SPATIAL PATTERNS IN PHENOTYPES AND HABITAT USE OF SICKLEFIN CHUB, MACRHYBOPSIS MEEKI, IN THE MISSOURI AND LOWER YELLOWSTONE RIVERS

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Doctor of Philosophy

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by

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The undersigned, appointed by the Dean of the Graduate School, have examined the dissertation entitled:

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SICKLEFIN CHUB, MACRHYBOPSIS MEEKI,

IN THE MISSOURI AND LOWER YELLOWSTONE RIVERS

presented by Douglas J. Dieterman,

a candidate for the degree of Doctor of Philosophy, and hereby certify that in their opinion it is worthy of acceptance.

Preface

Population Structure and Habitat Use of Benthic Fishes along the Missouri and Lower Yellowstone Rivers

This research is reported in 12 volumes. Final Report volumes are listed below and are available from the U. S. Army Corps of Engineers, the primary contracting agency for the overall project. Contact: Becky Latka, U. S. Army Corps of Engineers, CENWO-PM-AE, 106 South 15" Street, Omaha, NE 68102 (rebecca.j.latka@usace.army.mil, 4021221-4602) for copies. Volumes are currently available unless indicated otherwise (anticipated date of publication).

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SPATIAL PATTERNS IN PHENOTYPES AND HABITAT USE OF SICKLEFIN CHUB, MACRHYBOPSIS MEEKI, IN THE MISSOURI AND LOWER YELLOWSTONE RIVERS

Douglas J. Dieterman

Dr. David L. Galat, Dissertation Supervisor

ABSTRACT

The sicklefin chub, *Macrhybopsis meeki*, historically inhabited the mainstem Missouri River and Mississippi River downstream from the Missouri's confluence. Sicklefin chub declined from 70% of their historical range in the Missouri River following construction of reservoirs and river channelization. I studied two aspects of its autecology that could be useful in conservation and recovery efforts; phenotypic variation among isolated populations and factors associated with its distribution in the Missouri and Lower Yellowstone rivers.

Phenotypic variation reflects processes of local adaptation and evolutionary flexibility and can be used to identify distinct sub-populations or stocks that may require legal protection or specific management actions. Forty-two phenotypic traits were quantified and examined with principal components analysis, a multivariate statistical technique. Intra-population variation exceeded inter-population variation in all traits examined. However, a group of sicklefin chubs in the lower channelized river exhibited more stream-lined and hydrodynamic body morphologies. This partial divergence of body morphologies is postulated to be a response to increased water velocities in the channelized river.

Identification of habitats associated with sicklefin chub distribution can aid habitat creation and maintenance in restoration programs. Habitat associations were examined at segment and site spatial scales using logistic regression. Sixty-seven variables postulated to influence sicklefin chub distribution were examined. These included aspects of physical habitat, water quality, flow regime, and predation. Sicklefin chub presence was most highly predicted in segments far downstream from reservoirs, where turbidity in late summer-early autumn exceeded 80 NTUs and August flows were low, being generally < 10% of the total annual flow. Smaller-scale sites where adult sicklefin chubs were present were characterized by faster column velocities, a higher percentage of gravel, and a lower percentage of silt than sites where juveniles were present. Adult sicklefin chub presence at sites was most highly associated with current velocity and gravel substrates. These patterns are proposed to be related to conditions necessary for reproduction and successful recruitment and to moderation of predation and inter-specific competition.

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Chapter 1. Sicklefin chub (*Macrhybopsis meeki*) autecology and Dissertation Objectives.

Many of the world's large river systems have been anthropogenically altered for navigation, flood control, hydropower production, irrigation, waste disposal, agricultural, and municipal water supply purposes (Boon 1992, Allan 1995, Sheehan and Rasmussen 1999). Boon (1992) estimated that over 14,000 dams > 15 m high have been constructed worldwide for flood control, hydropower production, irrigation, and municipal water supply. In the United States, 26,550 km of rivers and streams were channelized by 1977 to aid navigation, flood control, and agriculture and an additional 16,090 km were proposed for work (Leopold 1977). Some human benefits, such as commercial and recreational fisheries and aesthetic beauty, declined concomitantly with alterations and fostered a growing awareness and appreciation for the environmental plight of large rivers (Green and Tunstall 1992, Welcomme 1992). Consequently, river improvement has become a priority for public and government institutions.

River improvement can encompass a variety of activities and depends on the degree of alteration. In nearly natural or minimally impacted rivers, improvement activities may only require preservation of the current environment with limitations on future development (Boon 1992). Alternatively, highly modified rivers require mitigation or restoration of abiotic and biotic resources (Boon 1992). Mitigation and restoration activities may include identification and reestablishment of flow patterns important to aquatic biota (e.g., Instream Flow Incremental Methodology, Bovee 1982; Range of

Variation Approach, Richter et al. 1996); construction of in-channel and off-channel aquatic habitats (e.g., Harberg et al. 1993, Gore and Shields 1995, Galat et al. 1998); water pollution regulation (Sheehan and Rasmussen 1999); removal of undesirable/exotic biota (Wydoski and Wiley 1999); and reintroduction of native species (Price 1989, Heidinger 1999, Rahel et al. 1999).

Successful restoration and mitigation efforts depend on adequate knowledge of the structure and function of the system under consideration (National Research Council 1992). Specifically, knowledge of the autecology of species (e.g., Schiemer and Waidbacher 1992) and of the historical structure of the system being restored (e.g., Hesse and Mestl 1993, Latka et al. 1993, Galat and Lipkin 1999) are critical for success of restoration/mitigation projects. Autecological information, such as habitat requirements and life-history traits (Baltz 1990), is of fundamental importance to recovery of imperiled fauna and their habitats and is an often cited research need for large river conservation and management (Boon 1992, Berry and Galat 1993, Gore and Shields 1995, Galat et al. 1996). Alternatively, life-history traits, such as reproduction and mortality, can be used to construct population viability, metapopulation, and spatially explicit population models (Pulliam and Dunning 1997). These models can subsequently be used to predict population responses to habitat restoration programs.

The 3,768 km long Missouri River is one large North American river having undergone substantial physical change since European settlement (reviewed in Hesse et al. 1989a, Galat et al. 1996). The lower one-third of the river has been channelized resulting in a loss of about 50% of the historic surface area (Funk and Robinson 1974). The middle

one-third of the river has been impounded for flood control and hydroelectric energy production (Hesse et al. 1989a), whereas the upper one-third is comparatively less altered. These alterations have resulted in substantial changes to the hydrology, habitat, and energy flow of the Missouri River. Concomitant with these changes have been noticeable declines in some native fish species (Pflieger and Grace 1987, Hesse et al. 1993, Galat et al. 1996, Grady and Milligan 1998). Reduction of habitat and of aquatic resources, including fishes, prompted political actions leading to mitigation and restoration activities (Hesse 1987, Hesse et al. 1989b, Galat et al. 1996).

The sicklefin chub (*Macrhybopsis meeki*) (Figure 1-1) is one fish species declining in the Missouri River. It is an archetypical, turbid water, large river, rheophilic fish, being once widely distributed in the mainstem Missouri River and that portion of the Mississippi River between the mouths of the Missouri and Ohio rivers (Bailey and Allum 1962). The species is thought to have originated in the ancestral, north-flowing Missouri River (Metcalf 1966). Sicklefin chubs have been reported from 13 states including all seven states adjacent to the Missouri River (Table 1-1).

Sicklefin chubs were captured infrequently in early collections leading to governmental concern for the species by the late 1980's. Sicklefin chubs were first collected from the Missouri River near St. Joseph, Missouri in August 1884, but were misidentified as sturgeon chub (*Macrhybopsis gelida*) (Jordan and Meek 1885). Meek (1892) again collected and misidentified sicklefin chub in the Missouri River near Sioux City, Iowa. The sicklefin chub was first correctly identified in 1896, from the Missouri River near the original collection site in Missouri (Jordan and Evermann 1896). Original

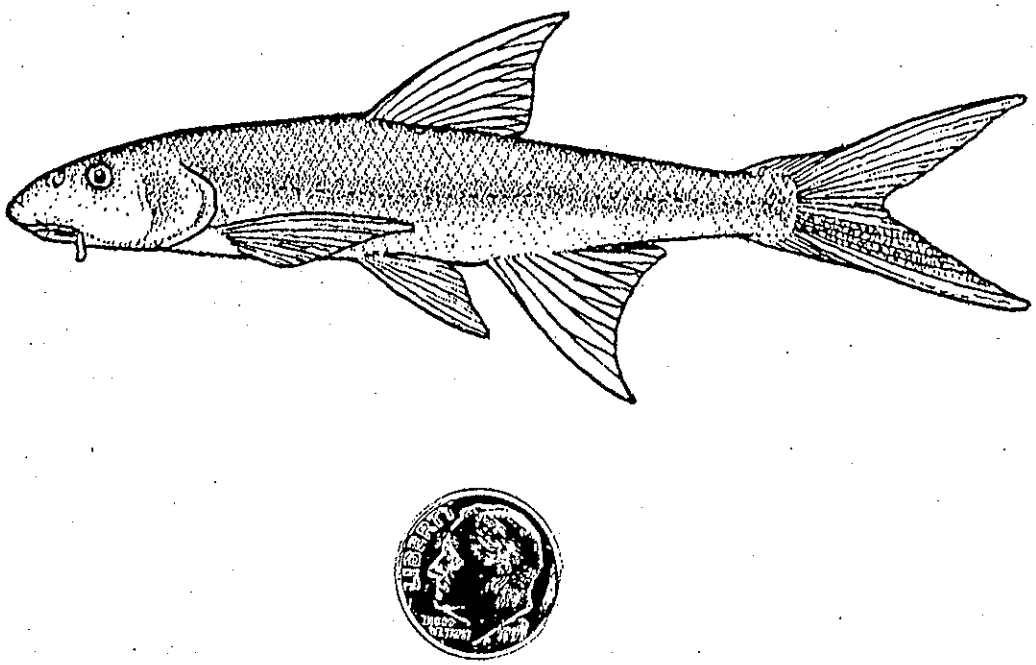

Figure 1-1. The sicklefin chub (*Macrhybopsis meeki*). Figure reproduced from: Eddy, S., and J. C. Underhill. 1978. How to know your freshwater fishes, 3rd edition. Wm. C. Brown Company, Dubuque, Iowa. The enlarged dime is included as a measure of scale.

Table 1-1. Summary of recorded sicklefin chub collections in the Missouri River by decade and state(s). Each collection site is considered separate if the geographic location *or* year differs. For example multiple collections during May, July, and October at the same site in 1940 would all be counted as one collection site. Collections made at the same site in 1940, 1941, and 1945 would equal three separate collections in the 1940 decade. MT=Montana, ND=North Dakota, SD=South Dakota, NE/IA=Nebraska/Iowa, KS/MO=Kansas/Missouri. Collections through 1992 are from Werdon (1993).

	State(s)				
Decade	MT	ND	SD	NE/IA	KS/MO
1880's	0	0	0	0	1
1890's	0	0	0	1	1
1900's	0	0	0	0	0
1910's	0	0	0	0	0
1920's	0	0	0	0	0
1930's	0	0	1	0	1
Fort Peck Dam, Montana completed in 1940					
1940's	0	0	2	4	30[a]
Fort Randall Dam, South Dakota completed 1953 *Garrison Dam, North Dakota completed 1955* *Gavins Point Dam, South Dakota completed 1955*					
1950's	0	2[b]	4	1	4[c]
Oahe Dam, South Dakota completed 1962 *Big Bend Dam, South Dakota completed 1964*					
1960's	0	0	0	1	30[d]
1970's	2	1	1	1	10
1980's	2	0	0	2	15

Table 1-1. continued.

Decade	State(s)				
	MT	ND	SD	NE/IA	KS/MO
Specific studies conducted to assess sicklefin chub status and distribution					
1990's[e]	195	106[f]	1	1	64
Total for all years	199	109	9	11	156
Grand total = 484					

[a] 1 site in Kansas River
[b] both sites in tributaries
[c] 2 sites in tributaries
[d] 1 site in Kansas River
[e] Collections after 1992 are from Dieterman et al. (1996), Gelwicks et al. (1996), Grisak (1996), Pegg et al. (1997), Grady and Milligan (1998), Everett (1999), and Etnier (unpublished data).
[f] 51 sites in Yellowstone River

type specimens from this collection are located in the United States National Museum at the Smithsonian Institution (USNM 35889). Sicklefin chubs were not collected again until the 1930's in South Dakota and Kansas/Missouri (Table 1-1). Collectors in the 1930's and 1940's predicted a reduced range following development of mainstem dams and associated turbidity reduction (Bailey and Allum 1962). For the next 50 years, the species was collected infrequently in general fish community surveys conducted in all seven Missouri River states (Table 1-1). Rarity led most states to propose legal or protective status for sicklefin chubs by 1992 (Table 1-2, updated from Werdon 1993).

