Rate of Food Exploitation by Littoral Fishes

by

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Abstract

The relationship between the amount of food consumed by the fish community and that present on the littoral zone of a lake was examined on a daily and annual basis. The method used to determine food consumption included a survey of fish biomass onshore and estimates of field daily ration for each fish group (combination of species and length class). The mean food consumption (0.30 g dry$\cdot$m$^{-2}\cdot$d^{-1}; 1.27 Cal$\cdot$m$^{-2}\cdot$d^{-1}) did not vary significantly during the season. Food types were classified as forage fish, benthic invertebrates, plankton and macrophytes. Macrophytes were, however, excluded from my definition of "potential food" because of their low occurrence in digestive tract content. Benthic invertebrate availability was determined on the basis of food distribution in the sediments and prey size. I estimated 68% of the benthic biomass to be potentially available to fishes. Food availability excluding macrophytes varied from 24.9 to 50.8 g dry$\cdot$m^{-2} (74.5 to 150.3 Cal$\cdot$m^{-2}). The geometric mean exploitation rate of littoral zone food by the fish community foraging there was 0.80% (dry weight) or 1.15% (caloric basis) per day (104% and 150% per year). These rates corresponded closely to P/B ratios of benthic invertebrates reported for the study area and for numerous North American lentic systems. Three possible regulators of fish exploitation rate are considered: time budget limitation, energetics of optimal foraging, and the ratio of real vs potential prey availability.

Résumé

La relation entre la quantité de nourriture consommée par la communauté de poissons et celle présente dans la zone littorale d'un lac a été examinée sur une base journalière et annuelle. La méthode utilisée pour déterminer la consommation de nourriture fait appel à des estimés de biomasses de poissons dans la zone littorale ainsi qu'à des estimés de ration journalière pour chacun des groupes de poissons (combinaison espèce - classe de longueur) capturés. La consommation moyenne de nourriture (0.30 g poids sec$\cdot m^{-2} \cdot j^{-1}$; 1.27 Cal$\cdot m^{-2} \cdot j^{-1}$) n'a montré aucune variation saisonnière significative. La nourriture fut classifiée en divers types; poissons fourrage, invertébrés benthiques, plancton et macrophytes. Les macrophytes ont cependant été exclus de ma définition de "nourriture potentielle" compte tenu de leur faible occurence dans les contenus du tractus digestif. La disponibilité des invertébrés benthiques fut déterminée en fonction de leur distribution dans le sédiment et de leur taille. En moyenne 68% de la biomasse benthique a été considérée comme potentiellement disponible aux poissons. La biomasse de nourriture disponible a varié de 24.9 à 50.8 g poids sec$\cdot m^{-2}$ (74.5 à 150.3 Cal$\cdot m^{-2}$). La moyenne géométrique du taux d'exploitation de la nourriture de la zone littorale par la communauté de poissons l'utilisant a été 0.80% (poids sec) ou 1.15% (en calorie) par jour (104% et 150% par an). Ces taux correspondent de près aux rapports P/B d'invertébrés benthiques déterminés dans la région d'étude ainsi qu'à ceux de systèmes lentiques nord-américains.

Trois possibilités de mode de régulation du taux d'exploitation par les poissons sont considérées: la limitation temporelle, l'énergétique de l'optimisation de la quête de nourriture et le rapport de la disponibilité réelle et potentielle des proies.

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INTRODUCTION

Fish production and/or biomass in lakes have been repeatedly linked to lake depth. Northcote and Larkin (1956) reported an inverse relationship between lake depth and total fish biomass in 100 British Columbia lakes. Rawson (1960) observed a similar inverse relationship between fish yield and lake depth in prairie and shield lakes. Ryder (1965) and Ryder et al. (1974) extended Rawson's analysis and documented the contribution of mean depth to explained variance in fish biomass and yield. Matuszek (1978) and Hanson and Leggett (1982) confirmed this result, and Prepas (1983) has recently shown that mean depth alone is a good predictor of fish population in both on-shield ($r^2 = 0.92$) and off-shield ($r^2 = 0.63$) lakes.

Ryder et al. (1974) and Hanson and Leggett (1982) speculated that the mean depth variable is an indirect measure of littoral zone area. The littoral zones of lakes support the highest levels of production at all trophic levels (Miller 1941; Anderson and Hooper 1956; Okland 1964; Kajak and Rybak 1966; Efford 1967; Kajak and Dusoge 1971; Werner et al. 1977; Keast et al. 1978). The higher food biomass supported by the littoral zone could explain the importance of the mean depth parameter in the several empirical predictors of fish biomass and/or yield developed to date (Ryder et al. 1974; Matuszek 1978; Hanson and Leggett 1982; Prepas 1983).

I evaluated the inferred relationship between mean depth and littoral zone area using data from Northcote and Larkin (1956; Figure 1) and literature data on mean depth combined with estimates of littoral zone area obtained directly from bathymetric maps (Figure 2). A highly significant relationship was obtained in both cases.

These findings suggest that the magnitude and efficiency of the transfer of littoral zone food to fishes may be a major determinant of total fish production and biomass in lakes. The magnitude and efficiency of this energy transfer is unknown. This thesis reports the results of a study designed to quantify the rate at which fish communities utilize the food biomass on the littoral zone. For that purpose, the amount of food consumed by the fish community on the littoral zone is quantified and compared to that present there. The computations are made on a dry weight and caloric basis.

Figure 1. Relationship between littoral zone area (% of total lake area < 30') and mean depth for 100 British Columbia lakes. (From Northcote and Larkin 1956).

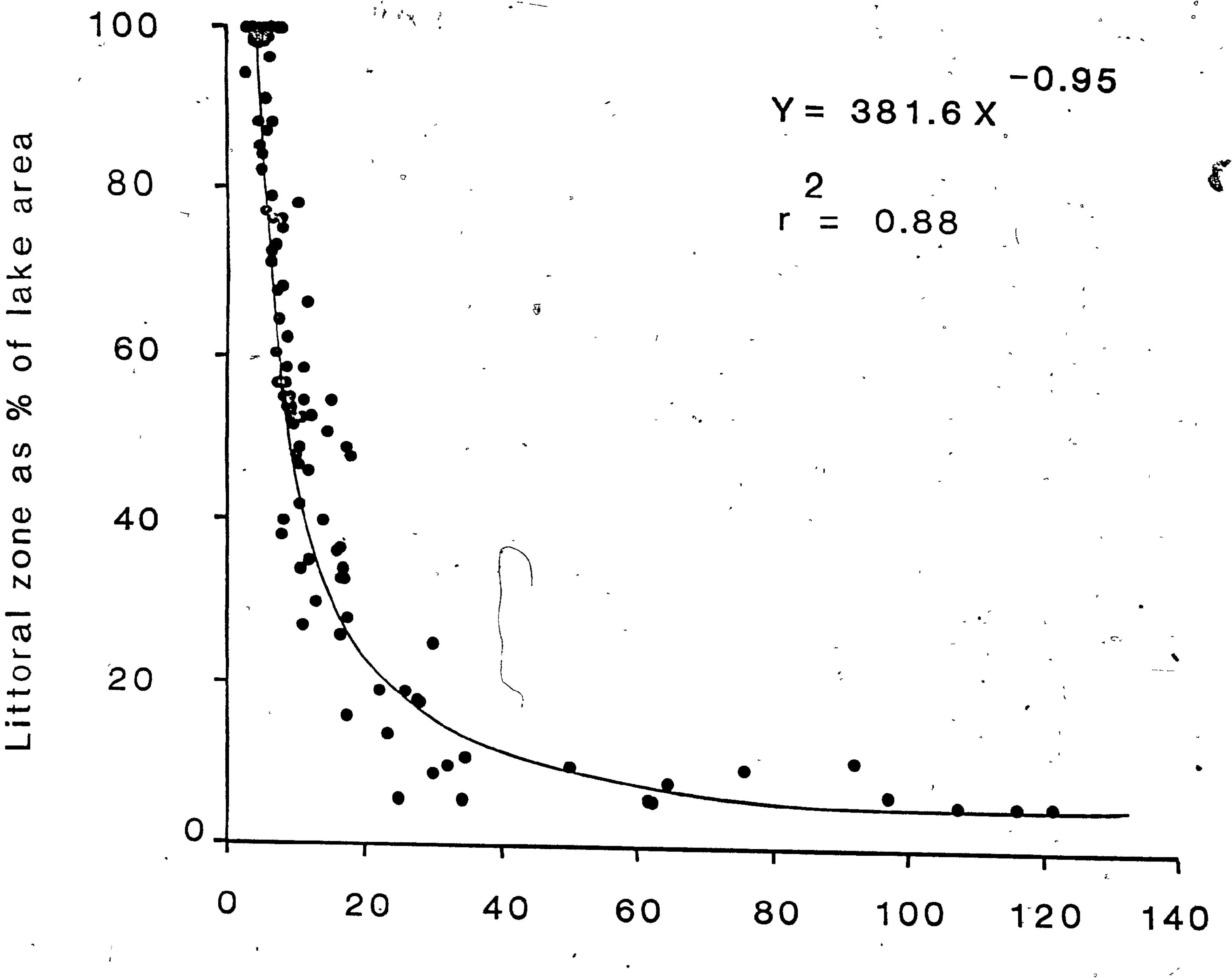
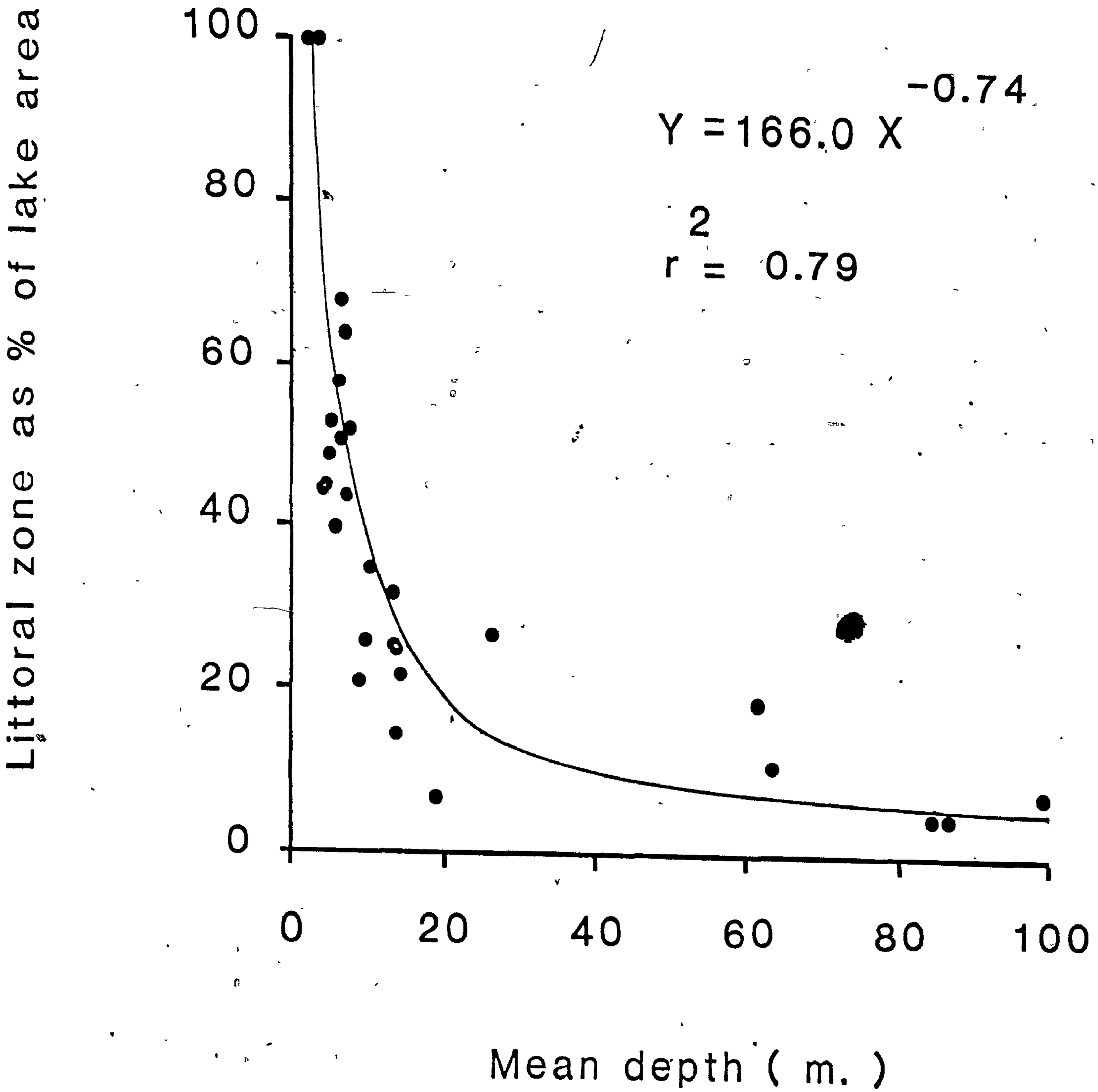

Y = 381.6 X^-0.95
r^2 = 0.88
Littoral zone as % of lake area
Mean depth (m.)
0
20
40
60
80
100
0
20
40
60
80
100
120
140

Figure 2. Relationship between littoral zone area (% of total lake area < 5 m) and mean depth for 28 North American lakes.


