

Selective foraging in the white sucker (*Catostomus commersoni*)

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Abstract: The white sucker (*Catostomus commersoni*) is a widespread and often abundant North American species. This benthivore can play an important role in the ecology of both fish and benthic communities in lakes and streams. However, the feeding behaviour and ecology of the white sucker have received limited study beyond a description of gut contents from small samples of fish. In this study, the diet of white suckers was determined in relation to season and depth distribution of the fish, as well as to the abundance and type of zoobenthos sampled at the site of fish capture. Suckers fed predominantly on either zoobenthos or zooplankton, with some seasonal variation. They specialized on particular prey and also on the largest individuals within their "speciality," thus exhibiting both resource partitioning and size-selective predation. These findings demonstrate that white suckers can be extremely flexible in their use of resources as opposed to being simple generalist feeders. This attribute, plus their tolerance of a range of environmental conditions, partly explains the abundance of white suckers and their wide distribution in temperate lakes and streams.

Résumé : Le Meunier noir (*Catostomus commersoni*) est une espèce répandue et abondante en Amérique du Nord. Ce poisson consommateur de benthos peut jouer un rôle important dans l'écologie des communautés de poissons et de benthos des lacs et des cours d'eau. Cependant, le comportement alimentaire et l'écologie du Meunier noir ont été peu étudiés et on ne connaît que la description des contenus stomacaux de petits échantillons de ce poisson. Dans ce travail, nous avons examiné le régime alimentaire du Meunier noir en fonction de la saison et de la répartition des poissons en profondeur, de même que l'abondance et le type de zoobenthos recueilli au site d'échantillonnage des poissons. Les meuniers consomment surtout du zoobenthos ou du zooplancton et leur régime subit des variations saisonnières. Ils se spécialisent et adoptent une proie particulière dont ils mangent les plus gros individus, faisant donc preuve de partitionnement des ressources et de prédation sélective en fonction de la taille. Ces résultats démontrent que les Meuniers noirs sont dotés d'une flexibilité extrême dans leur utilisation d'une ressource, et ce ne sont donc pas de simples consommateurs généralistes. Cette caractéristique, plus leur tolérance à une gamme étendue de conditions écologiques, peut expliquer en partie l'abondance et la répartition étendue des Meuniers noirs dans les lacs et les cours d'eau tempérés.

[Traduit par la Rédaction]

Introduction

The white sucker (*Catostomus commersoni*) is a widely distributed, frequently occurring North American benthivore (Scott and Crossman 1973) that can constitute half or more of the total fish biomass in lakes (Lalancette 1977; Trippel and Harvey 1987; Chen and Harvey 1994). It is referred to as an invader species (Magnan et al. 1994) and its success may be due in part to the paucity of other benthivorous fishes and to its capacity to exceed in size the prey taken by piscivorous fishes. White suckers' tolerance of a wide range of environmental and chemical conditions, and their ability to exhibit thermoregulatory behaviour, are thought to largely explain their distribution and competitiveness (Stewart 1926; Spoor and Schloemer 1938; Verdon and Magnin 1977; Kavaliers 1982; Marrin 1983; Trippel and Harvey 1987; Logan et al. 1991).

The ability of white suckers to compete for food resources may also explain their widespread distribution and abundance. They have been reported to affect the yield of walleye (*Stizostedion vitreum*; Anthony and Jorgensen 1977; Johnson 1977), perch (*Perca flavescens*; Johnson 1977; Hayes et al. 1992), and rainbow trout (*Oncorhynchus mykiss*; Barton 1980). Following white sucker introductions, brook trout (*Salvelinus fontinalis*) shifted spatial distribution and (or) feeding habits in response to increased interspecific competition for resources (Magnan 1988; 1989; Lachance and Magnan 1990; Tremblay and Magnan 1991; Lacasse and Magnan 1992; Magnan et al. 1994).

Two studies have indicated that of prey that are most available, white suckers feed preferentially on those that are larger (Lalancette 1977; Barton 1980); this is thought to be a mechanism for maximizing growth and (or) reproduction and thus the competitive ability of the fish (Paloheimo and Dickie 1966). However, the evasiveness of smaller prey (copepods in these studies) may explain their low frequency of occurrence in fish gut contents (O'Brien et al. 1985; Ahlgren 1990). Ahlgren (1996) also demonstrated that white suckers have the capacity to feed selectively. In this case, however, smaller fine detrital particles, which have the highest nutritional value, were selected.

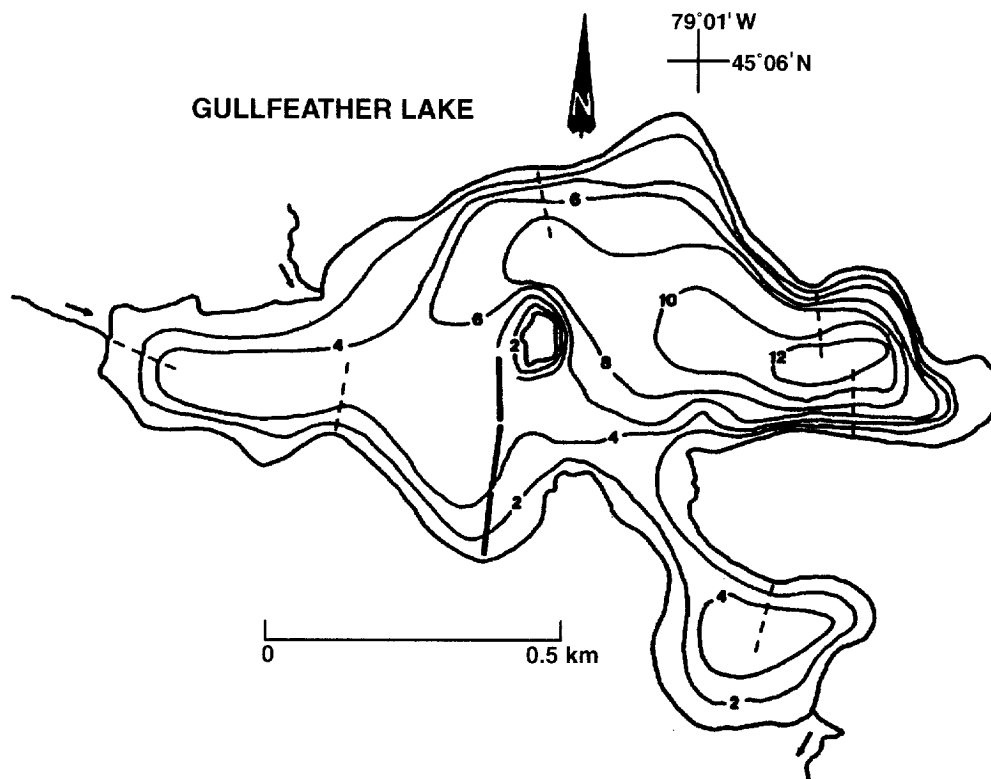
Thus, our study had two principal objectives: (1) to determine what white suckers eat in relation to what is available,

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Fig. 1. Bathymetric map of Gullfeather Lake. Contours are in metres; thick lines and broken lines indicate sampling locations.



and thus, to assess both their selectivity and flexibility in utilizing food resources, and (2) to determine if white suckers exhibit size-selective predation on the taxa consumed.

Methods

Study area

Gullfeather Lake (65.9 ha, maximum depth 13 m, mean depth 4.8 m) is located in south-central Ontario (45°06'N, 79°01'W) (Fig. 1). Detailed descriptions of lake morphometry and water chemistry are given in Jackson (1992). Prior to 1989, Gullfeather Lake supported a high-density population of white suckers characterized by slow growth, late maturation, and irregularity in age at maturity (Trippel and Harvey 1989, 1991). This slow growth and late maturation were attributed to the high density of the white sucker population, low densities of food organisms, and the anaerobic hypolimnion. Since 1989, the white sucker population has been reduced to one-third of its initial size (estimated at 11 330 fish) via the annual removal of approximately 1000 mature fish. Associated with this change was a marked increase in the density of chironomid larvae, common in the diet of benthivorous fishes, from 4330/m² in 1979 to 20 610/m² in 1994 (Trippel and Harvey 1989; Saint-Jacques 1996). Other lakes in the region inhabited by white suckers had chironomid densities (individuals/m²) of 5940 (Bigwind Lake), 9740 (Dickie Lake), 10 940 (King Lake), and 11 070 (Red Chalk Lake). This indicates that by 1993, the benthic community of Gullfeather Lake had a relatively large standing crop of these benthic organisms.