Rarity also prompted federal concern in the late 1980s and early 1990s. The U. S. Fish and Wildlife Service (USFWS) listed the species as Category 2 in 1991 (USFWS 1991). Category 2 designation indicated that a species was likely threatened or endangered and further studies of status were recommended. Two status surveys were subsequently conducted in the Missouri River (Stasiak 1990, Werdon 1990, Werdon 1992), however, no sicklefin chubs were collected. The USFWS published a formal status report on the sicklefin chub in 1993 (Werdon 1993), which concluded, "With the exception of the lower Missouri River, documented catches of sicklefin chub have been so rare over the past decade that the species may be in danger of extinction." This report recommended further status surveys in the Yellowstone River, the Wild and Scenic Missouri River in Montana, and lower portions of the Missouri and Mississippi Rivers. The species was reclassified as a Category 1 candidate species in 1994 (USFWS 1994). Category 1 designation indicated sufficient scientific information existed to support a listing proposal.

Table 1-2. State designated or proposed legal/protective status of sicklefin chub (*Macrhybopsis meeki*) (updated from Werdon (1993)).

State	Classification	Citation
	Missouri River	
Montana	Special concern	Hunter (1994)
North Dakota	Endangered	North Dakota Game and Fish Department (1994)
South Dakota	Threatened	Stukel and Backlund (1997)
Nebraska	Imperiled	Clausen et al. (1989)
Iowa	None	Iowa Department of Natural Resources (1988)
Kansas	Endangered	Cross and Collins (1995)
Missouri	Rare	Missouri Department of Conservation (1995)
	Middle and Lower Mississippi River	
Illinois	None	Illinois Natural Heritage Program (1990)
Kentucky	Special concern	Kentucky Department of Fish and Wildlife Resources (1991)
Tennessee	Special concern	Etnier and Starnes (1993)
Arkansas	Undetermined	Robinson and Buchanan (1988)
Mississippi	None	Mississippi Department of Wildlife, Fisheries, and Parks (1992)
Louisiana	Accidental in state	Louisiana Natural Heritage Program (1990)

A petition to list the sicklefin chub as endangered was received by the USFWS in August 1994 (USFWS 1994). The USFWS responded by funding status surveys in the Wild and Scenic Missouri River in Montana (Grisak 1996), the Yellowstone and Missouri Rivers in North Dakota (Everett 1999), and the Lower Missouri River in Kansas/Missouri (Gelwicks et al. 1996, Grady and Milligan 1998). These status surveys are the reason for increased numbers of sicklefin chub collection sites in the 1990s (Table 1-1). Within 90 days of receipt of a petition, the USFWS is required to issue a finding, based on all available information, regarding whether or not substantial scientific information exists to indicate that the petitioned action may be warranted. The USFWS issued a positive 90-day finding in response to the sicklefin chub petition on December 29, 1994 (USFWS 1995). This positive 90-day finding indicated that listing as endangered may be warranted.

Within 12 months of receipt of a listing petition, the USFWS is required to make a finding (i.e., a 12-month finding) of either; 1) listing not warranted, 2) listing warranted with a proposed rule to be published promptly, or 3) listing warranted but precluded by higher priority listing proposals. The USFWS established a listing team in April 1995 to develop a 12-month finding. Revision of the first draft was interrupted by a Congressional moratorium on new listings that lasted until May 1996. The listing package was updated in 1997 and again in 1999. The 1999 revised draft listing package indicates that the sicklefin chub presently occupies only 25% of its former range (R. Collins, U.S. Fish and Wildlife Service, North Dakota Field Office, Bismarck, personal communication). The sicklefin chub only exists in 30% of its former range within the Missouri River system, in three reproductively isolated populations, consisting of low overall numbers relative to

other species in the fish community. In April 2000, the USFWS received a 60-day notice of intent to sue by the Montana Rivers Coalition Inc., for failure to proceed with a 12-month finding in a timely manner (Montana Rivers Coalition Inc., 2000). The Montana Rivers Coalition Inc., officially sued the USFWS and Secretary of the Interior Bruce Babbitt in June, 2000 (*Montana Rivers Coalition Inc., v. Babbitt* 2000).

Clearly, sicklefin chub are an imperiled Missouri River fish and likely to be afforded federal protection in the near future. As such, autecological information will be required to guide development of recovery plans and Missouri River habitat restoration projects. What follows is a review of existing autecological information on sicklefin chubs and identification of critical knowledge gaps.

Baltz (1990) partitioned autecological studies into two areas, life-history traits and assessment of environmental requirements. Common life-history traits include age and growth patterns, reproductive aspects (e.g., age at first reproduction, spawning season and cues, fecundity), feeding habits, geographic variation in phenotypic and genotypic traits, and behavioral patterns (e.g., schooling, territorial defense). Assessment of environmental requirements refers to the spatial and temporal distribution and abundance of a species in various habitat types.

Life History Traits

Age and growth patterns.--Sicklefin chub age and growth has been examined in Montana, North Dakota, and Iowa/Nebraska/Kansas/Missouri areas of the river (Table 1-3). The oldest sicklefin chubs captured in 1994 and 1995 from the Missouri and

Table 1-3. Sicklefin chub, *Macrhybopsis meeki*, age and growth information from the Missouri and lower Yellowstone rivers.

Variable	Location	Year	N	Age group 1	2	3	4
Measured total length range (mm)	MT[a]	1994-95	59	29-42	43-75	73-93	95-109
Backcalculated length (mm) at age				27	62	79	96
Percent of individuals in each age group				29%	33%	34%	4%
Measured total length range (mm)	ND[b]	1995	64	39-53	53-85	86-99	107
Backcalculated length (mm) at age				46	75	94	105
Percent of individuals in each age group				6%	70%	22%	2%
Backcalculated length (mm) at age	[c]	1996	14	38	66		
Backcalculated length (mm) at age	[d]	1996	26	37	65		
Backcalculated length (mm) at age	[e]	1996	3	36	69		

[a] Missouri River in Montana upstream from Fort Peck Reservoir (Grisak 1996)
[b] Missouri and lower Yellowstone rivers in North Dakota (Everett 1999)
[c] Missouri River upstream from Fort Peck Reservoir and lower Yellowstone River in MT/ND (Pegg et al. 1997)
[d] Missouri River between Fort Peck Reservoir and Lake Sakakawea Headwaters (Pegg et al. 1997)
[e] Missouri River in Iowa, Nebraska, Kansas, and Missouri (Pegg et al. 1997)

Yellowstone rivers in Montana and North Dakota were age four (Grisak 1996, Everett 1999). Similarly, sicklefin chubs captured in the same areas between 1996 and 1998 were also age four (Pegg et al. 1997, Braaten 2000), but chubs captured in this time period only reached age three in the lower Missouri River in Iowa, Nebraska, Kansas, and Missouri (Braaten 2000). Grisak (1996) reported, based on a wide length range, that age 2 fish grew most in the Missouri River upstream from Fort Peck Reservoir, in Montana. Assuming a stable age distribution, declines in percent of individuals among age classes can represent ontogenic episodes of mortality (Van Den Avyle and Hayward 1999). Based on this assumption, mortality appears high after age 3 in the Missouri River above Ft. Peck Reservoir and between ages 2 and 3 and 3 and 4 in the Missouri and Lower Yellowstone rivers in North Dakota (Table 1-3).

Reproduction.--Reproductive aspects of sicklefin chubs are still poorly understood but anecdotal information exists. Werdon (1993) speculated that spawning is influenced by increasing water temperature and flow from snowmelt or precipitation events. Successful reproduction has been documented by presence of age-0 sicklefin chubs in the Missouri River, Missouri (Dieterman et al. 1996, Pflieger 1997, Braaten 2000). Larval *Macrhybopsis* chubs, including either or both sicklefin and sturgeon chubs, were collected in 1996 (Tibbs and Galat 1997). Spawning temperatures were estimated, based on larval fish development, to range from 20.5 to 26.2 ^{0}C, with peak spawning temperatures ranging from 20.5 to 25.3 ^{0}C. Although age-0 chubs were not reported in July-early October, 1996 collections in Montana and North Dakota, observations of individuals in

age groups 1-4 is suggestive of reproduction and recruitment there (Grisak 1996, Pegg et al. 1997, Everett 1999).

Grisak (1996) collected sicklefin chubs exhibiting signs of reproductive readiness in the Missouri River in Montana in 1994 and 1995 and reported sexual maturity at ages 2-4. Five gravid females and one ripe male were collected between 5 August and 17 August 1994, when water temperatures averaged 21.7 ^{0}C (range 19.7-22.7 ^{0}C), and discharge averaged 133.2 m^3/s (range 126.2-138.9 m^3/s). Eleven gravid females were collected between 18 July and 31 July 1995, when water temperatures averaged 21.3 ^{0}C (range 20.5-22.5 ^{0}C), and discharge averaged 507.2 m^3/s (range 336-693 m^3/s). Twenty-two ripe males were collected between 19 July and 16 August 1995, when water temperatures averaged 22.3 ^{0}C (range 18-28 ^{0}C), and discharge averaged 390.1 m^3/s (range 250-676 m^3/s). These temperature ranges are similar to those suggested by Tibbs and Galat (1997). Other than Tibbs and Galat (1997), environmental conditions prompting sicklefin reproduction have not been documented in other Missouri or Yellowstone river areas. Also, size and age at maturity and fecundity estimates are almost completely unknown.

Feeding habits.--Reigh and Elsen (1979) reported the only known food habits of sicklefin chubs. Stomachs from three chubs collected in North Dakota contained a black fly pupa (*Simulium* spp.), insect exoskeletons, and unidentifiable material.

Predation.--Although predation is typically an aspect of synecology (Baltz 1990, Crowder 1990), its supposed effect on sicklefin chubs necessitates mention here. Sauger predation on sicklefin/sturgeon chubs (undifferentiated) was reported in the Missouri

River in Montana (Gardner and Berg 1982). The two chubs in sauger diets had a combined relative importance value of 18.7. The relative importance index for a particular food item is calculated by summing the numerical percentage, volumetric percentage, and percent occurrence of the food item in the diet, then dividing this value by the summation of all food items in the diet (George and Hadley 1979, Gardner and Berg 1982). Increasing abundance of sight feeding predators in areas of reduced turbidity, such as downstream from impoundments (Pflieger and Grace 1987), has been suggested as possible factor contributing to sicklefin chub population declines (Werdon 1993, Everett 1999).

Geographic variation in phenotypic and genotypic traits.--Genotypic variation has not been examined, but was a cited research concern for sicklefin chub populations isolated by mainstem impoundment (Werdon 1993). Current literature describes phenotypic traits of sicklefin chubs, including morphometric and meristic characters (Table 1-4) and general body form and features. However, it is unknown whether regional taxonomic keys are based on observations of local specimens or simply report physical characters described by others. Also, many literature descriptions are based on historical records. Descriptions from across historical collection sites ranged from 40-50 lateral line scales, 4-4 or 1,4-4,1 pharyngeal tooth arrangements, maximum total lengths of 51-110 mm, and 8 anal fin rays (Table 1-4).

Sicklefin chubs developed unique morphological traits, likely in response to historical Missouri River conditions (i.e., a large turbid river). These include exceptionally long, sickle-shaped pectoral fins, an extremely falcate dorsal fin, a deeply forked caudal fin

Table 1-4. Sicklefin chub meristics as determined from regional fish identification books.

Characteristic	Citation
Lateral line scale count	
46-50	Freshwater fishes-Eddy and Underhill (1978)
45-50	South Dakota-Bailey and Allum (1962)
43-48	Iowa-Harlan et al. (1987)
>40	Kansas-Cross and Collins (1995)
43-48	Missouri-Pflieger (1997)
43-50	Tennessee-Etnier and Starnes (1993)
Pharyngeal teeth count	
4-4	Freshwater Fishes-Eddy and Underhill (1978)
1,4-4,1	South Dakota-Bailey and Allum (1962)
4-4	Iowa-Harlan et al. (1987)
1,4-4,1	Missouri-Pflieger (1997)
1,4-4,1	Tennessee-Etnier and Starnes (1993)
Maximum total length (mm)	
51	Freshwater Fishes-Eddy and Underhill (1978)
102	South Dakota-Bailey and Allum (1962)
102	Iowa-Harlan et al. (1987)
110	Kansas-Cross and Collins (1995)
102	Missouri-Pflieger (1997)
102	Tennessee-Etnier and Starnes (1993)
Anal fin ray count	
8	Missouri-Pflieger (1997)
8	Tennessee-Etnier and Starnes (1993)

and reduced eyes, sometimes partially covered with skin (Pflieger 1997). Fin developments minimize drag and aid individuals in maintaining themselves near the bottom in a swift current. Visual senses are of little importance in a turbid river, thus sicklefin chubs have developed sensitive cutaneous organs to compensate (Moore 1950, Davis and Miller 1967). These include a single, relatively long maxillary barbel and exceptionally dense concentrations of sensory papillae on the ventral surface, gular region, pectoral fin rays, and pelvic fin rays. Dense concentrations of these papillae can easily be seen on the pectoral and pelvic fin rays and have been termed compound taste buds by Moore (1950).

