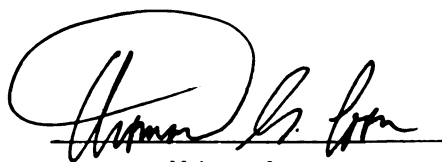This is to certify that the

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Among Populations of Redside Dace, a
Threatened Species in Michigan

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BEHAVIORAL, PHYSIOLOGICAL AND MORPHOLOGICAL SIMILARITY AMONG POPULATIONS OF REDSIDE DACE, A THREATENED SPECIES IN MICHIGAN

By

Douglas Craig Novinger

A THESIS

Submitted to
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MASTER OF SCIENCE

Department of Fisheries and Wildlife

ABSTRACT

BEHAVIORAL, PHYSIOLOGICAL AND MORPHOLOGICAL SIMILARITY AMONG POPULATIONS OF REDSIDE DACE, A THREATENED SPECIES IN MICHIGAN

By

Douglas Craig Novinger

I studied variation in behavior through observations of microhabitat use at sites in Michigan and New York. Redside dace occupied low velocity, mid-water positions in the deepest parts of pools. Differences among populations in habitat use corresponded with differences in habitat availability. I studied variation in physiological traits by measuring resting routine metabolic rate and critical thermal maximum for four temperature acclimated New York populations in the lab. Metabolic rate was also measured for naturally acclimated fish in the field in New York and Michigan. New York redside dace showed significant increases in metabolism and CTM with temperature. Michigan redside dace tested in the field had a significantly higher metabolic rate than that predicted for New York fish at the same temperature. Morphological variation was studied through a morphometric and meristic analysis and revealed that Michigan and Wisconsin specimens were most different in body shape and lateral line scale counts.

To my loving wife Sarah, for your unending patience and strength.

ACKNOWLEDGMENTS

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INTRODUCTION

The redside dace, *Clinostomus elongatus*, is a threatened minnow species in

Michigan. Successful management of the remnant Michigan populations is impaired by an

inadequate understanding of the ecological requirements of the redside dace and by the

current rarity of the fish. One solution to this problem is to look to other regions where

redside dace are abundant and more easily observed. However, significant heterogeneity

in phenotypic and genetic characters may exist among disjunct populations such as those

of redside dace (Shields and Underhill, 1993; Foster et al., 1992; White, 1988). The

similarity of populations of redside dace in Michigan to geographically separate

populations is not understood. If they are similar, populations of redside dace in other

states may adequately model the habitat needs, reproductive traits, and other attributes of

Michigan fish. Redside dace from outside of Michigan may also represent future sources

of fish for stocking into Michigan to reestablish Michigan populations. To assess the

potential of either use, it is necessary to determine the similarity of redside dace in

Michigan to redside dace from other parts of its range.

Background. - This project integrates observations of behavioral, physiological, and

morphological similarity and differences between geographically isolated populations of

redside dace to provide information useful to improving the species' status in Michigan

and elsewhere. Behavioral, physiological, and morphological traits describe phenotypic

attributes that are critical determinants of an organism's ecological niche and are at least

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indirectly related to evolutionary fitness; they are often studied separately (Foster et al., 1992; Ehrlich and Roughgarden, 1987; Kerr and Ryder, 1979). Several works suggest that aspects of the phenotype may evolve together in response to changing environmental conditions (Foster et al., 1992; Endler, 1986; Fry, 1971). The apparent interrelatedness of phenotypic traits further suggests that conclusions based on the examination of only one aspect of phenotypic variation may be misleading, thereby requiring detailed knowledge of a species' ecological requirements for the design of successful management policies. In the same way, approaches that only consider genotypic traits are usually unable to relate measures of genetic variation to the interactions of an organism with its environment. Despite their frequent use, molecular techniques have yet to prove their reliability in phylogenetic analysis over traditional morphological methods (Patterson et al., 1993). Rather, a genotypic approach to describing ecologically significant variation within and among groups should be complementary to a phenotypic approach.

Fry (1971) provided a framework in which to describe the relationships between environmental factors and behavioral capacities when he defined the metabolic "scope for activity" and complementary "zone of tolerance." The determination of metabolic rates and thermal tolerances are necessary components of Fry's models and may be used to measure the realized or potential functional status of an organism in units that are observable, common, and important to all organisms in a community (Kerr and Ryder, 1977). Estimation of resting metabolic rates and thermal tolerance have been useful for the prediction of optimum growth and food consumption rates as well (Jobling, 1983; Brett and Groves, 1979).

Patterns of habitat use have also been described in terms of the bioenergetic tradeoffs between metabolic requirements and the availability of critical resources such as food and shelter (Hill and Grossman, 1993; Hughes and Dill, 1990). It is generally understood that habitat use and inter- and intraspecific behavioral interactions are important in establishing fish community structure and species distributions (Grossman and Freeman, 1987).

Morphology has been linked to the ecology of fishes through intraspecific variation in life history and behavior, and has been used to predict patterns of habitat use and trophic position, and to infer phylogenetic relationships (Shields and Underhill, 1993; Foster et al., 1992; Reinthal, 1990; Felley, 1984; Gatz, 1979). Morphology has also been related to physiological performance through measurements of swimming and aerobic efficiency in fishes under a variety of environmental conditions (Brett and Groves, 1979; Webb, 1971).

The description and measurement of phenotypic attributes provides information that is readily usable by managers in the design and implementation of resource policies. Habitat elements including instream structures, channel morphology, and water quality may be manipulated or regulated to effect a response in aquatic organisms; achieving the desired result depends on a sound base of ecological knowledge that allows an accurate prediction of the response of individual species to environmental perturbation. Such understanding is essential in the case of endangered species which typically have narrow environmental tolerances and restricted distributions.

Redside dace belong to a unique assemblage of glacial relict species that inhabit the
Great Lakes basin and are distributed in disjunct populations characteristic of restricted
headwater stream fishes (White, 1988; Smith et al., 1981). In the western edge of their
range, redside dace are found in southeastern Minnesota and in the upper Mississippi
River and Lake Michigan basins of Wisconsin. East of Lake Michigan, redside dace occur
in southeastern Michigan, eastern Indiana, Ohio, northern Kentucky, West Virginia,
Maryland, and Pennsylvania, and are abundant in south-central New York. Redside dace
are also found in southern Ontario, Canada (Gilbert, 1980). Past geophysical processes
have undoubtedly played a major role in delineating the species' discontinuous
distribution. Redside dace probably occupied a more continuous northern range that was
disrupted during the Wisconsinan glacial advances as recently as 9 - 14,000 years ago
(Bailey and Smith, 1981). The importance of glacial refugia and routes of redispersal in
structuring the current patterns of distribution has been described for several species of
northern fishes (Underhill, 1986; Bailey and Smith, 1981; Hubbs and Lagler, 1964).
Current distribution of the redside dace is likely a historic product of migration and
changes in watershed boundaries through shifts in drainage outlets among the Great Lakes
and through headwater stream capture (Smith et al., 1981). In recent time, human
activities have further restricted the range of the redside dace and may threaten its
continued survival in Michigan (Coon, 1993; Smith et al., 1981; Trautman, 1981).

Green noted as early as 1935 that the redside dace exhibited a disjunct, extremely
localized, and shrinking distribution that was characteristic of a species threatened with
extinction. Factors identified as most responsible for the demise of native fishes in

southeastern Michigan and throughout North America include widespread degradation

and destruction of instream and riparian habitat, deteriorating water quality ascribed to

erosion and chemical alteration, overexploitation, and the introduction of nonindigenous

species (Warren and Burr, 1994; Cain, 1993; Miller et al., 1989; Karr et al., 1985; Smith,

1981). All are symptoms of the rapidly expanding influence of human activities on stream

ecosystems. Smith et al. (1981) demonstrated the influence of agricultural and urban

development and pollution on fish communities in the Raisin River system of southeastern

Michigan, noting that several species were restricted to the upper part of the drainage and

were threatened by the loss of critical habitat. They further documented the extirpation of

two headwater species from the watershed, the bigeye chub (*Hybopsis amblops*) and the

eastern sand darter (*Ammocrypta pellucida*) which, as suggested for redside dace

(Trautman, 1981), require clear water and gravel for spawning. The Raisin River drainage

is positioned between the two watersheds that hold the remaining extant populations of

redside dace in Michigan. Karr et al. (1985) presented similar findings for the Maumee

River drainage of northwestern Ohio and southeastern Michigan where one of the

remaining redside dace populations is located. They found that 50% of the headwater

species in the drainage had declined in abundance since 1850, and four headwater

invertivores that required clear water had been extirpated from the system. Human

impacts, particularly erosional inputs from intensive agriculture, have been implicated in

the decline of the redside dace in other parts of its range (Parker et al., 1988; Cooper,

1983; Trautman, 1981; Gilbert, 1980; Eddy and Underhill, 1974; Scott and Crossman,

1973).

Though locally abundant in certain regions, isolated populations of redside dace are especially vulnerable to chance catastrophic events because mortality in a local population is unlikely to be offset by immigration from other populations. Individual rosyside dace, *Clinostomus funduloides*, the closest relative of redside dace, have a small home range (Hill and Grossman, 1987). In addition, a disjunct distribution may have important implications for inter- and intrapopulation genetic diversity that have also been described for rosyside dace inhabiting headwater streams in southern Ohio (White, 1988). White (1988) found significant heterogeneity among populations at two polymorphic allozyme loci, which he interpreted as a minor degree of interpopulation differentiation. The most significant discovery, though, was of unexpectedly low levels of intrapopulation variability that supported an hypothesis of routine bottleneck episodes and coinciding founder effects (Hartl and Clark, 1989). Similar conditions may prevail among populations of redside dace that exhibit a similar, restricted pattern of distribution.

Several jurisdictions have provided protection of the redside dace. They are listed as species of special concern in Kentucky and West Virginia, and are under legal protection in Indiana (possibly extirpated; Gilbert, 1980). Redside dace have been extirpated from Iowa (Harlan and Speaker, 1987) and have decreased dramatically in Ohio (Trautman, 1981) and Ontario (Parker et al., 1988). Furthermore, Becker (1983) reported the "disappearance" and "severe decimation" of several populations in southeastern Wisconsin.

In other parts of their range, redside dace appear to be abundant and persistent. Populations in southeastern Minnesota, northern Wisconsin, and western New York have

not experienced the declines reported for redside dace elsewhere (J. Underhill, J. Lyons, and R. Daniels, personal communication).

The redside dace is known from the headwaters of the Upper and Middle River Rouge, a single tributary of the Huron River, and a tributary of the Maumee River near the Ohio border (Carl Latta, personal communication) in southeastern Michigan and is listed as a threatened species in the state. Redside dace have also been introduced into Fleming Creek, a tributary of the Huron River near Ann Arbor. Collection records of the University of Michigan Museum of Zoology suggest that the redside dace may have been more widely distributed in the River Rouge watershed in the recent past and survey efforts have demonstrated a decline in populations in the Upper River Rouge (G.Smith, personal communication); however, the full extent of their historical Michigan range is unknown. There is currently no evidence to suggest that redside dace were ever more widespread among southeastern Michigan watersheds nor has the complete loss of populations from a watershed been documented.

Adult redside dace average 65 - 70 mm in standard length and are easily identified from other cyprinids by their large eyes and large, upturned mouth with a projecting lower jaw. They are dark olive along the top of the back with a bright, golden stripe that stretches from the upper operculum to the base of the tail. A dark, midlateral stripe extends along the posterior portion of the body, and becomes mixed with silvery pink anterior of the dorsal fin. This region becomes a striking crimson in breeding males.

The biological literature offers little in the way of comprehensive life history research concerning the redside dace. Habitat use by redside dace has been described in detail at one

site by Koster (1939) and in general terms by several authors referenced below. Redside dace are found in cool, clear headwater streams with moderate gradient that offer a mixture of pool and riffle habitats (Meade et al., 1986; Becker, 1983; McKee and Parker, 1982; Trautman, 1981; Koster, 1939) . Though adults are most often collected in pools, they reportedly use riffles for spawning (Koster, 1939).

Riparian vegetation also appears to be an important attribute of redside dace habitat, perhaps due to the specialized feeding habits of redside dace (Daniels and Wisniewski, 1994; Parker et al., 1988; Schwartz and Norvell, 1958). In summer, redside dace feed primarily on terrestrial insects that land or fall to the water's surface, and regularly leap several inches into the air to catch hovering insects (personal observation; Daniels and Wisniewski, 1994; Schwartz and Norvell, 1958; Koster, 1939). Redside dace stomachs analyzed by Daniels and Wisniewski (1994) and Schwartz and Norvell (1958) contained 77 - 88% aerial terrestrial insects by number, primarily adult Diptera.

Information on the physiology and phylogeny of redside dace is more limited. Evans and Deubler (1955) gave a detailed description of the process of pharyngeal tooth replacement in redside dace. Bailey (1951) discussed the relationship of *Clinostomus* to *Richardsonius* and *Gila*, suggesting that the groups be combined into the single genus *Gila*. In contrast, Koster (1939) remarked on similarities of redside dace to *Chrosomus* (*Phoxinus*) spp. as well as to *Margariscus margarita*. The rosyside dace is the only congener of redside dace and has a more southern distribution (Gilbert, 1980); the ranges of the two species are adjacent but do not overlap.

Difficult questions concerning the continued survival of redside dace in Michigan are imminent. In at least two of the four populations in Michigan, immediate threats are posed by residential and commercial development in suburban Detroit and by the introduction of a potential predator, brown trout (*Salmo trutta*), a non-native sport fish. Research efforts that are directed to improve our understanding of the ecological requirements of redside dace in Michigan are warranted for several reasons. First, redside dace appear to have narrow habitat tolerances which make them a valuable indicator of stream quality (Smith et al., 1981). More importantly, redside dace fill a unique role as a significant piscivorous predator on aerial terrestrial insects. The specialized foraging strategy of the redside dace is distinct among members of the minnow family as well as among other North American stream fishes.

Objectives. - The purpose of this research project was to evaluate the potential for using redside dace outside of Michigan as models by comparing the phenotypic similarity of populations from Michigan, New York, and Wisconsin, populations representing the breadth of the species' distribution. This study describes ecological requirements of the redside dace and provides information that is immediately useful in formulating management plans for redside dace in Michigan and for declining populations threatened in other states.

My specific objectives were to describe (1) behavioral similarity between regions by comparing instream observations of microhabitat use, (2) physiological similarity among populations and regions by comparing metabolic rates; I also provided information on the thermal tolerance of New York redside dace as it related to variation in acclimation

temperatures, and (3) morphological similarity among populations and regions based on a comparison of morphometric and meristic traits.

To complete the three objectives, the project coordinated activities in the field, lab, and museum to make comparisons within and among geographic regions. Field work encompassed observations of behavior and microhabitat use of redside dace (first objective) in one stream in Michigan and two streams in New York. Physiological comparisons (second objective) were made in the field through the instream measurement of metabolic rates at one site in Michigan and one site in New York. Lab work also focused on comparisons of metabolic rates and thermal tolerances of redside dace (second objective) collected from four populations in New York that were returned to Michigan for study. I was restricted by state regulations from transporting Michigan redside dace to the lab. Research at the University of Michigan Museum of Zoology was performed with preserved specimens to satisfy the third objective, a comparison of morphology between redside dace originally collected from one watershed in Michigan and two watersheds each in New York and Wisconsin.

METHODS

Study Area

I performed field work at one site in Michigan and two sites in New York. Seeley Drain is a 7 km long headwater of the Upper River Rouge that flows southeasterly through the suburbs of Oakland County in southeastern Michigan (elevation 260 m, latitude 42°30'; Figure 1). The Upper Rouge joins with the Middle and Lower branches to flow east through the center of urban Detroit and into the Detroit River.

The study area included a 2 km reach between 12 and 13 Mile Roads approximately 2 km from the stream's origin. Seeley Drain flowed through an extensive wetland area just upstream of the study site and received inputs in the form of runoff from residential neighborhoods, parking lots, city streets, and construction sites as well as treated wastewater effluent from a facility upstream of the wetland (Coon, 1993; personal observation). In the study section, the stream was bordered by a golf course on the west and homes on the east. At a few points where riparian vegetation had been altered or eliminated, lawns and fairways met the stream bank.

Through most of the reach, a dense zone of grasses, willows, and woody shrubs overhung the stream. Seeley Drain was channelized at least twenty years ago and has been maintained as a public drain by the county, though it displayed a pool-riffle-run sequence dominated by pools and shallow runs. Sediments were relatively homogeneous: sandy with a thin layer of silt. Gravels were restricted to riffles and fast runs and there
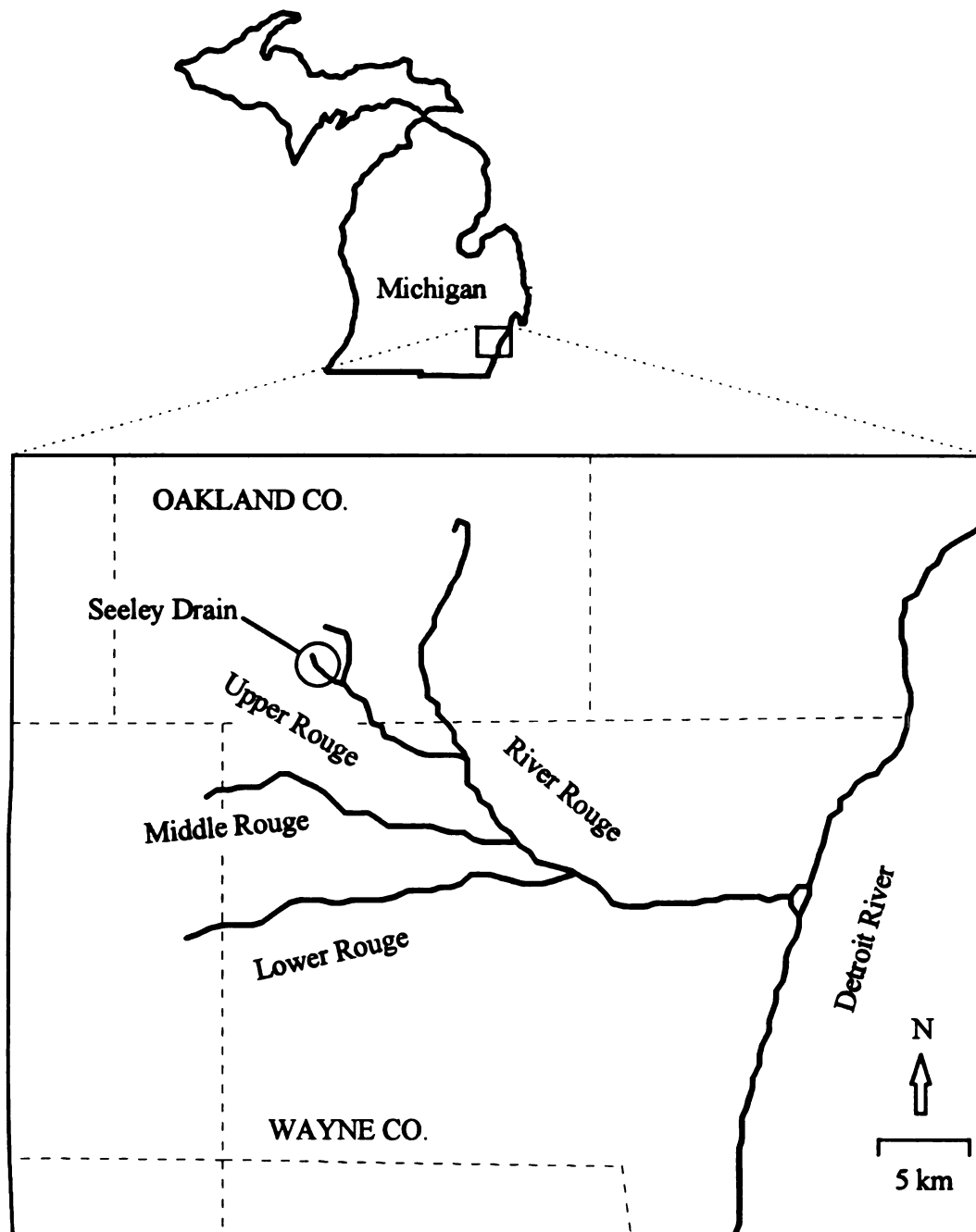
Figure 1. A map illustrating the Seeley Drain field site located in the Upper River Rouge watershed of southeastern Michigan.

was little instream woody structure or aquatic vegetation. Width was less than 2 m and depth was less than 0.75 m.

In New York, I conducted field work in two streams, Rice and France Brooks (Figure 2), both headwater streams in the Allegheny River drainage of Cattaraugus County at the southwestern edge of the state. The streams were within the boundaries of Allegany State Park and drained steep valleys of mature maple and oak forest. Human impacts to the streams were much more subtle than in Seeley Drain. Areas adjacent to the streams have undergone little modification other than the construction of seldom traveled gravel roads and associated bridge crossings. Oil and natural gas fields and timber resources have been exploited in the streams' watersheds, and brook trout (*Salvelinus fontinalis*) and brown trout have been introduced into both streams.