Fish sampling

White suckers were captured in overnight sets of three trammel nets (100 × 1.8 m) placed perpendicular to the shore and originating from Cabin Bay. The first net spanned 1–2.5 m depth, the second 2.5–3.5 m, and the third 3.5–4.5 m (Fig. 1). The initial sample size was set at 10 fish from each net per month between ice-out

and freeze-up (July–October in 1993; May–June in 1994). Analyses of the guts of five fish from each site yielded such significant differences that additional identification, enumeration, and measurement of prey organisms were deemed unnecessary. Fork length (± 0.1 cm), somatic mass (± 10 g), sex, and fish maturation were determined in the field and recorded for each fish. The first pectoral-fin ray was taken for age determination following the procedures of Beamish and Harvey 1969. As rates of ingestion and digestion in fish vary with size (Windell 1966; Jobling 1981; Dos Santos and Jobling 1991), white suckers in the size range 23–33 cm fork length were selected. Fish in this size range were largely in the age range 3–6 years. In a sample of 244 white suckers collected throughout the lake in early spring, 2% were older than 6 years.

Processing of intestinal contents

There is no clear demarcation between stomach and intestine in the white sucker. Studies on the gut contents of this species usually focus on the anterior third or half of the digestive tract, to reduce the amount of effort involved in identification and counting (Zuckerman 1980; Ringler and Johnson 1982; Tremblay and Magnan 1991). In this study, the anterior half of the gut, containing, on average, 60% of the total gut contents (Saint-Jacques 1996), was selected. All organisms in the anterior half were identified to the familial or ordinal level and counted using a dissecting microscope (Table 1). No empty guts were found. The biomass of ingested organisms was calculated as the product of numerical density and average dry mass of each taxon. The average dry mass was measured from intact whole organisms obtained from benthic cores (see the section Lake zoobenthos sampling). Chironomid larvae are important prey for white suckers (Ringler and Johnson 1982; Trippel and Harvey 1987; Tremblay and Magnan 1991; Hayes et al. 1992) and were therefore chosen for assessing size-selective predation. Preliminary investigation yielded a strong correlation between head-capsule length and body length of chironomid larvae ($\ln(\text{body length}) = 0.84 \ln(\text{head-capsule length}) + 2.18$; $r^2 = 0.82$, 74 df, $p < 0.0001$;

Table 1. Benthic invertebrates found in Gullfeather Lake (sediment cores and fish guts), 1993–1994, with abbreviations used in the figures.

Hirudinea (hir)	Insecta
Nematoda (nem)	Collembola
Oligochaeta (oli)	Isotomidae (iso)
Tubelaria	Coleoptera
Tricladida (tricl)	Elmidae (elm)
Crustacea	Diptera
Cladocera	Ceratopogonidae (cer)
Bosminidae (bos)	Chaoborinae (chao)
Chydorinae (chy)	Chironomidae
Daphnidae (dap)	Larvae (chl)
Holopedidae (hol)	Pupae (chp)
Macrothricidae (mac)	Ephemeroptera (eph)
Sididae	Neuroptera
<i>Diaphanosoma</i> (dia)	Sialidae (sia)
Ostracoda (ost)	Pyralidae (pyra)
Copepoda	Odonata
Calanoida (cal)	Anisoptera (ani)
Cyclopida (cyc)	Zygotera (zyg)
Nauplii (nau)	Tricoptera (tri)
Harpacticoida (har)	Acari
Malacostraca	Hydrachnida
Amphipoda	Halacaridae (hal)
Hyalellidae (hya)	Oribatei (ori)
	Mollusca
	Pelecypoda
	Sphaeriidae (sph)
	Gastropoda (gas)
	Tardigrada (tar)

Saint-Jacques 1996). Thus, head-capsule lengths measured with a scale micrometer were used to estimate the size of chironomids consumed by white suckers. Statistical resampling procedures (bootstrap) indicated that a minimum of 21% of the sample and not less than 80 individuals should be measured to obtain a reliable representation of the size distribution of chironomids in a given gut sample (Saint-Jacques 1996).

Lake zoobenthos sampling

During each period of white sucker sampling, 10 benthic cores (5.2 cm diameter) were collected by scuba divers along the nets to determine the density, biomass, and taxonomic composition of invertebrates available for fish consumption. In July 1994, 72 additional cores were taken along six transect lines passing through the three thermal zones of the lake (Fig. 1). Cores were taken according to a stratified random design based on the areal proportion of each lake stratum. These cores provided information on the spatial variation of the resources available for fish consumption over the whole lake. Sediment cores were preserved in 5% formalin in the field. Invertebrates were separated by sugar flotation at a specific gravity of 1.12 and sieved through 200- μ m mesh (Allison and Harvey 1980). Sediments were subsequently sorted for organisms to validate the effectiveness of the flotation method. Benthic organisms were stained in a mixture of eosine B and Biebrich scarlet to aid identification. The methods used for identification, enumeration, and measurement were the same as for intestinal organisms.

The biomass of organisms in each benthic core was calculated for each taxon from the average organism dry mass (mg), based on drying at 60°C for 24 h (Saint-Jacques 1996). Average dry mass of cladocerans (Bosminidae, *Diaphanosoma* spp., Daphniidae) and some

copepods (Calanoida and nauplii) were obtained from a 1983 Gullfeather Lake data set collected by the Ontario Ministry of the Environment (Hitchin and Yan 1983). The average dry masses of numerically less important taxa such as Tardigrada, Sialidae, and Elmidae were obtained from Strayer (1994) and Smock (1980).

Data analysis of gut contents

The data set of contents of the intestinal tracts of white suckers was analyzed using correspondence analysis (CA), a commonly used multivariate method of ordination known for its robust nature (Jackson 1993) and suitability for use with compositional data, such as gut contents (Jackson 1997). In this study, CA was used to summarize among-individual variation in the diets of the fish sampled. Following this analysis, the fish were classified in two groups according to their diet: zoobenthos feeders and zooplankton feeders. Zoobenthos feeders were defined as fish whose gut contents (biomass) consisted of more than 50% benthic prey items. Zooplankton feeders were defined as fish whose diet was dominated by zooplanktonic prey (>50% of biomass). The authors were intrigued by the possibility of two populations of white suckers resulting from this resource partitioning. Given the greater energetic gains from consuming zoobenthos versus zooplankton, the first step was to compare the size at age between zooplankton feeders ($n = 49$) and zoobenthos feeders ($n = 27$). Growth rates of white suckers of the two feeding groups were estimated by fitting the von Bertalanffy growth equation to back-calculated size at age (Ricker 1975), using SAS (PROC NLIN; Marquardt's method, Statistical Analysis Systems 1985; see Chen and Harvey 1994). Differences in growth rates between zoobenthos and zooplankton feeders were tested by examining the residual sums of the squares following Chen et al. (1992). Analysis of variance of logarithmically transformed or ranked data was used to determine whether fish mass, fork length, and age differed between the two feeding types. Differences in maturity status (mature versus immature) were tested using a χ^2 test.

Data analysis of gut contents versus resource availability

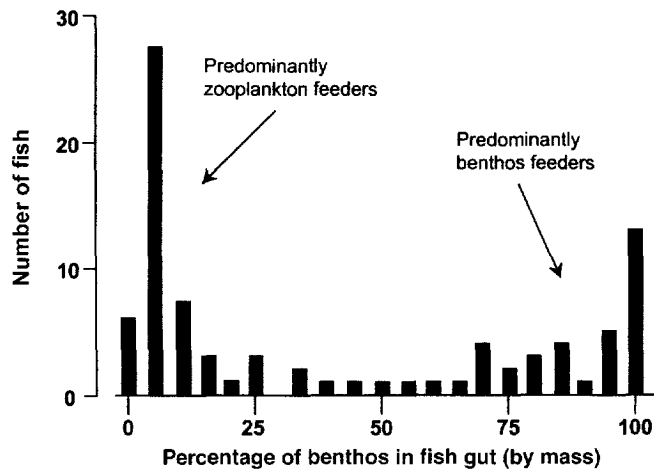
The prey items identified in the guts of the white suckers captured in Cabin Bay were analyzed using CA, and a parallel CA was done on the invertebrates found in the sediment cores from Cabin Bay. These analyses were based on the standardized logarithmically transformed biomass of the invertebrate taxa (each taxon ranging from 0 to 1). This method yielded a simple graphical assessment of the overlap between the diet of white suckers and the resources available in the sediments.