Behavioral patterns.--Behavioral patterns are unknown, however, a concentration of reproductively ripe sicklefin chubs was reported from the Missouri River in Montana (Grisak 1996).

Environmental Requirements

Distribution and abundance of fishes within and among habitats can be examined at multiple scales because habitats themselves can be classified at multiple hierarchical scales (Frissell et al. 1986, Hawkins et al. 1993). Processes associated with large-scale features are ultimate factors regulating structure and pattern of proximate small-scale habitat features (Hynes 1975, Platts 1979, Naiman et al. 1992). Habitat features at three hierarchically nested spatial scales that influence sicklefin chub distribution and abundance in the Missouri River and are amenable to restoration through management manipulation are recognized here; segments, macrohabitats, and localized sites (i.e., site scale). Segments are stretches of river, generally > 10 km, that are bounded by geomorphic (e.g.,

major tributaries, geologic discontinuities) and constructed (e.g., dams and impoundments) features. These features influence processes such as flow regime and sediment transport that ultimately affect smaller scale macrohabitat structure and pattern within and among segments. Macrohabitats are distinctive, continuous or repeatable, natural (e.g., sand bars, main channel, channel border, tributary confluence) and constructed (e.g., dike field, revetment) physical features within segments. Localized sites are areas within macrohabitats where fishes are collected with specific gears (e.g., gill nets, trawls, bag seines). The specific length and width of a localized site is defined by the area sampled by a gear, but lengths usually range from 10 to several hundred meters long. Physical habitat features are typically measured at fish collection sites and are considered representative of site-scale conditions regulating fish presence/absence and abundance there. The most common physical habitat features, and of likely importance to sicklefin chubs, are water depth, water velocity, substrate composition, and turbidity.

Some studies of sicklefin chub habitat use only qualitatively described physical features at collection sites. For example, Pflieger and Grace (1987) described sicklefin chub sites in the Lower Missouri River, Missouri/Kansas, as sites in open channels having swift current and firm substrate. Sites with sicklefin chubs in North Dakota were described as having sandy bottoms, moderate to swift current, and relatively high turbidity (Reigh and Elsen 1979). In Nebraska, sicklefin chubs sites were characterized as having sandy substrates, moderate current, and high turbidities (Hesse 1994). Etnier and Starnes (1993) considered sicklefin chub habitat to be sites in swift open channels over sand and gravel substrates.

Studies in the 1990's better quantified physical features at sicklefin chub collection sites (Table 1-5). Sicklefin chubs were collected at depths ranging from 0.1 to 11.0 m, bottom velocities from 0.15 to 1.06 m/s, and over a variety of substrate types. These wide ranges may reflect broad habitat use and availability of a variety of physical features in the Missouri River from Montana to Missouri. Alternatively, wide ranges may reflect ontogenic differences in habitat use as sicklefin chubs collected at various sites were not partitioned by age group.

Synthesis of reported macrohabitat use is difficult because some authors report *percent of sicklefin chubs* collected in various macrohabitats, others report *percent of collections* with sicklefin chubs in various macrohabitats, and still others did not assess macrohabitat use. Qualitatively, sicklefin chubs have been collected from almost every type of Missouri River macrohabitat; main channel, side channel, sand bar, revetted bank, channel border, backwater, tributary mouth, inundated floodplain (Gelwicks 1995, Dieterman et al. 1996, Gelwicks et al. 1996, Grisak 1996, Kubisiak 1997, Tibbs and Galat 1997, Young et al. 1997, Grady and Milligan 1998, Everett 1999, Fisher 1999). They have not been collected in oxbow lakes, though these areas may not have been adequately sampled for this species. Sicklefin chubs appear uncommon in backwaters and tributary mouths because generally < 10 individuals were reported collected from these macrohabitats. One exception was a report of 125 larval fishes, being sicklefin and/or sturgeon chubs, collected from connected scour holes (i.e., a backwater type habitat) created by the "Great Flood of 1993" in the Lower Missouri River (Tibbs and Galat 1997). Most sicklefin chubs have been collected in main channel, channel border, and

Table 1-5. Summary of physical features at sicklefin chub collection sites reported in the literature. N=the number of sicklefin chubs collected.

Citation and state	N	Gear	Depth(m)	Bottom Velocity (m/s)	Substrate
			Missouri River		
Grisak (1996) MT	4	seine	0.4-0.8	0.21-0.45	silt/gravel
	302	trawl	1.4-6.4	0.32-1.06	silt, sand and rock
Everett (1999) ND	57	trawl[a]	6.8[b]	0.47[b]	sand
	7	seine			
Bailey and Allum (1962), SD	[c]	seine	0.0-2.7		sand (100%) silt/mud(71%) fine gravel, boulder, clay (14% each)[d]
Gelwicks et al. (1996), MO	163	seine		0.15-0.25	sand/gravel
Grady and Milligan (1998), MO	59	trawl[a]	1.5-2.0 (70%)[e]	0.61-0.80 (60%)[e]	organic matter (46.7%) silt (23%) gravel/rock (6.7%)
	1	seine			
Dieterman et al. (1996), river wide	82	trawl[a]	0.1-11.0	0.00-1.60[f]	
	1	seine			
Young et al. (1997) river wide	210	trawl	0.1-8.0	0.00-1.60[f]	
			Mississippi River		
Carter and Beadles (1983), AR	2	seine	0.5-1.5		sand

[a]Physical features not partitioned by gear type.
[b]Only mean habitat values reported.
[c]Number of chubs collected not reported but seven sites were sampled.
[d]Percent of seven collection sites with substrate type indicated.
[e]Physical features are for percent of chubs indicated in parentheses.
[f]Column velocities measured, not bottom velocities.

sand bar macrohabitats. In summary, much contemporary autecological information has been gathered in the last ten years. However, some obvious data voids, such as assessment of the importance of large-scale features, still exist.

Selection of Autecological Aspects for Study and Objectives

Topics with little autecological information on sicklefin chubs are behavioral patterns, feeding habits, assessment of predation effects, geographic variation in phenotypic and genotypic traits, and assessment of large-scale environmental requirements. Age and growth, reproduction, and assessment of macrohabitat and site-scale environmental requirements are autecological aspects with more information, but need refinement through additional data. For example, knowledge of macrohabitat and site use could be refined by examination in other seasons, such as winter; or in multiple years with varying flows. Most years in the 1990's were characterized by above normal rainfall, resulting in higher than average river discharges (Hu et al. 1998, Pegg 2000). Some autecological aspects such as age and growth may change when drier conditions, as in the late 1980s, return. Also, current knowledge of macrohabitat use and physical features of used sites are based on status surveys conducted in areas of the Missouri River known to harbor populations and often at pre-determined sites where historical surveys had been conducted. Information on where a species is absent may be equally important as to where it is present to help define the range of conditions it will use (sensu Shelford's Law of Tolerance 1913, Allen and Hoekstra 1992).

Two autecological aspects important to understanding sicklefin chub life-history requirements, needed to develop recovery plans, and to aid in design of Missouri River habitat restoration and mitigation projects for sicklefin chubs were chosen for study: assessment of 1) phenotypic variation among isolated sicklefin chub populations, and 2) factors associated with sicklefin chub distribution at segment and site scales.

Identification of phenotypic variability among populations is important because it reflects the process of local adaptation and indicates the evolutionary flexibility of a species (Meffe and Carroll 1997). Population variability in phenotypic traits has been partially used to identify distinct sub-species or stocks requiring legal protection or specific management actions (Waples 1995, Dimmick et al. 1999). Also, phenotypic variability among populations may be used in re-introduction programs by identifying traits present in one population that may promote successful re-introduction in a particular habitat (Meffe 1986, Lesica and Allendorf 1995). In the original petition to list the sicklefin chub (USFWS 1995), petitioners suggested that sicklefin chub populations had declined partially because of the species' inability to adapt to human-induced alteration of the Missouri River. Phenotypic adaptations to differing environmental conditions, such as between least-altered habitats in the upper river and human induced channelization in the lower river are examined in Chapter 2. The specific objective was to examine phenotypic variation among geographic collections of sicklefin chubs throughout the Missouri River to determine if phenotypically distinct populations exist.

Associations between sicklefin chub distribution and environmental features have never been quantified at large spatial scales (e.g., segments) and these associations

often failed to include the full range of site-scale physical features present in riverine portions of the Missouri River system. Alteration of segment-scale processes such as, predation from introduction of non-native fishes, reduction of habitat diversity from channelization, inhibition of sediment movement resulting in turbidity reduction, and altered hydrologic and thermal regimes from river impoundment have been cited reasons for sicklefin chub declines in legal (e.g., USFWS 1995) and scientific literature (Werdon 1993, Hesse 1994). Although segment-scale phenomena have been qualitatively implicated in declines, no quantitative association has been assessed. Also, as stated previously, descriptions of physical features associated with sicklefin chub sites could be refined by incorporating randomly selected collection sites across the range of physical features available in riverine portions of the Missouri River. Further, partitioning sites used by adults and age-0 fish may refine the range of physical features used by sicklefin chubs. Quantitative assessment of these associations is examined in Chapter 3. Specific objectives are: 1) identify individual variables reflecting components of physical habitat, water quality, flow regime, and predation, that are most highly associated with sicklefin chub presence/absence in the Missouri River at segment and site scales using logistic regression; 2) describe sicklefin chub frequency-of-use patterns for these variables; 3) compare site-scale habitat measurements between sites used by age-1+ and age-0 sicklefin chubs; 4) define a range of optimum habitat conditions predicted from site-scale univariate logistic models and; 5) identify the relative importance of multiple combinations of these variables that best predict sicklefin chub presence/absence in the Missouri River at segment and site scales.

Subsequent chapters have been written as "stand alone" documents. Therefore some overlap in material and citations exists.

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Chapter 2. **Phenotypic variation of sicklefin chubs (*Macrhybopsis meeki*) in the Missouri and Lower Yellowstone Rivers**

Introduction

In the neo-Darwinian model of allopatric speciation, "a new species develops when a population that is geographically isolated from other populations, acquires during this period of isolation, characters that promote or guarantee reproductive isolation after the external barriers breakdown" (Mayr 1970). The process of developing characters that may ultimately differentiate populations as species can be termed evolution (Smith 1986, Futuyma 1998). A fundamental step in assessing the evolution of character traits and their potential adaptive significance is an examination of phenotypic differences among isolated populations (Mayr 1970, Toline and Baker 1993). Although mechanisms such as genetic drift and mutation may also lead to diverging characters (Mayr 1970, Templeton 1982), most evidence supports character divergence through adaptation to differing selection pressures (e.g., Schluter and McPhail 1992, Swain 1992, Jones et al. 1992, Foster et al. 1992, Toline and Baker 1993, Sturmbauer 1998).

Both natural and anthropogenic events isolate populations of riverine biota and subject them to differing selection pressures. Natural events include geologic/geomorphic actions such as stream capture (e.g., Strange 1998) or glaciation (Mayden 1988). Alternatively, anthropogenic events such as water withdrawal through irrigation or establishment of dams and impoundments can also isolate populations by severing aquatic connections between them (Pringle 1997). More than 14,000 dams greater than 15 m high have been constructed in the world (Boon 1992). In the United States, 98% of free-

flowing rivers greater than 200 km in length have dams and water diversion projects (Benke 1990). A primary effect of dams is to physically block fish movements and isolate populations (Allan 1995). Additionally, dams and impoundments can change habitat conditions by altering flow regime, water temperature, turbidity, dissolved oxygen, and sediment transport (Petts 1984, Ligon et al. 1995, Allan 1995). Thus, river regulation, in the form of dams and impoundments, can create the conditions necessary for initiating allopatric speciation: population isolation and differing environmental conditions which allopatric populations must either adapt to, emigrate from, or disappear.

The Missouri River in North America is one example of a large impounded river. Six mainstem dams were constructed along the middle one-third of its length between 1937 and 1963 (Sveum 1988). These dams range in height from 14 to 67 m (Sveum 1988) which likely impede fish movement (Keenlyne et al. 1994) and alter the river's flow regime, sediment transport, water temperature, and turbidity (Morris et al. 1968, Galat et al. 1996). In addition, the lower third of the river has been extensively channelized to aid navigation (Galat et al. 1996). The cumulative result is a river with a lower channelized zone characterized by a deep, high-velocity channel with moderate turbidity and warm-water temperatures, a middle inter-reservoir zone characterized by generally cold, clear dam outflows with moderate current velocity, and an upper zone characterized by relatively clear, warm waters also with moderate current velocity (Dieterman et al. 1996, Young et al. 1997).

Many fishes are considered to have been negatively impacted by these habitat alterations (Hesse et al. 1989, Galat et al. 1996) and include four species representing a

"big-river" faunal group (Pflieger 1971, Pflieger 1989), that have been globally classified by The Nature Conservancy as rare or imperiled; lake sturgeon (*Acipenser fulvescens*), pallid sturgeon (*Scaphirhynchus albus*), sturgeon chub (*Macrhybopsis gelida*), and sicklefin chub (*Macrhybopsis meeki*) (The Nature Conservancy 1999). Migratory patterns of other species also are considered to have been blocked by impoundments (Galat et al. 1996) likely isolating their populations. Though populations of many species have presumably been isolated by river impoundment, phenotypic traits of isolated populations of only two species, pallid sturgeon and shovelnose sturgeon (*Scaphirhnychus platorynchus*) have been examined (Keenlyne et al. 1994). However, only populations in the upper river were compared and adaptive benefits of phenotypic differences were only briefly discussed.