France Brook is a tributary of Red House Brook, a small stream that flows northwesterly into the Allegheny River. The 0.7 km reach that I studied (elevation 510 m, latitude 42°03') was 1 km upstream of the mouth and flowed northeast through a wetland dominated by grasses and shrubs that overhung stream margins. There were few trees near the stream, though a large beaver dam and pond were situated near the lower end of the study section. The reach was primarily pool and run habitat with large, rocky substrates covered with a fine layer of silt. Stream width was less than 1 m and depths under 0.5 m.

Rice Brook was the largest stream studied and flowed eastward through a more heavily wooded region. Just outside of park boundaries the stream joined Tonquin Creek to flow north to the Allegheny River. The study reach was a 1.2 km section, 4 km
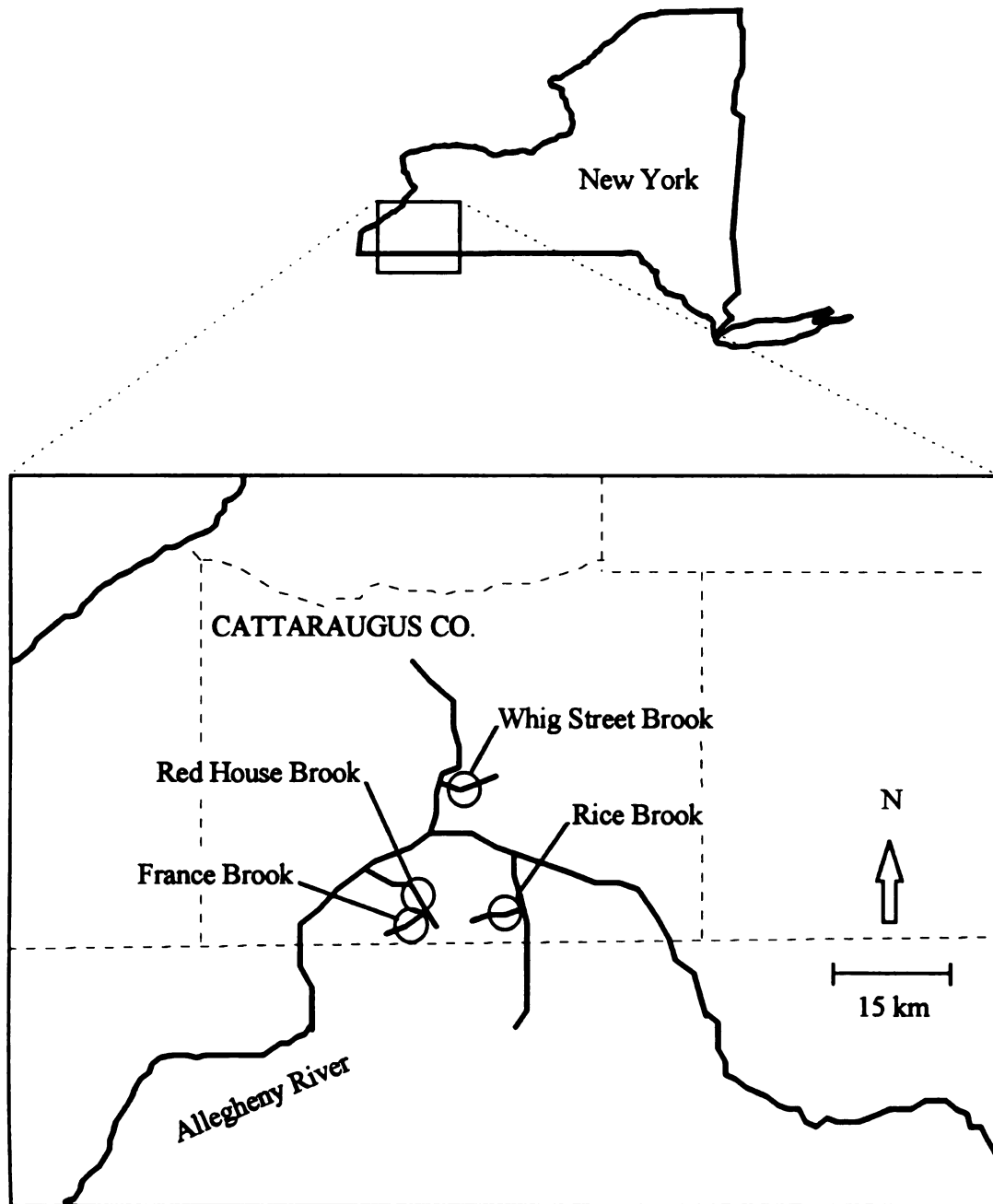
Figure 2. A map illustrating France, Red House, Whig Street, and Rice Brook field sites located in the Allegheny River watershed of southwestern New York.

upstream of the mouth (elevation 430 m, latitude 42°03'), composed of numerous deep pools (widths > 7 m, depths > 1 m) separated by riffles and runs. Substrates were dominated by pebble and cobble that were blanketed with a very thin layer of silt. Sand filled the interstitial spaces in most areas. Trees and shrubs overhanging the stream were less common and there was little instream woody structure.

I collected redside dace from two additional New York streams. Red House Brook was much larger than France Brook but contained similar habitat attributes. It flowed through heavily wooded areas and has been described by Daniels and Wisniewski (1994). Whig Street Brook was a small stream flowing from the north in the Allegheny River drainage and was bordered by roads and farmlands. The stream had been straightened and received direct runoff from cultivated row crops, though water clarity was high and depths up to 0.5 m were common. Substrates were rocky, lightly covered with silt, and there was an abundance of small, overhanging willows and shrubs.

Behavior

I studied microhabitat use by redside dace in Seeley Drain, Michigan, during June through August, 1994 and in Rice and France Brooks, New York, in mid-July, 1994. All observations were made during daylight hours between 7:00 am and 7:00 pm. Focal animal observations of individual fish (Altmann, 1974) lasted approximately 10 minutes and were conducted from the stream bank in Seeley Drain and by snorkeling in New York. Stream bank focal animal observations followed the covert tactics of Reighard (1910) and Hankinson (1920) and were facilitated by the use of polarized sunglasses and binoculars.

Good water clarity and the presence of high stream banks made this an effective method of observation in Seeley Drain where the small size of pools, shallow depths, and risks posed by urban inputs inhibited snorkeling. Direct observation of redside dace by snorkeling in an upstream direction proved most useful in the New York streams that I studied (Bovee, 1986; Grossman and Freeman, 1987).

The first minute of observation was sufficient to allow estimation of fish standard length to the nearest 5 mm, sex, location over the stream bed, and vertical position in the top, middle, or bottom third of the water column. Sex was visibly determined by coloration and by the relative length of the pectoral fins, males having a more intense red stripe and longer fins than females (Schwartz and Norvell, 1958). For the remainder of the observation period, I made a primarily qualitative description of behavior that focused on the use of instream cover, feeding activities, and intra- and interspecific interactions. Cover types were distinguished by their assumed function as providing either visual shelter (overhead structure), velocity shelter (structure projecting above the stream bottom), a combination (most woody debris), or no cover (Monahan, 1991). Information that I obtained while snorkeling was communicated through the snorkel to an assistant on the bank. Focal animal observations were terminated either by the end of the 10 minute period or by a behavioral response of the fish to the presence of the observer. Only data collected from undisturbed fish were included in further analysis.

At the end of a focal animal observation, a weighted, numbered marker was placed on the stream bottom beneath the location of the fish. I recorded microhabitat characteristics at each observation location later the same day that included the dominant

substrate particle type (diameter < 4 mm = sand/silt; 4-16 mm = gravel; 16 - 64 mm = pebble; 64 - 256 mm = cobble; > 256 mm = boulder), distance to the nearest physical structure, water column depth, stream width, mean water column velocity, and velocity at the midpoint of the vertical stratum occupied (hereafter termed focal velocity). I also recorded the distance to and the mean column velocity, width, and depth of the nearest fast water area. Riparian attributes measured included estimation of percent canopy coverage and the presence or absence of overhead structure within 1 m of the stream's surface at each marker location. Depths were measured to the nearest 0.01 m by use of a calibrated wading rod. Current velocities were measured by counting the rotations of a pygmy Gurley Meter and translating counts into m s^{-1} using a standard calibration. Mean column velocity was measured at 0.6 depth for depths < 0.75 m; at greater depths, mean column velocity was taken as the average of measurements at 0.2 and 0.8 depth (Bovee and Milhous, 1978). Focal velocity was measured in the middle of the vertical stratum occupied corresponding to 17% depth in the upper third, 50% depth in the middle third, and 83% depth in the lower third stratum.

I assessed the availability of habitat components by performing the measurements described above at 39 points in Seeley Drain and 59 points in the New York streams distributed randomly within the pools where I observed redside dace (Grossman and Freeman, 1987). Therefore, the data that I collected reflected only the relative distribution of habitat components found exclusively within pools used by redside dace and did not describe the availability of habitat attributes throughout the stream reach.

I also measured water temperature, pH, alkalinity, conductivity, and turbidity at each sampling site in addition to making a qualitative description of stream channel and bank condition. Water temperatures were measured with hand-held thermometers and pH with a Hanna Instruments waterproof pH tester that was calibrated before each use. Alkalinity was also measured in the field with a Hach portable water quality test kit and conductivity was measured with a YSI Model 33 conductivity meter. Samples for determination of turbidity were collected from mid-water. Sample bottles were immediately placed in an ice chest and analyzed at the lab within 24 hours by use of a Hach Model 2100A turbidometer calibrated with Hach gel standards prior to each use.

Frequency data for categorical habitat variables were analyzed with a χ^2 analysis of multidimensional contingency tables (Zar, 1984). I computed the electivities (L) for each category using Strauss' index (Strauss, 1979) to more clearly demonstrate selection or avoidance of specific habitat attributes in relation to their availability. Electivity scores of -1.00 to -0.50 indicated strong avoidance of the habitat attribute, -0.49 to -0.26 moderate avoidance, -0.25 to 0.25 neutral selection, 0.26 to 0.49 moderate selection, and 0.50 to 1.00 indicated strong selection of the habitat attribute (Baltz, 1990). Continuous habitat variables were tested using two-factor ANOVA (PROC GLM, SAS Institute Inc., 1988) on rank-transformed data (Potvin and Roff, 1993), and Tukey-type multiple comparisons were performed among mean ranks (Zar, 1984). For both procedures, $\alpha = 0.05$ was selected to judge the significance of test statistics.

Physiology

Fish capture and maintenance. - I collected a total of 100 adult redside dace in late October, 1993, from France, Red House, Rice, and Whig Street Brooks in southwestern New York by use of a battery-operated Wisconsin ABP-4 backpack electrofishing unit. The fish were immediately sealed in plastic bags that contained stream water and pure oxygen gas, placed in coolers, and returned to lab facilities at Michigan State University within 24 hours. We exercised extreme care in handling and transporting the fish and were rewarded by the 100% survival of the redside dace we captured. In the lab, fish were held in 90 L glass aquaria at densities of 25 fish per aquarium. The aquaria received a continuous flow of untreated, aerated well water that maintained a temperature of 12 ± 0.2 °C throughout the study. Dissolved oxygen was maintained at levels above 80% saturation and pH varied between 7.8 and 8.2. A combination of natural and artificial lighting conditions were controlled at 14:10 hours of daylight:darkness, and fish were fed daily to satiation on a diet of freeze-dried krill and prepared pellets, supplemented twice weekly with frozen adult brine shrimp. Fish were held for 5 months before experiments were initiated. Because of their protected status, Michigan redside dace could not be included in the lab study.

Metabolic Rate. - I used static-type respirometers and the sealed vessel method (Cech, 1990; Winberg, 1956) to measure the resting routine metabolic rates of mature redside dace. Oxygen consumption may be related to metabolic rate or the rate of energy expenditure through application of an appropriate oxycalorific coefficient that is dependent on fish condition and diet (Feldmeth and Jenkins, 1973; Elliot and Davison,

1975). Cech et al. (1985) defined resting routine metabolism as characteristic of quiescent fish, though not necessarily the lowest rate during the diurnal cycle (Cech, 1990). Resting routine metabolism is a slightly higher level of metabolism than the standard rate that was described by Fry (1971) as the minimum rate required to maintain life (zero activity).

I measured metabolic rate in two sets of experiments. In the first, I compared the metabolic rates of the laboratory-acclimated populations from New York with metabolic rates measured in the field for naturally-acclimated redside dace in New York and in Michigan. Lab experiments were carried out in May - June and field tests performed in late September and early October, 1994. Individuals from the four lab populations (n = 29) were tested for oxygen consumption rate in consecutive 10, 20, 30, 40, and 50 min trials. Each fish was tested once. In the field, 6 individuals from Rice Brook, NY and 12 from Seeley Drain, MI, were tested in single, 50 min trials.

In a second set of experiments, the lab populations were acclimated to temperatures of 6, 12, and 20 °C (n = 16, 29, and 31 respectively) and individual fish were tested for oxygen consumption rate in single, 50 min trials. A small number of the fish tested in experiment 1 were retested; these individuals were evenly represented among the temperature treatments. From a starting temperature of 12 °C, water temperature was adjusted 1 °C per day until the target acclimation temperatures were reached. Fish were then held at the new acclimation temperature for 14 days before testing.

The respirometers that I used were constructed from glass pint jars with a gasketed lid that was fitted with polystyrene inlet and outlet tubes (Figure 3). Water samples were taken from a short length of airline tubing connected to the outlet tube in the lid of the jar. Prior to testing, redside dace were starved for 40 - 48 h. Individual test fish
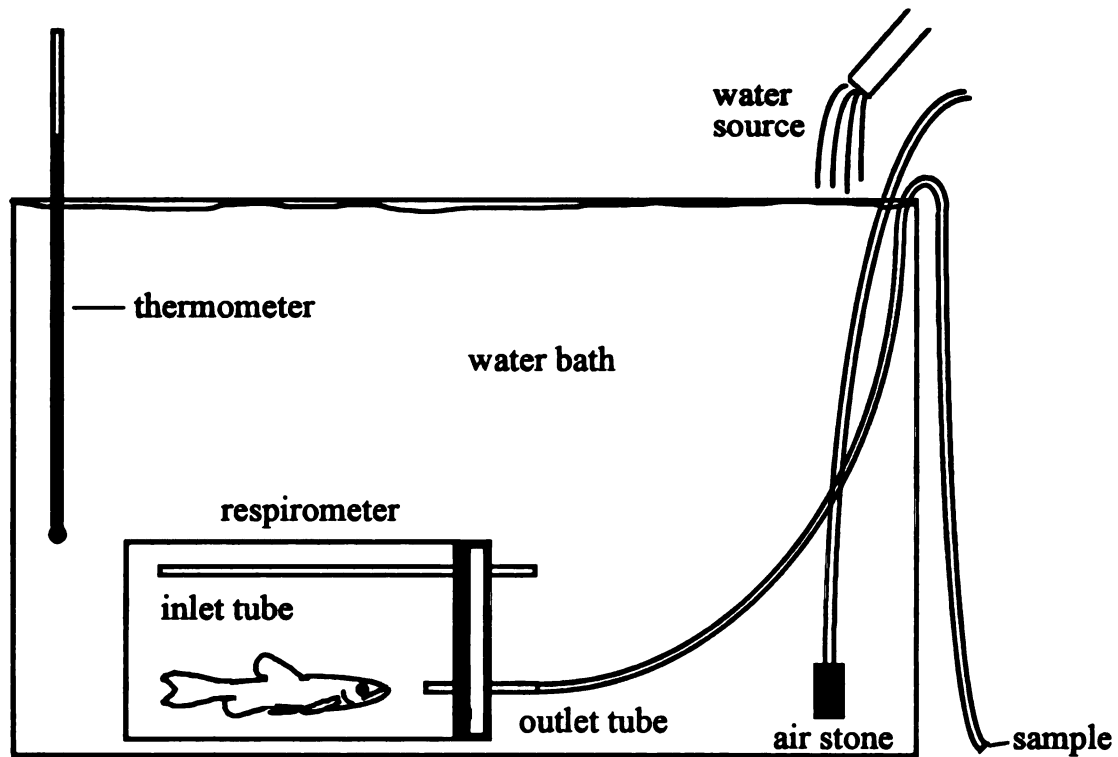
Figure 3. Diagram of the static respirometer used to collect samples for estimation of adult redside dace oxygen consumption rates.

were gently netted and sealed in the respirometers and submerged in glass aquaria that received a continuous flow of aerated, constant temperature well water. The respirometers were carefully debubbled and a siphon was started to maintain the circulation of fresh water through the respirometers. Test fish were then allowed an overnight acclimation period to become accustomed to the chambers. In addition, one blank respirometer was always set up and tested as a control to estimate oxygen consumption due to microbial metabolism. All oxygen consumption measurements were corrected for consumption recorded with the corresponding control. The aquaria were shielded from the movements of experimenters, and small mirrors allowed me to observe the behavior of fish in the respirometers.

To measure oxygen consumption, I took an initial water sample from the outlet tubing in a 60 ml glass bottle. I then plugged the end of the tube, thereby interrupting flow for the duration of the trial period. The amount of dissolved oxygen (mg L^{-1}) in the sample was immediately measured using a YSI Model 50B Dissolved Oxygen Meter and a Model 5730 polarographic probe with an automatic stirrer. At the end of the trial period, the outlet tube was unplugged and a final water sample taken and measured as above. Oxygen consumption rates (mg O_2 h^{-1}) were calculated by dividing the difference in dissolved oxygen concentration (initial - final) by the duration of the trial (h) and adjusting for the respirometer volume. The concentration of dissolved oxygen in the respirometers was not allowed to drop below 70% saturation to avoid the potential effects of hypoxic stress (Brett, 1964) and all measurements were taken between 8:00 am and 5:00 pm. At the conclusion of each trial, I measured standard length of the test fish to the nearest 0.1

mm and wet weight to the nearest 0.01 g. Test fish were also given a small fin clip to insure that they were tested only once. Sex was determined by coloration and the ratio of head length to pectoral fin length as outlined by Schwartz and Norvell (1958).

Field procedures were identical to those followed in the lab (described below) with a few exceptions. First, redside dace were captured by seine and held instream in plastic cages perforated with 3 mm openings prior to testing. Second, the respirometers were submerged in coolers placed just below natural beaver and debris dams. Stream water was directed over the dams and into the coolers with a piece of rain gutter to allow maintenance of the siphons that flushed the respirometers. Measurements were made on the stream bank with the same equipment used in the lab.

The oxygen meter was calibrated to Winkler titration (azide modification: APHA et al., 1989) on a regular basis, daily during periods of frequent use. Precision of the meter was reported by YSI to be within ± 0.02 mg L^{-1}, a claim supported by consecutive measurement of samples from the same source (range of differences = 0.004 - 0.04, mean = 0.018, n = 25). However, the degree of accuracy of the meter was more difficult to evaluate. Calibration records suggest that the absolute differences between the meter and titrations varied from 0.02 - 0.57 mg L^{-1}, with a mean deviation of 0.23 (n = 24). Because the data submitted to analysis was the difference in initial and final readings, precision was considered to be of primary importance. Deviations in accuracy were assumed to be consistent within a trial period, an assumption validated by the minuscule rates of consumption measured during trials with the blank respirometer. To account for error in the precision of the meter, all oxygen consumption rate standard errors were assigned a

minimum value of 0.01, the error associated with measurements using the pint-sized

respirometers (0.473 L; Cech et al., 1985). No attempt was made to correct for

measurement accuracy other than required maintenance and calibration of the meter.

Oxygen consumption rates were adjusted by an allometric relationship to account

for mass-specific differences among the fish tested:

$$Y = a X^b$$

where $Y = O_2$ consumption rate (mg min^{-1}), a = mass coefficient, X = mass (g), and b =

mass exponent (Cech, 1990). The parameters a and b were estimated from the linear

regression of the log-transformed oxygen consumption rates on log mass:

$$\log Y = -2.7364 + 0.7451 \log X$$

($r^2 = 0.732$, SE = 0.0448). The raw consumption rate data were then divided by (mass^b)

to create "mass-independent" metabolic rates that were analyzed in log-transformed form

(Winberg, 1956). The significance of treatment and group effects were assessed through

factorial ANOVA and Tukey's HSD (PROC GLM, SAS Institute Inc., 1988).

Thermal Tolerance. - I also studied a second physiological attribute of redside

dace, upper thermal tolerance, using the critical thermal maximum method (CTM)

originated by Cowles and Bogert (1944) and presented as a standardized methodology by

Hutchison (1961). Several authors have modified the procedure for application to fishes

(Cox, 1974; Hutchison and Maness, 1979; Becker and Genoway, 1979; Paladino et al.,

1980). Becker and Genoway (1979) defined CTM as a method for measuring the thermal

tolerance of poikilotherms by raising the temperature from ambient acclimation at a linear

rate so that no significant time lag exists between the temperature of the media and the

internal tissue of the test organism. Raising the temperature too fast may induce thermal shock, and a heating rate that is too slow may allow partial acclimation during the CTM test. Becker and Genoway (1979) further defined CTM as a parameter: the temperature where the test organism loses the ability to escape from conditions that promptly lead to its death.