A Mantel test was used to quantify the overlap between the gut contents of the white suckers captured in Cabin Bay and the invertebrates in the sediments of Cabin Bay. The Mantel test is a randomization procedure that compares two distance matrices (Manly 1986). Two distance matrices (Euclidian distance between taxa) were constructed from the first three axes of the ordinations when both the invertebrates in the guts of fish and those in the sediments were analyzed separately. This analysis was repeated for presence-absence data, to evaluate the robustness of the conclusions.

Selective feeding

Two forms of selective feeding were examined: selective predation on larger sized taxa and selective predation on larger individuals within a taxon. Selective feeding on larger sized taxa was investigated using both density and biomass information. Organisms in the fish guts and benthic cores were ranked by size. The difference between the proportions of a given prey found in fish and in the benthos was used to compare the potential for selective feeding between taxa. Selective feeding within a taxon was determined by comparing the frequency distributions of head-capsule lengths between chironomid larvae found in white sucker guts and

Fig. 2. Frequency distributions of white suckers, based on the proportion of zoobenthos in gut contents.



those found in benthic cores. The head capsule was measured because it is sclerotized and therefore less easily digested than the whole prey (Windell 1966; Borgmann and Ralph 1985).

No bias related to digestive processes was observed when the size distributions of head-capsule lengths of chironomids found in the first and last thirds of the fish guts were compared (paired t test, $t = 1$, $df = 328$, $p = 0.3$; Mann-Whitney U test, $U = 12\,008$, $n = 119$ and 211 , $p = 0.51$; see Saint-Jacques 1996). The same result was obtained when the mean dry mass of 200 Holopedidae (a commonly encountered taxon) collected in the first and last thirds of the guts were compared: no significant differences (paired t test, $t = 0.03$, 5 df , $p = 0.968$). In fact, a power analysis (Zar 1984; Peterman 1990) indicated that a minimum of 12 790 fish would be required to detect differences in the mass of Holopedidae between gut portions (note that the difference, δ , was estimated with a standard deviation value derived from a paired t test with 10 df , $\alpha = 0.1$, and $\beta = 0.1$). From the above, we concluded that digestive processes did not bias the size distributions of organisms taken from the guts of white suckers.

Results and discussion

Partitioning of zoobenthic and zooplanktonic resources

The proportions of zooplankton and zoobenthos in each white sucker sampled yielded a bimodal distribution (Fig. 2) showing that the majority of white suckers fed predominantly on zooplankton or zoobenthos and relatively few consumed similar quantities of each. A multivariate ordination based on the biomass of invertebrate taxa found in the intestinal tract of white suckers confirmed this segregation of fish into two feeding types (Fig. 3). The main axis of variation (CA1) contrasted fish that fed primarily on benthic invertebrates (Fig. 3, right-hand side of CA1, solid circles) with fish feeding primarily on zooplankton (Fig. 3, left-hand side of CA1, open circles). The diet of the zoobenthos feeders was composed mainly of chironomid larvae, Gastropoda, Odonata, and Amphipoda, whereas the zooplankton feeders consumed Holopedidae, Daphnidae, and Chaoborinae (Fig. 3). This dependence on zooplankton by more than half of the white suckers sampled may explain the weak relationship of white sucker growth to zoobenthos abundance and population size found by Trippel and Harvey (1987) and Chen and Harvey (1994, 1995).

There are several mechanisms that may explain this bimodal distribution. Under resource-limiting conditions, competitive mechanisms (both intra- and inter-specific) may drive the partitioning of resources (Diamond 1978; Ehlinger and Wilson 1988; Werner 1984; Malmquist 1992; Robinson and Wilson 1994; van Snik Gray et al. 1997). Under conditions of more abundant food resources, when both zoobenthos and zooplankton are highly abundant, the white sucker population (in whole or in part), like other species, may exploit or switch to any open or under-utilized resources (Werner et al. 1981; Robinson and Wilson 1994; Skúlason and Smith 1995). This partitioning may be expressed through a spatially related segregation of resources, where organisms feed predominantly in one type of environment (the inshore or offshore zone of a lake; Werner et al. 1977; Marrin 1983; Schmitt and Holbrook 1969; Malmquist 1992; see review by Robinson and Wilson 1994) and (or) through temporal segregation, resulting in resources being used in different proportions according to the season.

White suckers were sacrificed for analysis of gut contents and thus, as in all such assessments of gut contents, it was not possible to track prey consumption by individual fish over time. It was, however, possible to relate prey consumed by the population to season and location. Spatial patterns in the consumption of zoobenthos and zooplankton were examined for the three depth ranges sampled (Fig. 4). Zoobenthos consumption was greatest for fish captured in the inshore zone of the lake (1–2.5 m depth), where this resource was found to be more abundant (Fig. 5), whereas zooplankton consumption followed an inverse pattern. The nonrandom spatial distribution of the zoobenthos in the cores indicates that the bimodality in feeding may be attributable to a spatially related bias in feeding. However, the large variation in zooplankton consumption (Fig. 4), combined with the lack of simultaneous information about the spatial distribution of zooplankton in the lake, does not allow us to draw any firm conclusions about the role of spatially related bias in the feeding of fish.

There were temporal patterns in resource use by white suckers (Fig. 6). While zoobenthos consumption decreased during the later part of the season, zooplankton consumption remained important throughout the season. The decrease in the amount of zoobenthos ingested is associated with a marked increase in the variability of invertebrate abundance in the sediments (Fig. 7; note the logarithmic scale on the y axis). This suggests that white suckers (or at least a subgroup of them) may be switching to a more readily available food supply (zooplankton) as the availability of zoobenthos becomes more variable and perhaps decreases. Thus, the bimodal distribution of food items may be related in part to these temporal variations in feeding behaviour. Nonetheless, it cannot explain the entire pattern, because there is always a subgroup of white suckers feeding upon zooplankton despite abundant and less variable zoobenthic resources earlier in the season (Fig. 7).

Differences in the diet of fish sampled from the same population have frequently been related to bias due to sampling fish that differ in size, age, or sex (Werner et al. 1977; Zuckerman 1980; Marrin 1983; Werner and Gilliam 1984; Malmquist 1992; Platell et al. 1998; also see concerns expressed by Hartman and Brandt (1995)). In this study, white

Fig. 3. Biplot of invertebrate biomasses found in guts of white suckers captured in Cabin Bay (●, fish whose diet was dominated by zoobenthos; ○, fish that fed primarily upon zooplankton). See Table 1 for an explanation of abbreviations used for invertebrate taxa.

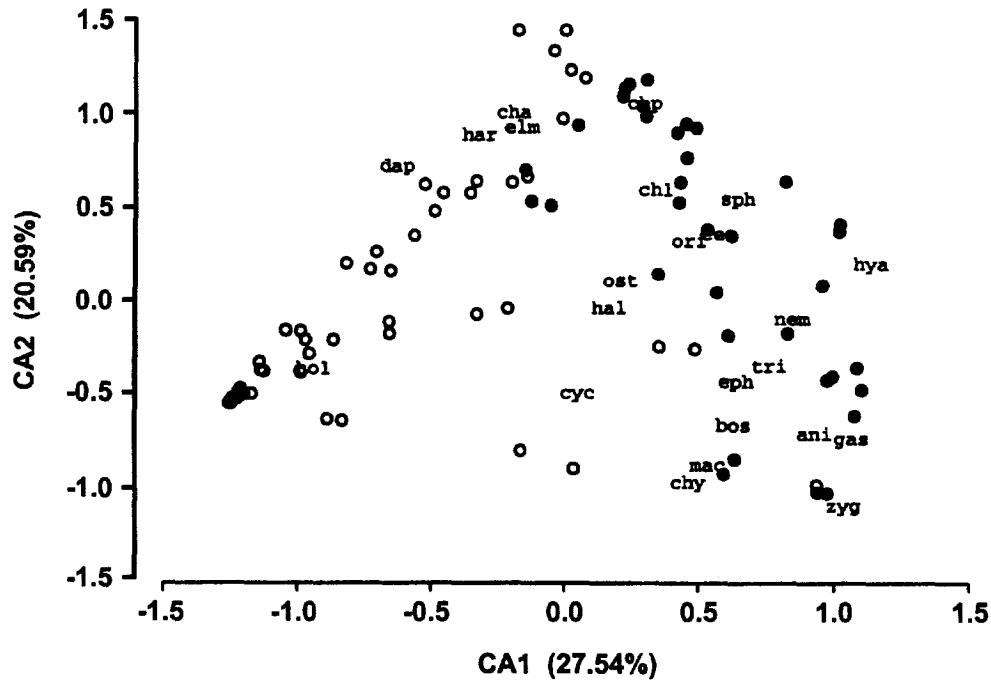
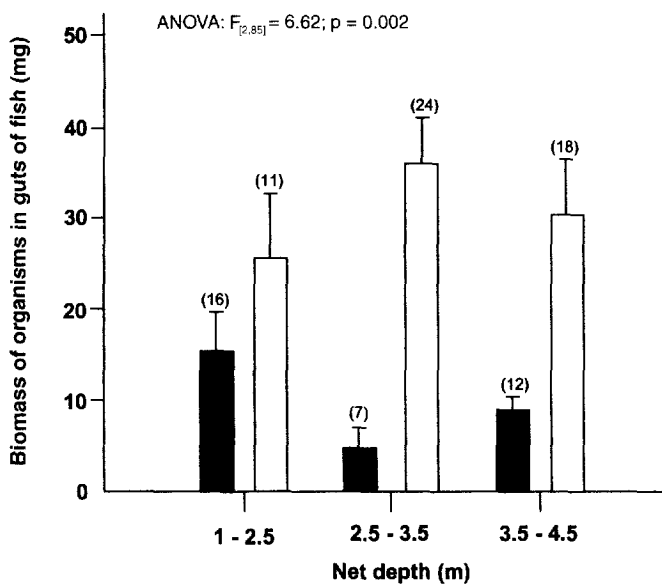