Y = 166.0 X^-0.74
r^2 = 0.79
Littoral zone as % of lake area
100
80
60
40
20
0
0
20
40
60
80
100
Mean depth (m.)

METHODS

The study was conducted in Newport Bay, a mesotrophic basin located at the southern tip of Lake Memphremagog (45°06'N; 72°17'W; Figure 3). Detailed descriptions of the morphometry and water chemistry of Lake Memphremagog are given in Morse and Flanders 1971; Pagé 1971; Lands et al. 1974; Ross and Kalff 1975.

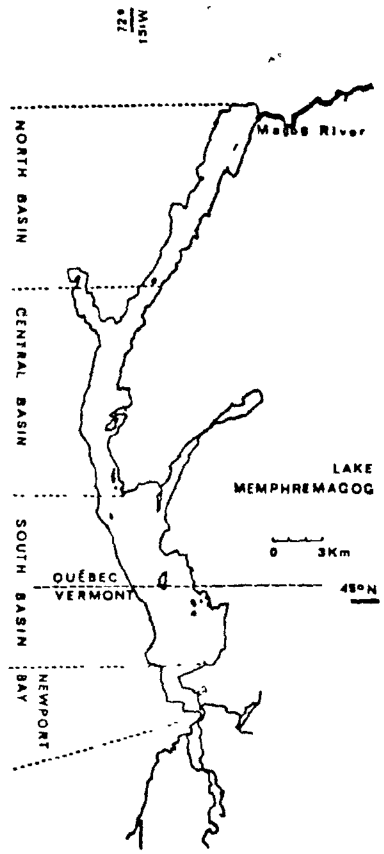
Definitions

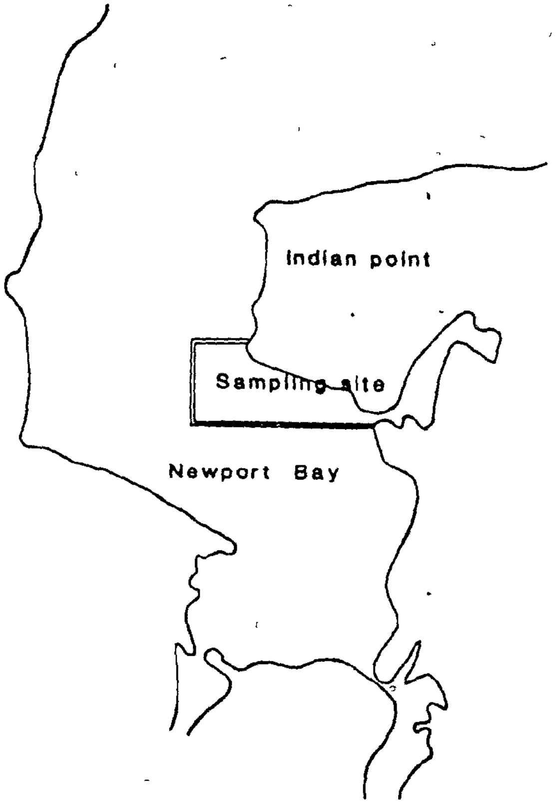
An essential step was to quantitatively define the littoral zone in the study area. For this purpose I adopted Westlake's (1981) definition of the littoral zone as that area within which the light intensity at the bottom is at least 1% of the surface irradiance.

Unpublished data (J. Kalff, McGill University, personal communication) show the 1% level of surface irradiance at Indian Point, adjacent to our study site (Figure 3), occurs at 5.5 to 7.5 m in May; 4.5 to 6.5 m in June and 3.5 to 5.5 m in July. Based on these data I defined the limit of the littoral zone as the 5 m isobath. This result is consistent with Wetzel's (1975) suggestion that depth of the littoral zone equates to the mixing depth. This depth averages between 5 and 6 meters in lakes lying between 40° and 50° N latitude (Straskraba 1981). The shallower littoral zone limits (2 and 3 meters respectively) reported by Gerking (1962) and Okland (1964) who worked in eutrophic lakes are not unexpected given the known inverse relationship between eutrophy and depth of light penetration.

My definition of the littoral zone biota potentially available to fishes as food (energy) was based on analysis of what the fish actually ate and included macrophytes and associated invertebrates, plankton, benthic invertebrates and forage fishes. This definition places fishes

Figure 3. Location of Study Area.


72°
15'W
Magog River
NORTH BASIN
CENTRAL BASIN
SOUTH BASIN
NEWPORT BAY
LAKE
MEMPHREMAGOG
0 3Km
QUÉBEC
VERMONT
45°N


Indian point
Sampling site
Newport Bay

< 6 cm T.L. such as cyprinids, into both the predator and prey categories. This definition was based on preliminary investigations of the diet of fishes in the study area.

Sampling

All components of the littoral zone community including fishes were sampled biweekly from June 20 to August 15, 1982. Fish > 6 cm T.L. utilizing the littoral zone for feeding were sampled seven times over a 24-hour interval beginning at 15:00 h from June 7 to August 16, 1982.

The biomass of littoral zone organisms potentially available as food was determined by quantitative sampling within 24 hours prior to the initiation of fish sampling.

Fishes > 6 cm T.L. were sampled with a 60 x 5 m knotless nylon standard seine (0.6 cm^2 mesh). The seine was deployed to fully enclose an area extending from the beach to the 5 m depth profile, and when hauled sampled a 700 m^2 area. By August 16 macrophyte growth had progressed to a point which made use of this seine ineffective. On this date a smaller 50 x 3 m knotless nylon bag seine was employed in a manner similar to the 60 m seine but extended only to the 3 m depth profile. When hauled it sampled an area of 460 m^2.

All fish in each sample were killed immediately after capture with an overdose of 2-phenoxy-ethanol. This successfully prevented regurgitation of stomach contents. The total catch was sorted by species. Each species was further sorted into 3 length classes determined *a priori* on the basis of similarities in adult size (Scott and Crossman 1973). This size separation was performed to accommodate known size related differences in daily ration and digestion rate (Ware 1975;

Elliott and Persson 1978; Allen and Wooton 1982; Persson 1982, 1983). In the balance of the thesis I use the term "fish group" to describe a specific combination of species and length class (Table 1).

Fishes < 6 cm T.L., i.e. those fishes considered to function as both predators and prey, were sampled (5 replicates prior to the initiation of 24 h sampling for fishes > 6 cm) with a 5.5 x 1 m knotted nylon bag seine (0.2 cm^2 mesh) which sampled a 30 m^2 area. These fishes were not sorted to species or to length class.

The total wet weight of fish (> 6 cm T.L.) in each fish group was determined immediately after capture with an electronic balance accurate to 0.1 g. The complete digestive tract was removed within 4 h of capture from a maximum of 15 fish per group per sample. The contents of the entire digestive tract of each fish group were pooled, weighed in the field to the nearest 0.01 g, and refrigerated. Dry weights of the pooled gut samples were determined within 3 days following drying at 60°C for 48 h. Dried gut contents were then stored in heat sealed plastic bags.

Total wet and dry weights of fishes < 6 cm T.L. were determined in the laboratory. Dry weights were taken following drying at 60°C for 48 h. No gut content analysis was performed on these fish.

Five replicate samples of benthos and plankton were collected at each of three stations located at the 1 m, 3 m and 5 m depths along a transect running perpendicular to the shoreline. A different transect was used on each sampling date. Benthos was sampled with a 0.023 m^2 Ekman dredge. All organisms retained on a 0.250 mm mesh seine were immersed in 70% ethanol for 15 min, transferred to 500 m Os saltwater

Table 1. Length class limits for fish species sampled.

Species	Common Name	Length Class Limits (mm) I	II	III
Ambloplites rupestris	Rock bass	< 140	140-240	> 240
Catostomus commersonii	White sucker	< 140	140-240	> 240
Esox niger	Chain pickerel	< 250	250-500	> 500
Etheostoma olmstedi	Johnny darter	< 80	80-110	> 110
Fundulus diaphanus	Banded killifish	< 80	80-110	> 110
Hybognathus nuchalis	Silvery minnow	< 80	80-110	> 110
Ictalurus nebulosus	Brown bullhead	< 140	140-240	> 240
Lepomis gibbosus	Pumpkinseed sunfish	< 140	140-240	> 240
Micropterus dolomieui	Smallmouth bass	< 250	250-500	> 500
Micropterus salmoides	Largemouth bass	< 250	250-500	> 500
Notemigonus crysoleucas	Golden shiner	< 80	80-110	> 110
Notropis atherinoides	Emerald shiner	< 80	80-110	> 110
Notropis volucellus	Mimic shiner	< 80	80-110	> 110
Osmerus mordax	Rainbow smelt	< 140	140-240	> 240
Perca flavescens	Yellow perch	< 140	140-240	> 240
Pimephales notatus	Bluntnose minnow	< 80	80-110	> 110
Salmo gairdneri	Rainbow trout	< 250	250-500	> 500
Stizostedion vitreum	Walleye	< 250	250-500	> 500

and refrigerated. Dry weights were determined following drying at 60°C for 48 h. This method of preservation prevented significant changes in calorific content between sampling and analysis ($t_\alpha = 0.66$, $n = 8$, $p > 0.05$).

Plankton was sampled via vertical net hauls obtained with a 0.5 m diameter, 0.064 mm mesh net. All plankton were killed by immersion in carbonated water and preserved in refrigerated 500 m Os saltwater. Dry weight was determined within two days of sampling by drying at 60°C for 24 h following filtration on 0.0012 mm glass fiber filters.

The potential loss of invertebrate biomass from the system through emergence was evaluated by operating three 1 m^2 emergence traps during the 24 h fish sampling period. No emergence was detected.

The maximum extension of macrophytes in the littoral zone throughout the season was the 2 m depth isobath. Macrophyte biomass was therefore determined only at the 1 m station. Macrophytes were sampled by hand removal of all plants from within a 0.10 m^2 quadrat. Dry weight biomass was determined following drying for 24 h at 60°C. Invertebrates sampled with the macrophytes were added to the benthic invertebrate samples when calculating invertebrate food availability.