I measured the CTM for a total of 23 redside dace from France and Rice Brooks, two of the New York lab populations used in the metabolic rate experiments. The fish were already acclimated to temperatures of 6, 12 and 20 °C and had been tested previously for metabolic rate. Individual redside dace were heated from ambient acclimation temperatures in a large beaker containing 3 L of water. The heating rate varied between 0.3 - 0.5 °C min^{-1} (Becker and Genoway, 1979), and was measured at regular intervals with an ASTM certified mercury thermometer (0.1 °C) to insure linearity of heating rate. The beaker was aerated to provide uniform mixing and adequate dissolved oxygen levels. Heating was initiated immediately after careful introduction of the fish to the beaker, and observations were made from behind a blind with a viewing slit.

I identified the CTM end point as the final loss of equilibrium (FLE), marked by a total loss of righting ability. At this point, the fish had lost the ability to escape from the thermal conditions that would promptly lead to its death (Becker and Genoway, 1979). I also identified four other behavioral markers that appeared to be related to increasing thermal stress:

1. BSW - sporadic burst swimming occurred when a continuous, consistent level of swimming became interspersed with sudden bursts of activity usually directed at the wall of the beaker.

2. SUR - surfacing, breaking the water's surface with the snout.

3. ESW - erratic swimming, characterized by sudden, directionless bursts, muscle spasms, and initial loss of equilibrium.

4. OPS - opercular spasms indicated by flaring and spasmodic movements of the gill covers and gulping motions (Feminella and Matthews, 1984). OPS soon followed FLE; if not immediately removed from the test conditions, the fish quickly died.

I recorded the time and temperature upon recognition of each behavioral landmark. At the conclusion of a test, fish were weighed and measured for standard length. It was determined from a small number of fish that immediate return to acclimation temperature following OPS allowed at least temporary recovery. No attempt was made to assess long term effects of the thermal tolerance tests.

Untransformed end point temperatures were analyzed by factorial ANOVA and Tukey's HSD (PROC GLM, SAS Institute Inc., 1988).

Morphology

Morphometrics. - I performed a landmark-based morphometric analysis (Bookstein, 1992) to examine variation in external body shape among populations of redside dace collected in Wisconsin, Michigan, and New York and with a congener, the

rosyside dace, that served as an outgroup. The preserved specimens were provided by the

University of Michigan Museum of Zoology (App.) and included lots that were collected

between 1925 and 1953. The redside dace specimens were selected to represent

populations from two watersheds in each state with the exception of Michigan, where

available material was limited to the River Rouge drainage (primarily individuals from the

Upper River Rouge). Included in the analysis were redside dace collected in the

Allegheny River and Susquehanna River watersheds in New York and the Black and

Wisconsin River watersheds in Wisconsin. Rosyside dace specimens from North Carolina

and Tennessee were pooled to obtain an adequate sample size of adult specimens.

Rosyside dace were selected as the outgroup as the only other member of the

genus *Clinostomus*. Patterns of habitat use, social, and foraging behaviors of the rosyside

dace (Freeman, 1990) are in many ways analogous to those of the redside dace (Koster,

1939), yet rosyside dace have a non-overlapping, more southern distribution and display

morphological differences from redside dace that have been summarized by other authors

(Page and Burr, 1991). The rosyside dace form provided a convenient reference from

which to judge the scale of shape differences among the groups of redside dace.

For the shape analysis, I selected 17 corresponding landmark points around the

bodies of the fishes (Figure 4, Table 1) chosen because they were representative of overall

body shape and could be identified with confidence on each specimen. The images of each

specimen and the x- and y-coordinates of each landmark were captured and digitized to

the nearest 0.1 mm using a Cohu RS-170 video camera (resolution 565×350) and Sony

Trinitron HR color monitor interfaced with a micro-computer and image-processing
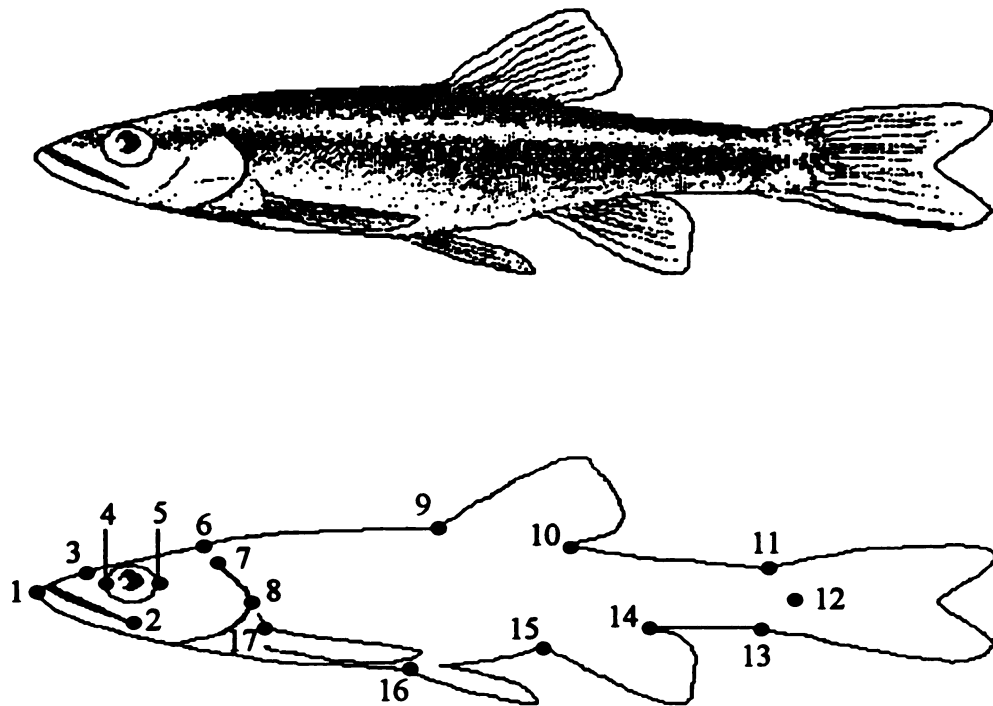
Figure 4. Locations of the 17 landmark points that were digitized around the body of each redside and rosyside dace museum specimen for morphometric analysis. Refer to Table 1 for a description of each point.

Table 1. Description of the 17 landmark points used in the morphometric analysis.

Point	Landmark Description
1.	Furthest anterior projection of the lower jaw.
2.	Furthest posterior projection of the mouth.
3.	Center position of the anterior naris.
4.	Most anterior edge of the eye.
5.	Most posterior edge of the eye.
6.	Occiput.
7.	Dorsal insertion of the operculum.
8.	Furthest posterior projection of the operculum.
9.	Anterior insertion of the dorsal fin.
10.	Posterior insertion of the dorsal fin.
11.	Dorsal insertion of the caudal fin.
12.	Posterior base of the vertebral column.
13.	Ventral insertion of the caudal fin.
14.	Posterior insertion of the anal fin.
15.	Anterior insertion of the anal fin.
16.	Anterior insertion of the pelvic fin.
17.	Dorsal insertion of the pectoral fin.

software (OPTIMAS, Optimas Corp.). In order to minimize measurement error within groups of specimens, I digitized the landmark coordinates of each fish on two nonconsecutive occasions (Yezerinac et al., 1992). The mean of these two estimates provided the working data set. For analysis, the landmark points were transformed to shape coordinates through the two point registration technique (Bookstein, 1986): the points were rotated and scaled to a common baseline drawn between landmarks 1 and 12 that were given arbitrary coordinates of (0,0) and (1,0). In this way, the method may be regarded as a size-independent analysis of shape differences. Only redside dace > 45 mm SL and rosyside dace > 40 mm SL were included in the analysis.

The untransformed shape coordinates were submitted to a multivariate test (Wilks Λ; PROC GLM, SAS Institute Inc., 1988) as dependent variables with group (a categorical variable) as the independent variable in the model. Experimentwise error was controlled by adjusting the significance level for the univariate tests of each coordinate (Hayes, 1993; Sokal and Rohlf, 1981). To maintain an experimentwise error rate of α_{exp} = 0.05 for the 30 individual tests, a significance level of α = 0.0017 was used.

I assessed the magnitudes and directions of shape change between groups by application of the thin-plate spline decomposed by its partial warps, a morphometric method recently presented by Bookstein (1989; 1992) and summarized in Rohlf and Bookstein (1990). The thin-plate spline is a multivariate function that may be used to interpolate surfaces over scattered data and is an effective tool for modeling biological shape change that is described by change in the configurations of landmark coordinates. The thin-plate spline can be visualized as the bending of an infinitely thin metal plate or

grid over one set of landmarks, the reference configuration or "starting form", so that its height over each landmark is equal to first the x-, then the y- coordinate of the corresponding landmark in another set, the "final form" (Zelditch et al., 1995). In this way, the thin-plate spline may be thought of as a distance function that maps the configuration of one object onto another, displayed as a deformation of the starting form (Bookstein, 1990). The thin-plate spline mapping quantifies the metaphorical "bending energies" associated with changes in the shape of the metal plate as the starting form is fitted to the final form.

The shape deformation described by the thin-plate spline mapping is decomposed into a uniform or linear part, the affine transformation, and a non-uniform, non-linear part. The affine transformation is a uni-directional change in the position of all landmarks that is proportional to the landmark's perpendicular distance from the selected baseline. By definition, it is a homogenious transformation over the entire form that keeps parallel lines parallel and is recognized as an apparent tilting or rolling of the thin-plate. The uniform transformation has zero bending energy. In contrast, non-uniform shape variation is localized at progressively smaller spatial scales as changes differing from one region to another due to the displacement of individual groups of landmarks.

The pattern of non-uniform bending is summarized in a bending energy matrix with the eigenvectors of the matrix termed "principal warps." Principal warps, Bookstein's (1992) "descriptors of deformation" are computed by the same subroutines that compute principal components in Principal Components Analysis. The bending energy depends on the location and spacing of the landmarks of the starting form and measures the

displacement of a landmark relative to its distance from other landmarks. Principal warps may be localized by eigenvalue (bending energy per unit summed squared landmark displacement) which corresponds to the inverse geometrical scale of the deformation. The largest eigenvalue corresponds to the smallest scale or local change, and the smallest eigenvalue corresponds to the largest scale change. The two-dimensional contribution of each principal warp to the shape deformation is described by a corresponding number of "partial warps," vectors that are computed by multiplying the principal warps by the landmark coordinates of the final form (Zelditch et al., 1995). Partial warps provide a graphical representation of how each principal warp alone bends the thin-plate. The principal warps represent the geometric terms in which shape differences can be described, and partial warps are the values assigned to those terms (Swiderski, 1993). Thus, the primary advantage of the method of thin-plate splines is that shape change, modeled as a deformation, may be attributed to uniform and non-uniform components of variation, and the non-uniform component may be further localized as changes at smaller spatial scales.

For this analysis, the mean shape coordinates of rosyside dace, the outgroup, were compared to individual redside dace shape coordinates using the TPSPLINE software package (version 9/14/94) developed by F.J. Rohlf. The x- and y-components of the uniform transformation were estimated using an algorithm provided in Bookstein (1990).

Meristics. - I also made three types of meristic counts on redside dace using specimens from the same lots examined in the morphometric study. The number of dorsal fin rays, anal fin rays, and scales in the lateral line were determined. Counts were made according to Hubbs and Lagler (1964). Scale counts were made at least twice on each

specimen to minimize counting error. Accuracy of fin ray counts were randomly verified

by a second investigator (D. Hondorp).

RESULTS

Behavior

Habitat Use. - Stream water quality characteristics of Seeley Drain were different in several respects from characteristics of the New York streams (Table 2). The temperature data presented in Table 2 is a summary of readings collected in July, 1994 in Seeley Drain and in mid-July in New York. A comprehensive temperature record for either of the New York streams was not available. Water temperatures were generally higher in Seeley Drain. Alkalinity, pH, and conductivity were all higher in Seeley Drain, perhaps reflecting regional geologic differences between Michigan and New York and differences in land and water uses. Turbidity tended to be somewhat higher in the New York streams, perhaps the result of deeper, richer soils in southwestern New York that do not have the high sand content of southeastern Michigan soils. However, all of the streams were very clear.

I searched for redside dace in pool, run, and riffle habitats, but only found them associated with pools. The Seeley Drain study reach was composed of approximately 50% pool, 30% run, and 20% riffle compared to the Rice Brook site which was 45 % pool, 30% run, and 25% riffle, and the France Brook site which was 40% pool, 25% run, 35% riffle. Observation was most difficult in riffles where turbulence and glare at the stream surface were greatest and runs were generally too shallow to navigate while snorkeling. Pools consequently received the greatest amount of observation effort.

Table 2. Range in stream water quality characteristics of Seeley Drain, Michigan and Rice and France Brooks, New York, during July, 1994. Sample sizes are given in parentheses.

	Seeley Drain	Rice Brook	France Brook
Highest recorded Temperature (°C)	24.4	19.4	21.1
Conductivity (μmhos)	820 (1)	27 (1)	32 (1)
pH	7.8 - 8.3 (5)	7.2 - 7.3 (6)	7.6 (5)
Alkalinity (mg/L CaCO₃)	210 - 268 (4)	17 - 22 (3)	15 - 17 (4)
Turbidity (ntu)	1.5 - 2.6 (9)	1.0 - 1.2 (9)	3.9 - 4.7 (9)

Redside dace were observed in 5 pools each in Seeley Drain and France Brook and 6

pools in Rice Brook.

Methods for observing habitat use were generally successful, and viewing

conditions allowed confident identification of individual redside dace and other co-

occurring fish species (Table 3). In Seeley Drain, 10 species were collected or observed

to occupy the same pools used by redside dace. Creek chub (*Semotilus atromaculatus*),

blacknose dace (*Rhinichthys atratulus*), and central mudminnow (*Umbra limi*) were most

common. In the New York streams, 19 species were observed with redside dace of which

blacknose dace, central stoneroller (*Campostoma anomalum*), creek chub, and common

shiner (*Luxilus cornutus*) were most prominent. Maintaining an observation period of

sufficient length prior to discovery by focal animals was difficult while snorkeling. The

quiet conditions of most pools required extreme care on the part of the observer, and

individual redside dace did not always orient upstream in the larger, slower pools.

Therefore, discovery was not easy to avoid but usually allowed at a minimum the

identification and determination of the location of the undisturbed fish over the stream

bed. Disturbance of individual fish was apparent by characteristic escape responses or

more often by exploratory movements towards the snorkeler.

Data from the two New York streams were pooled to obtain adequate sample

sizes for comparison to habitat use data from Seeley Drain, Michigan. The statistical

analysis of three categorical habitat variables, substrate, instream cover, and canopy, was

hindered by small cell sizes that violated the assumptions of χ^2. In the case of substrate

and canopy coverage, categories were meaningfully combined when necessary to eliminate

Table 3. Fish species co-occurring with redside dace in Michigan and New York. Names follow Robins et al. (1991).

SPECIES	MICHIGAN	NEW YORK
Campostoma anomalum		x
Catostomus commersoni	x	x
Cottus bairdi		x
Culea inconstans	x	
Etheostoma caeruleum		x
Etheostoma flabellare		x
Etheostoma nigrum	x	x
Hypentelium nigrum		x
Lepomis cyanellus	x	x
Luxilus cornutus	x	x
Nocomis biguttatus		x
Percina caprodes		x
Percina maculata		x
Phoximus eos	x	
Pimephales notatus		x
Pimephales promelas	x	x
Rhinichthys atratulus	x	x
Rhinichthys cataractae		x
Salmo trutta		x
Salvelinus fontinalis		x
Semotilus atromaculatus	x	x
Umbra limi	x	

empty cells (Zar, 1984). However, this was not possible in the analysis of instream cover, therefore χ^2 computations were considered biased.

Several of the habitat characteristics that I measured differed significantly in frequency of use by Michigan and New York redside dace; however, few of the same characteristics differed when frequency of use was compared to the inherent availability of the attribute within the pools that I sampled. The relationship between use and availability of substrate types illustrated this pattern (Figure 5). Substrate types were combined into two categories, fine (sand and clay) and coarse (gravel - boulder) for the χ^2 tests, and these confirmed that there were clear differences between Michigan and New York in both the use and availability of substrate types (P < 0.001). Pools in Seeley Drain had an overwhelmingly sandy bed in contrast to the New York streams where substrates were rocky and more diverse. However, the use of substrates in Seeley Drain and New York showed insignificant deviation from what was expected based on availability (P > 0.25). Electivity scores indicated that redside dace at both study sites exhibited neutral selection of substrate types.

There was a slight tendency for New York redside dace to be associated with the boulder substrate type (11.6 % use, 5.1% available), a finding that was related to observations of cover use (Figure 6). New York fish were associated with velocity shelters (41.9% use), usually boulders, more often than predicted by random choice (22% available; P < 0.10) and more frequently than redside dace in Seeley Drain; the electivity score suggested neutral to moderate selection by New York redside dace for this component as well. Seeley Drain contained more structures assumed to provide visual cover such as vegetation hanging in the water and small tree roots. In Michigan and in
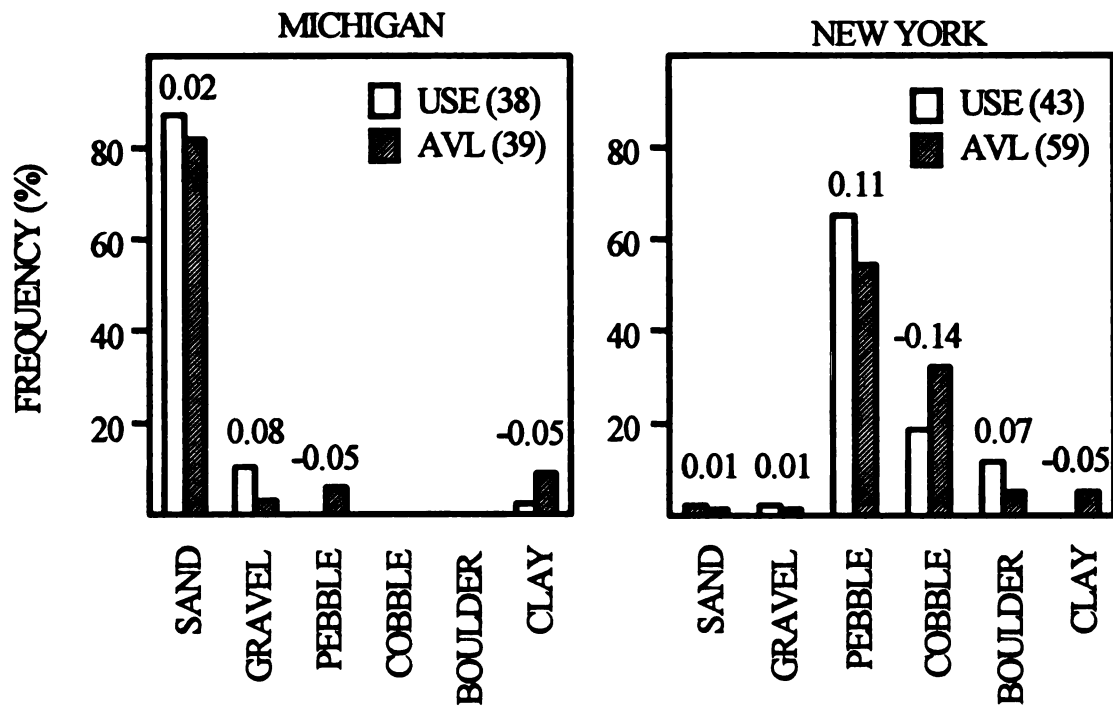
Figure 5. Stream bottom substrate percent frequency of availability and use by adult redside dace in Michigan and New York. Electivity (L) is given above the bars of each category and sample sizes are given in parentheses.
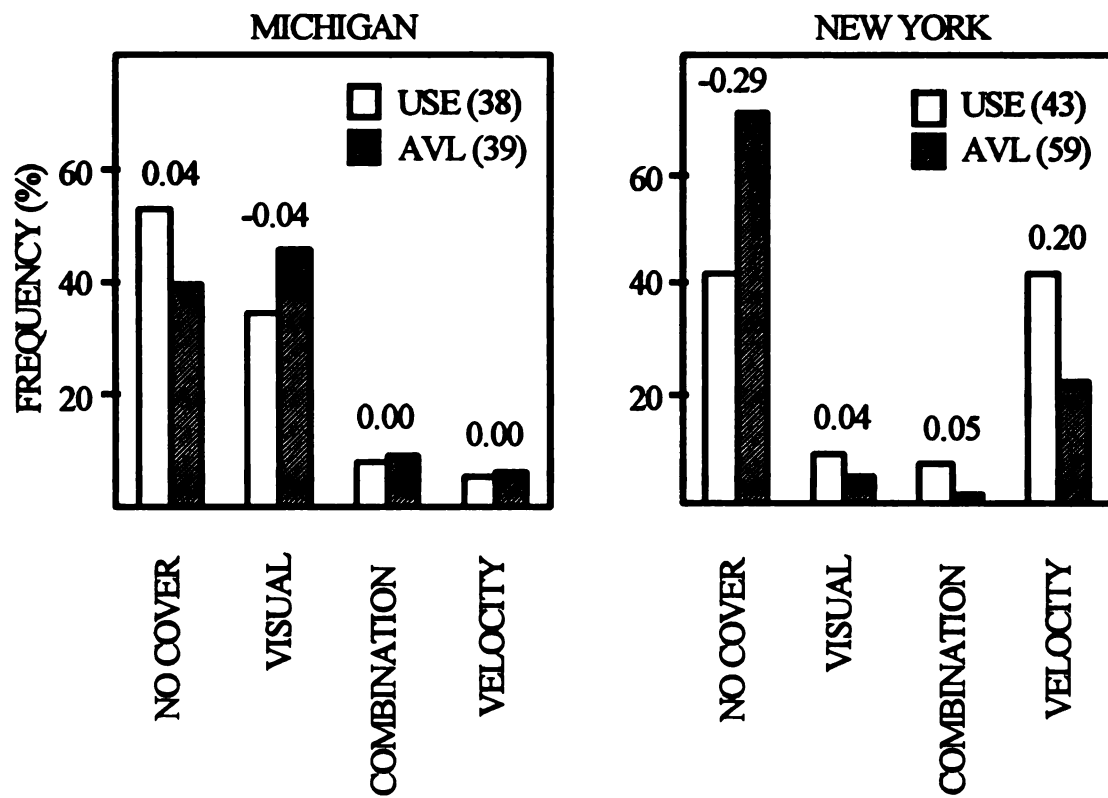
Figure 6. Instream cover type percent frequency of availability and use by adult redside dace in Michigan and New York. Symbol explanation follows Figure 5.

