Diet and annual production of two boreal river fishes following clearcut logging

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Synopsis

Diet and annual production of two cyprinid fishes in the Piscataquis River, Maine, were investigated before and after extensive deforestation of the surrounding watershed. Observed patterns were evaluated relative to post-logging changes in the benthic macroinvertebrate community, and to differences in ecomorphology between the two fishes. Prey selection was generally density-dependent for both predator species throughout the study, but significant exceptions to density-dependence were observed for several aquatic insect life-mode groups (e.g., swimmers, climbers, burrowers). This apparent preference/avoidance for certain prey taxa by fish predators could be adequately explained by differential availability (vulnerability) among prey taxa. Compared to the year before logging, significant post-logging changes in diet composition and gut fullness were observed for both blacknose dace, *Rhinichthys atratulus,* and creek chub, *Semotilus atromaculatus,* concomitant with post-logging changes in the availability of benthic prey. Annual production of blacknose dace was significantly lower (52.7 vs. 37.7 kg ha^{-1} y^{-1}) in the year following logging. In contrast, annual production of creek chub increased significantly after logging, from 8.6 to 17.4 kg ha^{-1} y^{-1}. Because post-logging changes in the physical environment were probably not sufficient to directly affect fish populations, we hypothesize that blacknose dace were morphologically constrained to feed on a declining aquatic prey resource, with a resultant decline in production. In contrast, the generalist creek chub switched to a non-aquatic prey resource (terrestrial arthropods) and no decline in production was observed for that species.

Introduction

The effects of logging practices on stream fishes in North America are well documented (see reviews by Gibbons & Salo 1973, Wydowski 1978, Moring & Garman 1986). In particular, changes in stream discharge (Bormann & Likens 1979), temperature (Anderson 1973, Feller 1981, Thedinga et al. 1989), substrate composition (Beschta 1978), and large woody debris (Beschta 1979, Murphy et al. 1986) are frequently associated with logging and may directly affect stream survival and recruitment in resident fish populations. Logging may also affect fish assemblages indirectly. Because fish are typ-

ically the top predators in small lotic systems, logging-induced changes in lower trophic levels may affect fish diet, growth, and production, even where fish are not directly affected by logging. Such indirect effects on stream fish populations may be as important as impacts involving direct alteration of fish habitat (Kingsbury & Kreutzweiser 1987).

Changes in stream fish feeding ecology have been associated with environmental disturbances such as channel modification (Benke et al. 1979, Schlosser 1982), impoundment (Mahon et al. 1979), and pesticide use (Kingsbury & Kreutzweiser 1987). Although all of the above studies document indirect effects of environmental disturbance on fish diet, only rarely have such changes been linked to concomitant shifts in fish production (Waters 1982, Portt et al. 1986, Kingsbury & Kreutzweiser 1987, Kreutzweiser 1990). In addition, no published studies have specifically investigated post-logging changes in fish diet and production in eastern North America.

Although temperate stream fishes are generally considered to be opportunistic foragers (Gorman & Karr 1978, Martin-Bergman & Gee 1985, Hansen et al. 1986), finer scales of prey resolution often reveal patterns of non-random exploitation (Allan 1981, Newman 1987). Such selective feeding may be quantified using one or more 'electivity' indices (e.g., Ivlev 1961, Chesson 1978, Strauss 1979), but indices based on relative abundances of prey taxa have been criticized on both statistical (Kohler & Ney 1982) and theoretical (Ware 1973) grounds. Results of feeding selection studies that use such indices are frequently interpreted, either explicitly or implicitly, as indicating active preference for, or avoidance of, particular prey items by the predator. Such an interpretation is, however, warranted only where all members of the prey spectrum are equally available to fish predators (Strauss 1979, Kohler & Ney 1982) — an unlikely situation in streams, considering the diversity of microhabitats occupied by stream-dwelling prey. Alternatively, patterns of apparent prey selection in fishes have been explained as resulting from differential prey availability (Ware 1973, Schlosser 1982, Konkle et

al. 1990), and predator ecomorphology (Wainwright 1988, Meyer 1989).

We initiated a study to: (1) test the hypothesis that deforestation had indirect effects on fish diet and production, and (2) evaluate fish diet in relation to both taxonomic and behavior-based descriptions of the benthic macroinvertebrate prey assemblage.