The capture efficiency of the 60 m seine was assessed by determining the recapture rate of marked fish introduced into the deployed seine. Twenty-five fish representing the three most abundant fish groups in the study area (Ambloplites II, Lepomis II, Perca II) were marked with fluorescent pigment (Phinney et al. 1967) and introduced into the seine on two occasions. The seine was hauled 10 to 15 minutes after their introduction and all fish captured were examined for marks under an ultra-violet lamp. Recapture rates were 24/25 and 25/25. On the basis of these results capture efficiency was assumed to be 100% and no corrections were applied to the catch.

Energy determination

Energy content (cal/g dry total weight) were calculated for digestive tract contents, and all potential food items (forage fish, benthic invertebrates, plankton and macrophytes). Energy values for benthic invertebrates and digestive tract contents were determined directly with a Phillipson microbomb calorimeter. Energy values for forage fish, plankton and macrophytes were obtained from Cummins and Wuycheck (1971).

A one-way anova revealed a significant variability in the caloric values of digestive tract contents between fish groups ($F_{2,28} = 4.94$, $p < 0.01$). This significant variability was due exclusively to Lepomis II. The lower energy content per unit weight of the food of this group was due to the high proportion of pelecypods (Sphaerium spp.) in the diet. The dry weight/calorie conversion for Lepomis II was 2046 cal/g dry total (95% C.I. = 1923-2169); that for all other fish groups was 5024 cal/g dry total (95% C.I. = 4714-5334).

The mean dry weight/calorie conversion for benthic invertebrates over the sampling season was 2878 cal/g dry total (95% C.I. = 2637-3199). This low value relative to that for the gut content of fish groups other than Lepomis II is, again, due to the presence of pelecypods in the benthos samples.

The dry weight/calorie conversions employed for plankton, macrophytes and forage fishes were 5308, 3402 and 5086 cal/g dry total weight respectively.

Data transformations

Prior to all statistical analysis both the normality (Kolmogorov-Smirnov test) and homogeneity of variances (F max test) were verified. Where required, transformations were applied. The details of these transformations are given in the text.

RESULTS

Fish biomass

A total of 18 fish species were sampled (Table 1). These were assigned to 36 fish groups for analysis (Table 2). Perca I and II, Lepomis II, Ambloplites II and Ictalurus III dominated the catch in terms of biomass (70% of the total). All other groups contributed less than 4% to the total biomass sampled (Table 2). In terms of numbers four fish groups (Perca I (22.9%); Hybognathus I (21.0%); Notemigonus I (15.2%) and Notropis volucellus I (13.2%)) dominated, comprising 72.3% of the total catch.

With the exceptions of rainbow trout (Salmo gairdneri, 2 specimens) and walleye (Stizostedion vitreum, 3 specimens) all other species were common in the catch throughout the summer.

The average biomass of fish on the littoral zone was 10.80 g wet$\cdot$m^{-2} (95% C.I. = 9.24–12.63). There was no significant diel (Figure 4) or seasonal (Figure 5) variability in the total biomass of fish sampled (ln transformed data; $F_{5,30} = 2.35$, $p > 0.05$; $F_{6,30} = 1.70$, $p > 0.05$).

Table 2. Geometric mean biomass and relative contribution of each fish group to total catch. Number of times one or two gut fullness peaks per day were observed. Mean "R", daily ration and daily food consumption for each fish group sampled.

Fish Group		$\overline{\text{Fish}}$ biomass (g wet·m^{-2})	%	Peak·day^{-1} 1	2	$\overline{R}$ (h^{-1})	$\overline{\text{Ration}}$ (g dry·100 g wet·$^{-1}$·d^{-1})	$\overline{\text{Food}}$ consumption (g dry·100 m^{-2}·d^{-1})
Perca	II	3.02	32.45	0	6	0.10	1.54	3.78
Lepomis	II	1.85	19.89	4	2	0.11	3.92	6.96
Ambloplites	II	0.66	7.07	4	2	0.13	3.15	1.26
Perca	I	0.56	6.02	0	5	0.10	1.26	0.74
Ictalurus	III	0.40	4.32	5	0	0.14		0.74
Esox	II	0.36	3.82	1	1	0.20		1.15
Notemigonus	III	0.35	3.80	0	3	0.18		0.54
Perca	III	0.32	3.47	5	0	0.15		0.37
Notemigonus	I	0.29	3.07	0	5	0.20	2.41	0.71
Catostomus	II	0.22	2.39	2	0	0.10		0.46
Hybognathus	I	0.16	1.69	3	2	0.12	1.46	0.31
Ambloplites	III	0.16	1.68	1	0	0.12		
Notemigonus	II	0.15	1.60	4	0	0.16	1.15	0.22
Lepomis	I	0.11	1.22	5	0	0.15	1.64	0.28
Ictalurus	II	0.11	1.14	2	0	0.18		0.13
x	I	0.10	1.09	2	2	0.17	2.26	0.13
Hybognathus	II	0.07	0.79	3	0	0.08		0.13
Notropis vo	I	0.05	0.56	0	3	0.13	3.73	0.08
Micropterus do	II	0.04	0.46					
Etheostoma	I	0.04	0.40	2	3	0.17	2.03	0.09
Esox	III	0.04	0.39					
Micropterus sa	I	0.03	0.37	0	4	0.17		0.02
Fundulus	I	0.03	0.36	2	3	0.12	1.37	0.06
Ambloplites	I	0.03	0.36	4	2	0.17		0.02
Notropis at	II	0.03	0.32			0.10		
Catostomus	I	0.03	0.28	4	0	0.12	2.84	0.05
Pimephales	I	0.03	0.28	5	0	0.08		0.01
Catostomus	III	0.02	0.22					
Salmo	II	0.01	0.15					
Stizostedion	II	0.01	0.12					
Notropis at	I	0.01	0.08	1	0	0.20		0.01
Ictalurus	I	0.01	0.05	1	0	0.12		
Micropterus	I	0.01	0.05					
Lepomis	III	0.01	0.05					
Stizostedion	I	<0.01	0.02					
Osmerus	I	<0.01	<0.01	2	0			

Figure 4. Daily variation in the geometric mean fish biomass on the littoral zone. Vertical lines represent 95% C.I. (dates used as replicates).

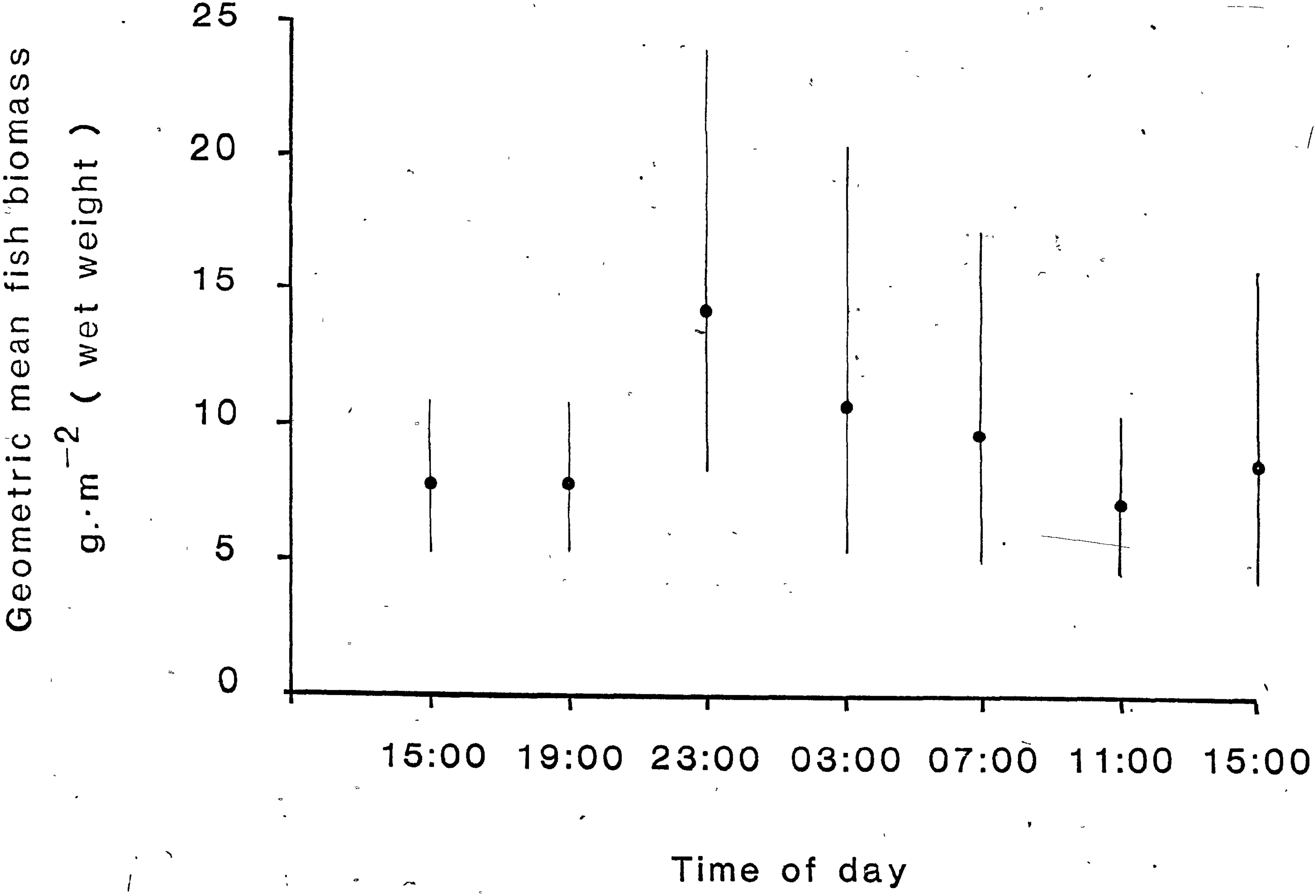
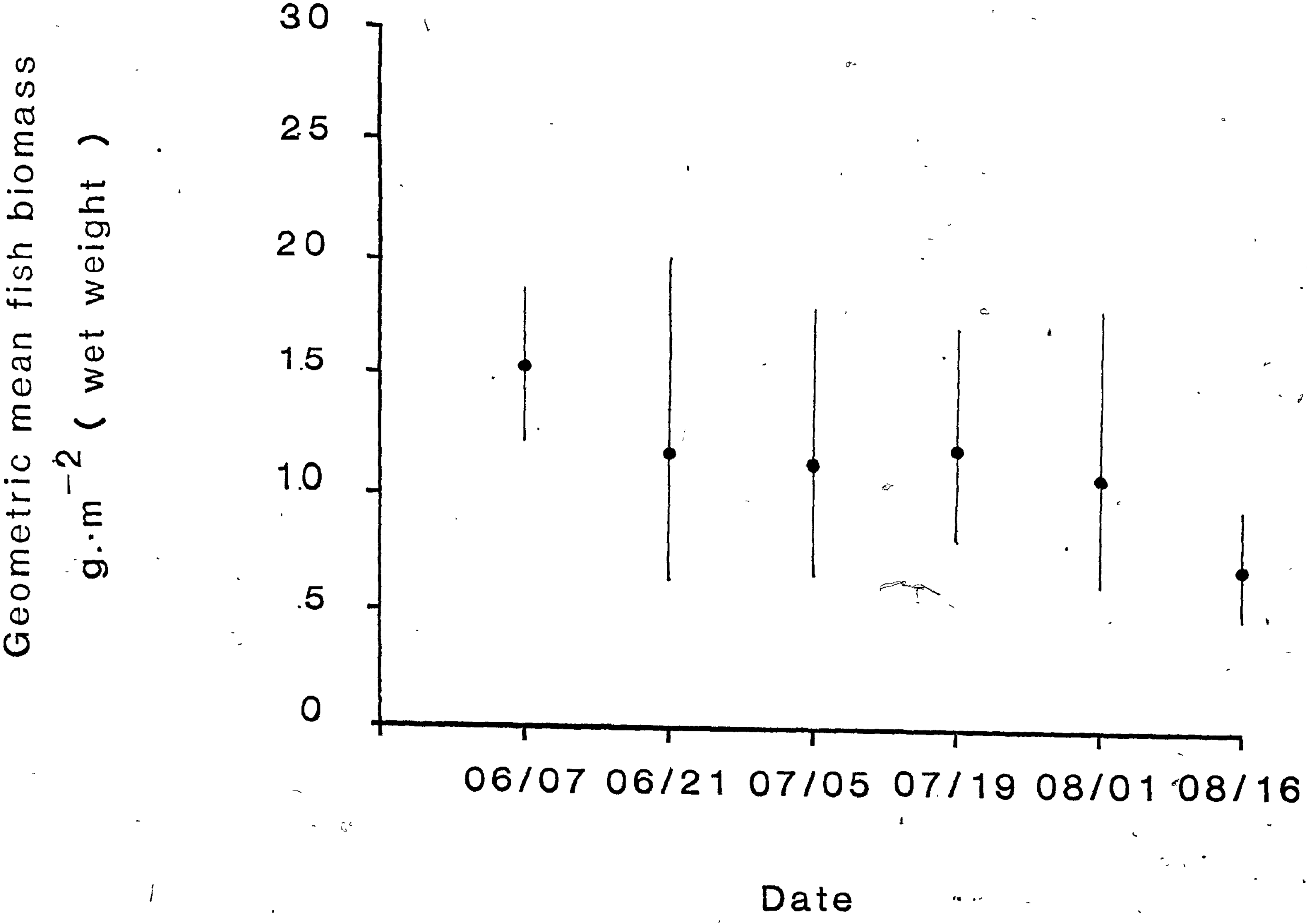