New York, use of locations with no cover was also frequently observed (52.6% MI and 41.9% NY). This lack of association with structure appeared to be directly related to the pelagic positions occupied by most of the redside dace: 73.7% of Michigan and 81.4% of New York fish held positions in the middle third of the water column (no difference; $P >$ 0.05; Figure 7), suggesting moderate to strong selection of this position. Focal animals were usually oriented upstream. Michigan and New York redside dace were also similar in their proximity to structure ($P > 0.50$), irrespective of cover use (median distance 0.20 m for both Michigan and New York), and use did not differ significantly from availability ($P > 0.20$).

The New York stream pools offered significantly greater ($P < 0.001$) median depths (0.27 m) and widths (3.10 m) than Seeley Drain (0.18 m and 1.30 m), and redside dace in both locations were consistently found in the deepest ($P < 0.005$; Figure 8) and widest ($P < 0.05$) locations (Michigan use: depth = 0.42 m, width = 2.00 m; New York use: depth = 0.40 m, width = 5.00 m). Yet, differences in stream dimensions did not equate to significant differences in the median mean column velocities ($P > 0.35$; Figure 9) available in Seeley Drain (0.072 m s^{-1}) or in New York (0.079 m s^{-1}); the available velocities also were not significantly different from the velocities associated with use (Michigan: 0.054 m s^{-1}, New York: 0.063 m s^{-1}). Corresponding median focal velocities encountered by redside dace also did not differ significantly ($P > 0.05$) between Michigan (0.050 m s^{-1}) and New York (0.083 m s^{-1}) and were not significantly different from the median mean column velocities associated with use described above (Mann-Whitney U, P > 0.5 for Michigan and New York).
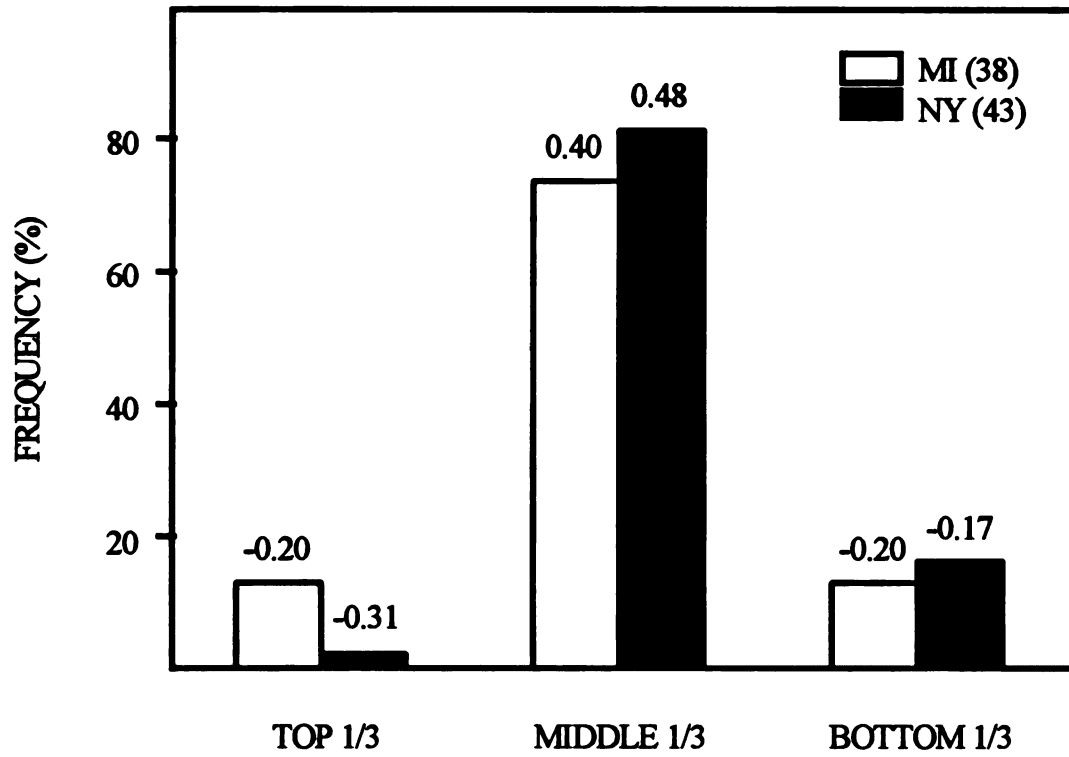
Figure 7. Vertical stratum in the water column occupied by adult redside dace in Michigan and New York. Symbol explanation follows Figure 5.
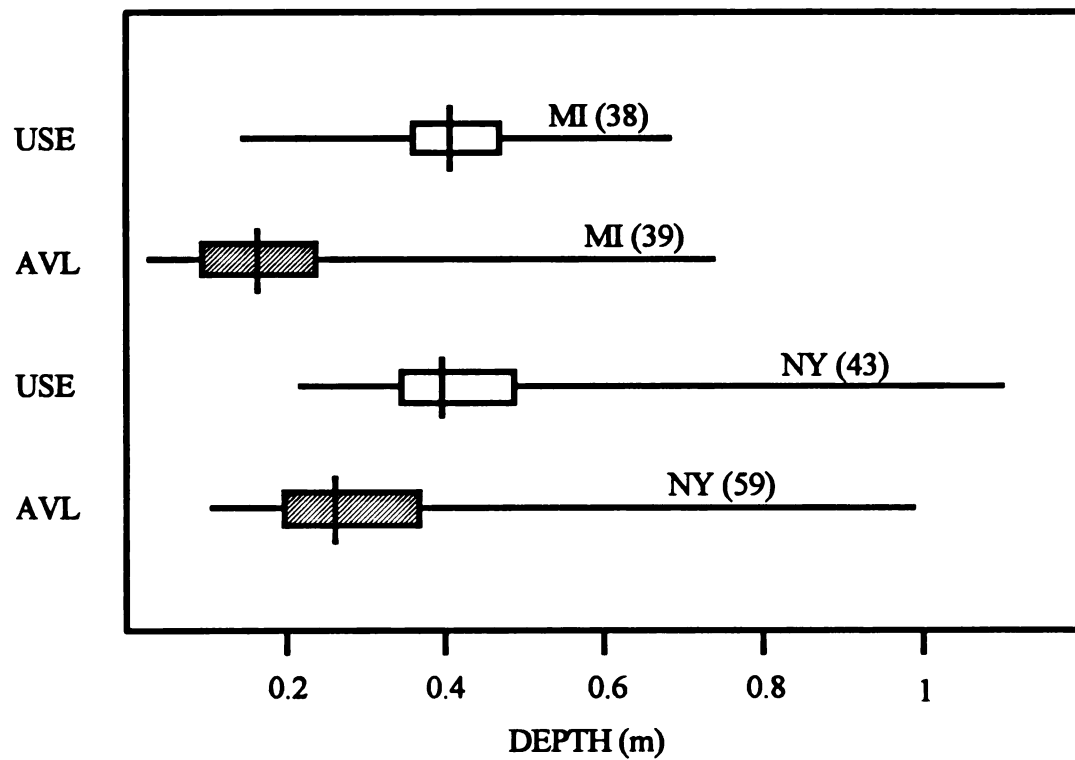
Figure 8. Depth availability and use by adult redside dace in Michigan and New York. Symbols: vertical bar represents median, box encloses 50% of the distribution, and horizontal bars mark the range. Sample sizes are given in parentheses.
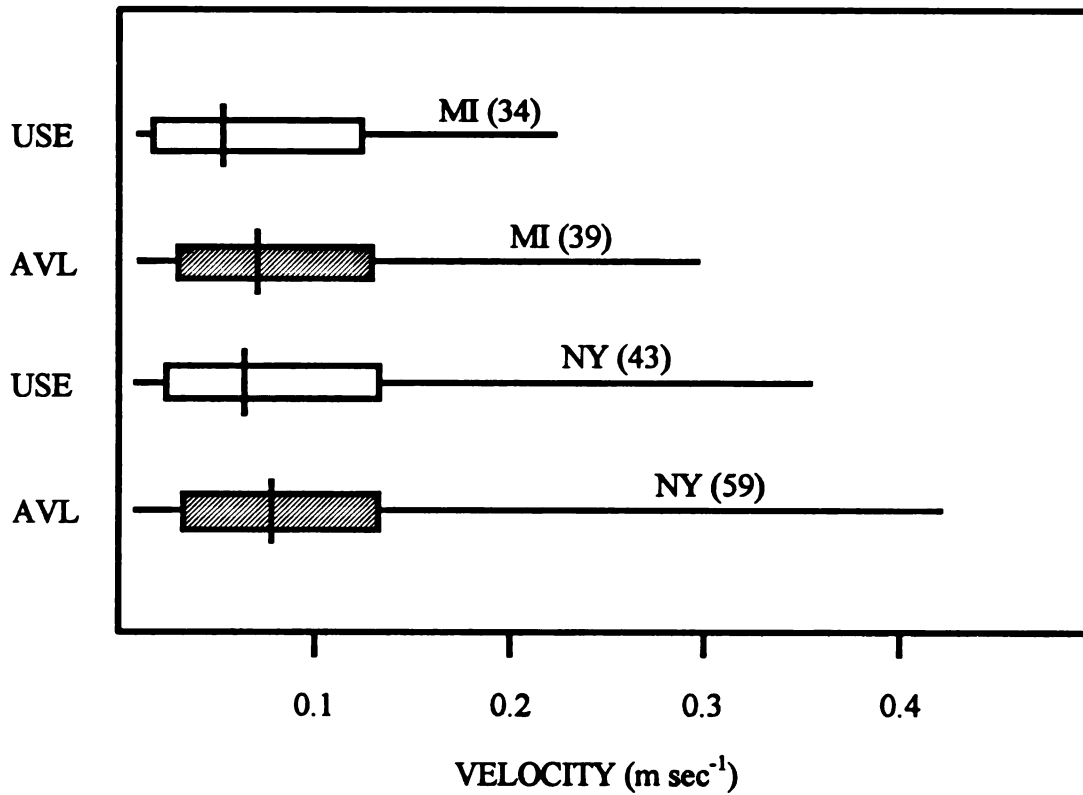
Figure 9. Mean column velocity availability and use by adult redside dace in Michigan and New York. Symbol explanation follows Figure 8.

I also evaluated four characteristics of the fast water areas that were nearest to the focal animal observation points. Designation of a fast water area was somewhat subjective; the requirements included a sudden and significant increase in velocity along a cross-channel transect, displayed by the formation of shear lines on the stream surface. Redside dace in New York were typically found farther from fast water areas than fish in Seeley Drain ($P < 0.025$; medians of 5.70 m and 3.60 m, respectively), a result expected from the greater width of the pools in New York than in Michigan. Like other pool dimension measurements, fast water areas were also wider ($P < 0.001$) in the New York streams (3.80 m) compared to Seeley Drain (1.00 m). However, median fast water depths (0.12 m for Michigan and New York) and velocities (0.256 m s^{-1} MI, 0.308 m s^{-1} NY) were not found to be significantly different ($P > 0.20$ and $P > 0.40$) between the sites.

Similar to instream habitat attributes, stream bank and riparian characteristics also differed greatly between Seeley Drain and the New York streams. Riparian vegetation along the pools in Seeley Drain was dense and close to the stream surface, with more than 75% of the points sampled having some form of structure within 1 m above the water. There was no difference between frequencies of use and the availability of locations associated with overhanging structure within 1 m of the stream surface in Seeley Drain. Riparian structure along Seeley Drain was composed mostly of tall fescue and short willow trees that hung in and over the stream. The New York streams possessed significantly fewer points associated with overhanging structures that were sampled for availability compared to Seeley Drain (42%; $P < 0.005$). Overhanging structure along the New York streams was represented by woody shrubs and a variety of small trees.

However, at these sites New York redside dace showed moderate selection of points beneath overhanging structure, using them more often than expected based on random choice (72%; $P < 0.025$).

Percent vertical canopy coverage high above the streams was also different between Seeley Drain and the New York sites ($P < 0.001$), but coverage associated with points of use were similar to proportions available ($P > 0.10$) indicating neutral selection of canopy density. Overall, the New York streams were located in regions of thicker forest; however, the larger New York streams created a wider opening in the tree coverage than Seeley Drain where smaller trees provided a dense canopy at most locations. For the New York streams, percent canopy coverage of less than 50% made up more than 80% of the observations associated with habitat use and availability. In contrast, coverage greater than 50% characterized 70 - 80% of the use and availability observations in Seeley Drain.

General Behavior. - I observed remarkably few interactions among redside dace or between redside dace and other species. Foraging dominated redside dace activities in Michigan and New York. During 35 out of 40 focal animal observations (88%) that lasted for the entire 10 min observation period, redside dace were observed holding stationary positions from which they intermittently struck at items in the water column or at the surface. They did not exhibit the aggressive, territorial behaviors that I observed simultaneously in blacknose dace, common shiners, and creek chubs. Individuals of these other species frequently came into physical contact with each other while attempting to maintain or regain positions in the pools. Lunges or even a brief chase often followed

these contacts. The other minnow species often held positions in the lower half of the water column, below the positions selected by most redside dace. When a mixed assemblage was present, the deepest pockets of the pool were usually held by large creek chubs and white suckers (*Catostomus commersoni*) that were seldom challenged by the other fishes. Redside dace did not respond to the locations or actions of other fishes and the only indication of interaction that I recognized was in competition for particles that entered the pool, especially items floating at the surface. Redside dace usually arrived at floating particles first, though it was not always possible to determine if the item was successfully eaten. Redside dace were not as successful at securing objects from the water column. Typically, small creek chubs or blacknose dace reached suspended particles first.

Redside dace displayed a characteristic feeding strategy that set them apart from the other minnows. From a mid-water position, redside dace launched sudden strikes at floating food particles, often leaping out of the water with the force of their momentum. They performed this behavior with greater frequency than other minnows sharing the pool and more often than they attempted to capture suspended particles. For 17 foraging redside dace, I quantified the number of strikes made at the surface compared to the number of strikes made at suspended items during the 10 min observation period. On average, the fish made 1 strike at the surface every 2.5 min, almost four times the frequency of strikes at particles in the water column (1 strike in 10 min). Two individuals made as many as 8 strikes at the surface during the 10 min period. Overall, redside dace struck at items once every 2 min and as often as once every 50 sec.

Physiology

Metabolic Rate. - Metabolic rates measured in the lab during the first experiment decreased in difference among the four populations as the length of trial periods increased (Figure 10). In several cases, variability in the data was less than that expected due to measurement error of the dissolved oxygen meter, so most SE were assigned a value of 0.01 to reflect the meter's sensitivity. Repeated measures ANOVA of the log-transformed oxygen consumption rates revealed a significant population effect ($P = 0.034$) but no mean difference between sexes ($P > 0.30$). Further inspection showed that the Whig Street Brook population had a significantly lower consumption rate than the other groups during the 20 min trial ($P < 0.05$); however, there was no detectable difference among populations in any of the other trial periods. The 50 min trial length appeared to offer the greatest potential for future repeatability of results among the trial lengths tested, and I selected it for use in later lab and field experiments. Redside dace consumed a mean of 0.114 mg O_2 $g^{-b} h^{-1}$ during the 50 min trial.

Mean oxygen consumption rates of redside dace tested in the field in Michigan and New York (Figure 11) were not different (Tukey HSD: $P > 0.34$; 0.130 and 0.143 mg O_2 $g^{-b} h^{-1}$), but New York field rates were found to be significantly higher than the rates measured in the lab (0.114 mg O_2 $g^{-b} h^{-1}$; $P < 0.005$). Michigan field rates also tended to be higher than lab rates but were not shown to be significantly different ($P > 0.05$). The standard errors shown in Figure 11 were assigned the value assumed for instrument error (0.01); however, the ANOVA procedure did not account for this adjustment. Assignment of these SE values negates the difference found between New York field and laboratory
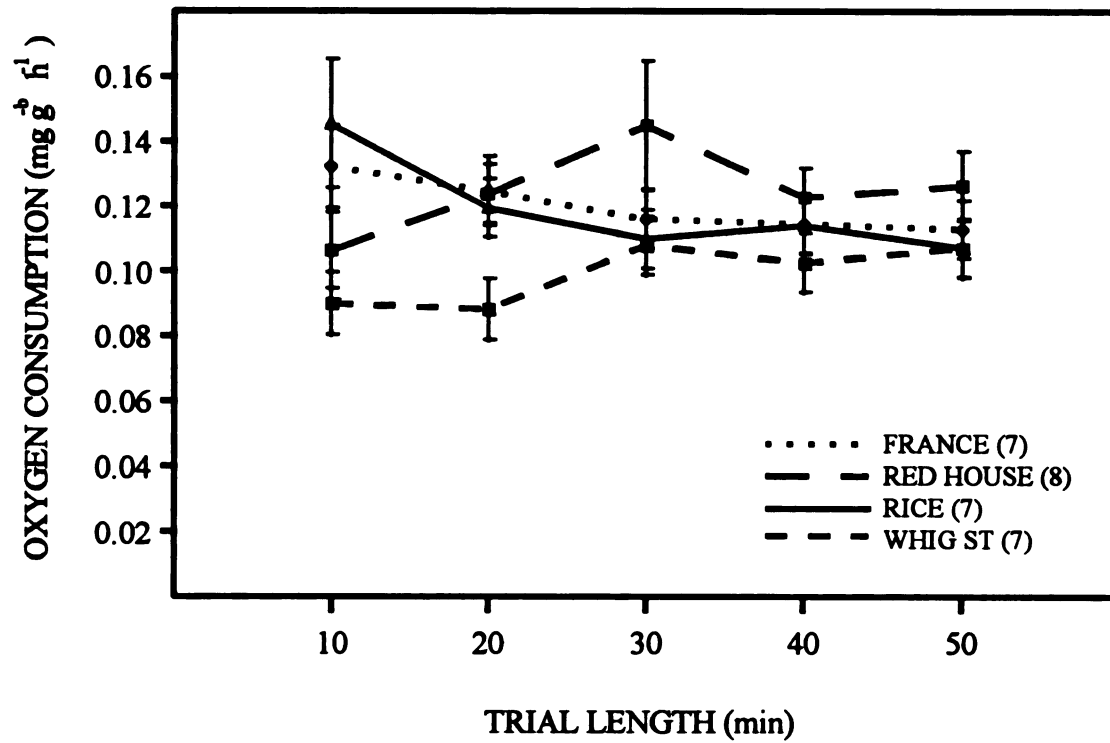
Figure 10. Mean oxygen consumption rates (± 1 SE) by adult redside dace from four New York streams during trial periods used in the first laboratory experiment. Sample sizes are given in parentheses.
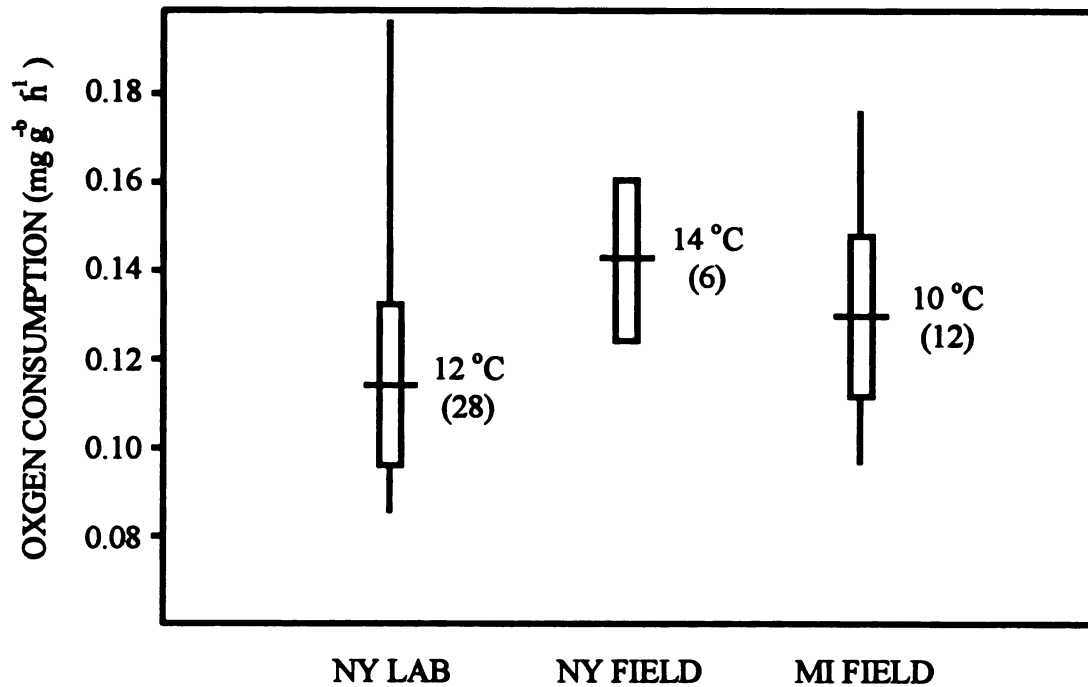
Figure 11. Mean oxygen consumption rates by adult redside dace from New York and Michigan during 50 min lab and field trials in the first experiment. The temperature that each group was tested at and sample sizes (in parentheses) are given next to the mean consumption rate. Symbols: horizontal bar represents mean, box encloses 2 SE, and vertical bars mark range.

measurements by ANOVA (Figure 11). There was, however, a definite tendency for estimates from field measurements to range higher than lab rates. Redside dace tested in the field in New York were acclimated to a slightly warmer temperature (14°C) compared to fish in the lab (12°C).