Study area

As part of a larger investigation of the effects of deforestation on trophic structure of a river community (Garman 1984, Garman & Moring 1991), fishes of the East Branch of the Piscataquis River, Piscataquis County, Maine, were studied from December 1980 to December 1982. A 1.2 km section of the river was selected as the study area. Within the study area, stream width and depth averaged 5 m and 1 m, respectively. Substrate was composed of large cobble (50–240 mm diameter) and gravel (10–49 mm diameter). Physicochemical traits were typical of small rivers within the spruce-fir forest biome of northeastern North America (Garman 1984). Approximately 90 percent of the standing timber – mostly white spruce, *Pinea glauca,* and balsam fir, *Abies balsamea* – was removed by a commercial clearcut in January 1982. Most riparian vegetation was also removed, but the river channel was undisturbed and introduction of large woody debris to the stream was insignificant.

A nearby watershed was initially selected as an experimental control, but a change in cutting schedules resulted in the watershed being logged in early 1981. No other suitable control stream was available in the vicinity, and the presence of extensive bogs on the East Branch Piscataquis River precluded the use of upstream areas as an experimental control.

Methods

Two cyprinid species, creek chub, *Semotilus atromaculatus,* and blacknose dace, *Rhinichthys atratu-*

lus, comprised over 90 percent (by number) of the Piscataquis River fish community and were selected for study. Brook charr, *Salvelinus fontinalis*, northern redbelly dace, *Phoxinus eos*, and white sucker, *Catostomus commersoni*, were occasionally collected in both years. Fish were sampled by electrofishing in May, August and November of 1981 and 1982 from randomly-chosen, 300 m sites within the study area; absolute abundance and associated variance for both fishes were estimated on each date by three-run removal (Zippin 1956). Individual fish were weighed to the nearest 0.1 g. Abundance estimates and the mean weights were used to estimate annual production of both species by the size-frequency method (Garman & Waters 1983, Kreutzweiser 1990). A subset of sampled fish (349 creek chub and 334 blacknose dace) were preserved in 10 percent formalin and stomachs were later removed for diet analysis. Stomach contents were indentified to genus (except Chironomidae), counted, and each prey taxon was expressed as the numerical percentage of all prey. Significant differential digestion of prey types, a potential source of bias in feeding selection studies (Strauss 1979), was not observed.

Several days before each estimate of fish abundance, benthic macroinvertebrates were quantitatively sampled with a modified Hess sampler (20 cm diameter, 256 μ mesh) at randomly-selected locations. Substrate was excavated to a depth of 20 cm and all material was carefully washed within the sampler; a minimum of six such samples were taken on each of the six dates. All organisms were identified to genus (except Chironomidae), and counted. The mean density (numbers per m²) of each macroinvertebrate taxon was determined on each date as an index of potential prey availability to Piscataquis River fish predators. Organisms were also assigned to one of five 'life-mode' categories (e.g., borrower, climber, swimmer, clinger, sprawler), following the classification of Merritt & Cummins (1978).

A Wilcoxon nonparametric ranking procedure (Kohler & Ney 1982) was used to determine if relative proportions of prey and potential prey types were significantly different, i.e. is selection

indicated? Statistical differences in annual production estimates were determined based on 95 percent confidence intervals (Newman & Martin 1983). Differences among mean macroinvertebrate densities and among mean prey number per fish stomach were inferred from approximate 95 percent confidence intervals ($\pm$ 2 SE).

Results

Following logging, some abiotic characteristics of the Piscataquis River were significantly altered, including diurnal and seasonal temperature regimes and suspended particulates (Garman & Moring 1991). None of these changes, however, reflected substantial alterations in physical features of fish habitat (Garman & Moring 1991). However, abundance and composition of the aquatic macroinvertebrate community did change after logging (Garman 1984). Specifically, overall mean density of aquatic macroinvertebrates within the study area was significantly higher and lower (P < 0.05) during spring and fall, 1982, respectively, compared to similar periods in 1981 (Table 1). Throughout the post-logging year, several insect taxa including Ephemeroptera, Plecoptera, and Odonata, were significantly less abundant in the benthos (P < 0.05), compared to 1981; chironomids (Diptera) increased substantially (3 ×) in abundance after logging. Taxonomic composition and relative abundance of the Piscataquis River fish community, however, was only slightly different between 1981 and 1982 (Garman 1984), indicating minimal direct impact of logging on the fish assemblage.