Geometric mean fish biomass
g.·m^{-2} (wet weight)
25
20
15
10
5
0
15:00
19:00
23:00
03:00
07:00
11:00
15:00
Time of day

Figure 5. Seasonal variation in the geometric mean fish biomass on the littoral zone. Vertical lines represent 95% C.I.


Geometric mean fish biomass
g.·m⁻² (wet weight)
30
25
20
15
1.0
.5
0
06/07
06/21
07/05
07/19
08/01
08/16
Date

Computations

In principal, total daily food consumption on the littoral zone could be estimated as the product of average fish biomass onshore and average daily ration. However, because of the large number of fish groups involved, the possibility of significant between group differences in daily ration (Ware 1975; Elliott and Persson 1978; Allen and Wooton 1982; Persson 1982, 1983) and the diel variance in the biomass of individual fish groups onshore, I could not assume a priori that this averaging approach would yield unbiased estimates. I therefore calculated total daily food consumption as;

$$D = \Sigma d_i \qquad (1)$$

where "D" is the total daily food consumption on any sampling date ($g\ dry \cdot m^{-2}$) and "d_i" is the daily food consumption of fish group "i" ($g\ dry \cdot m^{-2}$). "d_i" was calculated as;

$$d_i = \sum_{T=1}^{6} \bar{B}_{Ti} \cdot \bar{C}_{Ti} \qquad (2)$$

where "$\bar{B}_{Ti}$" ($g\ wet \cdot m^{-2}$) is the geometric mean biomass of fish group "i" during the time interval "T" and "C_{Ti}" is the partial daily ration of fish group "i" during the time interval "T" ($g\ dry \cdot 100\ g\ wet^{-1}$). "$\bar{B}_{Ti}$" was calculated as;

$$B_{Ti} = \exp \frac{(\ln (B_{(t+4)i} + 1) + \ln (B_{ti} + 1))}{2} - 1 \qquad (3)$$

where "B" is the fish biomass estimate of fish group "i" at time "t" or "t+4" ($g\ wet \cdot m^{-2}$). "C_{Ti}" was in turn calculated using the method of Elliott and Persson (1978).

$$\text{i.e. } C_{Ti} = \frac{(\bar{F}_{(t+4)i} - \bar{F}_{ti}\, e^{-R_iT})\, R_iT}{(1 - e^{-R_iT})} \qquad (4)$$

where "$\bar{F}_{ti}$" and "$\bar{F}_{(t+4)i}$" are, respectively, the mean gut fullness indices of fish group "i" at the time of sequential diel sampling periods "t" and "t+4" (g dry·100 g^{-1}); "R_i" is the relative digestion rate of fish group "i" (h^{-1}) and "T" the time interval between successive diel sampling = 4 h.

The mean gut fullness of fish group "i" at sampling time "t" was estimated as;

$$\bar{F}_{ti} = \frac{\sum_{j=1}^{n} G_{ji}}{\sum_{j=1}^{n} W_{ji}} \times 100 \qquad (5)$$

where "G_{ji}" is the dry weight of digestive tract (stomach + intestine) content of fish "j", group "i" (g); W_{ji} is the wet body weight of fish "j", group "i" (g) and "n" is the number of fish analyzed for digestive tract contents in group "i" at sampling time "t".

"R_i" is estimated as the slope of the relationship between digestion rate (r_i; g dry·100 g $wet^{-1}\cdot h^{-1}$) and mean gut fullness ($\bar{F}_i$) of fish group "i". Digestion rate is a positive linear function of gut fullness and passes through the origin (Elliott 1972). Hence a single observation of the relationship between digestion rate and gut fullness allows the calculation of "R_i". To equate rates of food disappearance to digestion rate, the assumption must be made that no consumption has occurred over the period considered. This assumption is most closely approached just following a peak in the fullness index. Thus, the digestive rate "r_i" of fish group "i" was estimated as;

$$r_i = \frac{\bar{F}_{(t+4)i} - \bar{F}^{\star}_{ti}}{T} \qquad (6)$$

where "$\bar{F}^{\star}_{ti}$" is the mean gut fullness of group "i" at the time of a gut fullness peak; "$\bar{F}_{(t+4)i}$" is the mean gut fullness of group "i" at the next sampling and "T" is the time interval between successive samples = 4 h. "R_i" in turn was estimated as,

$$R_i = \frac{r_i}{\bar{F}^*_{ti}} \qquad (7)$$

where "r_i" is the digestion rate estimate of fish group "i" and "$\bar{F}^*_{ti}$" is the value of mean gut fullness index of fish group "i" at a peak.

Relative digestion rate

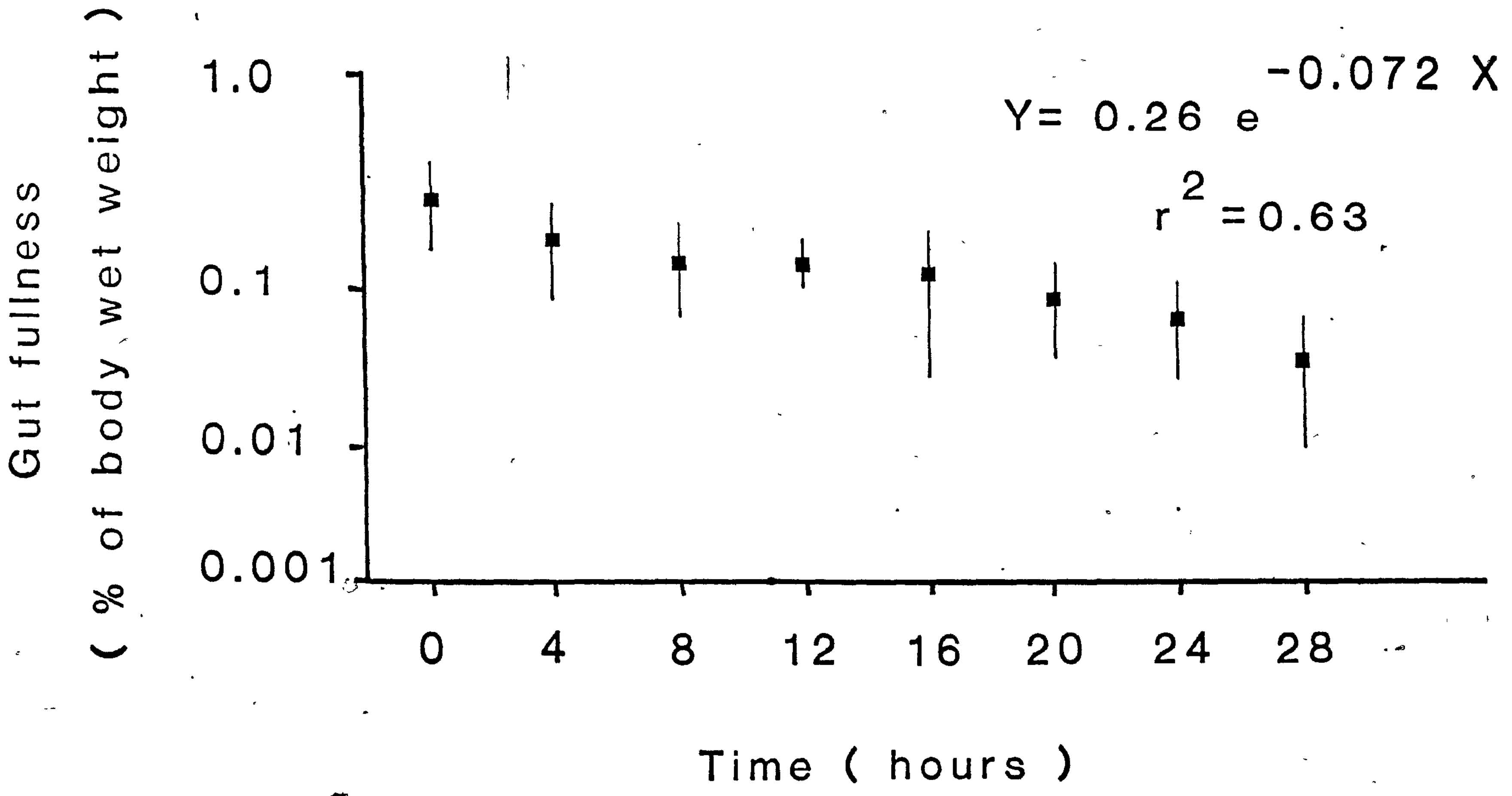
The average group specific relative digestion rate (R_i) varied between 0.08 and 0.20 h^{-1} (Table 2). The mean "R_i" for the 27 fish groups for which this value could be calculated was 0.14 (95% C.I. = 0.13 - 0.15). There were nine fish groups for which at least five independent estimates of "R_i" were possible. There was no significant seasonal variation of "R_i" for these groups ($F_{4,32} = 0.52$, $p > 0.05$). Differences between these 9 fish groups were, however, significant ($F_{8,32} = 3.52$, $p < 0.01$). Significant differences between fish groups were also underlined by the analysis of all groups taking sampling dates as replicates ($F_{26,83} = 1.89$, $p < 0.05$).

Of the 109 "R_i" values estimated, 8 were for a fish predator; Esox ($\bar{x} = -0.19$; 95% C.I. = 0.14 - 0.24), 18 for a macrophyte eater; Notemigonus ($\bar{x} = 0.18$; 95% C.I. = 0.16 - 0.20) and 83 for fish groups exploiting both planktonic and benthic foods ($\bar{x} = 0.12$; 95% C.I. = 0.11 - 0.13). No significant difference was found between the "R_i" values for macrophyte and fish eaters (Duncan's multiple range test, $p > 0.05$). Both macrophyte and fish eaters displayed "R_i" values significantly higher ($F_{2,107} = 12.72$; $p < 0.0001$; Duncan's multiple range test, $p < 0.05$) than fish groups feeding on plankton and benthos.