I designed a second experiment to explore the importance of temperature on metabolic rate in which redside dace were acclimated to two additional temperature treatments, one warmer and one cooler than the ambient temperature used in the first experiment. As in the first experiment, I was unable to find a difference between sexes ($P > 0.37$) or between the four New York populations ($P > 0.48$) included in the study, but treatment temperature had a pronounced effect ($P < 0.001$) on resting routine metabolic rate (Figure 12). Redside dace acclimated to 6°C had a significantly lower mean consumption rate (0.068 mg O_2 g^{+}h^{-1}; $P < 0.05$) than the control group maintained at 12°C (0.123 mg O_2 g^{+}h^{-1}) and the warm treatment group acclimated to 20°C (0.227 mg O_2 g^{+}h^{-1}). A comparison of the 12°C consumption rates between the two experiments failed to show a significant difference (two-tailed t-test, $P > 0.20$) and provided confidence in the repeatability of the results.

Thermal Tolerance. - Acclimation temperature also had a marked effect on the critical thermal maximum of New York redside dace (Figure 13). The CTM endpoint, FLE, differed significantly among all three temperature treatments ($P < 0.05$). Variation from the mean decreased as acclimation temperature increased. Bartlett's test and multiple comparisons (Zar, 1984) showed that the variance in CTM of redside dace acclimated to 6 °C (0.7079) was significantly higher ($P < 0.005$) than redside dace
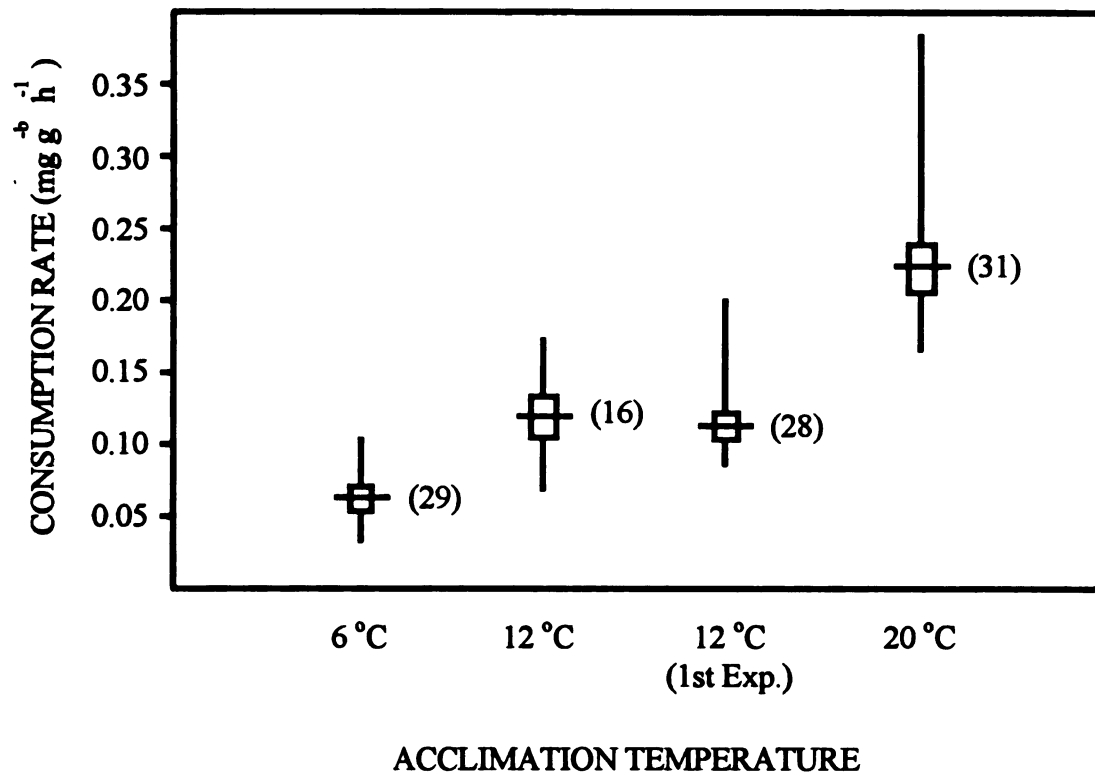
Figure 12. Mean oxygen consumption rates of adult redside dace from New York at three laboratory acclimation temperatures in the second experiment. Laboratory data from the first experiment is provided for comparison. Symbol explanation follows Figure 11.
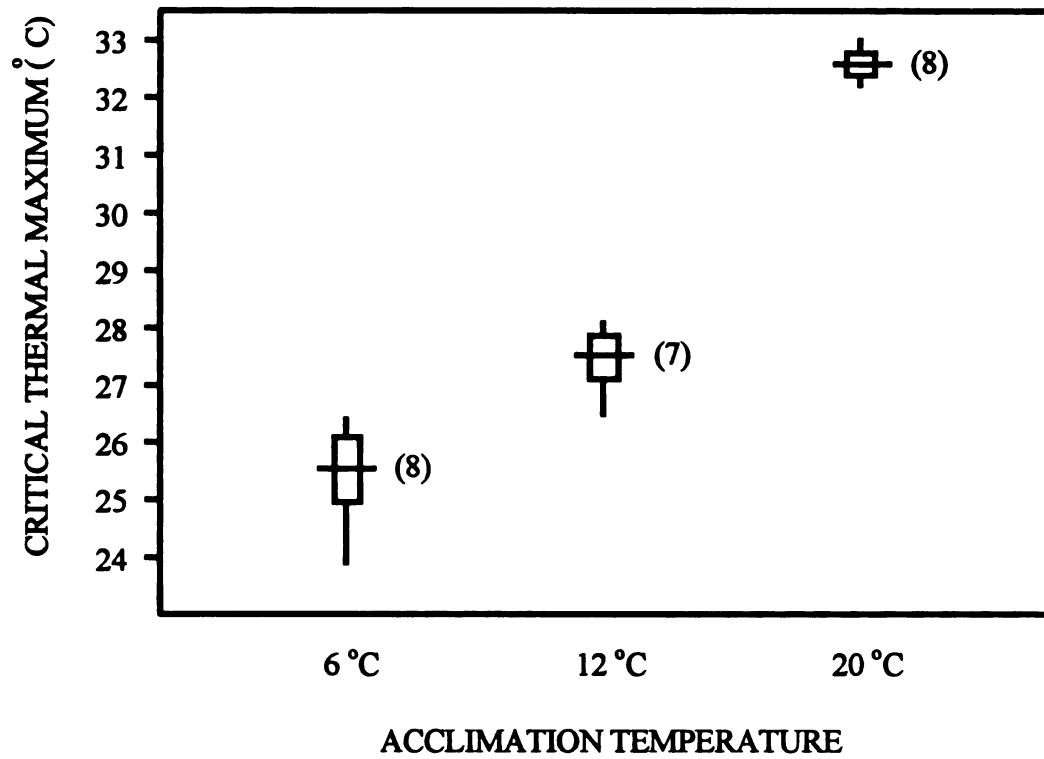
Figure 13. Mean critical thermal maximum of adult redside dace from New York at three laboratory acclimation temperatures. Symbol explanation follows Figure 11.

acclimated to 20 °C (0.0564). Variance was especially low for the latter group where the

SE was equal to the degree of measurement error in reading the thermometer (0.1 °C). I

detected no differences between the two populations (P > 0.49) used in the experiment. A

single individual in the control treatment died of unknown causes before completion of the

acclimation period.

The order of occurrence of the four other behaviors that I identified, BSW, ESW,

SUR, and OPS, was consistent among temperature treatments (Figure 14). Expression of

the behaviors was more constricted for the 20 °C treatment group, for which the

behavioral events were expressed at temperatures closer to the CTM than in the other

treatments. Only one individual failed to show all of the behaviors by not surfacing. The

occurrence of each behavior was also accompanied by a general increase in the level of

excitement and activity. During CTM tests, fish swam continuously against the slight

current produced by the aerator. Burst swimming activity (BSW) generally occurred well

before other apparent stress indicators and was the earliest sign of discomfort. Three

individuals died immediately after showing signs of OPS.

Morphology

Morphometrics. - Sample sizes and mean standard lengths of the specimens used in

the morphometric analysis are shown in Table 4. Preliminary viewing of the specimens did

not suggest any obvious differences among the five groups of redside dace that I studied

(River Rouge watershed, Michigan; Allegheny River and Susquehanna River watersheds,

New York; Black River and Wisconsin River watersheds, Wisconsin). There were,
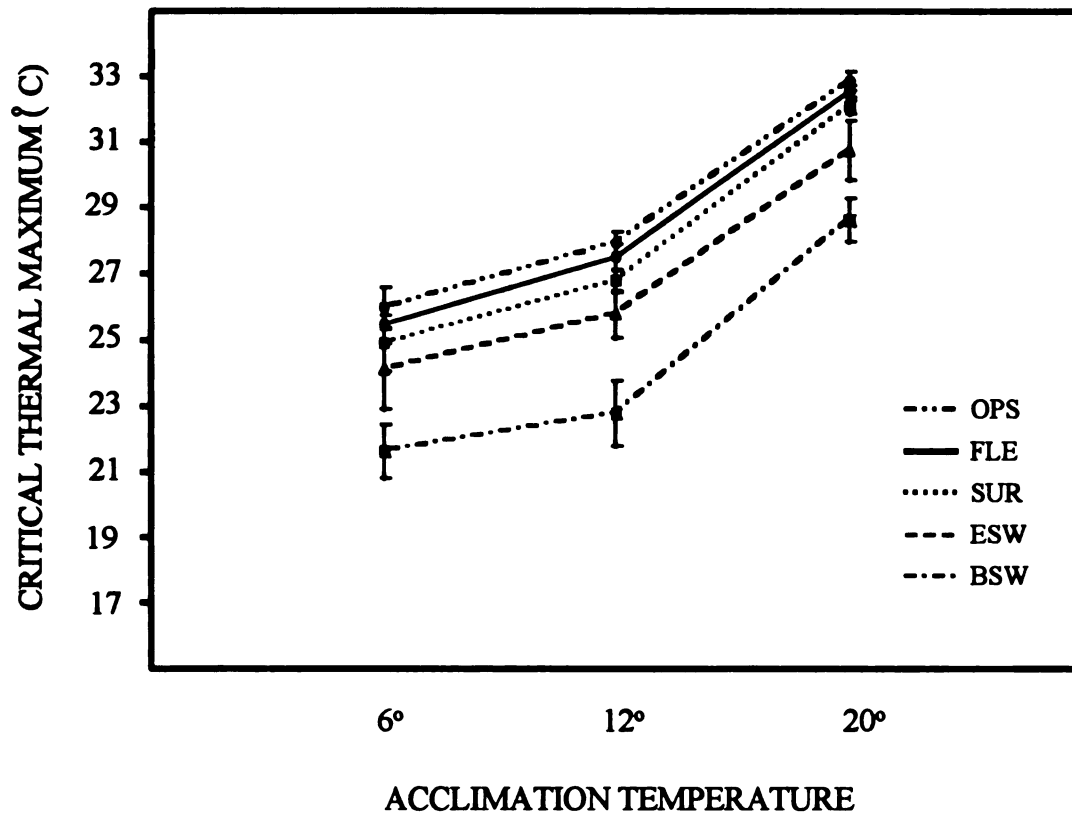
Figure 14. Sequence of behaviors observed during critical thermal maximum tests of adult redside dace from New York at three laboratory acclimation temperatures (means ± 2 SE). OPS = opercular spasms, FLE = final loss of equilibrium, SUR = surfacing, ESW = eratic swimming, BSW = burst swimming. See Methods - *Physiology - Thermal tolerance* for a description of each behavior.

Table 4. Sample sizes and standard lengths of redside and rosyside dace morphometric specimens.

	n	Mean SL (mm) ± SE
Wisconsin redside dace		
Black River	27	63.9 ± 2.1
Wisconsin River	18	62.1 ± 0.9
New York redside dace		
Allegheny River	23	58.7 ± 1.7
Susquehanna River	18	57.7 ± 1.2
Michigan redside dace	28	59.1 ± 1.3
Rosyside dace	30	51.0 ± 1.7

however, clear differences between redside dace and the rosyside dace. As described by Page and Burr (1991), the rosyside dace appeared to be a deeper bodied, stockier fish than the redside dace. Examination of the scatter plots of landmark points and statistical analyses confirmed this observation. Overall differences in the mean shape configuration of rosyside dace compared to the redside dace were most prominent along the dorsal surface of the form (Figure 15). The trend was for a heightening of the back and head and a slight deepening of the caudal peduncle of rosyside dace.

A preliminary within group analysis of differences in mean landmark coordinates (two separate MANOVA's) was performed to test the decision to pool watersheds within New York and within Wisconsin prior to an overall test for mean differences among regions. The mean configurations of the two New York watershed groups were not significantly different (Wilk's Λ, $F_{30,9} = 2.20$, $P > 0.10$), and those groups were pooled for further comparisons to the other groups of specimens. However, the two Wisconsin watershed groups did prove to be significantly different in mean landmark locations ($F_{30,14} = 6.91$, $P < 0.0002$). Corresponding univariate tests of the individual landmark coordinates suggested that the groups differed in the mean x-coordinate positions of points 9, 10, 14, 15, and 16, indicating horizontal shifts in points along the dorsal and ventral surfaces of the forms. Consequently, the Wisconsin redside dace were not pooled for further comparison to the other redside dace groups.

Wilk's test confirmed a significant group effect ($F_{120,436} = 12.18$, $P < 0.0001$) in an overall test of differences in mean shape configurations among Michigan, New York, and the Wisconsin groups of redside dace and the rosyside dace, and corresponding univariate
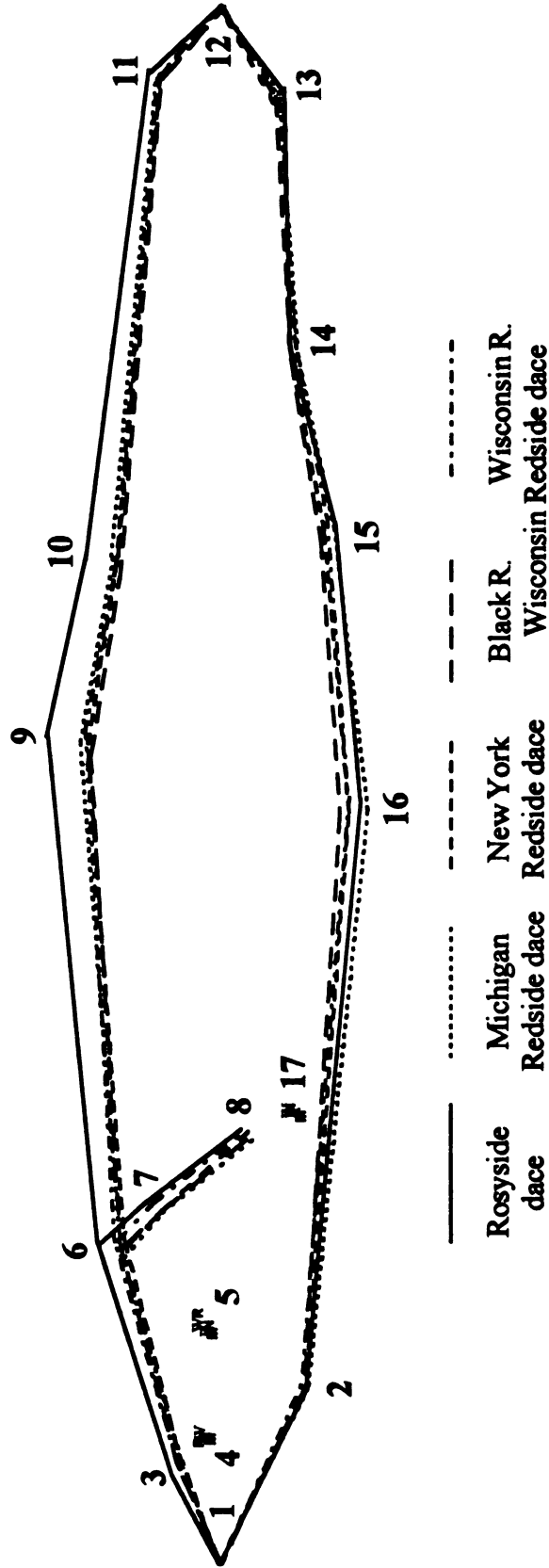
Figure 15. Outlines of mean shape configurations for redside dace from four regions and rosyside dace. Outlines have been scaled and superimposed on a baseline between points 1 and 12. Letters marking interior points represent Michigan (M), New York (N), Wisconsin - Black River (B), Wisconsin - Wisconsin River (W), and rosyside dace (R).

tests detected significant differences among groups for most x- and y-coordinates. There were fewer significant differences among the redside dace when the analysis excluded rosyside dace. The redside dace groups were significantly different overall ($F_{90,240}$ = 6.79, P < 0.0001) and in the x-coordinates of points 6, 9, 10, 14, and 16 and in the y-coordinates of points 2 - 7, 13, 15, and 16, despite substantial overlap among the groups in the coordinate scatters of individual landmarks.