Blacknose dace diet

Several benthic insect taxa (e.g., *Stenonema*, *Ephemerella*, *Hydropsyche*, and Chironomidae) were numerically important in the diet of blacknose dace, and in the benthos, during most sampling periods. Taxa that occurred infrequently in the benthos were generally uncommon in black-
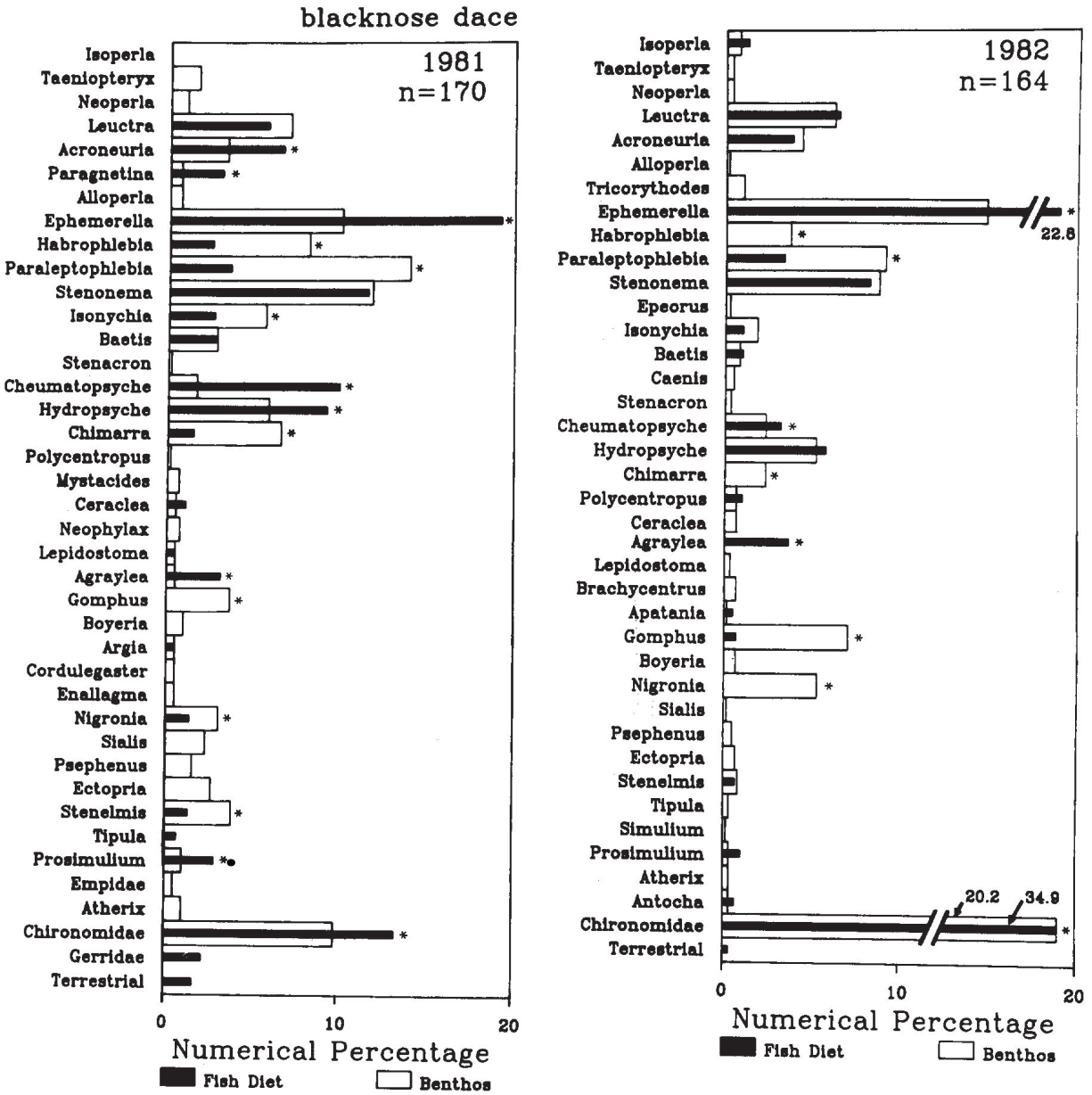
blacknose dace