As an independent test of the reliability of the values of "R_i" derived by my method I estimated "R_i", the most common fish group for Perca II, using the experimental method employed by Elliott (1972). While this method was originally applied to stomach evacuation estimates, it has since been effectively used to estimate "R_i" values for the foregut of fishes lacking stomachs (Persson 1982) or to the whole gut of fishes lacking (Kitchell et al. 1978) and possessing (Nakashima 1979) stomachs. Eighty specimens, collected by seining, were stocked into a 1 m^3 wading pool located at lakeside. A continuous flow of filtered lakewater was provided to the pool by pumping. Ten fish were sacrificed at the initiation of the experiment and an additional 10 were similarly sacrificed and examined each 4 hours for 28 h. All sacrificed fish were dissected immediately and the dry weight of the complete digestive tract contents were determined as previously described. Gut fullness indices developed for fish sacrificed at each sampling period were plotted against time since first sampling (Figure 6). The slope of the relationship ($\bar{x}$ = 0.072; 95% C.I. = 0.054 - 0.090) did not differ significantly from field derived estimates of "R_i" for Perca II ($\bar{x}$ = 0.10; 95% C.I. = 0.05 - 0.15; t_α = 0.48; n = 6; $p > 0.05$).

Caution should be exercised when comparing my whole gut derived "R" values with literature estimates. Grove and Crawford (1980) have shown that whole gut estimates may differ dramatically from estimates derived from evacuation rates determined for discrete digestive tract units. For example, "R_i" values derived from foregut of blennies (Blennius pholis), which lack a true stomach ($-0.36\ h^{-1}$) are six times greater

Figure 6. Food evacuation from the whole gut (stomach + intestine) of fish group Perca II during starvation. Vertical lines represent 95% C.I.


Gut fullness
(% of body wet weight)
1.0
0.1
0.01
0.001
0
4
8
12
16
20
24
28
Time (hours)
Y= 0.26 e^-0.072 X
r^2 =0.63

than the "R_i" value derived from whole gut analysis (0.06 h^{-1}; Grove and Crawford 1980). Comparisons with my values should therefore be restricted to whole gut derived "R_i" values.

Nakashima (1979), working with yellow perch of sizes equivalent to our Perca II, reported a mean "R_i" value of 0.16 (95% C.I. = 0.09 - 0.23) which does not differ significantly from my mean value of 0.10 (95% C.I. = 0.05 - 0.15; $t_\alpha = 1.71$; $n = 11$; $p > 0.05$) for this group. Kitchell et al. (1978) reported whole gut "R_i" values for 3 cyprinids (Pachychilon pictum, Leuciscus cephalus and Rutilus rubilio) fed exclusively on filamentous algae. The mean "R_i" value for these fishes was 0.24 (95% C.I. = 0.23 - 0.25). Although this value is higher than my group mean (0.14) it compares favourably with "R_i" values of the macrophyte ($\bar{x} = 0.18$; 95% C.I. = 0.16 - 0.20) and fish ($\bar{x} = 0.19$; 95% C.I. = 0.14 - 0.24) eaters (respectively Notemigonus and Esox). Similarly my value for benthos and plankton eaters ($\bar{x} = 0.12$; 95% C.I. = 0.11 - 0.13) approaches that given by Grove and Crawford (1980) for blennies fed on chopped clams, Mytilus spp. and lugworm Arenicola marina (~0.06).

Among factors known to influence the rate of food disappearance from the digestive tract following feeding (hence "R_i") are temperature, body size, food particle size, time between meals, digestibility, food composition (fat, protein etc.) and predator species (Hunt 1960; Molnar and Tolg 1962; Brett and Higgs 1970; Edwards 1971; Elliott 1972; Beamish 1972; Swenson and Smith 1973). While controversy is common, it is generally accepted that temperature and food type are the major regulators of "R_i" (Windell 1978). Given the diversity of food types consumed, the number of predators involved, and the seasonal water temperature differences that prevailed during my study, the variance in "R_i" values I report appears reasonable. This, plus the similarity of my estimates with available literature values for fishes consuming comparable diets and my experimentally and field derived values for Perca II, leads me to conclude that the "R_i" values reported adequately reflect the true "R_i" values for the species groups considered.

Daily ration

The mean daily ration for the 13 fish groups for which values could be obtained varied from 1.15% (g dry·100 g $wet^{-1}·d^{-1}$) to 3.92% (Table 2). The grand mean of all individual estimates was 2.31% (95% C.I. = 1.89 - 2.73). There was no significant seasonal variation in daily ration for the 4 fish groups for which at least 4 estimates were calculated (Lepomis II; Notemigonus I; Perca II, III; $F_{3,11} = 1.19$; $p > 0.05$). This finding justified the use of sampling dates as replicates in an analysis of the significance of differences in mean daily ration between groups. This analysis revealed significant differences between groups ($F_{12,23} = 3.18$, $p < 0.01$).

The grand mean caloric daily ration was 9.64 Cal·100 g $wet^{-1}d^{-1}$ (range: 5.78 (Notemigonus II) to 18.73 (Notropis vo. I)). This value, too, differed significantly between fish groups ($F_{12,23} = 2.27$; $p < 0.05$).

My estimates of daily ration for Perca II compare well with both theoretically and empirically derived estimates for yellow perch (Perca flavescens) of equivalent sizes. The basal metabolic rate (B.M.R.) of fish is described by the equation (Winberg 1956);

$$B.M.R. = aW^b \quad (8)$$

The exponent (b) normally assumes values between 0.70 and 0.80 (Peters 1983), while the intercept (a) typically ranges from 0.40 to 0.50 (Winberg 1956; Ware 1975). The result in Watt can be transformed in caloric units by a conversion factor (1 $\mathrm{cal \cdot s^{-1}}$ = 4.18 watts). Daily energy expenditure is believed to range between 2.0 and 3.0 times the basal metabolic rate (Ware 1975; Kerr 1982), and assimilation coefficients typically range from 0.75 to 0.85 (Winberg 1956; Beamish 1972; Ware 1975; Elliott 1976a,b). The surplus energy (Ware 1980, 1982) of Perca II in Lake Memphremagog was determined by Nakashima and Leggett (1975) to be 0.70 g $\mathrm{wet \cdot day^{-1}}$ (0.15 g $\mathrm{dry \cdot d^{-1}}$; 0.77 $\mathrm{Cal \cdot d^{-1}}$). Substituting these values and the mean weight of Perca II (80 g) into the equation;

$$\text{Daily ration} = \frac{aW^{b} \times (2.0 \text{ to } 3.0)}{\text{Assimilation coeff.}} + \text{Surplus energy} \qquad (9)$$

yields daily ration estimates of 3.35 - 7.83 $\mathrm{Cal \cdot d^{-1}}$ which is consistent with my daily ration estimate for 80 g Perca II ($\bar{x}$ = 6.17 $\mathrm{Cal \cdot d^{-1}}$; 95% C.I. = 3.13 - 9.22 $\mathrm{cal \cdot d^{-1}}$).

Persson's (1983) estimates of daily ration for Perch in age classes 2-3, which correspond to Perca II, ranged from 0.1 - 3.0 g $\mathrm{dry \cdot 100}$ g $\mathrm{wet^{-1} \cdot d^{-1}}$ or 0.54 - 16.0 $\mathrm{Cal \cdot 100}$ g $\mathrm{wet^{-1} \cdot d^{-1}}$ (calculated from food composition described by Persson 1983). My estimates were: mean 1.54 g $\mathrm{dry \cdot 100}$ g $\mathrm{wet^{-1} \cdot d^{-1}}$; 95% C.I. = 0.78 - 2.30 g $\mathrm{dry \cdot 100}$ g $\mathrm{wet^{-1} \cdot d^{-1}}$ (3.92 - 11.56 $\mathrm{Cal \cdot 100}$ g $\mathrm{wet^{-1} \cdot d^{-1}}$).

This correspondence between my estimates and the theoretical and empirical estimates given above suggests that the method I used to estimate daily ration for the fishes sampled in my study is valid.

Food consumption on the littoral zone

The total daily consumption of littoral zone food resources by the fish community foraging there averaged 0.30 g $dry \cdot m^{-2} \cdot d^{-1}$ (ln trans data; 95% C.I. = 0.20 - 0.44; Table 4) which corresponds to 1.27 $Cal \cdot m^{-2} \cdot d^{-1}$ (ln trans data; 95% C.I. = 0.87 - 1.85). The contribution of fishes < 6 cm T.L. to these values (ln trans data; $\bar{x}$ = 0.06 g $dry \cdot m^{-2} \cdot d^{-1}$; 0.30 $Cal \cdot m^{-2} \cdot d^{-1}$) was estimated by assuming their ration was equivalent to the average daily ration of all fish groups sampled (2.31 g dry·100 g $wet^{-1} \cdot d^{-1}$). The average daily consumption estimates for individual fish groups are presented in Table 2.

Food on the littoral zone

The mean biomass of fishes < 6 cm T.L. potentially available as prey to larger fishes was 0.77 g $dry \cdot m^{-2}$ (95% C.I. = 0.61 - 0.98; Table 3). Differences between sampling dates were significant (ln trans data; $F_{4,20} = 11.71$, $p < 0.001$).

The mean biomass of benthic invertebrates on the littoral zone was 45.98 g $dry \cdot m^{-2}$ (95% C.I. = 36.96 - 57.18). No significant difference in mean biomass occurred between sampling dates (ln trans data; $F_{4,68} = 1.57$, $p > 0.05$; Fig. 7). Significant biomass differences were, however, detected between depths (ln trans data; $F_{2,68} = 6.49$, $p < 0.01$). The mean benthic biomass at 5 meters was significantly less than that at 1 and 3 meters. No difference in mean biomass was evident between the 1 and 3 meter sites (Duncan's multiple range test; $p < 0.05$). This value is higher than estimates for 46 North American lakes and ponds (0.1 to 34.2 g $dry \cdot m^{-2}$; Hanson and Leggett 1982). The difference is believed to result from the inclusion of calcareous pelecypod shells in my weights.

