic mercury by an average yearling yellow perch was 2.470×10^{-6} g of organic mercury. Both food and water could serve as significant sources of pollutant for the observed accumulation of organic mercury but the extent to which each route contributed to the observed accumulation could not be resolved.

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