Fig. 1. Diet of blacknose dace, *Rhinichthys atratulus,* expressed as a numerical percentage (solid bars), and relative numerical composition of benthic taxa (open bars) in the Piscataquis River, Maine, before (1981) and after (1982) deforestation of the adjacent watershed. Fish diet values are means of three collections made in May, August and November of each year; benthos values are means of at least six replicate samples taken prior to each fish collection. An asterisk (*) indicates significant difference (P < 0.05) in the numerical percentages of the respective prey taxon between benthos and fish diet.

nose dace stomachs (Fig. 1). Departures from this general pattern were, however, observed in both years. Both before and after logging, *Ephemerella* prey were significantly more common (P < 0.05) in blacknose dace stomachs than in samples of the benthos, suggesting positive selection for that tax-

on. *Cheumatopsyche, Hydropsyche, Acroneuria, Agraylea* and *Prosimulium* were also frequently over-represented in the diet, relative to their abundance in the benthos. In contrast, the mayflies, *Habrophlebia, Paraleptophlebia* and *Isonychia,* the caddisfly *Chimarra,* the odonate *Gomphus,*
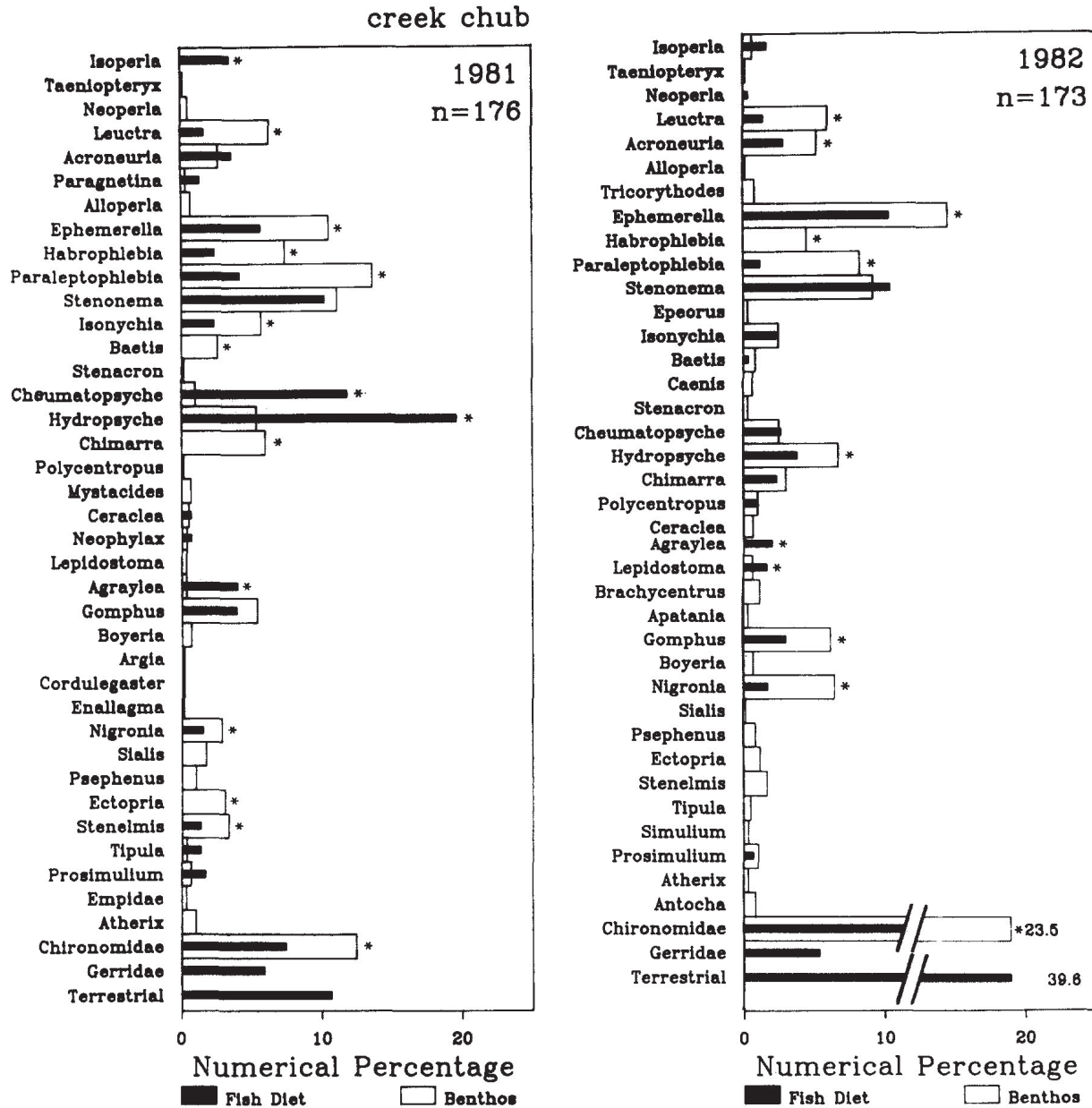
Fig. 2. Diet of creek chub, *Semotilus atromaculatus,* expressed as a numerical percentage (solid bars), and relative numerical composition of benthic taxa (open bars) in the Piscataquis River, Maine, before (1981) and after (1982) deforestation of the adjacent watershed. Fish diet values are means of three collections made in May, August, and November of each year; benthos values are means of at least six replicate samples taken prior to each fish collection. An asterisk (*) indicates significant difference (P < 0.05) in the numerical percentages of the respective prey taxon between benthos and fish diet.