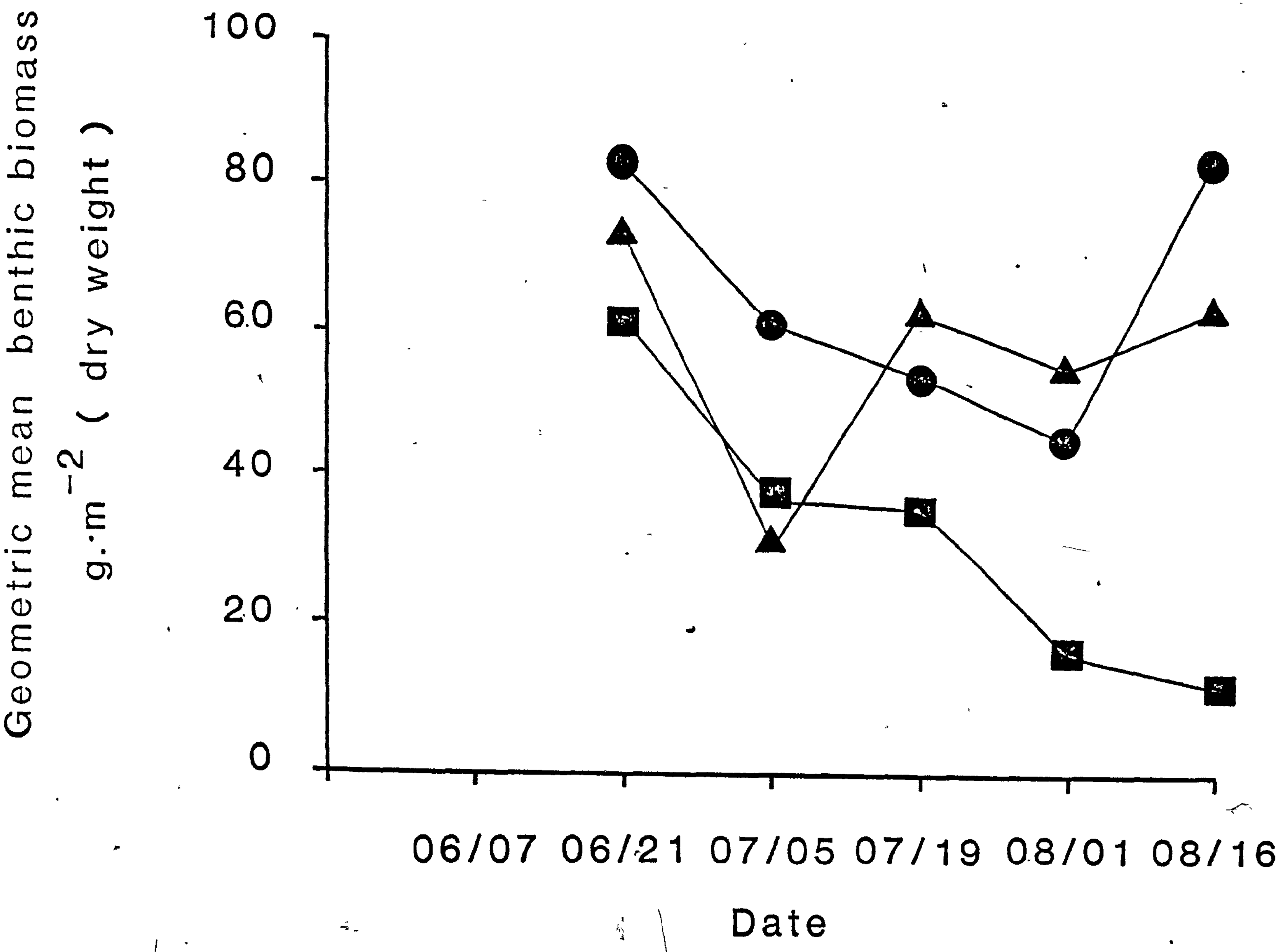
Table 3. Standardized geometric mean food biomass by type and date. g dry·m^{-2}; (Cal·m^{-2}).

	June		July		August	
Macrophyte	-	6.12 (20.82)	49.28 (167.66)	22.96 (78.11)	39.64 (134.86)	56.32 (191.61)
Plankton	-	0.86 (4.56)	0.26 (1.38)	1.77 (9.40)	0.52 (2.76)	1.57 (8.33)
Benthos	-	72.21 (207.82)	41.21 (118.60)	49.75 (143.18)	34.73 (99.95)	39.93 (114.92)
Fish	-	0.86 (4.37)	1.71 (8.70)	0.56 (2.85)	0.74 (3.76)	0.45 (2.29)

Table 4. Daily food consumption by the fish community, food available (including and excluding macrophytes) g dry·m^{-2} (Cal·m^{-2}) and fish exploitation rates (%) on a dry and caloric basis (in parentheses).

	June		July		August	
Fish community consumption						
	0.54 (2.07)	0.21 (0.89)	0.37 (1.67)	0.29 (1.35)	0.28 (1.24)	0.21 (0.81)
Total food available						
including macrophytes	-	56.94 (171.07)	79.27 (258.39)	59.12 (187.72)	64.52 (209.35)	85.49 (208.38)
excluding macrophytes	-	50.82 (150.25)	29.99 (90.73)	36.16 (109.61)	24.88 (74.49)	29.17 (88.77)
Fish exploitation rate						
including macrophytes	-	0.36 (0.52)	0.47 (0.65)	0.49 (0.72)	0.43 (0.59)	0.25 (0.29)
excluding macrophytes	-	0.41 (0.59)	1.23 (1.84)	0.80 (1.23)	1.13 (1.66)	0.72 (0.91)

Figure 7. Seasonal fluctuations of the geometric mean benthic biomass at the 1 (●), 3 (▲) and 5 (■) meter stations.


Geometric mean benthic biomass
g.·m^{-2} (dry weight)
100
80
60
40
20
0
06/07
06/21
07/05
07/19
08/01
08/16
Date

The mean plankton biomass (0.79 g dry·m^{-2}; 95% C.I. = 0.59 - 1.08) was comparable to values provided by Matuszek (1978) for twelve North American lakes (range: 0.15 to 1.65 g dry·m^{-2}). Plankton biomass showed significant seasonal (ln trans data; $F_{4,68} = 8.99$, $p < 0.001$) and depth (ln trans data; $F_{2,68} = 8.35$, $p < 0.001$) variation (Figure 8).

Macrophyte biomass averaged 101.0 g dry·m^{-2} over the season and ranged from 18.4 to 169.0 g dry·m^{-2}.

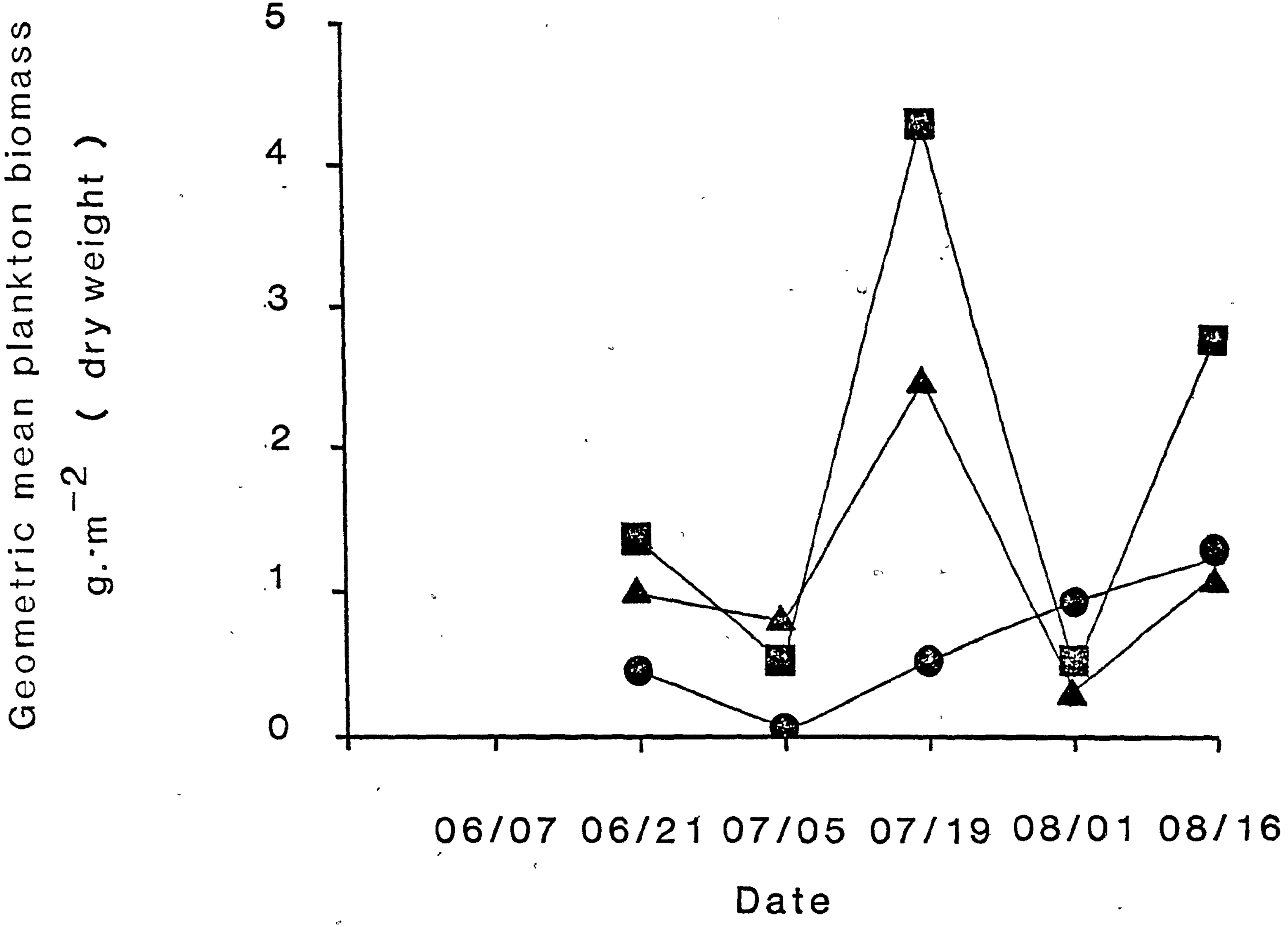
Comparison of the quantities of food consumed by the fish community foraging on the littoral zone with the quantities of food available there necessitates the weighing of the biomass of each food category to a standardized surface area. Field observations and bathymetric maps indicated that each station was representative of one-third of the littoral zone. Thus, an equal importance was given to each station in the weighing process. The weighed biomass of a food type "f" during the sampling day "s" (W_{fs}) was estimated as;

$$W_{fs} = \exp\left(1/3 \sum_{K=1}^{3} \ln \bar{B}_K\right) \qquad (10)$$

where "$\bar{B}_K$" is the geometric mean biomass of food type "f" at the station "K" (K = 1 represents 1 m depth station; K = 2, 3 m depth station; K = 3, 5 m depth station) during sampling day "s". This weighed biomass was calculated for all food types (Table 3) except fishes < 6 cm for which the biomass estimate was used directly.

Benthic organisms were by far the most abundant potential food source (62.1% of total biomass; 95.9% of non-macrophyte biomass). Since depth distribution in the sediment and individual size are known to

Figure 8. Seasonal fluctuations of the geometric mean plankton biomass at the 1 (●), 3 (▲) and 5 (■) meter stations.


Geometric mean plankton biomass
g.·m^{-2} (dry weight)
0
1
2
3
4
5
06/07 06/21 07/05 07/19 08/01 08/16
Date

influence the availability of benthos as prey I examined the distribution of benthos in the sediment column and the size of benthic organisms at my study site. With regard to depth distribution of the benthos and its effect on availability, Nikolski (1963) determined experimentally that perch can forage effectively on benthos to a depth of 1 centimeter in sand/silt sediments characteristic of the type occurring in Newport Bay.

The vertical depth distribution of the benthos was determined from 15 sediment cores (17 cm long, 7 cm diameter) taken at the three-meter station on two dates during the season (July 23 and August 28). Cores were obtained using scuba and were refrigerated immediately after collection. All cores were sectioned in 1 cm slices within 3 hours of collection. Eight core slices representing the top 8 cm of sediment were individually sieved through a 0.250 mm mesh screen. Retained organisms were refrigerated until sorting which was completed within 3 days of collection. The dry weight biomass of all organisms in each slice was determined to the nearest 0.01 g following drying for 48 hours at 60°C. The dry weight biomass of benthos varied significantly with depth (ln + 1 trans data; July; $F_{7,112} = 11.26$, $p < 0.001$; August; $F_{7,112} = 6.62$; $p < 0.001$). The biomass of invertebrates in the 0-1 cm strata ranged from 86% (July) to 63% (August) of the total in the 8 cm depth zone. These values did not differ significantly (Wilcoxon two samples test, $p > 0.05$) and combined gave a value of 68% (arithmetic mean). Weighed benthic biomass estimates (Table 3) were thus multiplied by 0.68 to correct for availability before summation of available biomass estimates of all food types (Table 4).