Fig. 4. Spatial variation in the biomass of zoobenthos (solid bars) and zooplankton (open bars) found in the gut contents of white suckers.



suckers from the two feeding groups did not differ in mass, length, or age (Table 2), therefore differences in diet could not be artefacts of dissimilarity in sample distributions.

The maturity versus diet data were tested to determine whether there was a nonrandom pattern in the 2 × 2 table. The χ^2 values were 1.45 for immature benthos, 0.96 for immature plankton, 1.52 for mature benthos, and 1.00 for mature plankton. The overall χ^2 value, 4.942 with 1 df, was significant at the $p = 0.026$ level, indicating a nonrandom relationship between maturity status and diet. Mature fish had

Fig. 5. Relationship between depth and abundance (A) and biomass (B) of invertebrates found in sediment cores from whole-lake sampling. Both Pearson's (r) and Spearman's (r_s) correlation coefficients are presented.

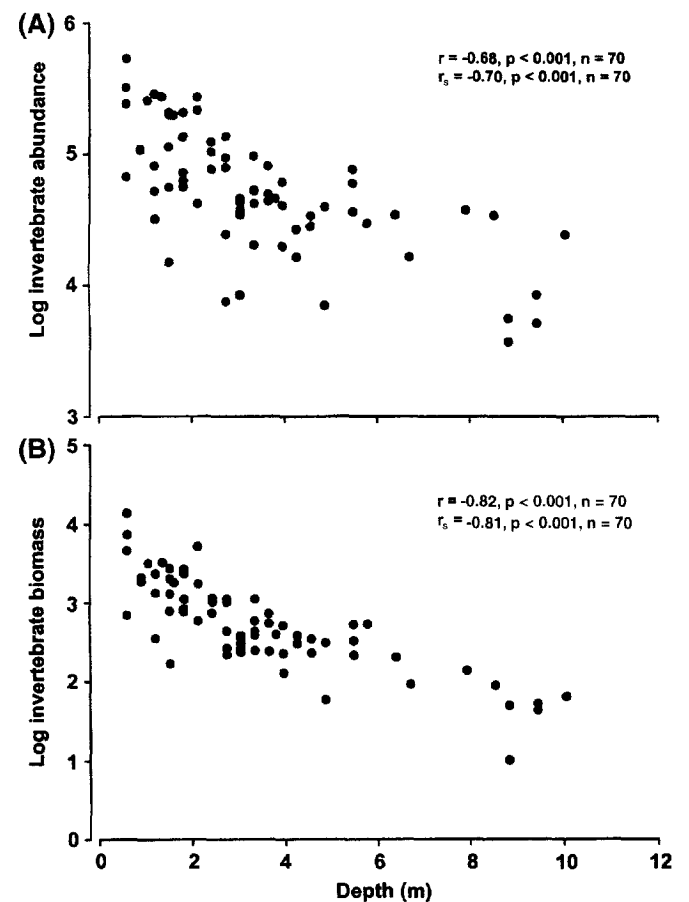


Fig. 6. Monthly variation in the biomass of zoobenthos (●) and zooplankton (○) found in white sucker gut contents. Error bars are 1 SE. Sample sizes (number of sediment cores) are 11 for May (M), 12 for June (J), and 10 for July (J), August (A), September (S), and October (O).

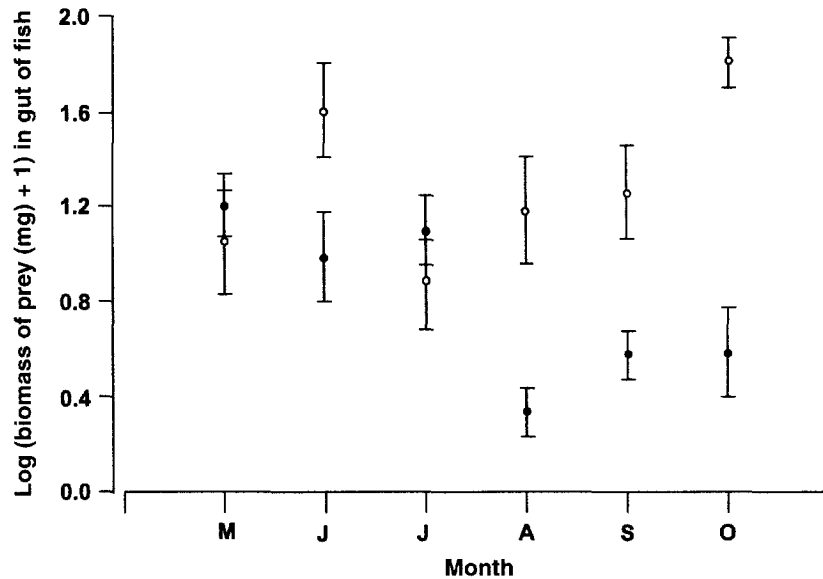


Fig. 7. Monthly variation in the mean biomass of zoobenthos found in Cabin Bay sediments (zooplankton excluded). Error bars are 1 SE. For sample sizes see Fig. 6.

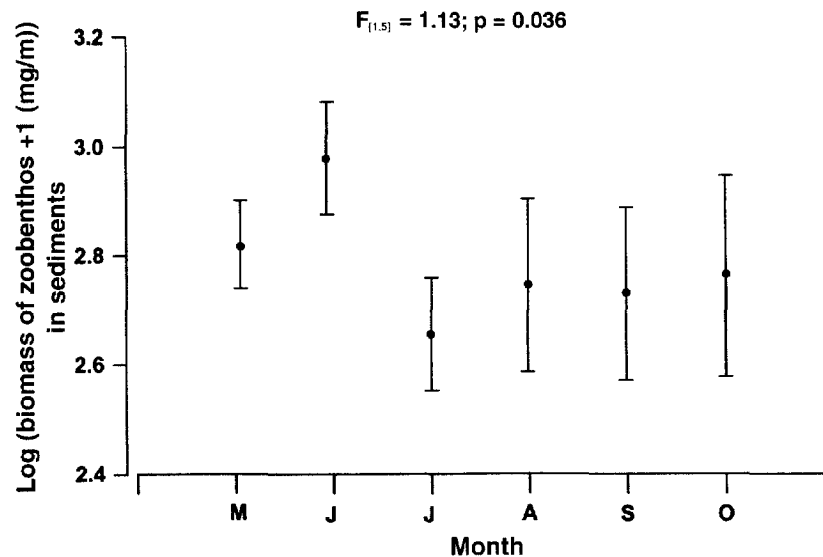


Table 2. Analysis of variance of attributes of zoobenthos- and zooplankton-feeding white suckers.

	df	Type III sum of squares	F	P > F
Fish mass (g)	1	2380.22	0.09	0.77
Fish length (cm)	1	0.74	0.04	0.85
Fish age (years)	1	4.92	1.01	0.32

a greater proportion of plankton in their diet relative to expected values under a null hypothesis of random association, and immature fish had fewer planktonic items in their diets. Fish feeding upon zoobenthos are thought to obtain a higher energetic return per unit cost than those feeding on zoo-

plankton (Paloheimo and Dickie 1966; Gascon and Leggett 1977; Magnan and FitzGerald 1982; Werner 1984; Hayes and Taylor 1990; but see Werner et al. 1981). In such a case, a higher growth rate may be expected among the zoobenthos feeders. Although zooplankton feeders had significantly more food in their gut ($F_{[1,76]} = 12.8, p = 0.0006$; see Saint-Jacques 1996) through most of the sampling season ($F_{[5,76]} = 4.6, p = 0.001$), their growth rate was not significantly different from that of zoobenthos feeders ($F_{[3,147]} = 2.4, p = 0.07$; Fig. 8).