and several other genera, were significantly under-represented in blacknose dace stomachs, relative to their apparent availability (P < 0.05). Non-insect and non-benthic insect (Gerridae) prey were consumed infrequently in both years by blacknose dace, as were terrestrial prey.

No major between-year differences in diet were apparent for blacknose dace, with the exception of chironomids, which more than doubled in numerical importance in the diet after logging. This increase was concomitant with a significantly higher (P < 0.05) density of chironomids in the benthos.

Chironomid larvae replaced *Ephemerella* as the dominant prey of blacknose dace in all post-logging samples, and on two occasions (May and August 1982) chironomids were significantly more abundant (P < 0.05) in blacknose dace stomachs than in benthos samples.

Creek chub diet

Although the diet of creek chubs in 1981 and 1982 reflected the same general patterns of composition and relative importance of prey taxa described for blacknose dace, several major differences were apparent (Fig. 2). *Ephemerella*, a major prey of blacknose dace in both years, was frequently under-represented in, or absent from, creek chub stomachs in 1981 and 1982. Chironomids were consumed less frequently by creek chub than by blacknose dace in both years, even though chironomids dominated the post-logging benthos. Also, non-benthic insects (Gerridae) and terrestrial prey were consumed frequently by creek chubs in both 1981 and 1982.

The numerical proportions of *Cheumatopsyche* and *Hydropsyche* in the diet of creek chubs were each significantly higher (P < 0.05) than in 1981 benthos samples (Fig. 2). After logging, however, hydropsychid caddisfly larvae were replaced by terrestrial arthropods as the most frequently-encountered prey in creek chub stomachs on all 1982 sampling dates, the latter ranging between 22 and 52 percent (number) of the diet in 1982.

Several taxa were consistently under-represented in creek chub diets compared to both 1981 and 1982 benthos samples. This difference between apparent prey availability and occurrence in the diet was significant (P < 0.05) for *Leuctra, Isonychia, Habrophlebia, Paraleptophlebia, Gomphus, Nigronia, Stenelmis* and chironomids on most dates. Many of these same genera were also less common in blacknose dace stomachs than random prey selection would predict.

The mean number of prey in fish stomachs, and mean density of benthic macroinvertebrates, was significantly lower (P < 0.05) in November 1982, compared to the same date in 1981 (Table 1). In contrast, creek chub stomachs contained a significantly higher (P < 0.05) number of prey (dominated by terrestrial arthropods) in August and November 1982, compared to the same months before logging.

Fish production

Estimates of annual production for blacknose dace and creek chub populations in the Piscataquis River showed significant (P < 0.05) between-year differences (Table 2). The direction of these changes was not, however, the same for the two species. In the year following logging, the production of creek

Table 1. Mean number of prey in stomachs of blacknose dace, *Rhinichthys atratulus* (n = 334) and creek chub, *Semotilus atromaculatus* (n = 349), and in benthic samples (numbers per m²) from the Piscataquis River, Maine before (1981) and after (1982) deforestation. Numbers in parentheses are approximate 95 percent confidence intervals.