The thin-plate spline analyses provided insight into the scale and magnitude of shape differences between groups and was useful in visualizing the directions of landmark displacement. Linear transformation did not suggest significant relationships among the groups of redside dace. Uniform variation was virtually unrecognizable in the affine mappings of the thin-plate spline transformations from the rosyside dace reference configuration to mean redside dace shape configurations. A scatter-plot of the uniform x- and y-factors (Figure 16) showed that uniform variation was primarily in a negative direction along the x- and y-axes. A principal components analysis of the uniform factors (Tabachnick and Bookstein, 1990) showed that uniform factor y loaded highest on the first of two principal components that described 58% and 42% of the total uniform variation, respectively. The linear transformation was characterized by a slight tilting of the thin-plate in which landmarks above and below the baseline displayed anterior, dorso-ventral displacements that were proportional to their distance from the baseline. The deformation corresponds to a homogeneous narrowing of the body and head of the outgroup rosyside dace form in the transformation to the form of redside dace.
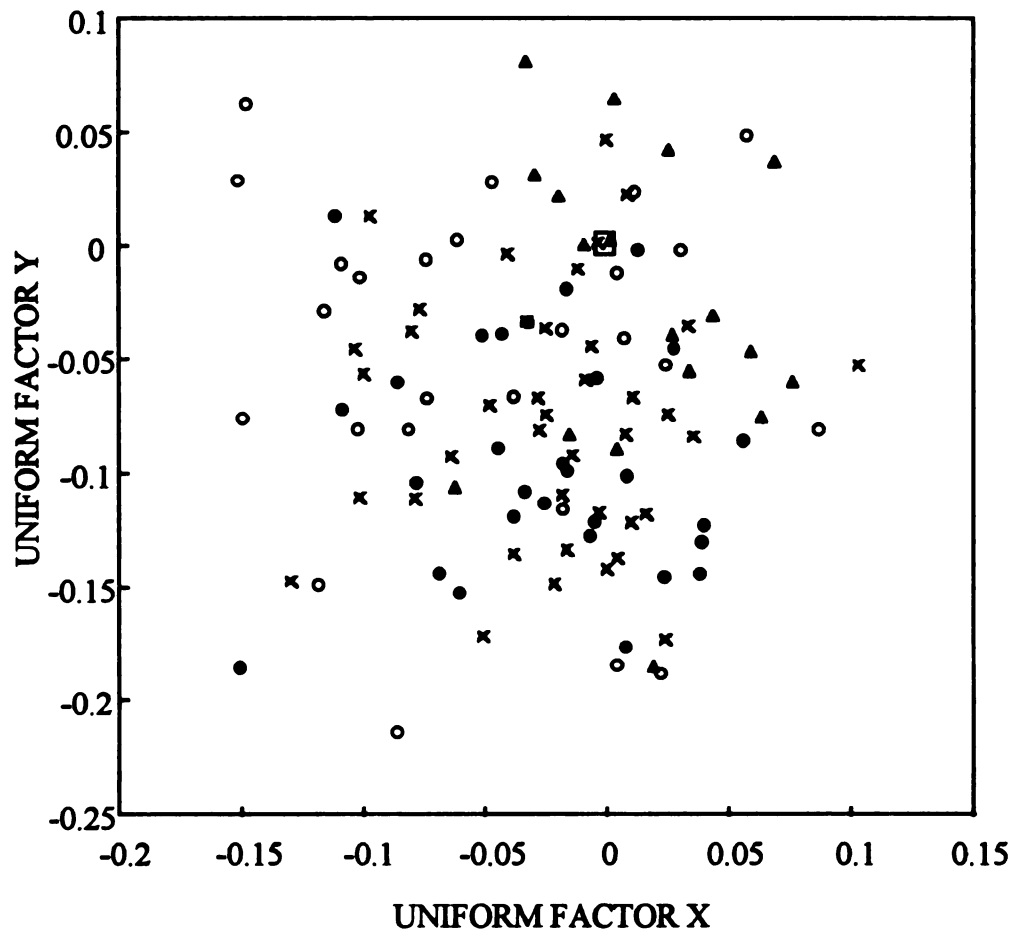
Figure 16. Scatter-plot of the uniform factor x- and y-dimensions of the affine transformation from the mean rosyside dace starting configuration to individual redside dace shape configurations. Symbols: (□) rosyside dace at (0,0); (•) Michigan redside dace; (×) New York redside dace; (o) Wisconsin - Black River redside dace; (Δ) Wisconsin - Wisconsin River redside dace.

Non-uniform shape change had a much greater impact than uniform change on the shape of the thin-plate splines. Non-uniform variation among the groups of redside dace and the outgroup was observed as heterogeneous stretching of the thin-plate caused by the independent movements of separate neighborhoods of landmark points. The spline analyses produced a set of 14 principal and partial warps that corresponded to non-uniform components of shape change for each comparison of the rosyside dace starting form to individual redside dace specimens. The partial warps were ordered by eigenvalue in that the first partial warp had the largest eigenvalue and corresponded to the smallest scale shape change. Progressively smaller scale partial warps described variation not already attributed to larger scale warps.

Overall, the thin-plate spline analysis identified several non-uniform differences in shape that distinguished redside dace from rosyside dace, but few distinctive shape differences were found among the groups of redside dace. Figure 17 and 18 illustrate the thin-plate spline transformation from the rosyside dace starting form to each of the mean redside dace shape configurations by mapping the deformation of a cartesian grid. Total bending energies of the non-uniform transformation were comparable among all redside dace groups (New York 0.0093, Michigan 0.0094, Wisconsin - Black River 0.0114, Wisconsin - Wisconsin River 0.0119) suggesting that the overall degree of bending was similar.

The most profound difference between redside dace and rosyside dace was regularly displayed in the largest scale partial warp 14 (Figure 19) though this warp was not useful in distinguishing among the groups of redside dace. Partial warp 14 described a
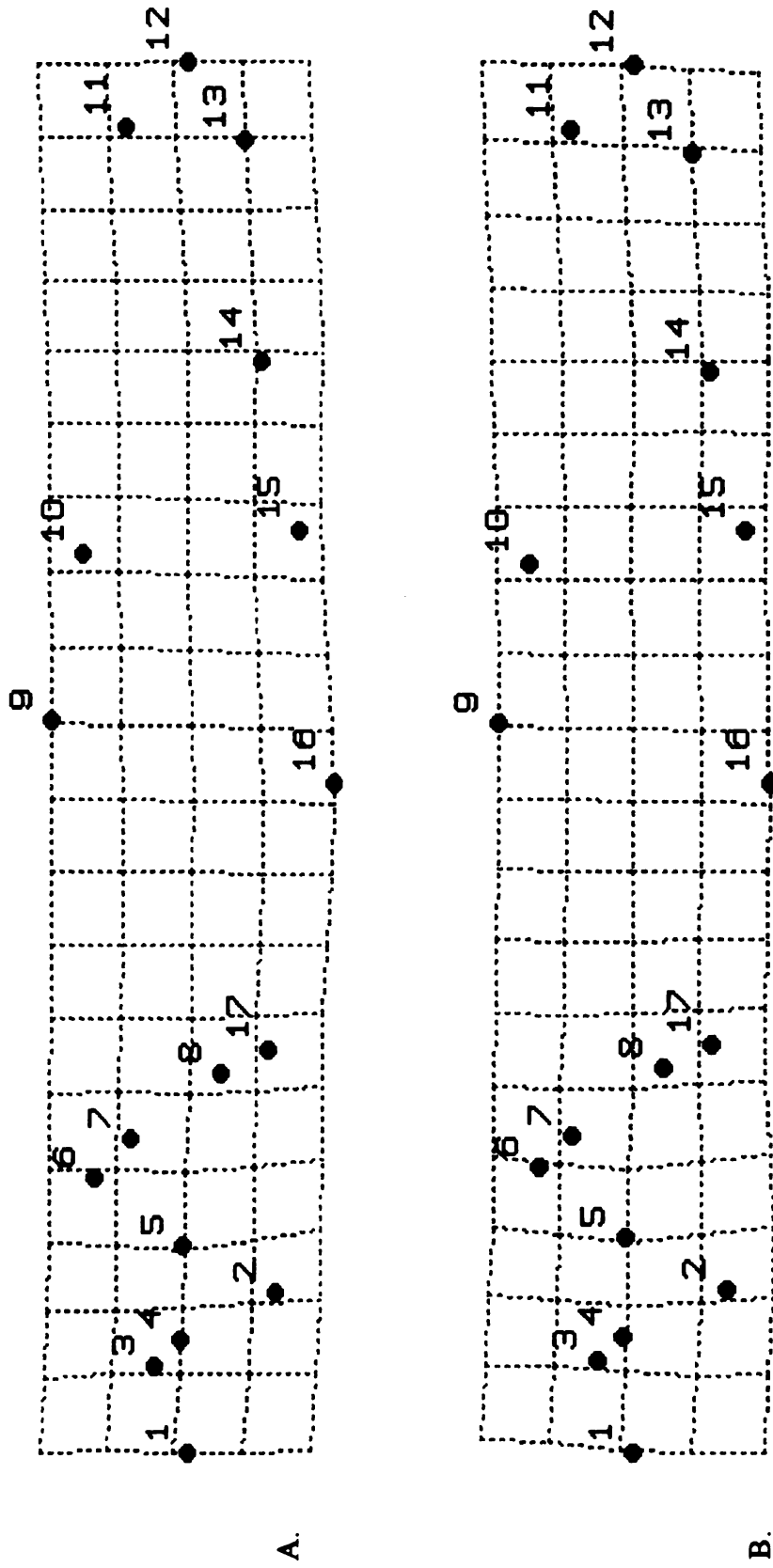
Figure 17. Cartesian mappings of the thin plate spline transformation of the rosyside dace starting configuration to redside dace mean shape configurations. The mappings depict the combined effects of the affine and non-uniform components of shape change. A) The transformation from the rosyside dace configuration to the Michigan redside dace configuration. B) The transformation from the rosyside dace configuration to the New York redside dace configuration.
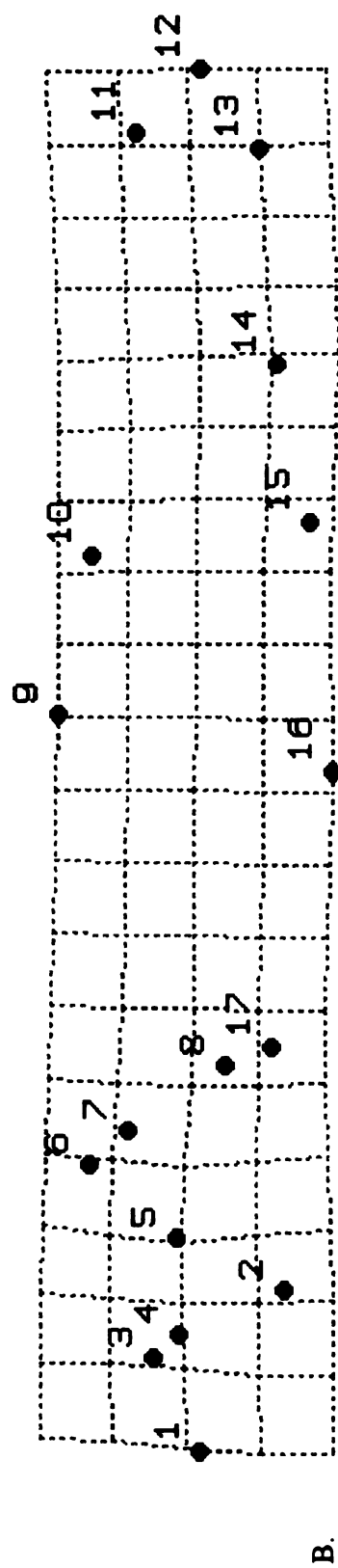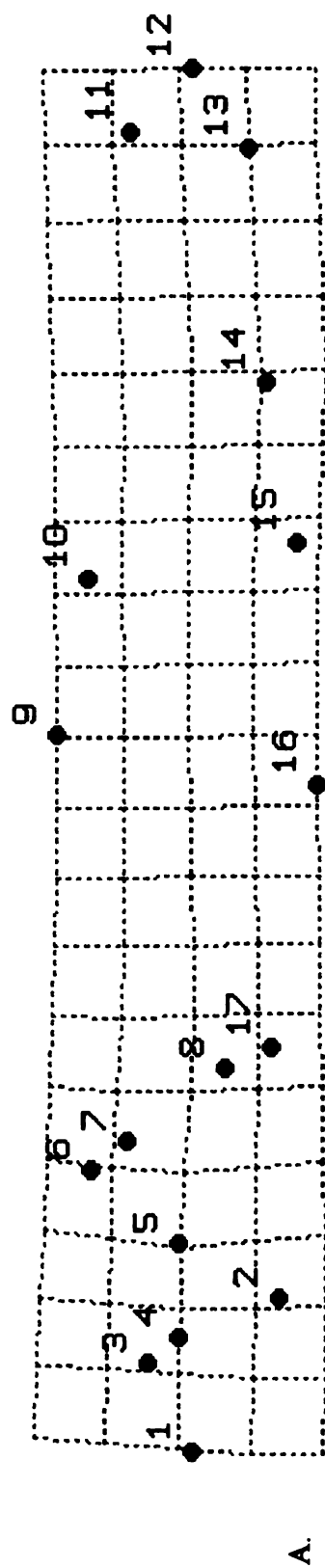
Figure 18. Cartesian mappings of the thin plate spline transformation of the rosyside dace starting configuration to redside dace mean shape configurations. The mappings depict the combined effects of the affine and non-uniform components of shape change. A) The transformation from the rosyside dace configuration to the Wisconsin - Black River redside dace configuration. B) The transformation from the rosyside dace configuration to the Wisconsin - Wisconsin River redside dace configuration.
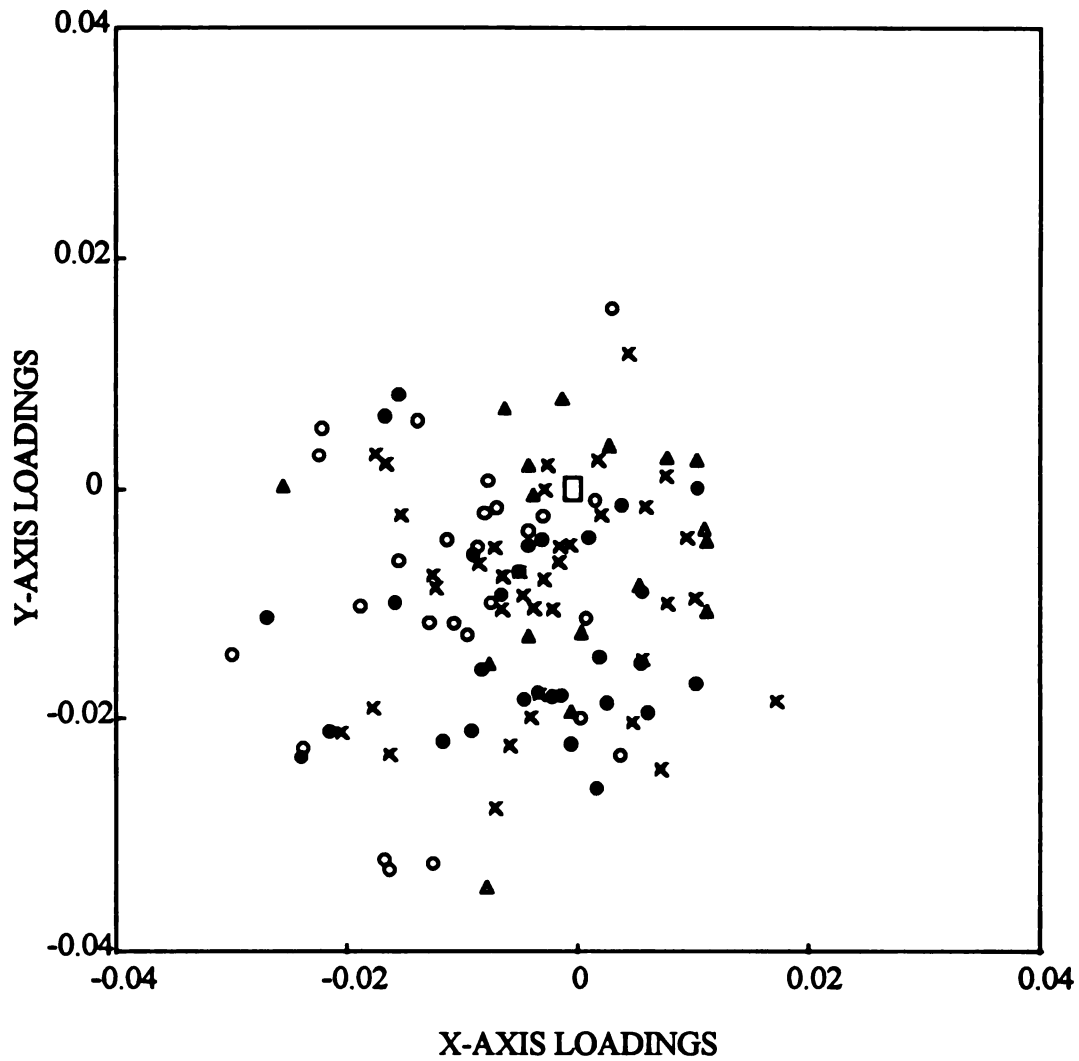
Figure 19. Distribution of loadings on the x- and y-dimensions of partial warp 14 for the thin-plate spline transformation from the mean rosyside dace starting configuration to individual redside dace shape configurations. Symbols: (□) rosyside dace at (0,0); (•) Michigan redside dace; (x) New York redside dace; (o) Wisconsin - Black River redside dace; (Δ) Wisconsin - Wisconsin River redside dace.

transformation characterized by dorso-ventral depression of the trunk of rosyside dace through downward shifts at points 9 and 16, and corresponding upward shifts at the ends of the baseline, points 1 and 12. The displacement of the central landmarks relative to the anterior and posterior ends of the baseline is a common feature of the largest scale principal warp (Swiderski, 1993; Bookstein, 1991). Large-scale transformations contributed most to the shape of the splines (high magnitude) but had low bending energies (< 10% of the total) because their effects were distributed over broad regions (low eigenvalues). Depression along the dorsal surface was consistent among the redside dace and suggested an overall decrease in the height of the rosyside dace back relative to redside dace, a difference apparent in the outlines of the mean shape configurations (Figure 15) and in the total spline mappings (Figure 17 and 18).

Large-scale features of shape change were the most distinguishing shape characteristic among the redside dace. Partial warp 11 (Figure 20) described primarily dorso-ventral shifts along the ventral surface with high y-axis loadings on point 16, 14, and 2. This transformation suggested that Wisconsin redside dace from both watersheds had a shallower keel than New York or Michigan redside dace relative to the rosyside dace starting form; however, the scale of these shape differences is small and the scatters of all redside dace groups overlap. Michigan redside dace were more similar to the outgroup in this deformation than were the other redside dace groups.