The sicklefin chub is an excellent species for examining the influence of river regulation on phenotypic traits because its historical riverwide distribution is now fragmented into allopatric populations that exist in differing local abiotic conditions (Werdon 1993, Dieterman et al. 1996, Young et al. 1997). Additionally, its small size and adaptations for existence in historical Missouri River conditions, such as high turbidity, may show recent adaptations to river regulation, such as turbidity reduction. The sicklefin chub is considered an archetypical big river species (Pflieger 1971, Cross and Moss 1987, Pflieger 1989) and formerly inhabited most of the mainstem Missouri River, lower reaches of some tributaries, and the Lower Mississippi River (Lee et al. 1980). Sicklefin chub exhibit numerous adaptations to aid existence in turbid, moderate velocity water. These adaptations include exceptional numbers of compound taste buds on various body

segments, reduced eyes sometimes partially covered by skin, reduced optic brain lobes, a single relatively long maxillary barbel, and extremely falcate dorsal, pectoral, and pelvic fins (Moore 1950, Davis and Miller 1967). Its small size aids laboratory examination. Factors precluding use of other big river imperiled species are federal protection discouraging physical disturbance (pallid sturgeon), limited distribution or abundance of allopatric populations (lake sturgeon, sturgeon chub), and large body sizes (pallid sturgeon, lake sturgeon). My objective was to examine phenotypic variation among geographic collections of sicklefin chubs throughout the Missouri River to determine if phenotypically distinct populations exist. If phenotypically distinct populations are identified, potential mechanisms responsible for differences can be suggested based on correlations with other variables (e.g., Riddell and Leggett 1981, Beacham and Murray 1987, Fleming and Gross 1989, Matthews 1998). Also, phenotypic variability can be used to identify unique population units for conservation and management (e.g., stocks, Nehlsen et al. 1991) and may prove useful for re-introduction programs.

Methods

I sought to identify populations by examining sicklefin chubs collected from throughout their current range in the Missouri and Lower Yellowstone Rivers, measuring a range of phenotypic traits, and using multivariate statistical techniques to explore patterns of spatial variation that might suggest phenotypically distinct populations. Many techniques can be used to assess spatial variation, including visual examination of descriptive statistics (e.g., plots of data means and standard deviations plotted against

spatial distance), univariate tests, and multivariate methods. Of these, multivariate methods are considered most appropriate for exploratory analyses of spatial variation because they consider many variables simultaneously and most methods do not require *a priori* designation of populations, a typical requirement for most univariate tests (Thorpe 1976).

Sicklefin Chub Collection

Thorpe (1976) discussed two collection problems related to analysis of spatial variation; sampling enough sites to represent the geographic area under consideration and completing this without the influence of temporal variation on phenotypes. In order to assess phenotypic variation in sicklefin chubs from throughout the Missouri and Lower Yellowstone Rivers, fish had to be collected from about 2,000 river kilometers in a short time period. A study examining habitat use and population structure of benthic fishes in the Missouri and Lower Yellowstone rivers (Dieterman et al. 1996, Young et al. 1997) provided specimens that met these criteria. This study partitioned these rivers into 27 segments based on geomorphic, hydrologic, and constructed features (e.g., major tributaries, dams). Fishes were sampled from late July to early October in 17 segments in 1996 and 14 segments in 1997 (Figure 2-1) following standardized procedures (Sappington et al. 1996, 1997). Small fishes such as sicklefin chubs were sampled in deep (i.e., generally > 1.2-m) and shallow (generally < 1.2-m) habitats with a benthic trawl and bag seine, respectively. The benthic trawl was 2-m wide by 0.5-m high with a 3.2-mm

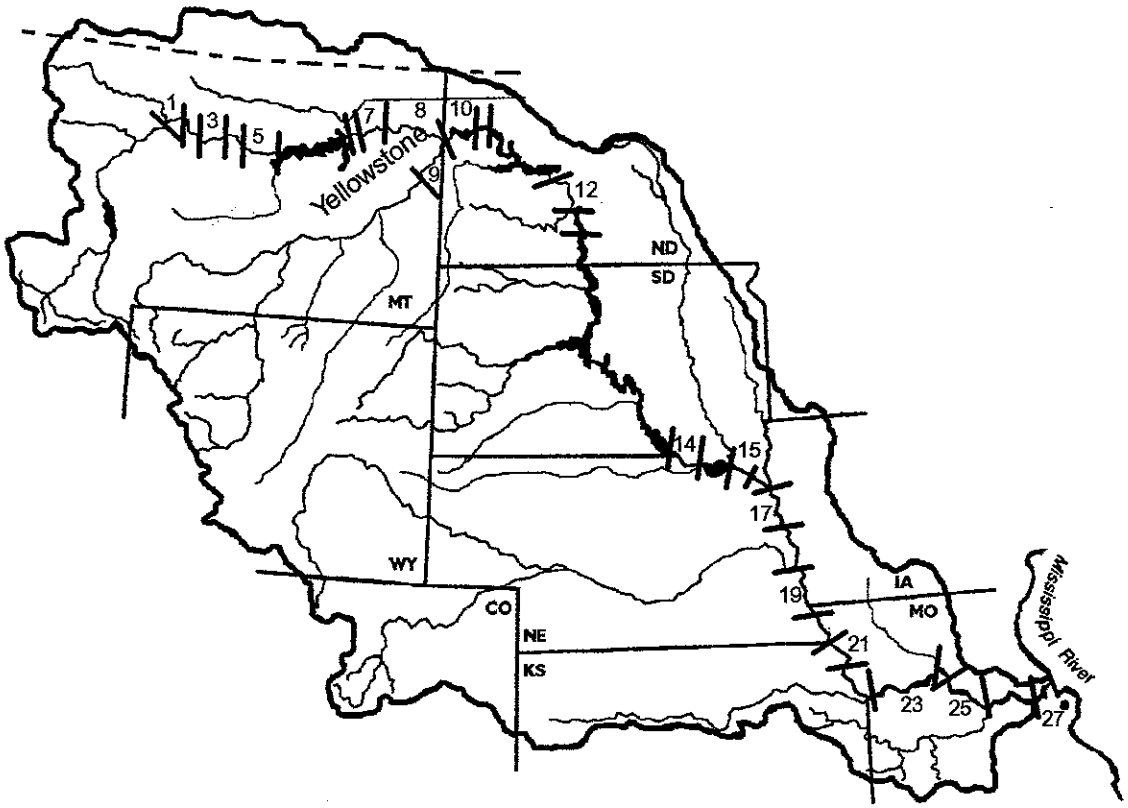


Figure 2-1. Approximate location of Missouri and lower Yellowstone river study segments. Segments 3, 5, 6, 7, 8, 9, 10, 12, 14, 15, 17, 18, 19, 21, 22, 23, 25, and 27 were sampled in 1996. Segments 3, 5, 7, 8, 9, 10, 12, 14, 15, 17, 19, 22, 23, 25, and 27 were sampled in 1997.

inner mesh net. The bag seine was 10.7-m long by 1.8-m high with 5-mm mesh and a 1.8-m by 1.8-m by 1.8-m bag at the center. Sicklefin chubs were fixed in 10% formalin for about 12 months, then soaked in tap water, and preserved in 75% ethanol (Haedrich 1983). Phenotypic measurements were made on preserved specimens.

Measurement of Phenotypic Traits

Selection of an adequate number of features to characterize the phenome is another important decision when studying spatial variation in phenotypic traits (Thorpe 1976). Forty-four morphometric and 18 meristic traits have been widely used in assessment of phenotypic variation among fish populations (Strauss and Bond 1990). Twelve of these morphometric features, that might vary in a species inhabiting the historically turbid Missouri River, were measured following standard methods (Strauss and Bond 1990): eye diameter, barbel length, anal fin base length, body depth, caudal peduncle depth, dorsal fin base length, head length, inter-orbital width, length of longest dorsal ray, length of longest pectoral fin ray, length of longest pelvic fin ray, snout length, and standard length. Features such as eye diameter and barbel length aid food and predator detection while snout and fin lengths aid hydrodynamic capabilities (Moore 1950, Pflieger 1997, Matthews 1998). Six meristic counts also were enumerated: number of anal-, dorsal-, and pelvic-fin rays, number of lateral line scales, and number of scale rows above- and below- the lateral line. Such meristic traits are known to vary in response to environmental factors, especially temperature (Hubbs 1922, Fowler 1970). All morphometric measures (nearest 0.1 mm) and meristic counts were made from the

left side of the fish with either a dial calipers for traits > 5 mm or a Nikon SMZ-2B binocular dissecting scope with an ocular micrometer for traits < 5 mm.

A meristic trait common to the barbeled minnows inhabiting turbid Great Plains streams also was enumerated. Moore (1950) documented the presence of elevated chemical sense organs along the first interradial membranes of the pectoral and pelvic fins and termed them compound taste buds. Counts of compound taste buds were higher in species inhabiting turbid waters than in species from less turbid waters, suggesting the importance of this adaptation for food detection. Turbidity reduction from sediment entrapment in impoundments has been an important alteration of the Missouri River (Morris et al. 1968, Pflieger and Grace 1987) that could influence local adaptation of *Macrhybopsis* chubs. I recorded the number of compound taste buds on the first inter-radial membrane of the pectoral and pelvic fins to assess recent adaptations, if any, to reduced turbidity in the Missouri River. Counts on left and right fins were enumerated separately, but combined for analyses. Compound taste buds are technically a meristic trait because they are enumerated rather than measured. However, unlike most other meristic traits, compound taste bud counts increase with fish size (Davis and Miller 1967). Thus, counts of compound taste buds could differ among individuals simply because of body size differences among them. Therefore, compound taste buds were grouped with morphometric data because morphometric data were analyzed with a multivariate technique that can examine data independent of size effects (see below).

Traditional morphometric measures have been criticized by Strauss and Bookstein (1982) and Bookstein et al. (1985) because they are primarily length, depth, and width

measurements; they tend to be repetitious and overlapping; they provide uneven coverage of the body with most measurements clustered on or near the head, fins, and caudal peduncle resulting in analyses biased towards these body regions; and many characters represent greatest or least distances (e.g., greatest body depth, length of longest fin ray), so precise measurement locations can vary from specimen to specimen (Strauss and Bond 1990). To alleviate these concerns Strauss and Bookstein (1982) developed the truss system to provide more even areal body coverage and to better quantify patterns in overall body shape. I followed the recommendation of Strauss and Bond (1990) by using both traditional measures and the truss system to examine morphological variation in sicklefin chubs.

Ten identifiable landmarks giving 21 morphometric truss measures that have been used for other cyprinids (Wood and Bain 1995) were chosen (Figure 2-2). Truss distances were measured following methods in Strauss and Bookstein (1982) and Winans (1984). Each specimen was placed on water resistant paper. A pin was poked through the specimen at each landmark and into the paper underneath. Pinned papers were then placed on a digitizing pad. Pin holes were digitized as X-Y coordinates into a computer spreadsheet. Landmarks were digitized in the same sequence for each specimen. Morphometric distances were then calculated by geometry with a computer.

Fish that had damaged traits (e.g., missing scales, damaged fins, mutilated bodies), due to field sampling or collection of aging structures, were eliminated only from analysis of that trait. Consequently, samples sizes differed among meristic,

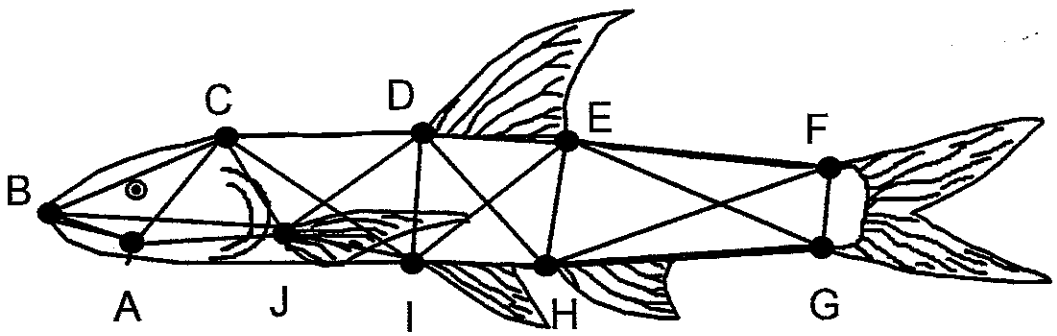


Figure 2-2. Locations of 10 truss landmarks used on sicklefin chubs collected from the Missouri and lower Yellowstone rivers in 1996 and 1997. Landmarks are denoted by filled circles. Truss distances (21 total) are denoted by lines. Landmarks refer to (A) most posterior point of maxillary, (B) most anterior point of jaw, (C) most posterior part of neurocranium, (D) anterior insertion of dorsal fin, (E) posterior insertion of dorsal fin, (F) anterior attachment of dorsal membrane from caudal fin, (G) anterior attachment of ventral membrane from caudal fin, (H) anterior insertion of anal fin, (I) anterior insertion of pelvic fin, (J) anterior insertion of pectoral fin.

morphometric, and truss analyses. Two workers initially measured or enumerated traits and significant differences in their precision were found to be minor (i.e., precision assessed on 81 of the 216 specimens with a paired t-test).