	May		August		November	
Blacknose dace						
1981 (n = 176)	3.1	(0.4)	3.0	(0.2)	3.3	(0.6)*
1982 (n = 173)	3.0	(0.6)	2.9	(0.4)	2.1	(0.4)
Creek chub						
1981 (n = 170)	3.5	(0.6)	3.0	(0.6)*	3.4	(0.4)*
1982 (n = 164)	3.4	(0.4)	4.5	(0.3)	4.2	(0.3)
Benthos						
1981 (n = 20)	1085	(84)*	1347	(136)	4060	(504)*
1982 (n = 22)	2056	(194)	1312	(204)	1478	(338)

* P < 0.05, between-year comparisons.

chub was 102 percent higher than in 1981. In contrast, blacknose dace annual production declined by 28 percent, compared to the pre-logging estimate. Total production of the Piscataquis River fish assemblage, conservatively estimated by combining values for creek chub and blacknose dace, declined slightly (61.3 vs. 55.1 kg ha^{-1} y^{-1}) after logging. Ratios of annual production/mean biomass (P/B) were 1.0 and 1.1 for blacknose dace and 0.6 and 0.7 for creek chub, in 1981 and 1982, respectively.

Discussion

Feeding ecology

The feeding ecology of blacknose dace and creek chub – common, stream-dwelling cyprinids of central and eastern North America – in the Piscataquis River was similar to the findings of other investigators. Blacknose dace typically feed on small aquatic insects, and on chironomid larvae in particular (Johnson 1982). Composition of the diet generally reflects that of the benthos, and terrestrial prey are rarely consumed (Johnson & Johnson 1982). Creek chubs are highly opportunistic feeders and, unlike blacknose dace, may feed extensively on non-insect aquatic invertebrates and on terrestrial arthropods (Barber & Minckley 1971). Although large creek chubs may be piscivorous (Fraser & Emmons 1984, Schlosser & Ebel 1989), no evidence of pisci-

Table 2. Estimates of annual production (P) and production/biomass ratios (P/B) for blacknose dace, *Rhinichthys atratulus*, and creek chub, *Semotilus atromaculatus*, from the Piscataquis River, Maine, before (1981) and after (1982) deforestation. Numbers in parentheses are 95 percent confidence intervals.

	P (kg ha^{-1} y^{-1})	P/B
Blacknose dace		
1981	52.7 (8.0)*	1.0
1982	37.7 (4.6)	1.1
Creek chub		
1981	8.6 (3.9)*	0.6
1982	17.4 (4.1)	0.7

*P < 0.05, between-year comparisons.

vory was found in the present study. Results of this study support the view of the creek chub as a generalist predator, feeding on a wide range of aquatic and terrestrial macroinvertebrates, and of blacknose dace as a less opportunistic predator of benthic aquatic insects.

Feeding by creek chub and blacknose dace in the present study generally conformed to a model of random prey choice (Gorman & Karr 1978, Hansen et al. 1986), but examples of apparent feeding selection were observed for both predator species. Departures from random feeding in the present study could be interpreted as indicating active preference for, or avoidance of, certain prey taxa by fish predators. However, such an interpretation is justified only when availability of all prey taxa is equivalent (Strauss 1979, Kohler & Ney 1982), and this is unlikely in a structurally-complex environment like the Piscataquis River. Alternatively, aquatic insect behavior, such as swimming duration, burrowing and overall activity level (Ware 1973, Janssen 1982, Dixon & Baker 1988, Konkle et al. 1990, McPeek 1990) and microhabitat choice (Crowder & Cooper 1982, Angermeier 1985), may differentially mediate detection and/or capture of macroinvertebrate taxa by fish predators.

Prey size may also be an important determinant of prey choice by stream-dwelling fish (Allan 1978, Newman 1987). However, because most Piscataquis River macroinvertebrates were small (< 10 mm; G. Garman unpublished data), fish predators were not considered to be gape-limited (Schmitt & Holbrook 1984). A possible exception was the prey genus *Nigronia* (Megaloptera), which frequently exceeded 30 mm in length (G. Garman unpublished data), and occurred rarely in fish diets.

Differential utilization of the same food resource by co-occurring fishes may also result from differences in predator feeding morphology that affect capture efficiency for, or availability of, certain prey types (Keast & Webb 1966, Wainwright 1988, Meyer 1989). The large terminal mouth and fusiform body of the creek chub are characteristic of a highly-mobile, generalist predator (Keast & Webb 1966). In contrast, the smaller, sub-terminal mouth

and negative buoyancy of the blacknose dace are adaptations of a benthic life (Hynes 1970).