Local changes in the positions of one or two points contributed the most bending energy (> 75% of the total) to the thin-plate spline transformation from rosyside to redside dace. Partial warp 4 (Figure 21) was consistently of highest bending energy (> 45% of the total) and was of second highest magnitude after partial warp 14. Partial warp 4 was
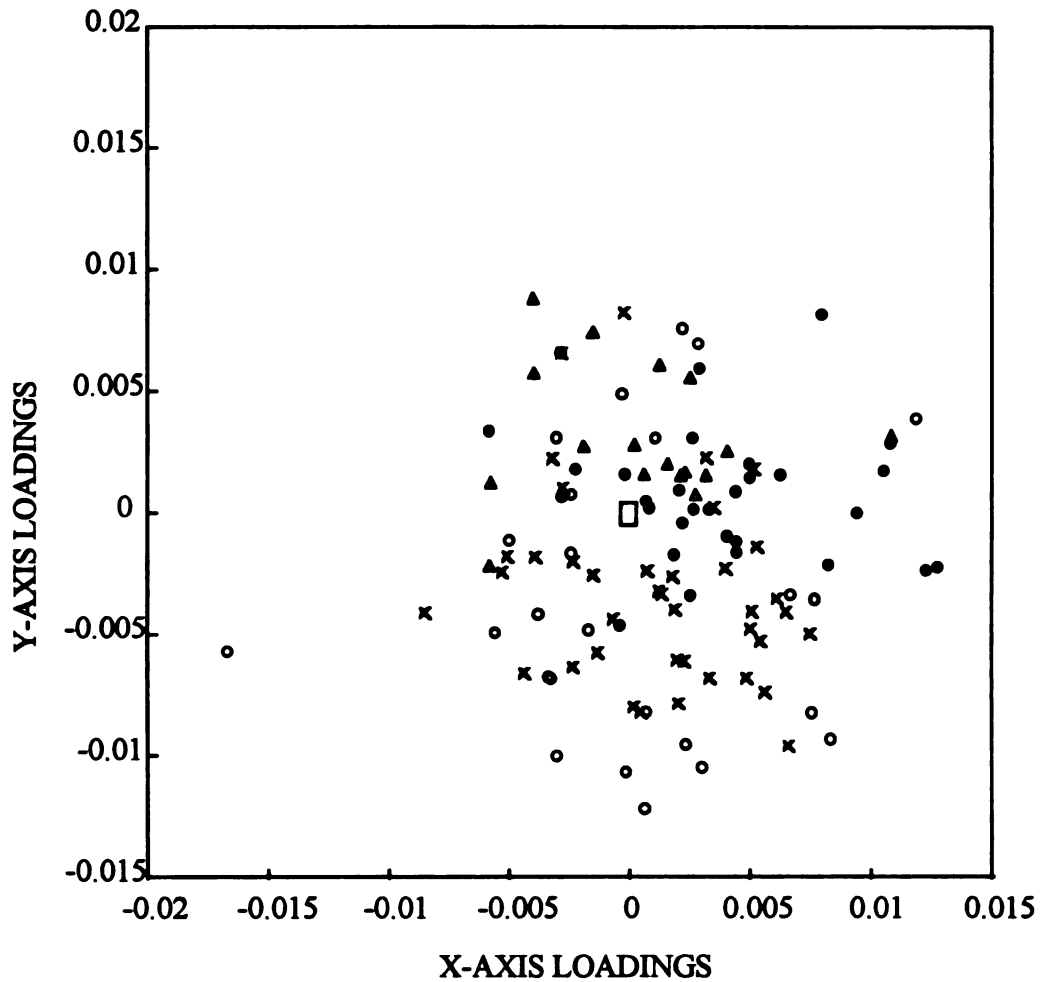
Figure 20. Distribution of loadings on the x- and y-dimensions of partial warp 11 for the thin-plate spline transformation from the mean rosyside dace starting configuration to individual redside dace shape configurations. Symbols: (□) rosyside dace at (0,0); (•) Michigan redside dace; (x) New York redside dace; (o) Wisconsin - Black River redside dace; (Δ) Wisconsin - Wisconsin River redside dace.
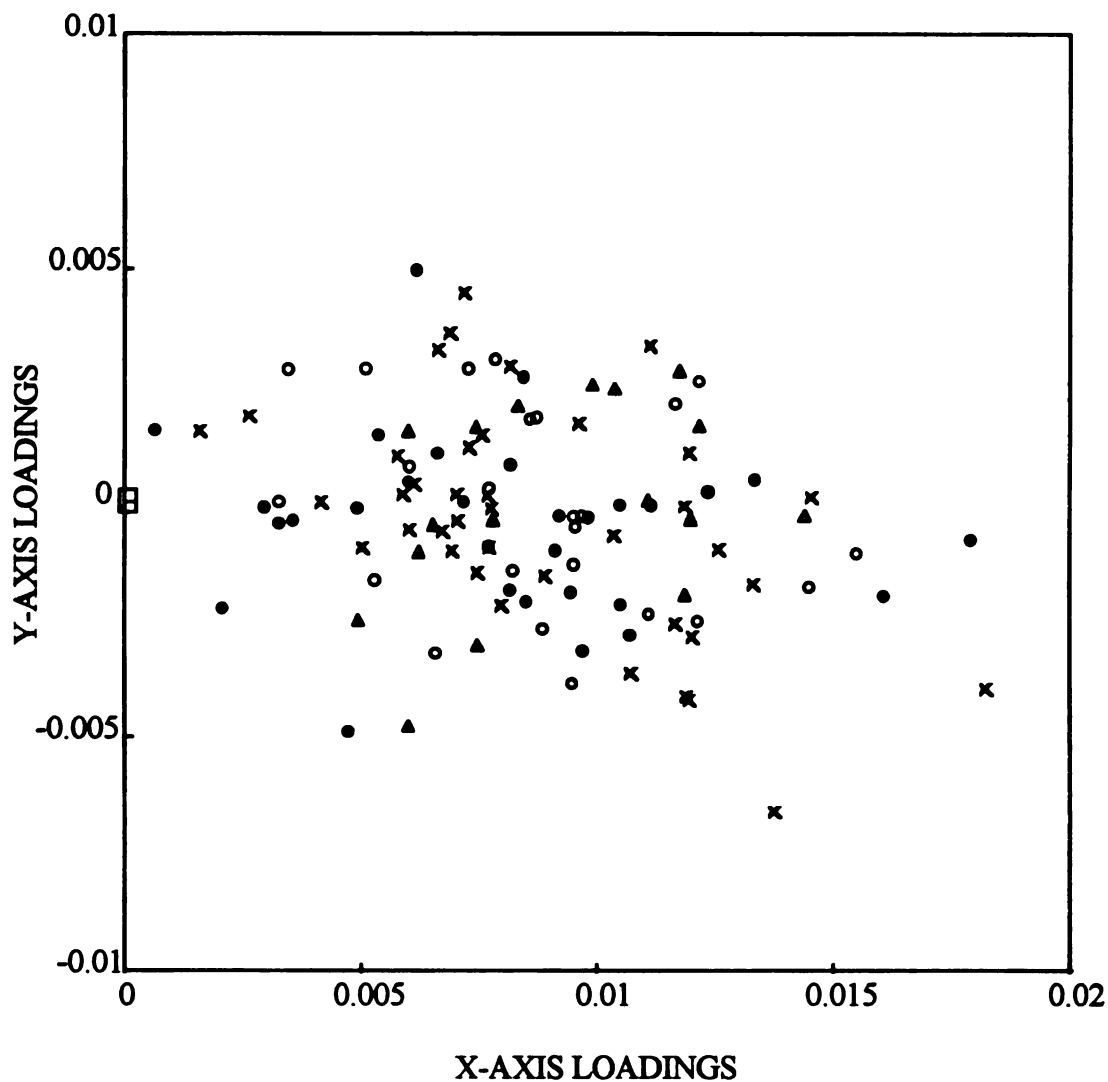
Figure 21. Distribution of loadings on the x- and y-dimensions of partial warp 4 for the thin-plate spline transformation from the mean rosyside dace starting configuration to individual redside dace shape configurations. Symbols: (□) rosyside dace at (0,0); (•) Michigan redside dace; (×) New York redside dace; (o) Wisconsin - Black River redside dace; (Δ) Wisconsin - Wisconsin River redside dace.

driven by the horizontal, posterior movement of point 5, the posterior edge of the eye. High loadings on the horizontal axis indicated that redside dace possessed a significantly narrower intraorbital diameter than rosyside dace, though no difference was indicated among groups of redside dace specimens.

Rosyside dace were further differentiated from redside dace through a second, small-scale transformation, partial warp 2. This warp described inward movements in landmarks located along the operculum and base of the skull (points 6 and 8) of redside dace relative to rosyside dace. Anterior displacement of these landmarks was most pronounced for Michigan redside dace and least for Wisconsin - Wisconsin River redside dace, though distributions of the two group's loadings overlapped. Additional partial warps depicted inward, posterior movement of the anterior naris (partial warp 1, point 3) and the dorso-ventral displacement of landmarks identifying the caudal peduncle (warp 5 and 10, points 11, 13, and 9). Collectively, these shifts implied a decrease in relative head dimensions and in the width of the caudal peduncle of the redside dace compared to the rosyside dace. Redside dace did not differ appreciably in their loadings on these partial warps.

Meristics. - There was no discernible pattern to minor variation in dorsal and anal fin ray counts. Redside dace from Michigan, New York, and Wisconsin consistently possessed 8 separate dorsal fin rays (Table 5); only 2 individuals from New York had 7 dorsal fin rays. Counts of anal fin rays were more variable (Table 6), though most individuals (>86%) had 9 anal rays.

Table 5. Frequency distribution of dorsal fin ray counts for redside dace morphometric specimens from five locations.

| | | Number of Dorsal Fin Rays | |
	n	7	8
Wisconsin			
Black R.	26		26
Wisconsin R.	22		22
New York			
Allegheny R.	36		36
Susquehanna R.	17	2	15
Michigan	43		43

Table 6. Frequency distribution of anal fin ray counts for redside dace morphometric specimens from five locations.

	n	Number of Anal Fin Rays		
		8	9	10
Wisconsin				
Black R.	27		23	4
Wisconsin R.	19		18	1
New York				
Allegheny R.	42		34	2
Susquehanna R.	17	3	14	
Michigan	43	3	37	3

Differences among the redside dace were evident from lateral line scale counts

(Figure 22). Michigan redside dace had a lower median scale count (63) than either of the

New York watershed groups (Allegheny Susquehanna Rivers = 65) or Wisconsin groups

(Black River = 65; Wisconsin River = 66). A χ^2 contingency table analysis confirmed that

Michigan had significantly fewer lateral line scales ($P < 0.001$) than New York and

Wisconsin (watersheds pooled within state).
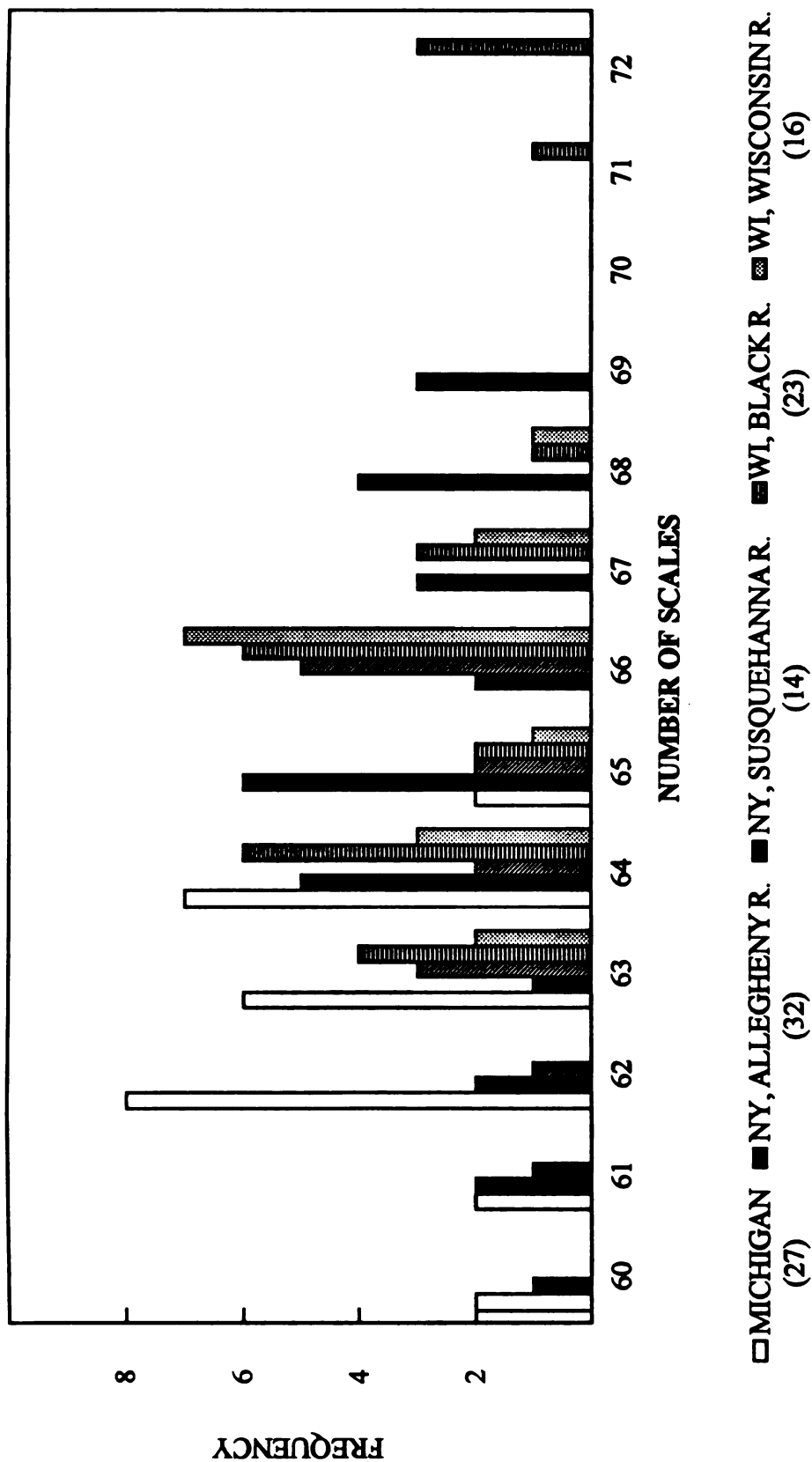
Figure 22. Frequency distribution of lateral line scale counts for redside dace morphometric specimens from five regions. Sample sizes are given in parenthesis.

DISCUSSION

Behavior

Redside dace in Michigan and New York used depth and current velocity attributes of microhabitat in similar ways, but differed in their use of other microhabitat attributes. Most individuals occupied mid-water positions in the deepest parts of pools. From this position, redside dace struck repeatedly at items floating on or hovering above the stream surface. They struck less frequently at objects suspended in the water column. It was difficult to generalize about the importance of substrate type or instream cover to foraging redside dace because the substrates and cover types available in Seeley Drain and the New York streams were different and redside dace use of these attributes differed accordingly.

In Seeley Drain, instream visual cover was the only type of abundant instream cover, and its use by redside dace was only slightly less than that expected from random choice. Use of no cover was recorded for most observations. It is also possible that depth was being used as a form of cover from avian piscivores by redside dace in Seeley Drain and New York (Baltz and Moyle, 1984), but I was unable to test this hypothesis with the data I collected. In the New York streams, boulders provided velocity shelters that received a disproportionate amount of use by redside dace. Velocity shelters were the only form of instream cover abundant in the New York streams. Structure overhanging the stream was used in the New York streams, but the importance of overhanging

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structure was less obvious in Seeley Drain where it was abundant over all of the pools surveyed.

Differences in the availability of habitat attributes have been shown to limit the degree to which habitat use information may be reliably transferred from one site to another (Barrett and Maughan, 1994). The importance of a habitat attribute may be masked by its general abundance or attributes deemed important in one locality may not be available in others. A comparative approach involving artificial manipulation of microhabitat components would be useful to clarify the significance of the patterns of microhabitat use that I observed. It would be valuable to know if redside dace in Seeley Drain would make use of velocity shelters if they were made available or would respond to the selective removal of some overhanging cover. Velocity shelter did appear important to rosyside dace that were observed to aggregate in eddies or depositional areas next to fast water during high flow conditions (Freeman, 1990). Redside dace did not appear to make special use of areas adjacent to fast water (depositional areas at the heads of pools), and there was no identifiable relationship between the distribution of redside dace within pools and the proximity of fast water areas.

My observations of microhabitat use are in close agreement with the detailed observations of Koster (1939) who noted that redside dace primarily inhabited pools and devoted the largest portion of their activities to foraging at or near the surface. It should also be emphasized that the use and availability of microhabitat characteristics that I measured are specific to mid-summer, daylight conditions and may differ at night and during other parts of the year. Grossman and Freeman (1987) found that rosyside dace

occupied more benthic, low velocity positions during winter months. Also, the attributes and significance of spawning and overwintering microhabitats were not evaluated in this study and may play a crucial role in determining redside dace distribution. Gravels hypothesized to be necessary for spawning (Koster, 1939) may be limited in the sand-dominated substrates of Seeley Drain, and increased siltation may pose an especially serious threat to the reproductive success of redside dace.

The patterns of redside dace microhabitat use that I described appeared to correspond closely to selective tradeoffs associated with the fish's distinctive mode of feeding, the activity that dominated nearly all observation periods. Natural selection should favor individuals that maximize their fitness through the selection of high quality microhabitats and efficient foraging strategies (Hill and Grossman, 1993). Through their use of mid-water positions and exploitation of aerial, terrestrial prey, redside dace incurred higher energetic costs associated with swimming at higher velocities (Facey and Grossman, 1990) and perhaps increased their risk of predation by other aquatic and aerial predators compared with deeper positions. However, at mid-water positions redside dace could increase their net energy intake by reducing their distance from potential food items and could increase their chances at detecting and capturing prey compared to deeper positions (Wilzbach, 1985). In another sense, a mid-water position would reduce the risk of predation by avian predators compared to a near-surface position that would be closer to prey. Piscivorous fishes may also present a threat to foraging redside dace; brook and brown trout were observed at the New York study sites and brown trout are known to co-occur with some redside dace populations in Michigan. Redside dace were observed to

form small aggregations when feeding, similar to rosyside dace (Freeman, 1990).

Aggregative social behaviors may offer a defense against other fish predators (Moyle and Cech, 1988).

Redside dace may reduce direct competition for food with other fishes by displaying such a specialized foraging strategy (Daniels and Wisniewski, 1994). A correspondence between net energy intake and microhabitat use has been shown for other fishes inhabiting stream water-column microhabitats (Hill and Grossman, 1993; Hughes and Dill, 1990). A bioenergetic model constructed by Hill and Grossman (1993) predicted microhabitat use (focal velocities) for rosyside dace with 75% success and found that prey capture success was the most important model component. They showed that the energetic costs incurred by holding position at a given velocity was much less than the energy available at that velocity, indicating that the benefits of the position outweighed the costs. In the same way, redside dace appear to balance the costs of swimming, predation risk, and perhaps decreased food availability against the benefits of increased prey capture success and reduced competition. The redside dace foraging strategy appears to rely heavily on visual accuity, a hypothesis supported by the uncommon observation of redside dace in streams of low water clarity. Increased turbidities in the streams inhabited by redside dace may pose a serious threat to redside dace foraging abilities and should be guarded against by appropriate management efforts.

Physiology

Metabolic rate. - Redside dace displayed a clear metabolic response to trial period lengths and acclimation temperatures. Estimates of oxygen consumption rate became

more stable as the duration of the test increased. Presumably, test fish became more accustomed to the change in water quality that accompanied the interruption of flow. One of the disadvantages of static respirometry methods that employ the sealed vessel technique is the inability to maintain constant conditions during a trial (Winberg, 1956). Subtle changes in temperature and in the concentrations of dissolved gasses and ions in the respirometer may elicit a physiological response in test fish. The activity levels of test fish were also beyond control and varied to a minor extent among individuals. These criticisms make the sealed vessel method less attractive as an estimator of standard (resting) metabolic rate, though the procedure was a dependable method for measuring resting routine rates for comparative purposes (Cech, 1990). The rates that I measured were expected to overestimate standard metabolism and to include some variability associated with spontaneous activity. Observation showed that such activity was minimal.

The rate of metabolism is a product of the environmental conditions that fish encounter as well as their evolutionary history (Fry, 1971). The oxygen consumption rates that I recorded for redside dace tended to be higher than rates determined for other cyprinids using similar methodology (Figure 23). Central stoneroller and common shiner, minnows that were abundant in the New York streams where I studied redside dace, had similar oxygen consumption rates in a study by Clausen (1936). In addition, metabolic rates measured for rosyside dace at 15°C (Facey, 1987) were identical to redside dace tested at 14°C in the field. Similar rates were also recorded for the plains minnow, *Hybognathus placitus*, which has a more midwestern distribution but reaches similar dimensions as the redside dace (Bryan et al., 1984). Minnows that had the lowest rates

Acclimation Temperature (C°)

Species	5	10	15	20	25	30	Investigators
Campostoma anomalum				0.19			Clausen, 1936
Carassius auratus				0.09	0.12	0.14	Konstantinov et al., 1990
C. auratus							Fry and Hart, 1948
Clinostomus elongatus	0.07	0.12	0.14	0.12			Present study
Clinostomus funduloides[1]	0.16	0.33	0.14	0.23			Facey, 1987
Cyprinus carpio				0.12	0.25	0.28	Konstantinov et al., 1990
Gila bicolor mohavensis				0.04	0.07	0.10	McClanahan et al., 1986
Hesperoleucus symmetricus		0.01			0.04		Cech et al., 1990
Hybognathus placitus			0.11	0.18	0.27	0.45	Bryan et al., 1984
Luxilus cornutus				0.13			Clausen, 1936
Ptychocheilus grandis		0.04	0.06	0.07	0.08	0.12	Cech et al., 1990
Rhinichthys osculus		0.24	0.26	0.38	0.45	0.61	Baltz et al., 1982

[1]standard rates estimated by extrapolation of active consumption rates to 0 activity.

Figure 23. Oxygen consumption rates (mg g^{-1} h^{-1}) associated with resting metabolism for several cyprinid fishes.

compared to redside dace, Sacramento squawfish *Ptychocheilus grandis* (Cech et al.,

1990) and the tui chub *Gila bicolor* (McClanahan et al., 1986), have western distributions;

the squawfish occupies warmer environments and is much larger than the redside dace.