Statistical Analyses

Baltz (1990) distinguished between those multivariate analyses that examine population discrimination versus those that analyze population identification. The former examines differences among populations defined *a priori* using analyses such as discriminant function analysis or multivariate analysis of variance. The latter is a more exploratory technique that examines similarities and differences among individuals to assess population groups. Ordination techniques, such as principal components analysis (PCA), are extremely useful for examining these similarities and differences among individuals (Thorpe 1976, Baltz 1990).

Cluster analysis is another multivariate technique typically used to identify population groups and their affinities. However, its limitation for only categorizing populations makes it unsuitable for detecting specific spatial patterns in variation such as clines (Thorpe 1976). Principal components analysis can identify specific spatial patterns such as clines and can also assess population affinities by examining the spatial distance between population groups identified in bivariate plots of principal component scores (Manley 1994).

Principal components analysis was used to examine similarities and differences among individual sicklefin chubs collected from study segments. Data were generated at

the level of individuals but were presented and discussed for each segment. For example, principal component scores were presented for each individual but all individuals collected within a specific segment were identified by a segment-specific symbol in bivariate plots. Data are presented in this manner because segments provide a geographic reference for identifying spatial patterns such as clines, yet allow phenotypically distinct populations, that could encompass individuals from more than one segment, to still be identified. Segments were not intended to be *a priori* defined populations. A brief summary of the PCA techniques used is provided here, but more detail can be found in Appendix 2A; and Humphries et al. (1981), Bookstein et al. (1985), Johnson and Wichern (1992), Hatcher and Stepanski (1994), and Manley (1994). Principal components were calculated on covariance matrices of measurements. The components are linear combinations of trait values that summarize the major trends in variation of correlated traits among individuals. Sheared PCA (Humphries et al. 1981, Bookstein et al. 1985) was used to analyze the morphometric and truss data because body size of collected specimens varied among geographic collections. This technique quantifies shape differences independent of fish size (Bookstein et al. 1985).

Morphometric, meristic, and truss data were analyzed independently with PCA to obtain separate principal component scores for each individual from these character systems. In this way, individual PC-scores from different character systems can be plotted together to identify population groups. Principal component scores from morphometric and meristic data are typically plotted together to identify populations (e.g., meristic principal component 1 scores are often plotted against sheared morphometric principal

component 2 scores, examples in Poss and Miller 1983, Smith et al. 1983, Matthews 1987, Stauffer and van Snik 1997).

Morphometric, meristic, and truss data were also analyzed independently to maximize sample size within character systems. Principal components analysis requires each observation, or individual specimen, to have a measurement for every trait variable used in the analysis. If one trait measurement is missing the entire observation is omitted from the analysis (Hatcher and Stepanski 1994, Manley 1994). Combining morphometrics and truss data reduced overall sample sizes in PCA from 176 to 129 fish. The effect was especially pronounced for individuals in the lower river (i.e., river segments 19-27) where sicklefin chubs were uncommon and sample size was reduced from 31 to 20.

Two criteria for PCA are normality and adequate sample size. Normality assumptions were met with $\log_{10}$ transformed data based on bivariate scatter plots of data showing symmetrical ellipses among all possible combinations of variables and univariate stem-leaf plots (Johnson and Wichern 1992). Also, Wood and Bain (1995) summarized other studies which demonstrated that morphometric data typically satisfy multivariate normal assumptions. Hatcher and Stepanski (1994) cautioned that principal components analysis is a large-sample procedure. They recommend having at least 100 samples or five times the number of variables being analyzed. The sample size criterion was met as at least 100 specimens contributed data for each PCA.

Results

Meristic Analysis

Scale rows above and below the lateral line contributed most to meristic PC1 because of their high loadings (Table 2-1). Individuals with more scale rows above and below the lateral line had higher positive meristic PC1 scores. Numbers of anal-fin rays and lateral line scales were predominant in meristic PC2 and individuals with high positive scores along this component had more of them (Table 2-1). For example, the two extreme scores along meristic PC2 (Figure 2-3) reflected two sicklefin chubs with nine anal-fin rays in segments 5 and 10 (Appendix 2B, Table 2B.1). Pelvic-fin rays and lateral line scales contributed most to meristic PC3 (Table 2-1). Scale rows above and below the lateral line (i.e., meristic PC1 scores) displayed the most inter- and intra-segment variation, though meristic PC2 and PC3 scores had greater maximum values (Figure 2-3). Little variation among segments in anal-fin rays and pelvic-fin rays (i.e., meristic PC2 and PC3 scores) indicated that they would contribute little to population identification. In general, meristics varied more in segments in Montana and North Dakota than in downstream areas in Iowa, Nebraska, Kansas, and Missouri. However, there was no clear longitudinal pattern (Figure 2-3). No sicklefin chub population could be identified solely on meristic traits because meristic PC-scores exhibited substantial overlap among individuals and the segments they were collected in (Figure 2-4, 2-5).

Table 2-1. Principal component loadings for meristic characters of 167 sicklefin chubs (*Macrhybopsis meeki*) collected from the Missouri and lower Yellowstone rivers in 1996 and 1997.

Character	PC1	PC2	PC3
Anal-fin rays	-0.117	0.862	-0.113
Dorsal-fin rays	-0.047	-0.036	-0.015
Pelvic-fin rays	-0.107	-0.055	0.916
Lateral line scales	0.193	0.422	0.293
Scale rows above the lateral line	0.597	0.001	-0.164
Scale rows below the lateral line	0.611	-0.094	0.028
Proportion of variance	24%	17%	16%

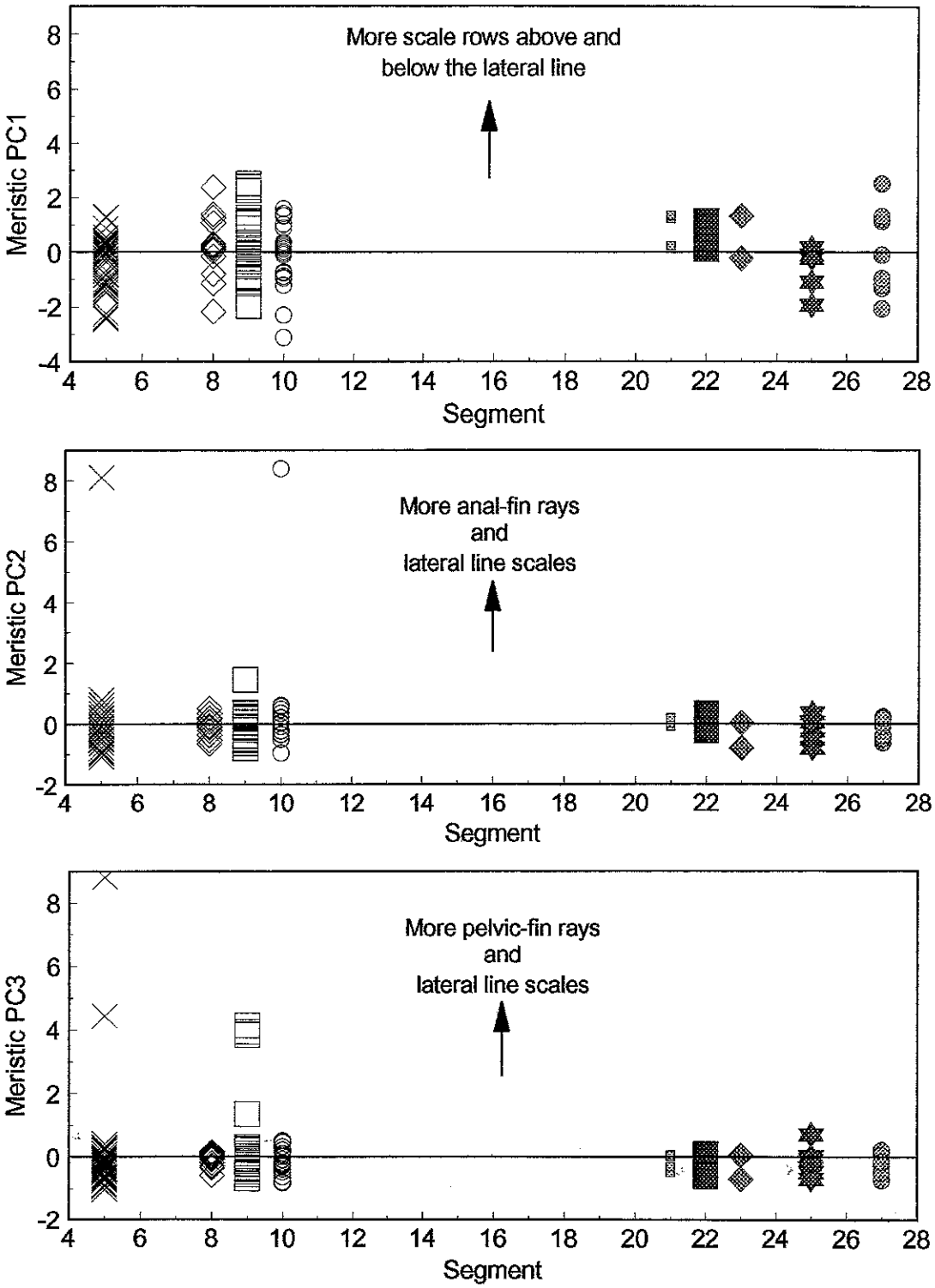


Figure 2-3. PC1, PC2, and PC3 scores from principal components analysis of sicklefin chub meristic traits plotted against Missouri and lower Yellowstone river study segments. Symbols represent PC-scores for individual fish collected in each segment. Study segments are as shown in Figure 2-1. Interpretation of PC axes is based on loadings in Table 2-2. Sicklefin chubs were collected in 1996 and 1997.

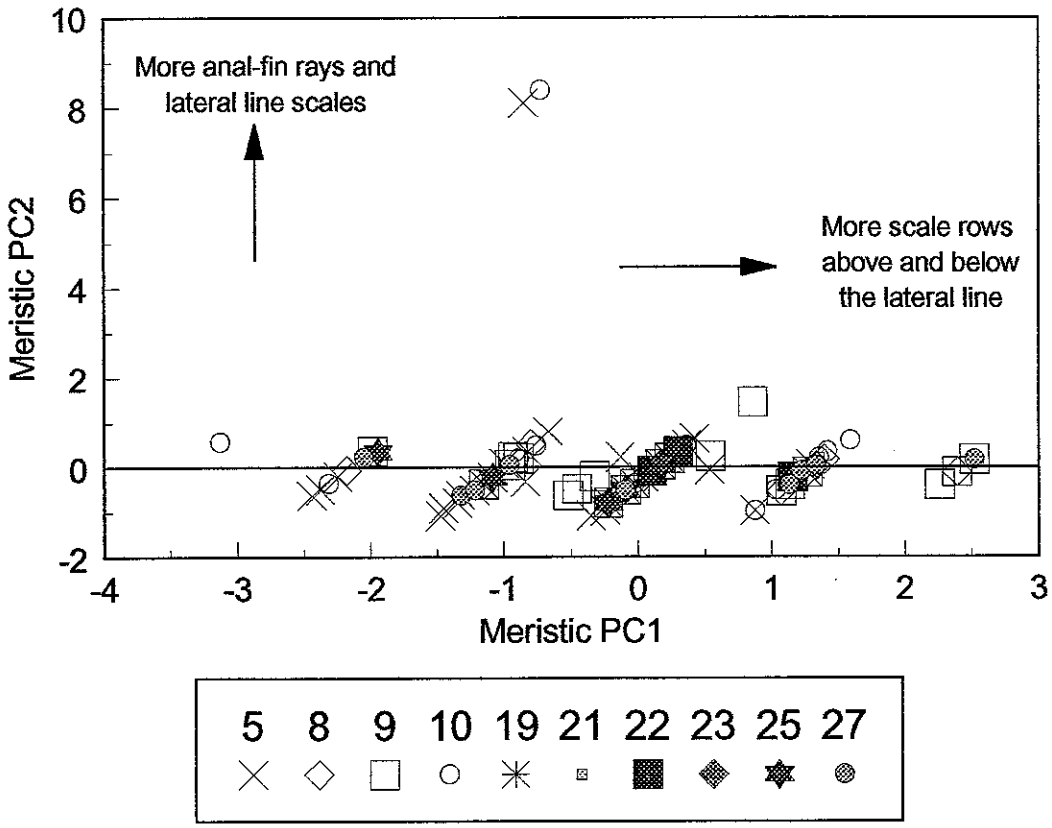


Figure 2-4. Scatterplot of first and second principal component scores of meristic traits of sicklefin chubs, *Macrhybopsis meeki* collected in 1996 and 1997 from 10 study segments (symbols) in the Missouri and lower Yellowstone rivers. Interpretation of PC axes is based on loadings in Table 2-2.