Fish can respond adaptively (i.e. optimize energy intake) to changes in the food resource (Dill 1983). In this study, creek chubs responded to shifts in the quantity and quality of autochthonous aquatic prey by increasing consumption of terrestrial arthropods, thereby maintaining or increasing the average number of prey in the gut in the year after logging. A similar response to declines in autochthonous prey was shown for brook charr by Allan (1981) and Kingsbury & Kreutzweiser (1987).

In a Virginia stream, water-column fishes (*Notropis* spp.) with terminal mouths consumed terrestrial arthropods, while co-occurring benthic genera (e.g., *Etheostoma, Percina*) fed only on the benthos (Garman 1991). In the same study, terrestrial arthropods were collected almost exclusively from the uppermost 2 cm of the water column. Blacknose dace in the Piscataquis River may have been constrained, either morphologically or through behavioral interaction with creek chub (Fraser & Emmons 1984), from exploiting alternate prey, particularly terrestrial arthropods, during 1982.

Fish production

Few estimates of annual production are available for stream-dwelling cyprinid fishes in North America (Neves 1981, Neves & Pardue 1983, Mahon & Balon 1985). Annual production and P/B ratios in the Piscataquis River generally agree with available values for creek chub (Lotrich 1973, Mahon et al. 1979) and blacknose dace (Mahon et al. 1979, Neves & Pardue 1983) elsewhere. The significant between-year difference in annual production observed for creek chub in the Piscataquis River was generally greater than annual variation reported elsewhere for stream-dwelling fishes under undisturbed conditions (Hunt 1974, Egglishaw & Shackley 1977, Newman & Waters 1989). However, the smaller decline in blacknose dace annual production between 1981 and 1982, although statistically significant, may be the result of natural variation.

The lower annual P/B ratios for creek chub, com-

pared to blacknose dace ratios, were consistent with the larger size and greater longevity of the former species (Neves 1981, Waters et al. 1990). Because P/B ratios are a reflection of growth (Whitworth & Strange 1983), and ratios were relatively constant between years for both fishes, it is not possible to explain annual production differences solely on the basis of observed changes in fish diets. However, both predators altered their diets in response to changes in the quantity and quality of the prey resource, and did so in ways that would appear to be adaptive (Dill 1983). The constancy of P/B values after logging may be due to shifts in age and size structure of the populations as a result of emigration from, or immigration to, the study site (Newman & Waters 1989). However, no information on fish movements during the study is available.

Conclusions

Behavioral and morphological characteristics of aquatic insects have been used to classify taxa into 'life-modes' (Merritt & Cummins 1978), which might be expected to reflect prey availability, irrespective of prey taxon. For example, insects classified as burrowers and swimmers may be infrequently detected or captured by fish predators, due to cryptic habits or the ability to avoid capture. Aquatic insects in other life-mode groups (e.g., clingers, sprawlers, and climbers) inhabit substrate surfaces, are generally poor swimmers, and may be more vulnerable (i.e. available) to fish predators. In this study, most prey genera for which apparent positive selection was observed were classified as clingers (e.g., *Hydropsyche, Cheumatopsyche, Ephemerella*), climbers (*Agraylea*), or groups that could not be assigned to a single life-mode category (e.g., Chironomidae). In contrast, apparent negative selection was consistently observed for insects classified as burrowers (e.g., *Gomphus*) and moderate to strong swimmers (e.g., *Habrophlebia, Paraleptophlebia, Isonychia*).

Although changes in the abiotic character of the Piscataquis River after logging appeared relatively innocuous and did not directly affect fish habitat or

fish community structure (Garman 1984, Garman & Moring 1991), diets and production rates of two cyprinid species were significantly different between years. The post-logging changes in fish production followed a disturbance that altered prey abundance, but did not substantially affect fish habitat. Because an experimental control for the logging treatment could not be used during the study, however, the relationship between logging and changes in fish production and diet cannot be described as causal.

Long-term changes in trophic structure of stream fish assemblages after disturbance may include shifts toward omnivory (Schlosser 1982, Karr et al. 1985) and increased dependence on autochthonous energy sources (Karr & Schlosser 1978, Vannote et al. 1980, Minshall et al. 1985), particularly where disturbance includes removal of riparian vegetation. For that part of the Piscataquis River affected by logging, the future fish community will likely be characterized by increased dominance by resident omnivores (e.g., white sucker), declines in resident insectivore species (e.g., brook charr and blacknose dace) and recruitment of fishes more typical of downstream sections of the Piscataquis River.

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