Size-selective predation

Fish are capable of spatially partitioning habitats and thus specializing on a given prey type; they also are able to feed selectively on the largest prey within their specialty (Werner

Fig. 8. Back-calculated sizes at age and von Bertalanffy growth functions for predominantly zoobenthos feeders (●, solid line, $n = 27$) and zooplankton feeders (○, broken line, $n = 49$).

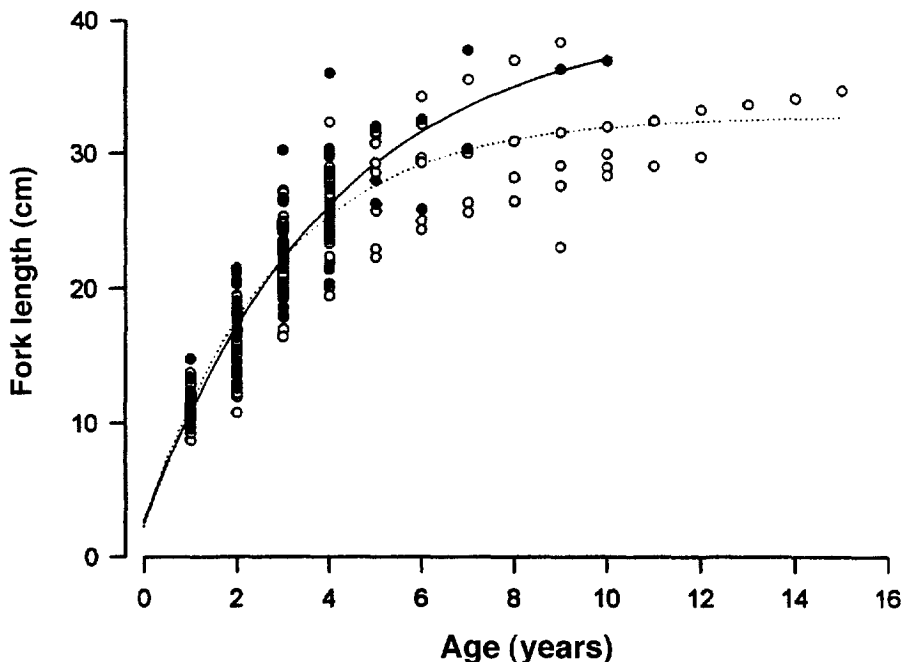
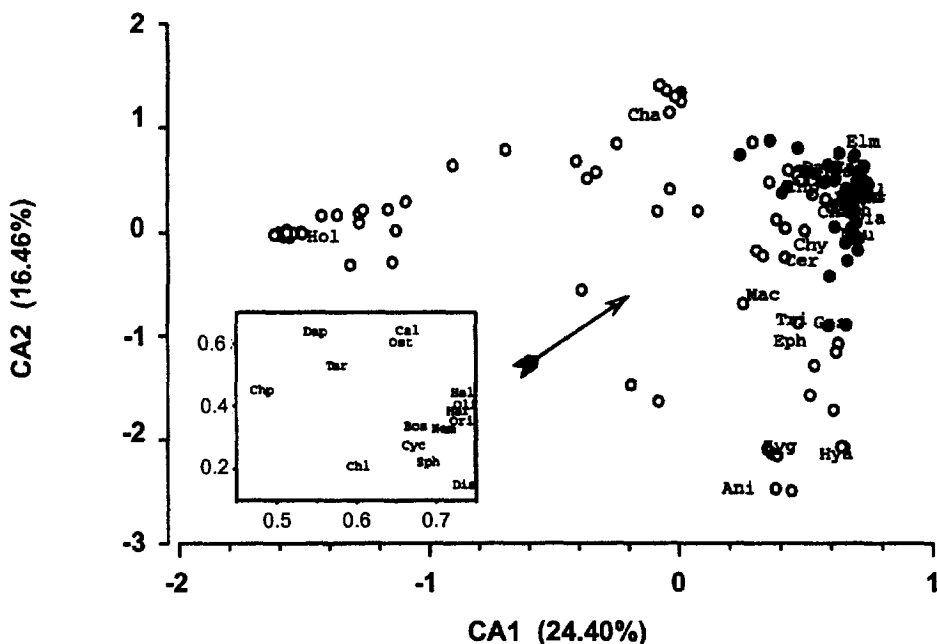


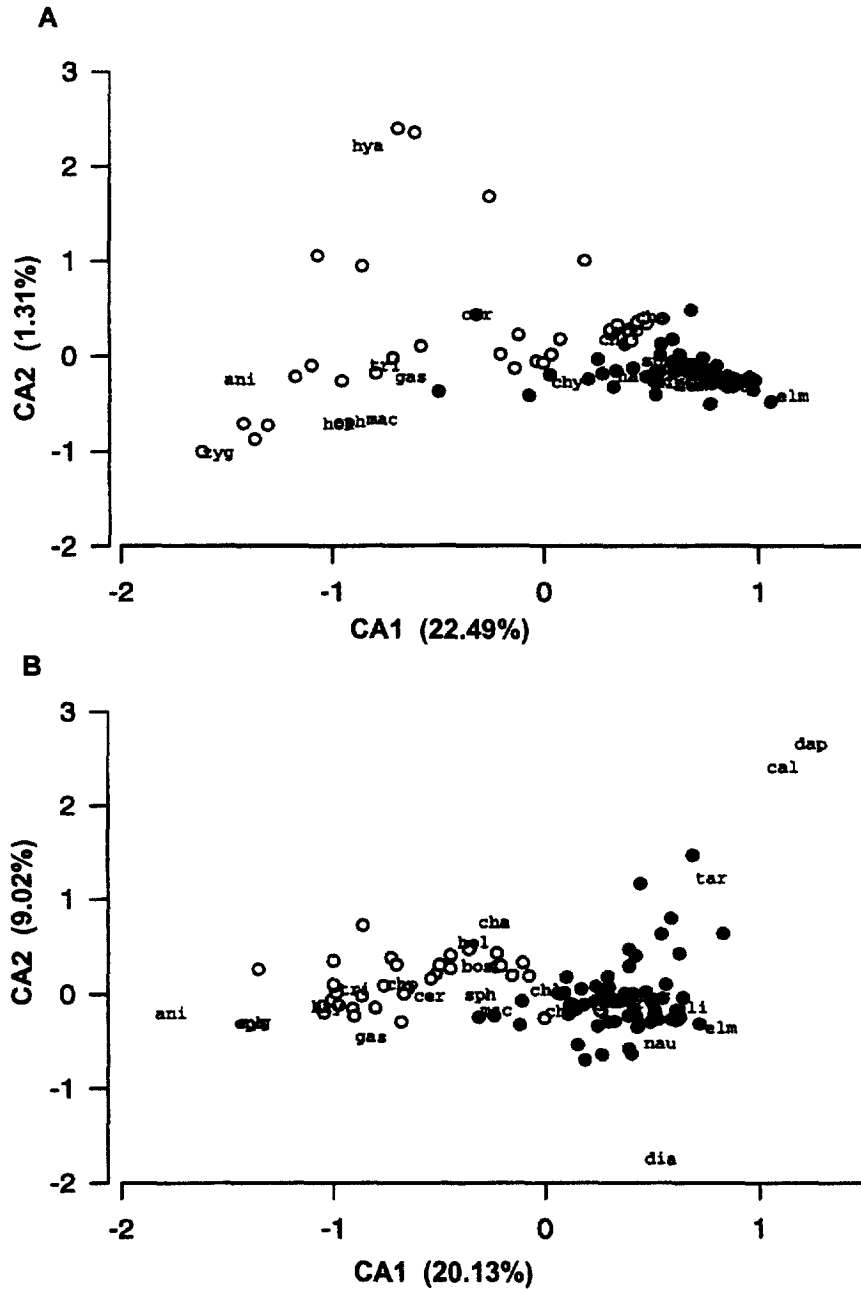
Fig. 9. Biplot of invertebrate biomasses found in sediment cores (●) and white sucker guts (○). See Table 1 for an explanation of abbreviations used for invertebrate taxa.