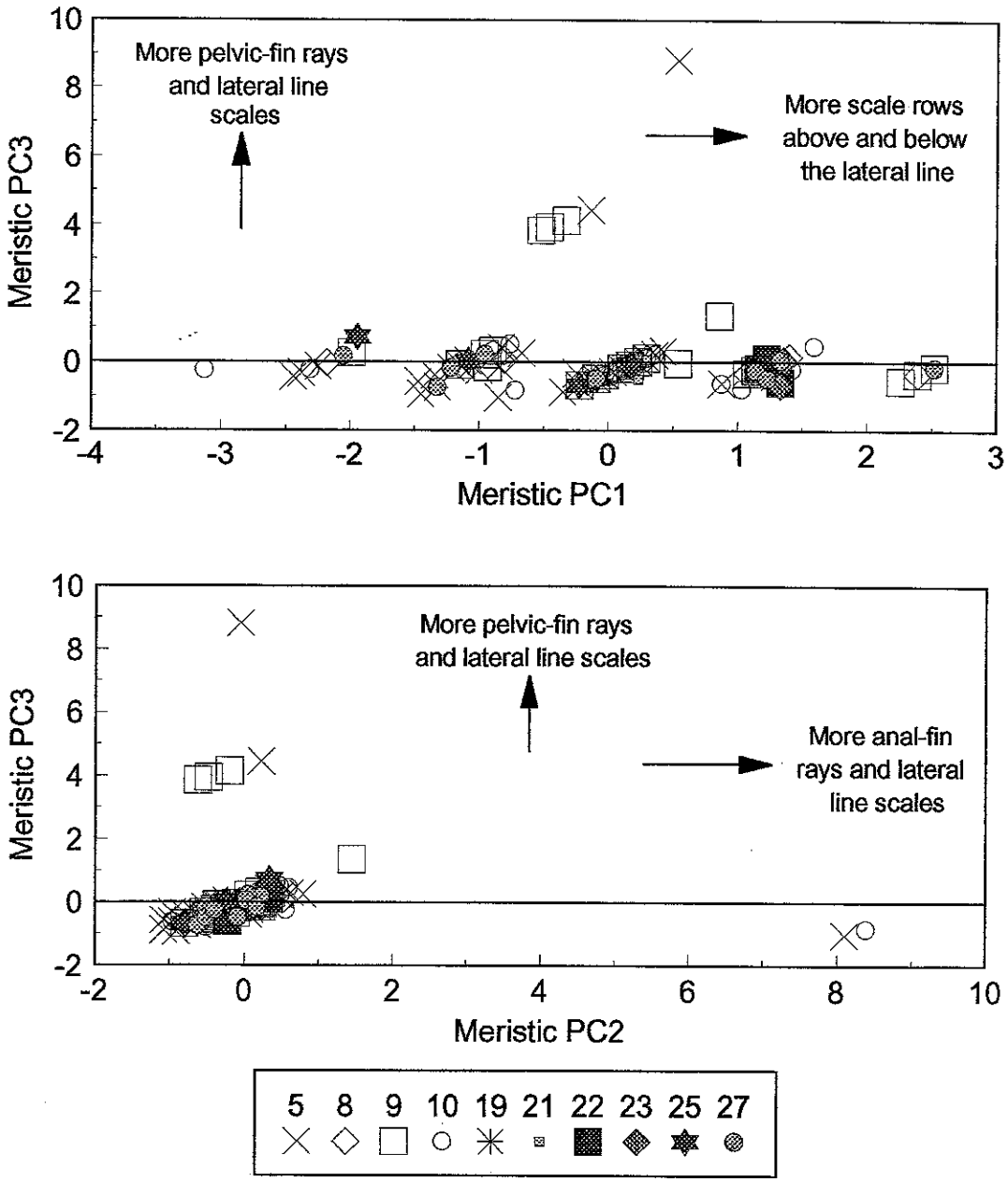


Figure 2-5. Scatter plots of first and third (top) and second and third (bottom) principal component scores of meristic traits of sicklefin chubs, *Macrhybopsis meeki*, collected in 1996 and 1997 from 10 study segments (symbols) in the Missouri and lower Yellowstone rivers. Interpretation of PC axes is based on loadings in Table 2-2.

Morphometric Analysis

Body size varied among individuals (Figure 2-6, Appendix 2B, Table 2B.2), but was removed by the shear procedure. General body size was reflected by PC1 because all variables loaded nearly even and high (Table 2-2). Also, a relationship between morphometric PC1 scores and standard length was evident (Figure 2-6). Sheared morphometric PC2 and PC3 scores were considered body size independent because all variables did not load evenly and highly (Table 2-2) and relationships between their scores and standard length were weak (Figures 2-7, 2-8). Three to four small fish in segments 21, 23, and 27 were exceptions on sheared morphometric PC2 as they had smaller negative scores than conspecifics with longer standard lengths (Figure 2-7). This may mean that sheared morphometric PC2 is not entirely body size independent and that ontogenetic variation may be present. Alternatively, other fish of equal or lesser length did not have smaller negative scores suggesting that the three to four outliers reflected actual morphometric differences independent of size effects.

Compound taste buds on pectoral and pelvic fins contributed most to sheared morphometric PC2 because of their high loadings (Table 2-2). They helped explain 33% of the variation not accounted for by body size. Fish with greater numbers of compound taste buds had lower sheared morphometric PC2 scores (i.e., high negative values) because of high negative loadings. There was no clear upstream to downstream pattern in sheared morphometric PC2 scores, but rather, substantial intra-segment variation was present in lower river segments (Figure 2-7).

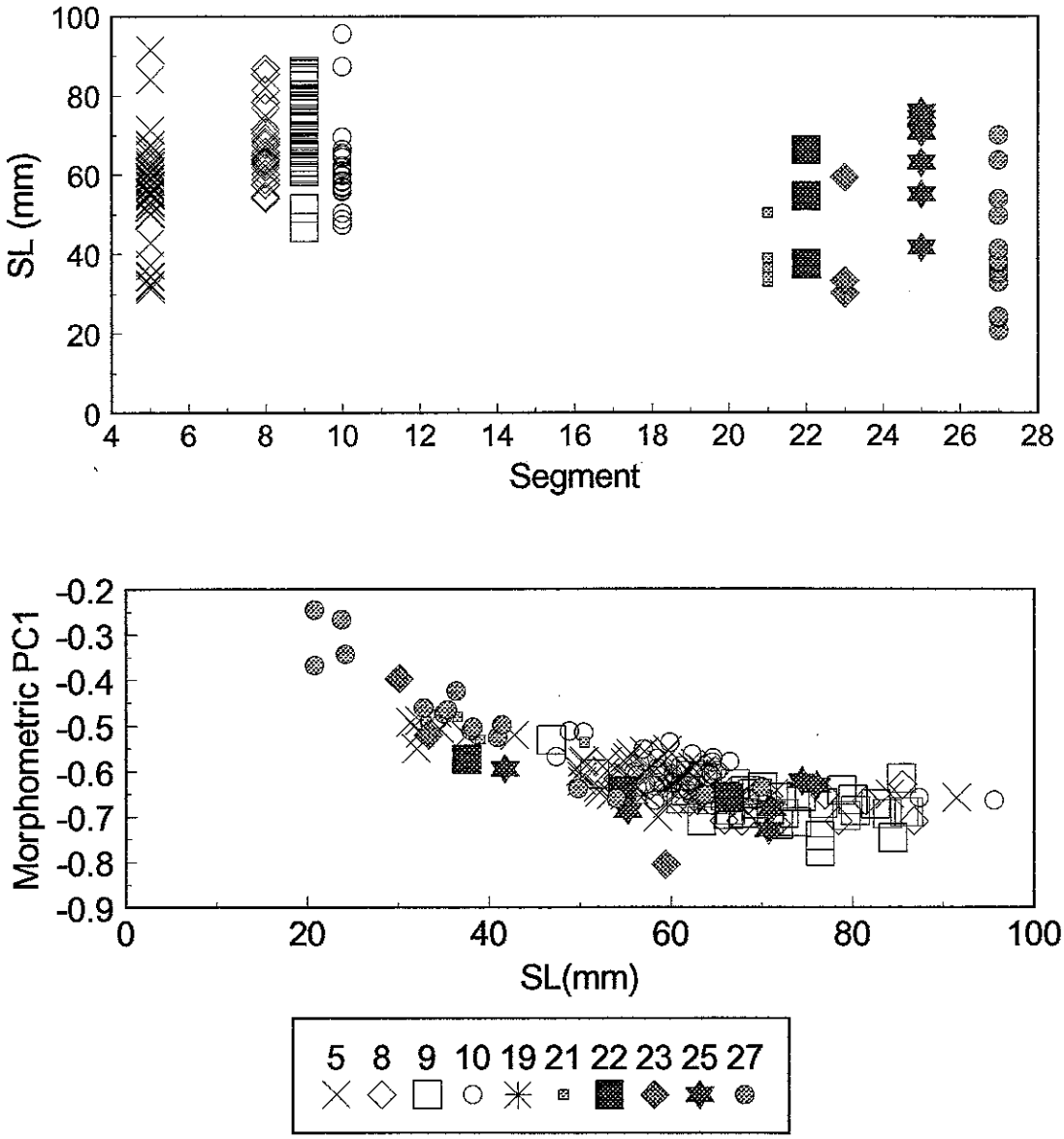


Figure 2-6. Plots of sicklefin chub standard lengths (SL) against Missouri and lower Yellowstone river study segments (top) and individual first principal component scores of morphometric traits against standard length (bottom). Morphometric PC1 is interpreted as a general measure of body size. Sicklefin chubs were collected in 1996 and 1997.

Table 2-2. Variable loadings on first, second, and third principal components of morphometric characters for 176 sicklefin chubs (*Macrhybopsis meeki*) collected from the Missouri and lower Yellowstone rivers in 1996 and 1997.

Character	PC1 (size)	Sheared PC2	Sheared PC3
Standard length	0.235	-0.120	0.106
Horizontal eye diameter	0.106	-0.048	0.090
Barbel length	0.190	0.072	0.262
Inter-orbital width	0.266	-0.094	-0.021
Head length	0.208	-0.033	0.121
Anal-fin base length	0.228	-0.090	0.121
Dorsal-fin base length	0.231	-0.106	0.114
Length of longest dorsal ray	0.265	-0.166	0.211
Length of longest pectoral fin ray	0.268	-0.178	0.158
Length of longest pelvic fin ray	0.255	-0.160	0.115
Body depth	0.250	-0.118	0.109
Caudal peduncle depth	0.228	-0.099	0.074
Snout length	0.267	-0.075	0.157
Pectoral fin taste buds	0.368	-0.799	0.406
Pelvic fin taste buds	0.383	-0.864	0.046
Proportion of variance	88%	4%	2%