The prey handling capability of fish is known to be determined by gape (Keast and Webb 1966). Numerous authors have reported that the maximum breadth of prey animals consumed corresponds closely to the mouth width of the predator (Northcote 1954; Lawrence 1958; Yasuda 1960; Okada and Taniguchi 1971; Wong and Ward 1972; Wankowski 1979). Burko (1975) found the handling time for prey $>$ 0.8 times the mouth width increased 6 to 7 fold. I therefore adopted 0.8 times gape width as the upper limit of the benthos available size fraction. The mouth gape of 26 specimens belonging to the three main benthivorous fish groups (Ambloplites II, Lepomis II, Perca II) measured using the method of Keast and Webb (1966) ranged from 1.2 to 3.8 cm ($\bar{x}$ = 2.08; 95% C.I. = 1.82 - 2.34). The maximum width of benthic invertebrates found in the top centimeter of sediments ranged from 0.22 to 2.15 cm ($\bar{x}$ = 0.70; 95% C.I. = 0.61 - 0.79). I therefore considered 100% of the benthos in this depth zone to be available to the suite of fish predators foraging on the littoral zone. Available benthos biomass (B_A) was determined by;

$$B_A = B_e \cdot p_1 \qquad (11)$$

where "B_e" is the benthos biomass estimate and "p_1" is the proportion of benthos biomass sampled by the Eckman dredge that lies within the surface first centimeter (p_1 = 0.68).

Fish exploitation rate on the littoral zone

The daily fish exploitation rate on the littoral zone was calculated by dividing the food consumed by the food biomass on the littoral zone. This calculation was made in two ways; one including and one excluding macrophytes as a food source for fishes (Table 4). When macrophytes were included, the mean exploitation rate was 0.0039 on a dry weight basis and 0.0053 on a calorific basis. When macrophytes were excluded, the mean dry weight exploitation rate was 0.0080 and the caloric rate was 0.0115. Because of the low occurrence of plant material in the diets of the fish studied, I believe the latter values represent a more reliable estimate of true rates.

Assuming an annual feeding period of 130 days, the biomass/energy necessary to support these exploitation rates on an annual basis are estimated to be 1.04 times the mean summer standing crop (dry weight) and 1.50 times the mean summer caloric standing crop on the littoral zone.

My estimate of a 130-day feeding period is based, in part, on data in Keast (1968) which indicates that feeding of the rock bass Ambloplites rupestris, the pumpkinseed sunfish Lepomis gibbosus and the yellow perch, the major components of the total fish biomass in my study, begins in the spring when temperatures average approximately 9°C. The annual duration of temperatures > 9°C in Lake Memphremagog is approximately 160 days (Nakashima and Leggett 1975; J. Kalff, unpublished data). However, Nakashima and Leggett (1975) showed that growth in yellow perch is restricted to approximately 100 days. This observation is consistent with Keast's (1968) finding that food consumption in 9 north temperate fish species including the yellow perch, the rock bass and the pumpkinseed sunfish, increases 3-4 fold as temperature increases from 8-15°C in the spring. Apparently food consumption early in the feeding season (and perhaps also late in the season) is inadequate to meet the demands of maintenance and growth. This effect would also be compounded by the known effect of temperature on assimilation efficiency (Brett 1979; Brett and Groves 1979). I have therefore assumed an intermediate annual feeding period of 130 days and assume further that the average feeding rates I observed apply over this interval.

I assessed the influence of variability in my estimates of "F" (gut fullness index), fish, benthic and plankton biomass, and the availability coefficient on the derived exploitation rate in two ways. First, I recalculated fish exploitation rate using, at each step of the computation, the upper and lower value of the 95% confidence interval of the mean value for each of the parameters involved. This "worst case" analysis yielded estimates of dry weight exploitation rates ranging from 0.0003 to 0.0731 on a daily basis and from 0.04 to 9.50 on an annual basis. The average daily and seasonal exploitation rates calculated from mean values of all parameters were 0.0079 and 1.03 respectively. Caloric exploitation rates derived by this method were 0.05 - 10.23 on a daily basis ($\bar{x} = 1.13$) and 6.50 - 1330 on a yearly basis ($\bar{x} = 146.9$).

The assumption, implicit in the "worst case" analysis, that extreme values of all parameters used to calculate fish exploitation rate would occur simultaneously, is questionable. I therefore performed a second error analysis. In this analysis the values of the input parameters used to calculate daily exploitation rates were drawn at random, following a normal distribution, from within the upper and lower 95% confidence interval of the ln normalized data. There were two exceptions to this procedure: first, the distribution of "F" values was normal and hence no transformation was necessary. Second, distribution of values of the coefficient of availability could not be normalized by standard transformations. I therefore divided the observed distribution into five equal classes. During the iterative process, a class was selected in proportion to its frequency and individual values from within the class were then chosen at random assuming a uniform distribution. Annual estimates of exploitation rate were generated in a similar fashion with the addition that the length of the feeding season was allowed to vary between 100 and 160 days. Values for the length of the feeding season were selected at random assuming a normal distribution having a mean of 130 days.

One thousand daily and annual estimates (dry weight and caloric basis) were generated by iteration. The distribution of these variables were not normal (Figure 9). The distributions were normalized by ln transformation (Figure 10). In my analysis I assumed that the five biweekly exploitation rate estimates derived from field sampling were members of the same population as those derived by this analysis. This assumption is strengthened by the similarity of the mean values of exploitation rates generated by the iterative process and the mean of the field estimates (Table 5). I then used the standard deviation of the ln normalized distributions of generated exploitation rates to estimate the upper and lower 95% confidence interval around my field derived mean values. My analysis indicates that the upper and lower 95% confidence intervals of fish exploitation rate (dry weight) were 0.0023 - 0.0275 on a daily basis and 0.28-3.88 on an annual basis. Those on a caloric basis were 0.0036 - 0.0366 (daily) and 0.43-5.26 (annual) (Table 5).

Figure 9. Frequency distributions of dry weight and caloric exploitation rates derived from error analysis (1000 iterations).

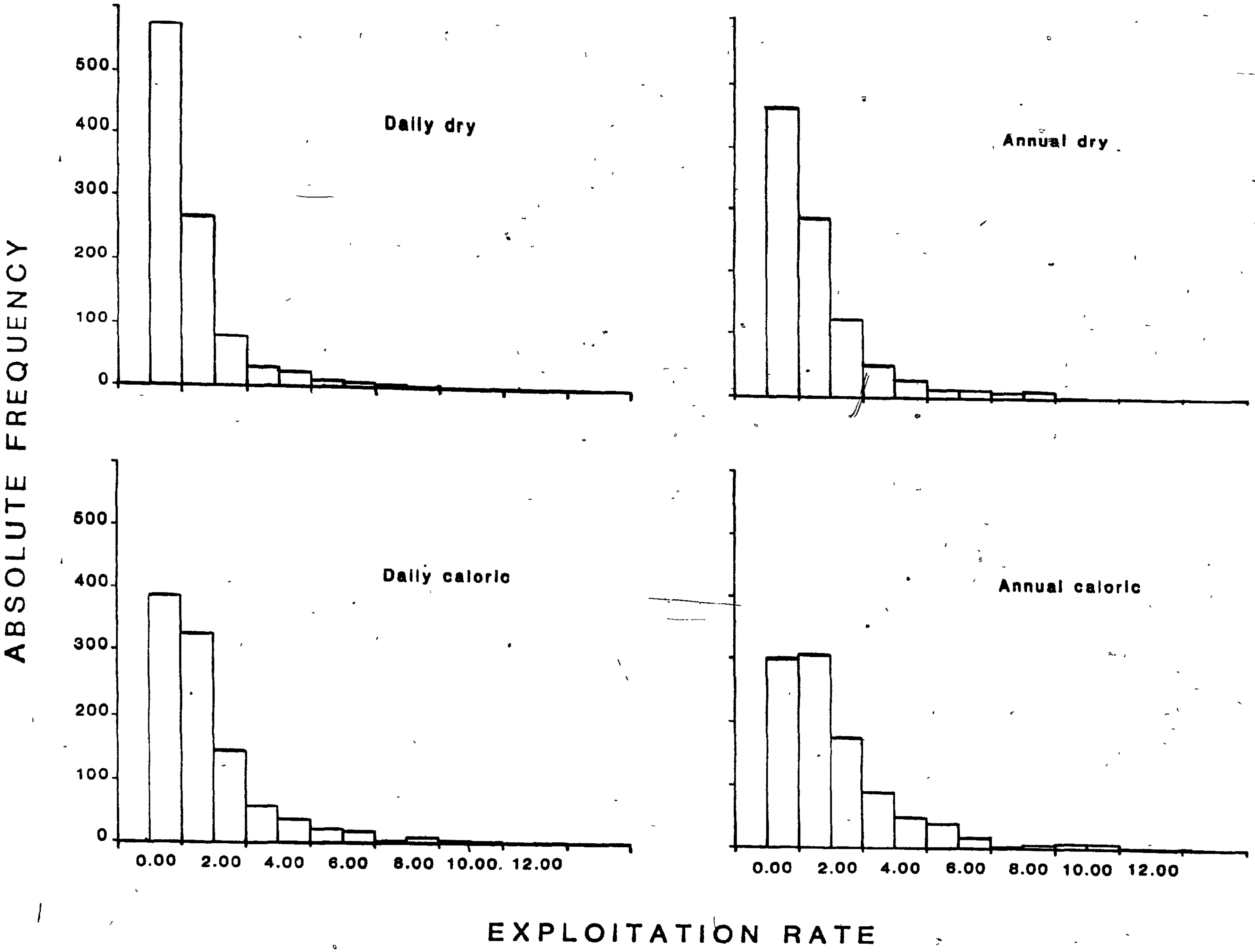

Daily dry
Annual dry
Daily caloric
Annual caloric
ABSOLUTE FREQUENCY
500
400
300
200
100
0
0.00
2.00
4.00
6.00
8.00
10.00
12.00
EXPLOITATION RATE

Figure 10. Frequency distributions of dry weight and caloric exploitation rates based on 1000 iterations using ln transformed data.