et al. 1981). The multivariate comparison of gut contents and benthos in the sediments showed a significant lack of overlap (Mantel test, $p = 0.39$; Fig. 9). Sediment cores sample benthic rather than zooplanktonic invertebrates, therefore the overlap between the availability of benthic resources and the amount consumed by fish may be better assessed by removing fish that feed predominantly on zooplankton from the analysis. The result was nonsignificant when the assessment was based on biomass data (Mantel test, $p = 0.103$);

however, when it was based on presence-absence data, the overlap increased (Mantel test, $p = 0.03$; Fig. 10). Thus, the white suckers that consume zoobenthos are doing so as part of a nonrandom feeding strategy, given that there is no proportional representation of prey from sediments in the fish guts. The biplots show that the larger sized taxa such as Anisoptera, Zygoptera, Ephemeroptera, Hyalellidae, and Gastropoda were ingested in greater proportions relative to their abundance in the sediments (Figs. 10 and 11). Smaller

Fig. 10. Biplot of invertebrate biomasses (A) and presence-absence data (B) for sediment cores (●) and white sucker guts (○), with zooplankton-feeding fish omitted. See Table 1 for an explanation of abbreviations used for invertebrate taxa.

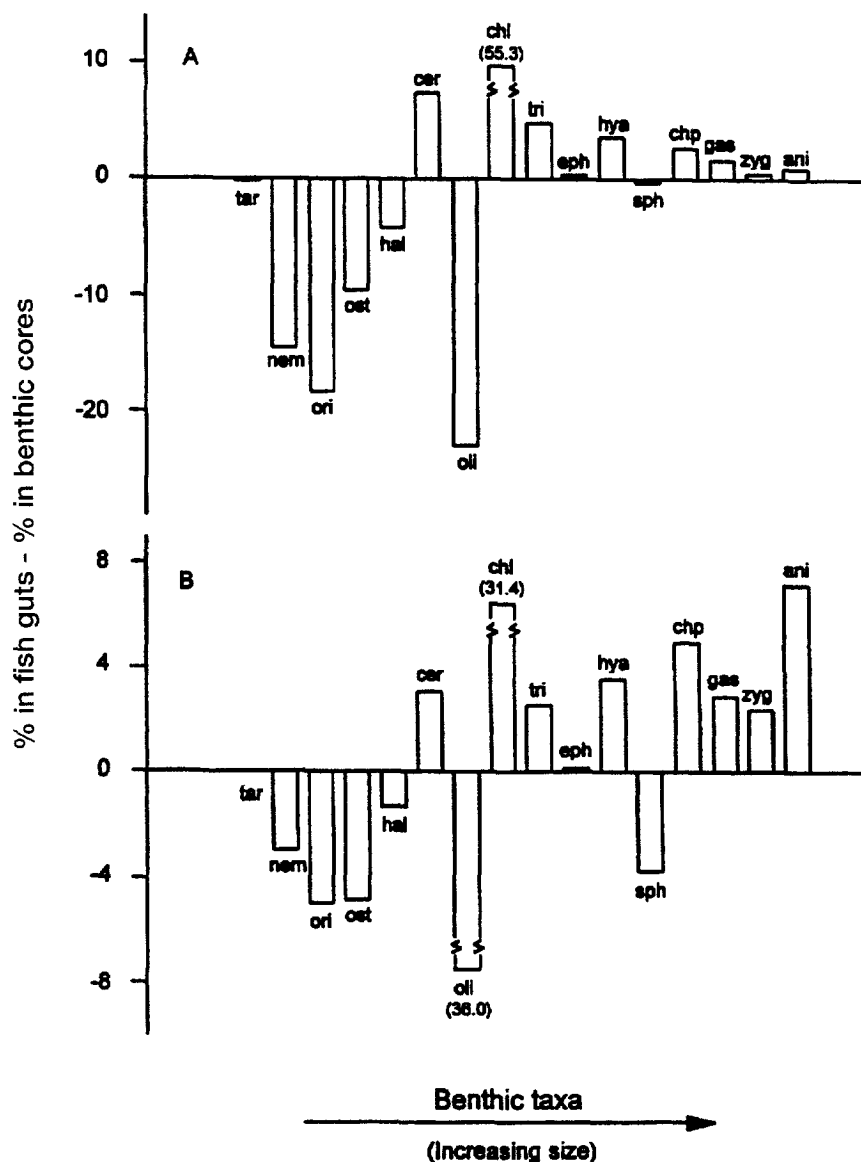


sized taxa such as Tardigrada, Halacaridae, Oribatei, Nematoda, Ostracoda, and the majority of the smaller Cladocera were common in the sediment cores but not in the fish diets.

Size-selective predation within a single taxon was tested for chironomid larvae, an important component representing 30% of the white sucker diet (Saint-Jacques 1996). Chironomids in gut contents were consistently and significantly larger than those from sediment cores throughout the 6-month sampling period (Kolmogorov-Smirnov test, $p < 0.0001$ for every month; Fig. 12). A comparison of the sizes of chironomids in benthic cores taken along the six transect lines revealed remarkably similar size profiles ($F_{[5,6]} = 0.03$, $p = 0.62$; see Saint-Jacques 1996). Thus, it appears unlikely that

white suckers were preferentially feeding in any of the six regions of the lake, but rather that feeding pressure may have been relatively uniform throughout the lake. Collapsing the data from the six benthos transects into three thermal regimes yielded significant differences ($F_{[2,6]} = 5.6$, $p = 0.04$; see Saint-Jacques 1996), as the very few chironomids collected in the hypolimnion tended to be larger than those collected in the epilimnion and metalimnion. It is unlikely, however, that white suckers are choosing to forage to a large extent in the hypolimnion, where larger chironomids are found. Fish usually forage in areas of highest prey density, assuming that other factors such as predation risk are equal (Ringler 1979; Werner et al. 1981; Marrin 1983), and both

Fig. 11. Relative proportions of benthic invertebrates in sediments and white sucker guts, ranked according to increasing size of the benthic invertebrates, based on numerical density (A) and biomass (B). See Table 1 for an explanation of abbreviations used for invertebrate taxa.



the density and biomass of prey were significantly lower at greater depths in the lake (Fig. 5). Also, in Gullfeather Lake a substantial portion (seasonal average 38%) of the lake-bottom area has an oxygen concentration $<1.0 \text{ mg}\cdot\text{L}^{-1}$ during the period of thermal stratification (Trippel and Harvey 1989; Nürnberg 1995). White suckers have never been captured in the nearly anaerobic portion of the lake.