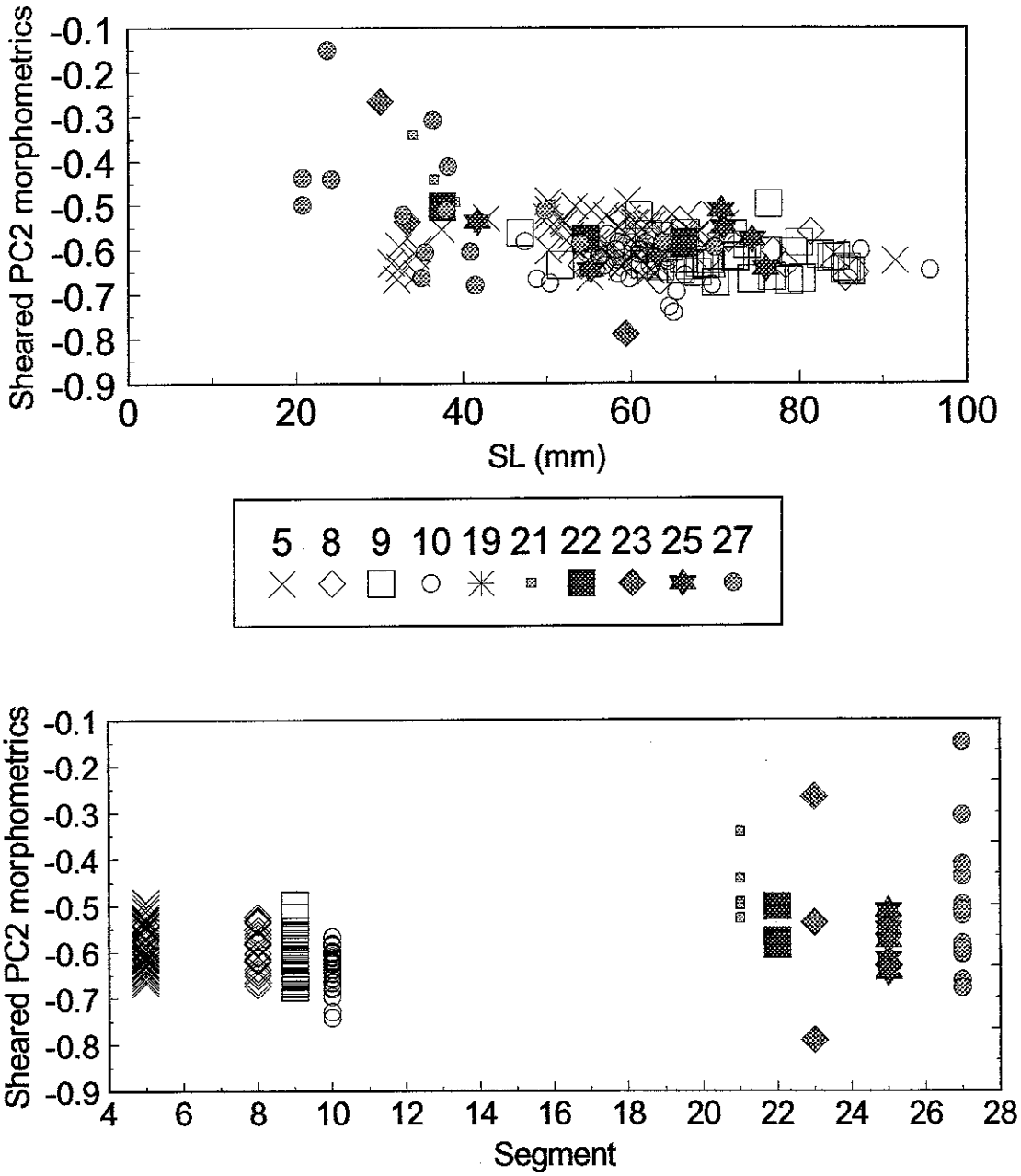


Figure 2-7. Individual sheared PC2 morphometric scores plotted against standard length (SL) (top) and against Missouri and lower Yellowstone river study segments (bottom) for sicklefin chubs collected in 1996 and 1997.

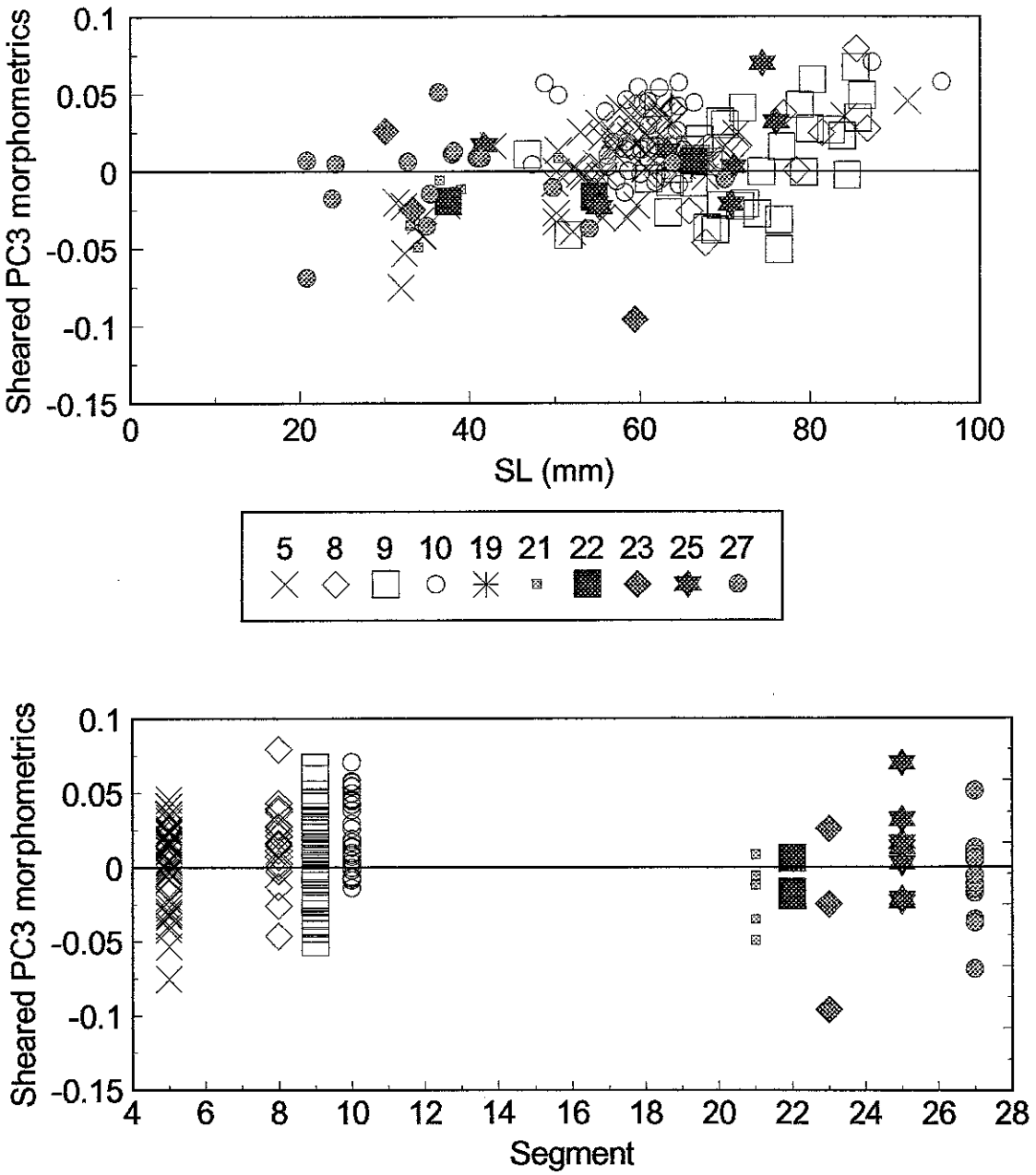


Figure 2-8. Individual sheared PC3 morphometric scores plotted against standard length (SL) (top) and against Missouri and lower Yellowstone river study segments (bottom) for sicklefin chubs collected in 1996 and 1997.

Pectoral fin taste buds, barbel lengths, and longest dorsal ray lengths contributed most to sheared morphometric PC3 (Table 2-2). This PC accounted for 2% of overall variation, but 17% of the variation not explained by body size. Fish scoring high along this component (i.e., high positive scores) had more pectoral fin taste buds, longer barbels, and longer dorsal fin rays (Table 2-2). Sheared morphometric PC3 scores showed no upstream to downstream pattern, but rather substantial intra-segment variation as was observed for sheared morphometric PC2 (Figure 2-8).

No phenotypically distinct population could be clearly identified based on these traits because individual sheared morphometric PC2 and PC3 scores and meristic PC1 scores plotted against each other exhibited substantial overlap (Figures 2-9, 2-10). Still, there was a tendency for sicklefin chubs in segments 8, 9, and 10 to have many taste buds as only six of 91 sicklefins from these segments (6.5%) had sheared morphometric PC2 scores less negative than -0.55 (Figure 2-9). Alternatively, about half the sicklefin chubs in the lower river had scores greater than -0.55 indicating greater variability in taste bud counts in segments 19-27 (Figure 2-9). Lack of variation in meristic PC2 and PC3 scores precluded their use in identifying populations.

Truss Analysis

General body size was again reflected by the first principal component of truss data (93% of total variance) because all variables loaded nearly even and high (Table 2-3) and PC1 truss scores appeared related to standard length (Figure 2-11). Body size variation was removed from sheared PC2 and PC3 truss scores as indicated by variable

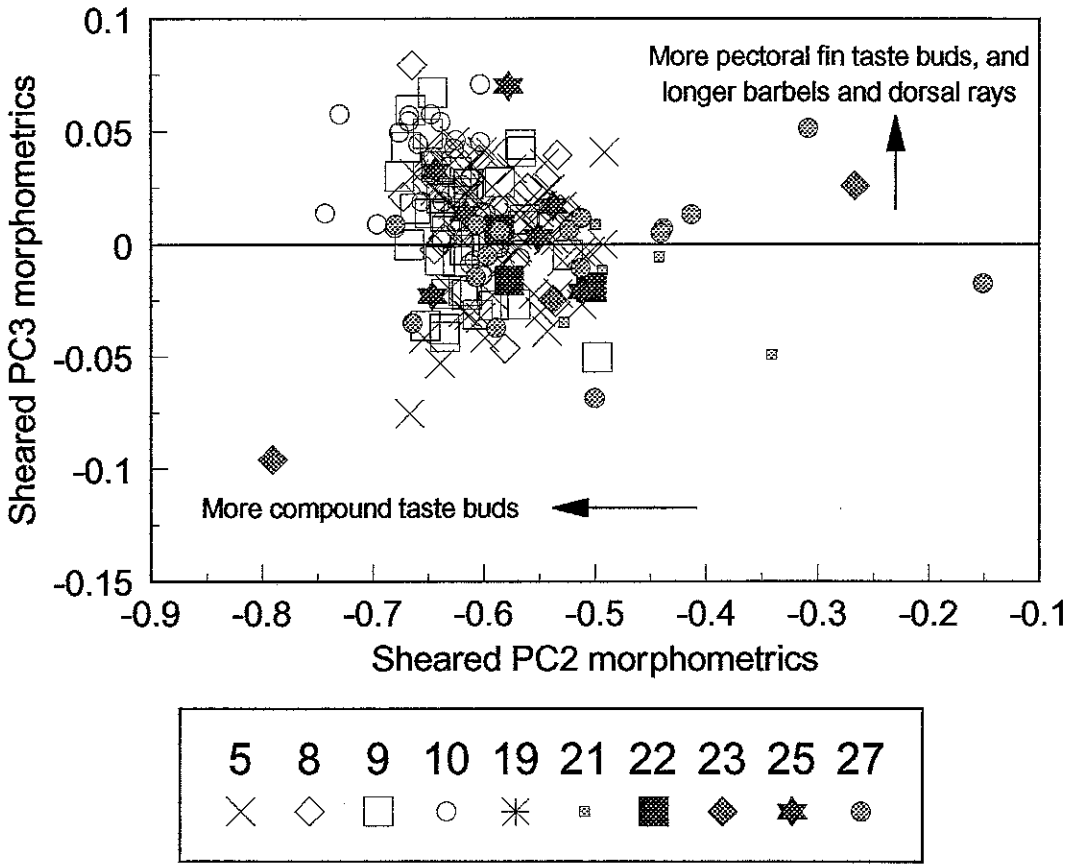


Figure 2-9. Exploratory scatter plot of individual sheared PC2 morphometric scores plotted against individual sheared PC3 morphometric scores from sicklefin chubs collected in ten Missouri and lower Yellowstone river study segments in 1996 and 1997. Interpretation of sheared PC2 and PC3 morphometric axes based on loadings in Table 2-3.