Redside dace showed a significant, steady increase in metabolic rate with

acclimation temperature in the second experiment. The upward trend in intensity

appeared to explain the differences between New York field and lab results observed in

the first experiment. Considered together, the results of the two experiments showed that

the mean resting routine metabolic rates of redside dace fit a predictable exponential

function:

$$y = 0.0416e^{0.0861x} \ (r^2 = 0.993)$$

where y = oxygen consumption rate (mg g^{-b} h^{-1}) and x = acclimation temperature ($^\circ$C;

Figure 24). Many researchers have demonstrated the influence of temperature on standard

metabolic rates (Ege and Krogh, 1914; Brett, 1964; Beamish, 1964b, and Mookherji,

1964; Cech et al., 1979, 1985, 1990; Kaufman and Wieser, 1992; Smirnov et al., 1987;

Konstantinov et al. 1990). The general relationship for temperate fishes was synthesized

by Ege and Krogh (1914) who developed the "standard" curve from static respirometry

data for temperature acclimated goldfish, *Carassius auratus*. Winberg (1956) found that

the rate of standard metabolism of many fishes followed a similar trend, though the

standard curve has been shown to offer a poor approximation of actual oxygen

consumption rates for some species (Fry, 1947, 1971; Brett and Groves, 1979). The

resting routine metabolic rates that I measured for redside dace showed close

correspondance to those predicted by the goldfish curve (Figure 24). The standard curve
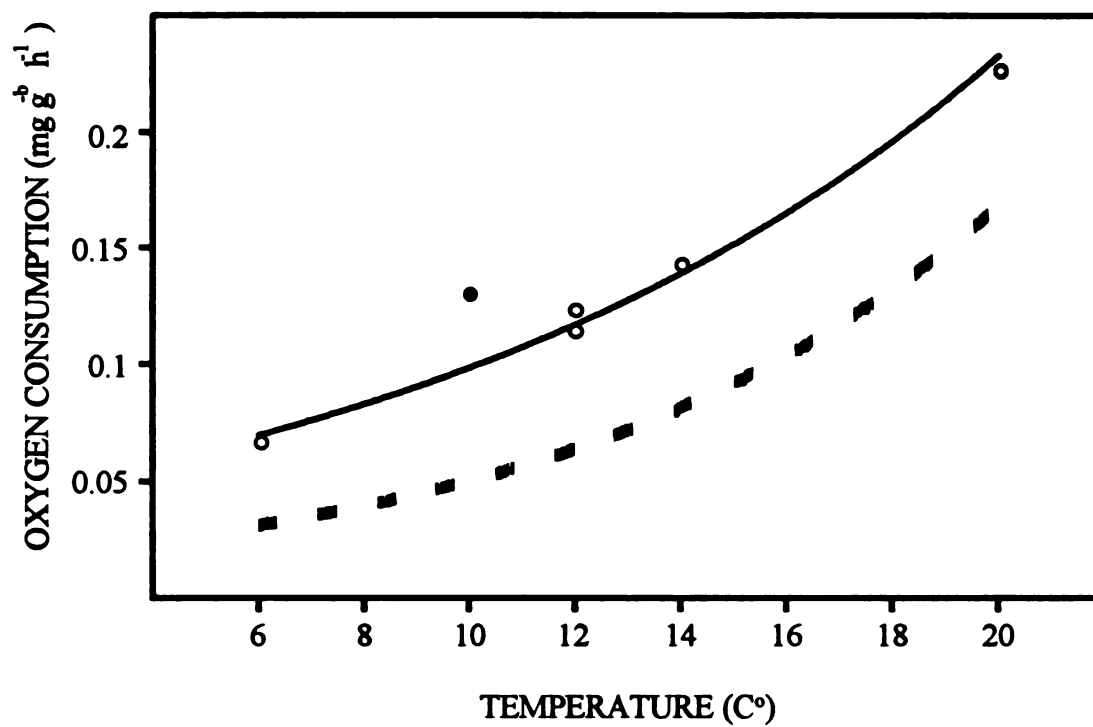
Figure 24. Redside dace mean oxygen consumption rates in relation to Krogh's "standard curve" (dotted line) adapted from Winberg (1956). New York data are indicated by the open circles and solid line, Michigan by the closed circle.

(Ege and Krogh, 1914) has a mean Q_{10} (increase in rate with a 10°C increase in temperature) of 2.0 compared to a mean Q_{10} of 2.4 for redside dace. The metabolic rates of redside dace were elevated above the standard curve but fit within the 2.0 - 2.5 range reported for freshwater fishes (Fry, 1971; Brett and Groves, 1979).

Redside dace tested in the field in Michigan showed a significantly higher metabolic rate compared to the value predicted for New York fish at the same temperature (Figure 24). The Michigan mean consumption rate (0.13 mg g^{-b} h^{-1}) was beyond the 95% confidence interval around the estimated rate of New York redside dace at 10 °C ($\tilde{Y}_i$ = 0.09, 95% CI: 0.09 - 0.10). However, in comparing standard errors the difference is not great. I was restricted from testing more Michigan redside dace by Michigan Department of Natural Resources policy regarding the handling of protected species. Therefore, I did not have the opportunity to collect oxygen consumption data for Michigan redside dace at other temperatures, so it is difficult to generalize about physiological differences in metabolism between redside dace in Michigan and New York. The relatively higher rate for Michigan fish at 10 °C may indicate a true difference between the groups, suggesting that redside dace in Seeley Drain are adapted to a different set of environmental conditions than redside dace in New York or that redside dace in Seeley Drain are stressed by an unmeasured environmental factor. It is unlikely that seasonal influences separate from temperature were responsible for this difference because field experiments in Seeley Drain and New York were not more than one month apart and occurred well outside of the reported spawning season of redside dace in either state.

Static respirometry methods worked well in the lab and in the field. Although metabolic rates have been estimated by other techniques at field sites (Feldmeth and Jenkins, 1973), few studies have utilized field respirometry methods and equipment that were nearly identical to those used in the lab (Mukhamedova, 1978). Field techniques allowed the testing of naturally acclimatized fish in their native stream water, avoiding the handling stress and lengthy acclimation periods necessary for fish transferred to lab conditions. The method also eliminated the expense and effort required to maintain fish in the lab. I was able to control most significant external factors to the same degree as in lab experiments (with the exception of a few rainy days), and the method required a minimum of equipment and preparation. Field respirometry methods should be considered as a credible alternative to lab approaches for simple experimental designs.

Thermal tolerance - Increasing acclimation temperatures produced a significant rise in redside dace CTM but at a lower rate than the increase observed in standard metabolic rates. Mean CTM showed a 1.3 rate of increase from 6 - 20 °C acclimation temperatures (1.2 for each 10 °C increase in acclimation temperature). It is not possible to predict the relationship of Michigan redside dace CTM to the data measured for New York redside dace without a comprehensive, detailed base of ambient monitoring data for the New York and Michigan streams. I would expect redside dace from Michigan to have higher thermal tolerances if environmental conditions in Seeley Drain proved to be more variable than conditions in Rice Brook. Feminella and Matthews (1984) showed that populations of orangethroat darter, *Etheostoma spectabile*, from streams with wide temperature fluctuations exhibited higher CTM than darters in spring-fed streams with

homogeneous temperature regimes. This prediction assumes that redside dace in Seeley Drain are under no other forms of stress and are comparable in condition to redside dace from New York.

The CTM of redside dace was similar though consistently higher than maxima determined for other Cyprinidae (Figure 25), many of which are also found in the New York streams studied. The fact that *Clinostomus* CTM ranged higher than the values recorded for most minnows was in part explained by differences in the experimental endpoints chosen. Kowalski et al. (1987) used the onset of muscular spasms to mark CTM, and Scott (1987) chose initial rather than final loss of equilibrium, the endpoint that I used. Muscle spasms and initial loss of equilibrium corresponded to the ESW behavior that I recorded for redside dace and occurred at lower temperatures than the final loss of equilibrium (Figure 14). The two minnows that displayed a CTM higher than that of redside dace, red shiner *Cyprinella lutrensis* (Matthews, 1986) and tui chub *Gila bicolor* (McClanahan et al., 1986), have western distributions and red shiner inhabit warmer environments.

The measurement of thermal tolerances has been critical to understanding the temperature requirements and preferences of different fish species and has been used to model fish response to various environmental perturbations (Fry, 1971). Upper CTM is regarded as an acute measure of thermal tolerance that has been shown to overestimate the upper bounds of the "zone of tolerance," defined by Fry (1947) as the upper incipient lethal temperature (UILT), where 50% mortality occurs. CTM places an upper bound on the "zone of resistance," where mortality is an unavoidable function of exposure time and

Acclimation Temperature (C°)

0   10   20   30

Species					Investigators
Clinostomus elongatus	25.5		32.6		Present study
Cyprinella lutrensis		27.5	36.1		Matthews, 1986
Gila bicolor mohavensis			33.5	34.9	36.2	McClanahan et al., 1986
Luxilus cornutus			31.9		Kowalski et al., 1978
Nocomis micropogon			30.9		Kowalski et al., 1978
Notropis rubellus			31.8		Kowalski et al., 1978
Pimephales notatus			31.9		Kowalski et al., 1978
Phoximus erythrogaster	18.2	29.3	32.3		Scott, 1987
Rhinichthys atratulus			31.9		Kowalski et al., 1978
Rhinichthys cataractae			31.4		Kowalski et al., 1978

Figure 25. Critical thermal maximum determinations for several cyprinid fishes.

temperature. That mortality quickly follows CTM was evident in this study by the death of three test fish immediately after showing signs of OPS.

Lethal temperature estimates, including CTM, may provide a reasonable approximation of the optimum growth temperatures of temperate fishes, though it is acknowledged to be less accurate for this purpose than measures of final preferenda (Jobling, 1983; Reynolds and Casterlin, 1979). I applied the CTM value for redside dace acclimated to 20 °C (32.6) to two linear regression equations developed by Jobling (1983) from a compilation of values reported in the literature that related lethal temperature to growth optima (r^2 = 0.86) and to final preferenda (r^2 = 0.88). The predicted growth optimum for redside dace was 24.7 °C, almost identical to the predicted preferendum of 24.5 °C. These estimates are in the range of values measured directly for other minnows. Cherry et al. (1977) reported final preferenda of 26.2 °C for central stoneroller and 26°C for rosyface shiner (*Notropis rubellus*). I have successfully acclimated a small number of redside dace to temperatures approaching 23 °C with no visible signs of stress, though no observations pertaining to tolerance at higher temperatures were made. The predicted optimum growth temperature and final preferendum are beyond the highest water temperatures measured at the study sites in New York during July and were above measurements made at the same sites in June by other invesitigators in previous years (R. Daniels, unpublished data). However, redside dace are known to inhabit streams in western New York that displayed August temperatures that were warmer than the predicted growth optimum and final preferendum. The predictions were close to the high temperature recorded in Seeley Drain during the present study (24.4 °C; Table 2). This

was the highest temperature recorded in Seeley Drain during the past three years (T.

Coon, unpublished data). This suggests that redside dace in Seeley Drain and the New

York study streams were not challenged by extreme temperatures during the study period;

however, the temperature optima of many temperate fishes have been shown to be near

the upper bounds of the zone of tolerance, the incipient lethal temperature (Fry, 1971).

Therefore, management efforts should be sensitive to changes in the stream ecosystem that

result in increased ambient temperatures, especially in streams where summer

temperatures may already surpass growth optima.

Morphology

Morphometric analyses employing thin-plate splines have been used to describe the

evolution of morphological structures among taxonomic groups (Swiderski, 1993;

Tabachnick and Bookstein, 1990) and to model the complex integration of ontogenetic

processes (Zelditch et al., 1992). The method was also useful in the present study to

clarify the morphological similarity of external body shapes among four groups of redside

dace in relation to a congener, the rosyside dace. Despite several significant differences

suggested by a MANOVA of shape coordinates, the thin-plate spline analysis suggested

only minor differences in external body shape among groups of redside dace from

Michigan, New York, and Wisconsin; in general, variation in the geometric shape

descriptors was at least as great within as among groups. Differences in mean body shape

that were identified among the redside dace were minute in comparison to differences in

shape between redside and rosyside dace and support only tentative conclusions about

patterns of morphological differentiation among geographically separate populations of

Clinostomus elongatus.

The redside dace differed from the rosyside dace in two respects. First, redside dace demonstrated an overall body shape that was less robust than that of the rosyside dace. This included both uniform and non-uniform dorso-ventral depression of the redside dace form in the trunk and head, indicated by loadings on the uniform y-factor, on the largest-scale partial warp, and on several intermediate and smaller-scale partial warps. Second, a highly localized shape difference showed that rosyside dace had a proportionately wider intraorbital diameter than redside dace. This posterior widening of the eye appeared to follow the outward shifts observed in other regions of the head of rosyside dace relative to redside dace.

The Wisconsin redside dace specimens appeared to diverge from the other groups and from rosyside dace in the largest number of morphometric characteristics. Wisconsin - Black River redside dace differed slightly from Michigan redside dace in large and small-scale partial warps (warps 10 and 2) while Wisconsin River specimens differed from Michigan redside dace in partial warps 11 and 10. In two cases (warps 11 and 10), the Michigan form deviated in the direction of the rosyside dace mean configuration. Mean shape outlines (Figure 15) also implied that shape similarities between Michigan redside dace and rosyside dace were greater than were similarities between rosyside dace and either Wisconsin group of specimens. New York redside dace were intermediate in most respects. The spline mappings (Figure 17 and 18) suggested that the Michigan mean form

was deeper than either Wisconsin form; however, the high degree of intrasample variation and intersample overlap even at this scale was demonstrated in Figure 19.

The fin ray and lateral line scale counts that I made in this study fell within ranges reported for the redside dace by Page and Burr (1991), Smith (1987), and Becker (1983). Page and Burr (1991) described a range of 59 - 75 lateral line scales for redside dace compared to a range of 60 - 72 counted in the present study. Counts of lateral line scales also suggested a relationship in which Michigan specimens differed from the Wisconsin redside dace. Michigan specimens had the fewest number of scales (median = 63), a difference that, like body shape, was in the direction of scale counts presented for the rosyside dace (43 - 57; Page and Burr, 1991). Numbers of dorsal and anal fin rays were not different among redside dace groups.

Collectively, the morphological evidence showed that differences among the redside dace were minute, but suggested that Michigan redside dace were most similar to redside dace from New York and least similar to redside dace from Wisconsin, especially from specimens representing the Black River drainage. Also, Michigan redside dace exhibited a morphology that was more similar to that held by rosyside dace than were the morphological characteristics exhibited by the other redside dace.

Results of the morphological comparisons described relationships among *Clinostomus* that may have important evolutionary implications for the description of post-glacial recolonization of the Great Lakes Basin by redside dace. In the absence of parallel or convergent evolution, the results suggested that Michigan redside dace displayed a more ancestral morphology than the New York or Wisconsin redside dace.

This hypothesis presumes that rosyside dace may be considered an approximation of the ancestral form in that their external morphology has been influenced minimally by derived characteristics. In addition, the hypothesis also assumes that the differences in morphology that I measured were genetic in origin and not a function of environmental differences between the collection localities. Similarities among the groups may therefore reflect a complex history of migration or local evolutionary differentiation.

The Mississippi drainage is believed to have offered glacial refugia for numerous cyprinids, including redside dace (Bailey and Smith, 1981). Migration routes into deglaciated parts of the basin would have been afforded by broad drainage connections as early as 14,000 years ago in the upper Mississippi and the Illinois River drainages in Wisconsin and Illinois, the Wabash - Maumee River connection in Michigan, and the Ohio River drainage in New York. Michigan redside dace probably entered Detroit River tributaries from the Wabash - Maumee River connection, a route that is believed to have been open only briefly after the retreat of glacial ice, closing approximately 13,600 years ago (Bailey and Smith, 1981). Closure of the route would have isolated Michigan populations of redside dace from eastern and western populations in New York and Wisconsin. Consequent founder effects (Hartl and Clark, 1989) could have played a role in maintaining ancestral morphological traits in the Michigan populations.

The biological and historical processes underlying the morphological variation that I uncovered are unknown, and it would be inappropriate to invoke theories of adaptation and natural selection or evolution through any other avenue to explain them. The landmarks that I selected for analysis were arbitrary (Bookstein, 1990). Gross changes in body dimensions as indicated in this study, for example, are not descriptive of the variation

in internal features that were likely responsible for the large-scale deformations. Because of this, the true homology of the landmarks between forms is left uncertain as is the structure or trait that might have been under selective pressure. The landmarks that I selected conform to the definition of operational homology (Smith, 1990) that is simply a correspondence of landmark positions from form to form. In this sense, the landmark analysis at the scale I selected was less useful for phylogenetic or cladistic analyses because it did not identify individual structures. However, the method was valuable as a tool for the preliminary testing of hypotheses of overall shape similarity among groups and serves as a guide to the more detailed study of external and internal anatomical structures. The morphological similarities described in this study should be compared to the results of a molecular analysis to clarify the significance of the subtle shape differences among the redside dace and to corroborate the relationships indicated by this study.

CONCLUSIONS

This study was designed to assess the phenotypic similarity of populations of redside dace remaining in Michigan to populations in New York and Wisconsin, regional centers of redside dace abundance. In doing so, this study provided information concerning the species' ecological requirements that can be used to guide management decisions that will affect the continued survival of redside dace in Michigan. It was not known if the phenotypic traits selected for study were necessarily genetic or environmental in origin. Research has shown that phenotypic variation may be attributed to either influence (Shields and Underhill, 1993; Foster et al., 1992).

Redside dace in New York were similar to Michigan populations in some aspects of microhabitat use, despite differences between Michigan and New York in the availability of microhabitat attributes. In general, redside dace were found at low-velocity, mid-water positions in the deepest parts of pools and were associated with locations that possessed overhanging structures within 1 m of the stream surface. Redside dace at both locations were observed to feed primarily at the surface, often leaping out of the water in pursuit of flying insects. Foraging dominated the activities of redside dace, and it was only during competition for food items that redside dace appeared to interact directly with other stream fishes. The New York streams maintained a more diverse fish fauna, yet observations of interspecific interactions with redside dace were rare. The Michigan and New York streams were clear and offered well developed pools but differed markedly in some aspects of water chemistry.

Resting routine metabolic rates and critical thermal maxima were shown to increase for New York redside dace at several acclimation temperatures and followed a trend that is well established for other minnows and temperate fishes. Metabolic rates measured at a single temperature for Michigan redside dace were slightly higher than expected from the relationship determined for New York fish; however, because we were prohibited from testing metabolic rates of Michigan redside dace at more than one temperature, the overall significance of this difference was not clear. The critical thermal maxima of redside dace in New York suggested an optimum growth temperature that is near the maximum stream temperature recorded during this study in Seeley Drain. Redside dace in Seeley Drain could be threatened by minor, prolonged temperature elevations because optimum growth temperatures and final preferenda are near the upper incipient lethal tolerance limit of most temperate fishes (Fry, 1971).

Only minor differences in morphology were found among groups of redside dace from Michigan, New York, and Wisconsin. The differences suggested that Michigan specimens were more similar to New York than to Wisconsin specimens in body depth, though overall differences between New York and Wisconsin redside dace were extremely subtle as were differences between watersheds within states. Michigan redside dace specimens appeared to differ most from specimens collected in the Wisconsin - Black River watershed, the western-most group included in the analysis. The ecological significance of these differences was not ascertained. The scale and number of shape differences was much greater between redside dace and rosyside dace than among the groups of redside dace. Among the redside dace, Michigan specimens bore the closest

resemblance to rosyside dace in external body shape and in lateral line scale counts. The apparent retention of some ancestral traits by Michigan redside dace relative to the other groups may be related to the early, post-glacial isolation of the southeastern Michigan watersheds following the closure of a major southern dispersal route.

There are several avenues of future study that should be considered. Artificial manipulation of instream microhabitat characteristics would be helpful in clarifying ambiguous results due to differences in habitat availability within and between study sites. Some habitat attributes that were available in the New York streams were not available at the Michigan study site, impeding a direct comparison of habitat use between sites for those attributes. It was also difficult to assess the importance of habitat attributes when use followed availability. In that case, it was not possible to separate selection of an abundant habitat attribute from random choice. Cover types could be experimently added and removed from pools in Michigan and New York streams to assess redside dace response to structure that is not normally available. Another set of research needs includes the direct determination of a more detailed array of physiological parameters including measurement of active metabolism, final preferenda, growth optima, and defining the zone of temperature tolerance for redside dace. This information would allow more accurate prediction of the species' physiological tolerances and suggest conditions that would maximize (or threaten) fish condition. Finally, a phylogenetic analysis that includes representatives from more regions across the species' range and integrates detailed features of external and internal anatomy with measures of molecular similarity

would help to resolve the historical relationships of the isolated populations of redside dace included in this study.

The results of this project emphasize that efforts to enhance the prospects for redside dace survival in Michigan will be strongly tied to the maintenance of beneficial aspects of the stream corridor and to ensuring a level of high water quality in the stream reaches that redside dace occupy. This study suggested that redside dace require cool, clear pools that are bordered by well-developed riparian vegetation. A suitable riparian corridor including dense, low vegetation would promote the production and concentration of terrestrial insects that serve as the primary food source of redside dace. Riparian vegetation would also provide shade to encourage cooler stream temperatures and serve to reduce erosional inputs that add sediment to pools, decreasing depth and water clarity. Though not evaluated in this study, gravel riffles are reported to provide necessary spawning habitat for redside dace suggesting that a pool - riffle configuration should also be protected.

APPENDIX

APPENDIX

Museum Specimen List

All specimens used in the morphometric and meristic analyses of this study were obtained from the University of Michigan Museum of Zoology, Ann Arbor, MI.

Clinostomus elongatus:

Middle River Rouge, Detroit River drainage, Northville, Wayne County, Michigan. UMMZ 061357, 066545.

Upper River Rouge, Detroit River drainage, Farmington, Oakland County, Michigan. UMMZ 136878.

Mud Creek, Allegheny River drainage, Cherry Creek, Chautauqua County, New York. UMMZ 180797, 180960.

Cold Spring Creek, Allegheny River drainage, Randolph, Cattaraugus County, New York. UMMZ 180823.

Dunderburg Creek, Susquehanna River drainage, Gilbertsville, Otsego County, New York. UMMZ 109773.

Unnamed stream, Black River drainage, Medford, Taylor County, Wisconsin. UMMZ 078727, 078740.

Big Eau Pleine River, Wisconsin River drainage, Colby, Marathon County, Wisconsin. UMMZ 075738.

Clinostomus funduloides:

Tributary of Hyco Creek, Roanoke drainage, Leasburg, Caswell County, North Carolina. UMMZ 177051.

Dry Creek, Tennessee River drainage, Hardin County, Tennessee. UMMZ 200924.

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