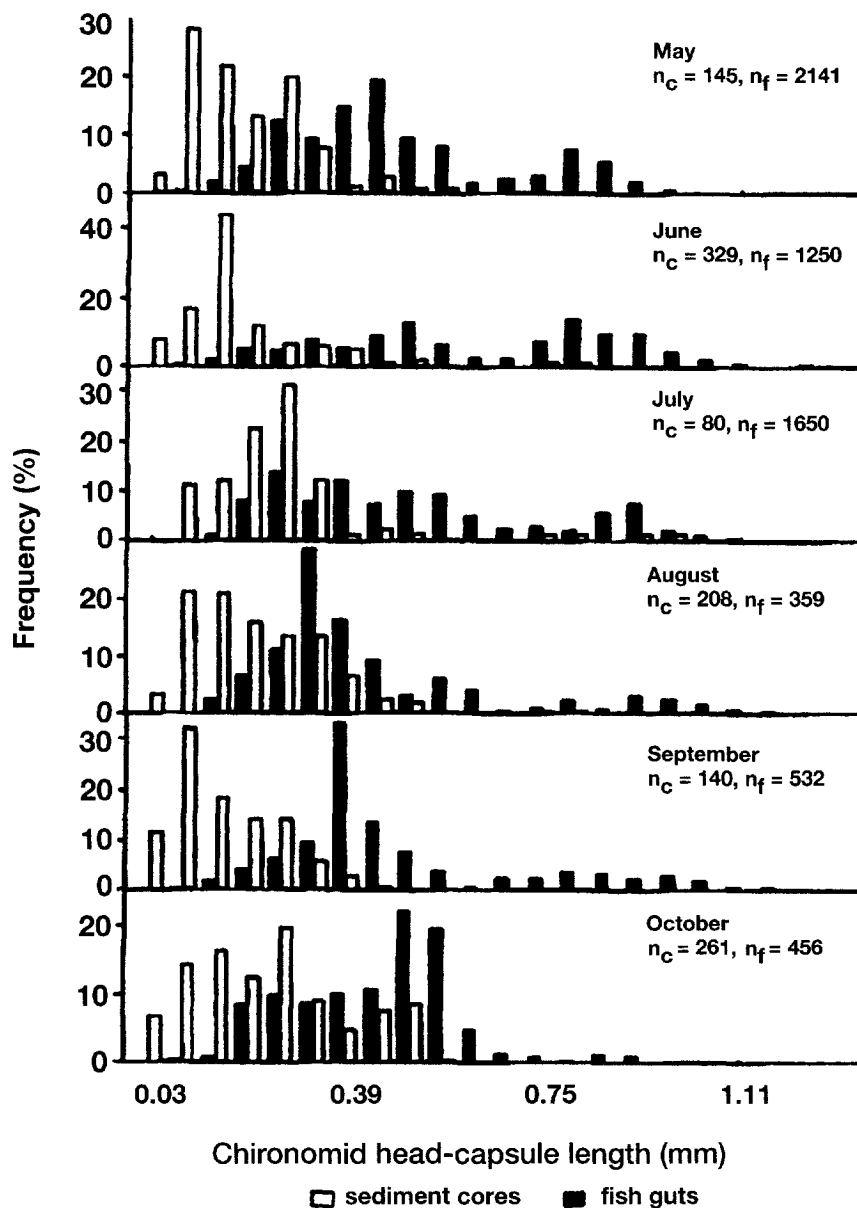
Conclusions

This study demonstrates that white suckers can be adaptive in their use of resources. In feeding, they can specialize on particular prey types (i.e., partition resources) and also upon the largest individuals within a taxon (size-selective predation). These findings refute the widely held belief that the species forages randomly upon the bottom fauna. Also, despite their morphological adaptations for feeding on benthos,

such as a subterminal mouth and papillate lips, more than half of the biomass consumed by Gullfeather Lake white suckers was zooplankton. This may explain some of the past difficulties (Trippel and Harvey 1987; Chen and Harvey 1995; Chen and Harvey 1999) in modelling white sucker growth rates in relation to the abundance of benthos and white sucker population density.

Nonrandom feeding by white suckers in Gullfeather Lake could be due to the abundant food base following the reduction in population density. Whether this selective behaviour would be found in a resource-poor or more competitive environment is an important subject for future study. In past studies, Magnan and co-workers (Lachance and Magnan 1990; Tremblay and Magnan 1991; Lacasse and Magnan 1992) asserted that when resources were shared between competing species, white suckers were very opportunistic, using the

Fig. 12. Frequency distributions of head-capsule lengths of chironomids from sediment cores (open bars) and white sucker guts (solid bars). Sample sizes are shown as follows: n_c , cores; n_f , fish guts.



entire size spectrum of available benthic resources. That is, white suckers are possibly capable of augmenting their food intake by broadening their diet when resources are scarce.

Thus, the ability of white suckers to partition resources, exhibit size-selective feeding behaviour when resource availability is high, and change to a different mode of feeding in a potentially resource-poor environment demonstrates that this species can exhibit considerable flexibility in foraging behaviour. The combination of these attributes, together with their tolerance of a wide range of environmental conditions, makes them a very successful species in terms of abundance and frequency of occurrence.

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References

Ahlgren, M.O. 1990. Diet selection and the contribution of detritus to the diet of the juvenile white sucker (*Catostomus commersoni*). *Can. J. Fish. Aquat. Sci.* **47**: 41–48.
 Ahlgren, M.O. 1996. Selective ingestion of detritus by a north temperate omnivorous fish, the juvenile white sucker, *Catostomus commersoni*. *Environ. Biol. Fishes.* **46**: 375–381.
 Allison, W.R., and Harvey, H.H. 1980. Methods for assessing the benthos of acidifying lakes. *In Effects of Acidic Precipitation on Benthos: Proceedings of a Symposium of the North American Benthological Society.* Edited by R. Singer. North American Benthological Society, Hamilton, N.Y. pp. 1–13.

- Anthony, D.D., and Jorgensen, C.R. 1977. Factors in the declining contribution of walleye (*Stizostedion vitreum vitreum*) to the fishery of Lake Nipissing, Ontario, 1960–76. *J. Fish. Res. Board Can.* **34**: 1703–1709.
- Barton, B.A. 1980. Spawning migrations, age and growth, and summer feeding of white and longnose suckers in an irrigation reservoir. *Can. Field-Nat.* **94**: 300–304.
- Beamish, R.J., and Harvey, H.H. 1969. Age determination in the white sucker. *J. Fish. Res. Board Can.* **26**: 633–638.
- Borgmann, U., and Ralph, K.M. 1985. Feeding, growth, and particle-size-conversion efficiency in white sucker larvae and young common shiners. *Environ. Biol. Fishes*, **14**: 269–279.
- Chen, Y., and Harvey, H.H. 1994. Maturation of white sucker, *Catostomus commersoni*, populations in Ontario. *Can. J. Fish. Aquat. Sci.* **51**: 2066–2076.
- Chen, Y., and Harvey, H.H. 1995. Growth, abundance, and food supply of white sucker. *Trans. Am. Fish Soc.* **124**: 262–271.
- Chen, Y., and Harvey, H.H. 1999. Spatial structuring of length-at-age of the benthivorous white sucker (*Catostomus commersoni*) in relation to environmental variables. *Aquat. Living Resour.* **12**: 351–362.
- Chen, Y., Jackson, D.A., and Harvey, H.H. 1992. A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. *Can. J. Fish. Aquat. Sci.* **49**: 1228–1235.
- Diamond, J.M. 1978. Niche shifts and the rediscovery of interspecific competition. *Am. Sci.* **66**: 322–331.
- Dos Santos, J., and Jobling, M. 1991. Factors affecting gastric evacuation in cod, *Gadus morhua* L., fed single meals of natural prey. *J. Fish Biol.* **38**: 697–713.
- Ehlinger, T.J., and Wilson, D.S. 1988. Complex foraging polymorphism in bluegill sunfish. *Proc. Natl. Acad. Sci. U.S.A.* **85**: 1878–1882.
- Gascon, D., and Leggett, W.C. 1977. Distribution, abundance and resource utilization of littoral zone fishes in response to a nutrient/production gradient in Lake Memphremagog. *J. Fish. Res. Board Can.* **34**: 1105–1117.
- Hartman, K.J., and Brandt, S.B. 1995. Trophic resource partitioning, diets, and growth of sympatric estuarine predators. *Trans. Am. Fish. Soc.* **124**: 520–537.
- Hayes, D.B., and Taylor, W.W. 1990. Reproductive strategy in yellow perch (*Perca flavescens*): effects of diet ontogeny, mortality, and survival costs. *Can. J. Fish. Aquat. Sci.* **47**: 921–927.
- Hayes, D.B., Taylor, W.W., and Schneider, J.C. 1992. Response of yellow perch and the benthic invertebrate community to a reduction in the abundance of white suckers. *Trans. Am. Fish. Soc.* **121**: 36–53.
- Hitchin, G.G., and Yan, N.D. 1983. Crustacean zooplankton communities of the Muskoka–Haliburton Study lakes: methods and 1976–1979 data. Data report DR 83/9 of the Limnology Section, Water Resources Branch, Ontario Ministry of the Environment, Dorset, Ont.
- Jackson, D.A. 1992. Fish and benthic invertebrate communities: analytical approaches and community–environment relationship. Ph.D. thesis, University of Toronto, Toronto, Ont.
- Jackson, D.A. 1993. Multivariate analysis of benthic invertebrate communities: the implication of choosing particular data standardizations, measure of association, and ordination methods. *Hydrobiologia*, **268**: 9–26.
- Jackson, D.A. 1997. Compositional data in community ecology: the paradigm or peril of proportions? *Ecology*, **78**: 929–940.
- Jobling, M. 1981. Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. *J. Fish Biol.* **19**: 245–257.
- Johnson, F.H. 1977. Responses of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations to removal of white sucker (*Catostomus commersoni*) from a Minnesota lake, 1966. *J. Fish. Res. Board Can.* **34**: 1633–1642.
- Kavaliers, M. 1982. Seasonal and circannual rhythms in behavioural thermoregulation and their modifications by pinealectomy in the white sucker (*Catostomus commersoni*). *J. Comp. Physiol. A*, **146**: 235–243.
- Lacasse, S., and Magnan, P. 1992. Biotic and abiotic determinants of the diet of brook trout, *Salvelinus fontinalis*, in lakes of the Laurentian Shield. *Can. J. Fish. Aquat. Sci.* **49**: 1001–1009.
- Lachance, S., and Magnan, P. 1990. Performance of domestic, hybrid, and wild strains of brook trout, *Salvelinus fontinalis*, after stocking: the impact of intra- and interspecific competition. *Can. J. Fish. Aquat. Sci.* **47**: 2278–2284.
- Lalancette, L. 1977. Feeding in white suckers (*Catostomus commersoni*) from Gamelin Lake, Québec, over a twelve-month period. *Nat. Can.* **104**: 369–376.
- Logan, C., Trippel, E.A., and Beamish, F.W.H. 1991. Thermal stratification and benthic foraging patterns of white sucker. *Hydrobiologia*, **213**: 125–132.
- Magnan, P. 1988. Interactions between brook charr, *Salvelinus fontinalis*, and nonsalmonid species: ecological shift, morphological shift, and their impact on zooplankton communities. *Can. J. Fish. Aquat. Sci.* **45**: 999–1009.
- Magnan, P. 1989. The impact of cyprinid and catostomid introductions on brook charr, *Salvelinus fontinalis*, populations: a review. *Physiol. Ecol. Jpn. Spec.* **1**: 337–356.
- Magnan, P., and FitzGerald, G.J. 1982. Resource partitioning between brook trout (*Salvelinus fontinalis* Mitchell) and creek chub (*Semotilus atromaculatus* Mitchell) in selected oligotrophic lakes of southern Quebec. *Can. J. Zool.* **60**: 1612–1617.
- Magnan, P., Rodríguez, M.A., Legendre, P., and Lacasse, S. 1994. Dietary variation in a freshwater fish species: relative contributions of biotic interactions, abiotic factors, and spatial structure. *Can. J. Fish. Aquat. Sci.* **51**: 2856–2865.
- Malmquist, H.J. 1992. Phenotype-specific feeding behaviour of two arctic charr *Salvelinus alpinus* morphs. *Oecologia*, **92**: 354–361.
- Manly, B.F.J. 1986. Multivariate statistical methods, a primer. Chapman and Hall, New York.
- Marrin, D.L. 1983. Ontogenic changes and intraspecific resource partitioning in the tahoe sucker, *Catostomus tahoensis*. *Environ. Biol. Fishes*, **8**: 39–47.
- Nürnberg, G.K. 1995. Quantifying anoxia in lakes. *Limnol. Oceanogr.* **40**: 1100–1111.
- O'Brien, W.J., Evans, B., and Luecke, C. 1985. Apparent size choice of zooplankton by planktivorous sunfish: exceptions to the rule. *Environ. Biol. Fishes*, **13**: 225–233.
- Paloheimo, J.E., and Dickie, L.M. 1966. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. *J. Fish. Res. Board Can.* **23**: 1209–1248.
- Peterman, R.M. 1990. Statistical power analysis can improve fisheries research and management. *Can. J. Fish. Aquat. Sci.* **47**: 2–15.
- Platell, M.E., Potter, I.C., and Clarke, K.R. 1998. Do the habitats, mouth morphology and diets of the mullids *Upeneichthys stotti* and *U. lineatus* in coastal waters of south-western Australia differ. *J. Fish Biol.* **52**: 398–418.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* No. 191.
- Ringler, N.H. 1979. Prey selection by benthic feeders. In *Predator–prey systems in fisheries management*. Edited by R.H. Stroud and H. Clepper. Sport Fishing Institute, Washington, D.C. pp. 219–229.