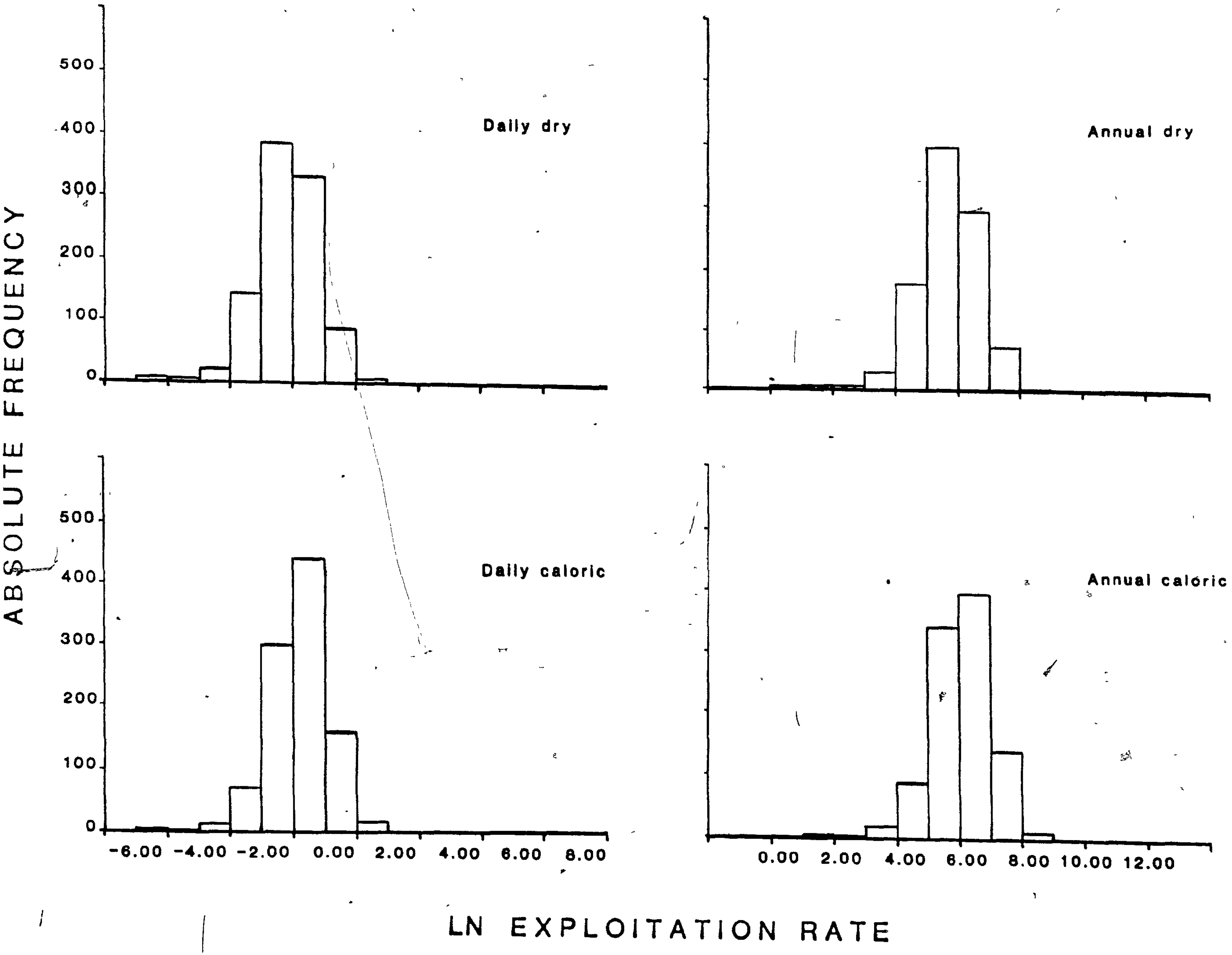

ABSOLUTE FREQUENCY
Daily dry
Annual dry
Daily caloric
Annual caloric
500
400
300
200
100
0
-6.00
-4.00
-2.00
0.00
2.00
4.00
6.00
8.00
10.00
12.00
LN EXPLOITATION RATE

Table 5. Geometric mean food exploitation rates and 95% C.I. derived for error analysis (1000 iterations). Values in percentage.

Exploitation rate	n = 1000			n = 5	
	$\bar{x}$	s	95% C.I.	$\bar{x}$	95% C.I.
Daily	0.82 (1.22)	1.0 (0.93)	0.77 - 0.87 (1.15 - 1.29)	0.80 (1.15)	0.23 - 2.75 (0.36 - 3.66)
Annual	104.2 (144.8)	1.1 (1.0)	97.6 - 111.3 (136.0 - 154.2)	104 (150)	27.88 - 387.93) (42.51 - 525.79)

DISCUSSION

This is the first study in which community exploitation rates have been determined for fishes foraging on the littoral zone of lakes. It is also the first study in which estimates of community consumption have been determined directly through an analysis of feeding rates and biomass for individual species and size groups; previous studies having estimated rates of consumption from growth data using physiologically based models. The latter approach, first applied to fish in Allen's (1951) study of Horokiwi Stream, yielded estimates of consumption ranging from 40 to 150 times the mean annual invertebrate biomass. This implies a P/B ratio for the invertebrate fauna of Horokiwi Stream ranging from 40 to 150 if the invertebrate population is to sustain the predation imposed by brown trout (Salmo trutta) in the system. Gerking (1962) argued that Allen had overestimated consumption by his use of adult growth efficiency values for trout (Pentelow 1939) which he then extended to the total population. Gerking (1962) proposed that Allen's values were at least two or three times too high. More reasonable estimates would thus lie in the range 13-75 times the mean annual biomass. Horton (1961), again using the physiological approach, estimated that the exploitation rate of the brown trout in Dartmoor Stream ranged from 8.7 to 26.0 times the mean annual food biomass. Using data from Mann (1964) I calculated that the consumption rates of roach and bleak in the River Thames ranged from 18.7 times the mean annual food biomass if fish not directly sampled (Mann 1965) were not included in the analysis to 47.4 times when these fish were included. I similarly used data from Gerking (1962) to calculate the annual exploitation rate of the bluegill (Lepomis macrochirus) population of Lake Wyland. I obtained estimates ranging from 1.8 times the mean annual biomass if the food supply is equated to the July peak standing crop to 8.0 times the mean annual biomass if the August biomass is considered representative of mean annual food supply.

The annual consumption rates I derived for Lake Memphremagog (1.04, dry weight; 1.50 on a caloric basis) are much lower than those reported above for lotic environments. This is not unexpected since lotic systems have generally been shown to be more productive than lentic systems (Wetzel 1975; Hynes 1979). My estimates are, however, generally consistent with those I derived using data from Gerking (1962), these being the only other lentic consumption rates I was able to find.

The method I have employed, while itself complex, obviates the need to assume specific assimilation and growth efficiencies (which, as noted above, has created significant biases in previous estimates), and the uncertainty involved in applying laboratory derived estimates of these and other parameters to field situations. Moreover, as my error analysis clearly demonstrates, the complexity of my approach can be significantly reduced by using as input parameters seasonal mean biomass and the seasonal mean daily ration for the community (9.64 Cal·100 g $wet^{-1} \cdot d^{-1}$; 0.023 g dry·g wet body weight·d^{-1}; 0.082 g wet·g wet body weight·d^{-1}) without meaningfully altering the resulting estimate of community consumption. Thus, when considering the community as a whole, species and time specific differences in relative digestion rate and daily ration can be ignored. This greatly reduces the work required to obtain community consumption rates for fishes.

In my calculation of annual consumption rates I assumed both a fixed feeding season and reduced feeding rates in the early and late portion of this period. This is consistent with observations on seasonal variability of daily ration (Nakashima and Leggett 1978; Allen and Wooton 1982). While my error analysis suggests the method I propose is relatively insensitive to reasonable variation in the rate of change of feeding in the spring and fall period I believe greater attention should be given in future studies to defining these rates of change, as well as to the length of the period of peak feeding activity. Given my finding that community mean values for relative digestion rate and daily ration are adequate, this additional effort to define the feeding period becomes more possible.

I believe that my analysis demonstrates quite conclusively that the littoral zone fish community consumes only a small fraction of the caloric or dry weight food resources potentially available on a daily or annual basis (Table 5). Taking a longer term view of the relationship between food availability and rates of consumption it is reasonable to suppose, as many have done (Lindeman 1942; Slobodkin 1960; Ivlev 1945; Sheldon, Sutcliffe and Paranjape 1977), that for systems in equilibrium consumption should approximate production of food items. This suggests, then, that community exploitation rates should approximate the ratio of production/biomass (P/B) in the prey community.

Very few community estimates of P/B are available for limnetic systems, and none are available for littoral zones. The limited data available do, however, support the prediction. For Lake Memphremagog, Dermott et al. (1977) estimated the daily P/B ratio for three diptera in the south basin adjacent to the study site to be in the range 0.005 - 0.04 ($\overline{x}$ = 0.015). This corresponds closely with my estimate of community exploitation rate ($\overline{x}$ = 0.0080; 95% C.I. = 0.002 - 0.028). The annual dry weight P/B ratio for benthic invertebrates in 20 temperate lakes (Waters 1969; Banse and Mosher 1980) averages 3.88 (95% C.I. = 2.36 - 5.40). My estimate of annual dry weight exploitation rate overlaps strongly with these values ($\overline{x}$ = 1.04; 95% C.I. = 0.28 - 3.88).

The correspondence between measured P/B ratios for lentic benthos (which comprise > 90% of the biomass consumed by the littoral zone fish community of Lake Memphremagog) and my estimates of community exploitation rates offers the first direct empirical support for the prediction/assumption that community exploitation rates in fish should balance production (Lindeman 1942; Slobodkin 1960; Ivlev 1945; Sheldon, Sutcliffe and Paranjape 1977). It also provides a mechanistic basis for the observation that differences in biomass of 1+ and older yellow perch between the south and north basins of Lake Memphremagog (2.5/1, Nakashima and Leggett 1975) are closely linked to differences in the mean benthic biomass (2.8/1; Dermott et al. 1977).

On a larger scale these findings are consistent with the assumption that the demonstrated linear relationship between fish yield in lakes and mean benthic biomass (Hanson and Leggett 1982) is causal. It is interesting, and perhaps indicative of the generality of my findings, that the slope of this relationship is 0.012, i.e. fish yield is linked to benthic biomass by the approximate daily P/B ratio of the benthos.

The factor or factors limiting higher exploitation rates by individual fishes or by the total community in the short term are presently unknown. Given the very low daily and seasonal rates determined here, the potential for such short term gain appears substantial at first glance. Three possible limiting factors are suggested by recent findings in related fields.

First, Mills (1982) has shown that the time budget of individual fish is complex and the time actually available for foraging is limited. These time constraints could restrict the total foraging capacity of individual fish and hence community exploitation rates. This hypothesis does not, however, explain why fish numbers would not increase over the medium term leading to temporary imbalances in the production/exploitation ratio. Such increases would ultimately lead to serious overexploitation of the food production base and subsequent sharp reductions in fish biomass and yield. Such medium to large scale fluctuations in fish community biomass do not appear to be characteristic of unexploited systems.

A second possibility is that foraging rates of individual fish are constrained by the energetic cost/benefit equation relating to foraging. For example, Brocksen and Bugge (1974), Elliott (1976a,b) and Caulton (1978) have shown convincingly that assimilation efficiency is inversely proportional to daily ration. Moreover, growth efficiency in fish is known to decrease with daily ration (Paloheimo and Dickie 1966). Hence the marginal energetic value of each prey item declines as ration increases. Feeding rates could, therefore, be limited by the interaction between the per item energetic cost of feeding and the marginal energetic value of the prey. Empirical support for this hypothesis is found in Ware's (1975) analysis of Ivlev's (1960) study of bleak (Alburnus alburnus). In this planktivorous species the interaction function describing net food intake and cost of foraging as a function of swimming speed (foraging cost) defined an optimal swimming speed (111 $m \cdot h^{-1}$) beyond which both growth and growth efficiency declined monotonically. This effect of foraging cost on the marginal value of prey organisms provides a possible mechanism by which exploitation rates of individual fish may be limited. This could explain the low exploitation rates observed in the short term. However, it again fails to deal with the question of why fish numbers/biomass would not increase in the medium term to more fully exploit the apparent surplus of available biomass.

A third hypothesis, and one which I favour at the present time, is that the low community exploitation rates observed result from the difference between potential and real food availability. In my model I have assumed that 68% of the total benthos biomass (i.e. that located in the top 1 cm) is available. It is well known, however, that few fish systematically mine the benthos for prey. Hence while a significant fraction of the prey items in the top 1 cm are potentially available as prey, a much smaller proportion are likely to be visible, and hence truly available, at any given time. Moreover, only a fraction of those prey at or on the surface of the sediment and hence potentially visible will be pursued by fishes. This fraction will depend on the interacting effects of fish density, reactive distance (Ware 1971; Werner and Hall 1974), prey colour (Ginetz and Larkin 1973), fish preference (Sutterlin and Sutterlin 1970; Sutterlin 1975) prey contrast (Ware 1975; English 1983) and apparent prey size (O'Brien et al. 1976).

Consequently, I suggest that prey availability is low relative to biomass. It is probable also that the absolute biomass of available prey will increase in proportion to total prey biomass. Based on my observations of the community exploitation rate of littoral zone fishes in Lake Memphremagog, which rely heavily on the benthos for their prey, and on the correspondence between my finding and the slope of the more general relationship between fish yield and benthic biomass in lakes, I predict that the ratio of available biomass to total biomass will approximate 1/100 or 1%. This value is expected to vary between systems, primarily as a result of differences in substrate type, habitat complexity, density of vegetation, and the species composition of the predator and prey communities. A better quantitative definition of availability, and of the effects of these parameters on availability, are badly needed to provide a more realistic interpretation of fish exploitation rates.

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