- Ringler, N.H., and Johnson, J.H. 1982. Diet composition and diet feeding periodicity of some fishes in the St. Lawrence River. *N.Y. Fish Game J.* **29**: 65–74.
- Robinson, B.W., and Wilson, D.S. 1994. Character release and displacement in fishes: a neglected literature. *Am. Nat.* **144**: 596–627.
- Saint-Jaques, N. 1996. Flexibility, and the foraging behaviour of the white sucker *Catostomus commersoni*. M.Sc. thesis, University of Toronto, Toronto, Ont.
- SAS Institute Inc. 1985. SAS user's guide: statistics, version 5. SAS Institute Inc., Cary, N.C.
- Schmitt, R.J., and Holbrook, S.J. 1969. Seasonally fluctuating resources and temporal variability of interspecific competition. *Oecologia*, **69**: 1–11.
- Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. *Bull. Fish. Res. Board Can.* No. 184.
- Skúlason, S., and Smith T.B. 1995. Resource polymorphisms in vertebrates. *Trends Ecol. Evol.* **10**: 366–370.
- Smock, L.A. 1980. Relations between body size and biomass of aquatic insects. *Freshwater Biol.* **10**: 375–383.
- Spoor, W.A., and Schloemer, C.L. 1938. Diurnal activity of the common sucker, *Catostomus commersoni* (Lacépède), and the rock bass, *Ambloplites rupestris* (Rafinesque), in Muskellunge Lake. *Trans. Am. Fish. Soc.* **68**: 211–220.
- Stewart, N.H. 1926. Development, growth, and food habits of the white sucker *Catostomus commersonii* Lesueur. *Bull. U.S. Bur. Fish.* **42**: 147–184.
- Strayer, D.L. 1994. Body size and abundance of benthic animals in Mirror Lake, New Hampshire. *Freshwater Biol.* **32**: 83–90.
- Tremblay, S., and Magnan, P. 1991. Interactions between two distantly related species, brook trout (*Salvelinus fontinalis*) and white sucker (*Catostomus commersoni*). *Can. J. Fish. Aquat. Sci.* **48**: 857–867.
- Trippel, E.A., and Harvey, H.H. 1987. Abundance, growth, and food supply of white suckers (*Catostomus commersoni*) in relation to lake morphometry and pH. *Can. J. Zool.* **65**: 558–564.
- Trippel, E.A., and Harvey, H.H. 1989. Missing opportunities to reproduce: an energy dependent or fecundity gaining strategy in white sucker (*Catostomus commersoni*)? *Can. J. Zool.* **67**: 2180–2188.
- Trippel, E.A., and Harvey, H.H. 1991. Comparison of methods used to estimate age and length of fishes at sexual maturity using populations of white sucker (*Catostomus commersoni*). *Can. J. Fish. Aquat. Sci.* **48**: 1446–1459.
- van Snik Gray, E., Boltz, J.M., Kellogg, K.A., and Stauffer, J.R., Jr. 1997. Food resource partitioning by nine sympatric darter species. *Trans. Am. Fish. Soc.* **126**: 822–840.
- Verdon, R., and Magnin, E. 1977. Dynamique de la population de meuniers noirs *Catostomus commersoni commersoni* (Lacépède) du lac Croche dans les Laurentides, Québec. *Nat. Can. (Que.)*, **104**: 197–206.
- Werner, E.E. 1984. The mechanisms of species interactions and community organization in fish. *In Biological communities, conceptual issues and the evidence. Edited by D.R. Strong, Jr., D. Simberloff, L.G. Abele, and A.B. Thistle.* Princeton University Press, Princeton, N.J. pp. 360–382.
- Werner, E.E., and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.* **15**: 393–425.
- Werner, E.E., Hall, D.J., Laughlin, D.R., Wagner, D.J., and Wilsman, L.A. 1977. Habitat partitioning in a freshwater fish community. *J. Fish. Res. Board Can.* **34**: 360–370.
- Werner, E.E., Mittelbach, G.G., and Hall, D.J. 1981. The role of foraging profitability and experience in habitat use by the bluegill sunfish. *Ecology*, **62**: 116–125.
- Windell, J.T. 1966. Rate of digestion in the bluegill sunfish. *Invest. Indiana Lakes Streams*, **7**: 185–214.
- Zar, J.H. 1984. *Biostatistical analysis*. 2nd ed. Prentice Hall, Englewood Cliffs, N.J.
- Zuckerman, L.D. 1980. Life history regulation in populations of white sucker (Osteichthyes: Catostomidae) as determined by resource availability. M.S. thesis, State University of New York, Syracuse.