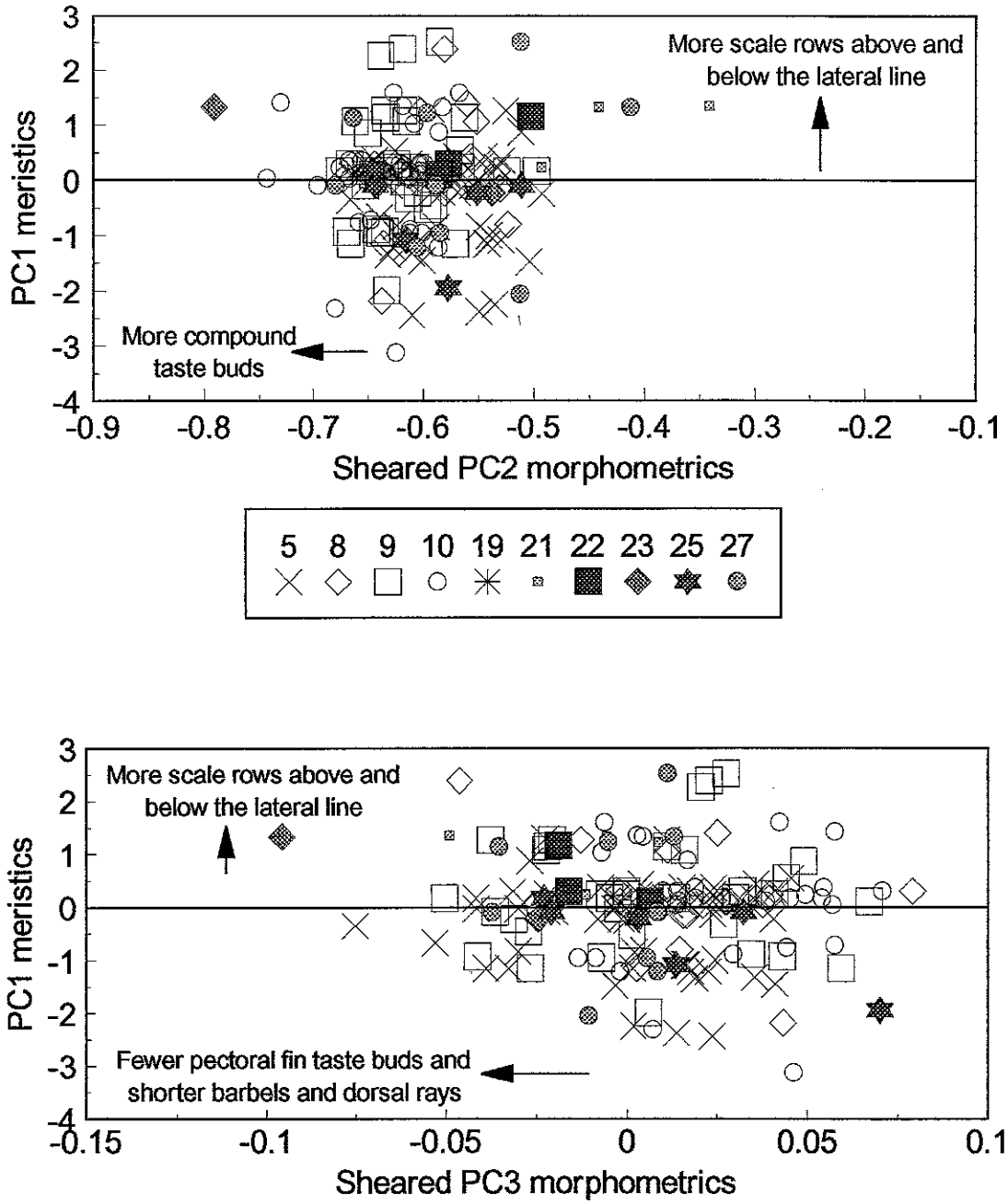


Figure 2-10. Exploratory scatter plots of individual PC1 scores (meristics analysis) plotted against sheared PC2 morphometric scores (top) and sheared PC3 morphometric scores (bottom) from sicklefin chubs collected in ten Missouri and lower Yellowstone river study segments in 1996 and 1997. Interpretation of PC1 meristic axis based on loadings in Table 2-2. Interpretation of sheared PC2 and PC3 morphometric axes based on loadings in Table 2-3.

Table 2-3. Variable loadings on first, second, and third principal components of truss distances for 148 sicklefin chubs (*Macrhybopsis meeki*) collected from the Missouri and Lower Yellowstone rivers in 1996 and 1997.

Truss distance	PC1 (size)	Sheared PC2	Sheared PC3
A-B	0.148	0.190	0.348
A-C	0.198	-0.022	0.154
A-J	0.178	-0.456	0.350
B-C	0.191	-0.141	0.122
B-J	0.166	-0.204	0.327
C-D	0.226	0.024	0.055
C-I	0.213	-0.115	0.031
C-J	0.189	0.300	0.268
D-E	0.208	0.053	0.001
D-H	0.238	-0.147	0.053
D-I	0.232	0.119	0.127
D-J	0.234	0.174	0.012
E-F	0.237	-0.253	0.082
E-G	0.235	-0.240	0.088
E-H	0.260	-0.144	0.056
E-I	0.231	0.231	0.074
F-G	0.228	-0.125	0.109
F-H	0.227	-0.119	0.050
G-H	0.224	-0.124	0.055
H-I	0.235	-0.022	0.055
I-J	0.237	-0.232	-0.149
Proportion of variance	93%	2%	1%

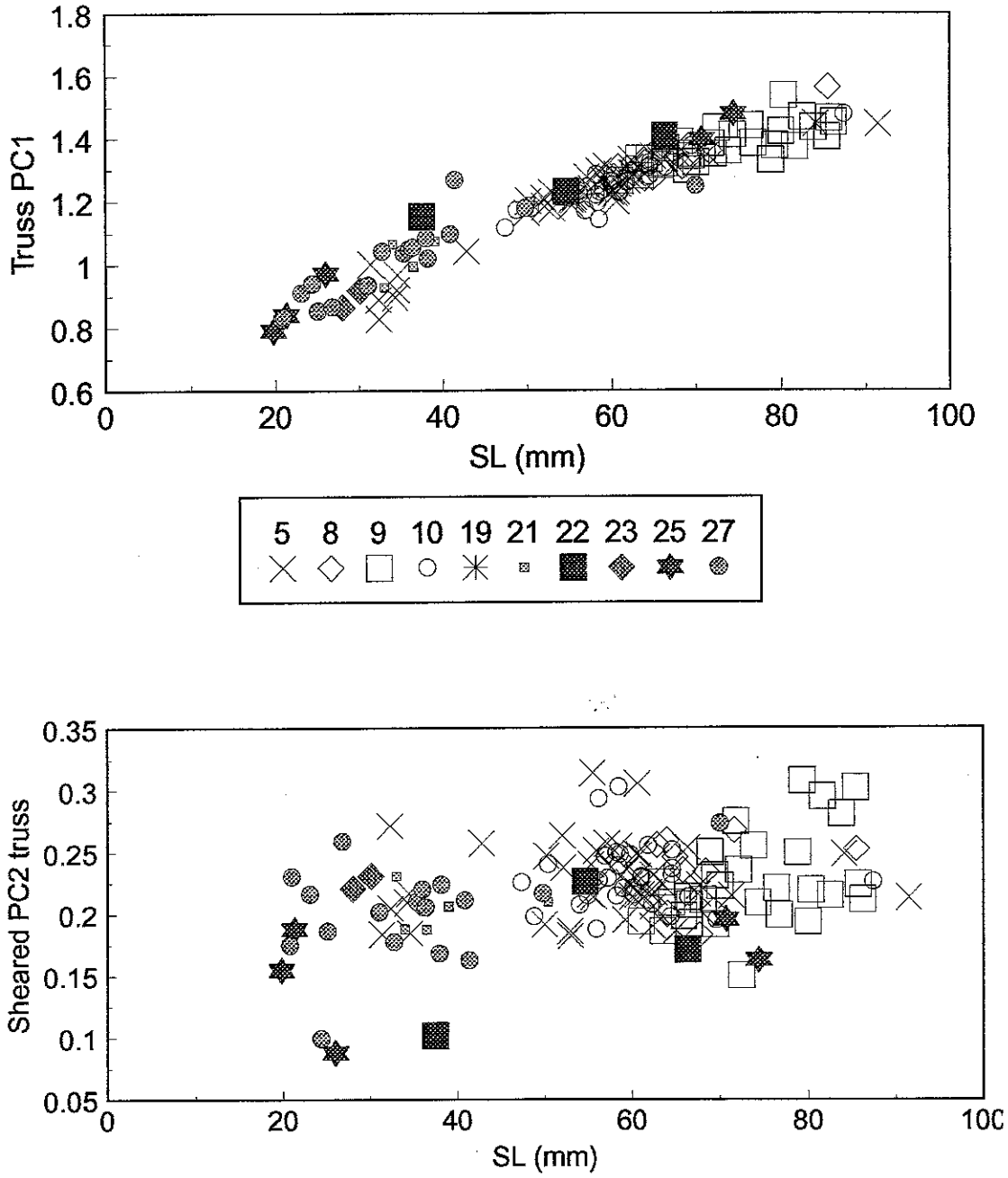


Figure 2-11. Individual PC1 truss scores (top) and sheared PC2 truss scores (bottom) plotted against standard lengths (SL) from sicklefin chubs collected in ten Missouri and lower Yellowstone river study segments in 1996 and 1997. Truss PC1 is interpreted as a general measure of body size.

loadings (Table 2-3) and plots of sheared PC-scores against standard length (Figures 2-11, 2-12). A selected head distance (A-J), body height distance (C-J) and caudal distances (E-F, E-G) loaded highest on sheared PC2 truss. These variables helped explain 2% of total variance, but 29% of the variation not accounted for by body size (Table 2-3). Fish with longer head distances A-J, shorter body height distances C-J, and longer trunk distances E-F and E-G scored lower along this component (i.e., low positive numbers) (Figure 2-13). Sheared PC3 truss data (1% of total variance) was interpreted as a measure of head lengths A-J, A-B, and B-J (Table 2-3). Fish scoring high on this component had longer heads (Figure 2-13) because these variables loaded positively on this component.

Individual sheared PC2 truss scores plotted against individual sheared PC3 truss scores showed greater separation of populations than either meristic or morphometric traits with two population groups emerging (Figure 2-14, 2-15). One population group was composed of individuals from lower river segments 19-27. These chubs had longer head and caudal regions, and a shorter body depth. The other population was composed of individuals from upper river segments 5-10. These chubs had shorter head and caudal regions, and a taller body depth.

Discussion

Intra-segment variation in sicklefin chub meristic and morphometric traits currently exceeds inter-segment variation, suggesting that no phenotypically distinct populations exist in the Missouri River, despite river regulation. Phenotypic traits are a product of a variety of genetic and environmental mechanisms (e.g., genetic drift, selection pressures,

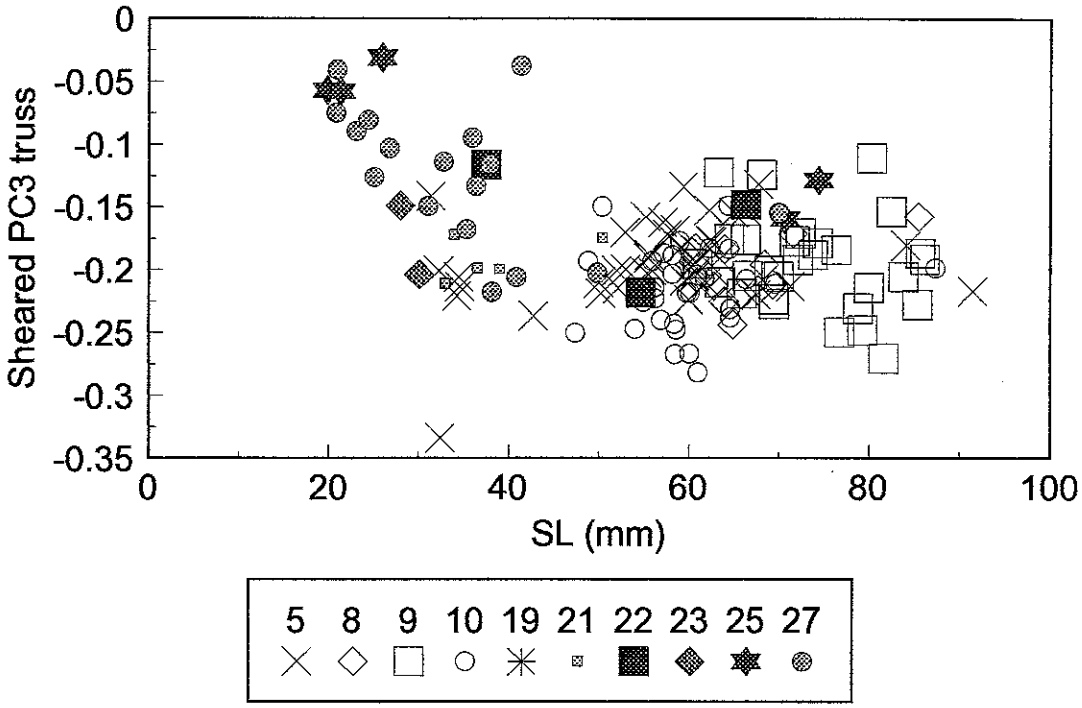


Figure 2-12. Plot of individual sheared PC3 truss scores plotted against standard length (SL) of sicklefin chubs collected in ten Missouri and lower Yellowstone river study segments in 1996 and 1997.

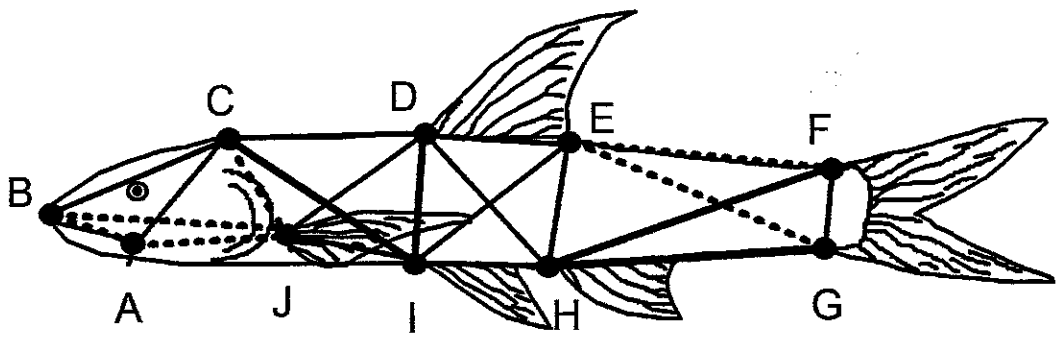


Figure 2-13. Truss distances of sicklefin chubs that are interpretated as important elements defining sheared PC2 and PC3 truss scores. Interpretation is based on loadings in Table 2-4. Sicklefin chubs were collected from the Missouri and lower Yellowstone rivers in 1996 and 1997.

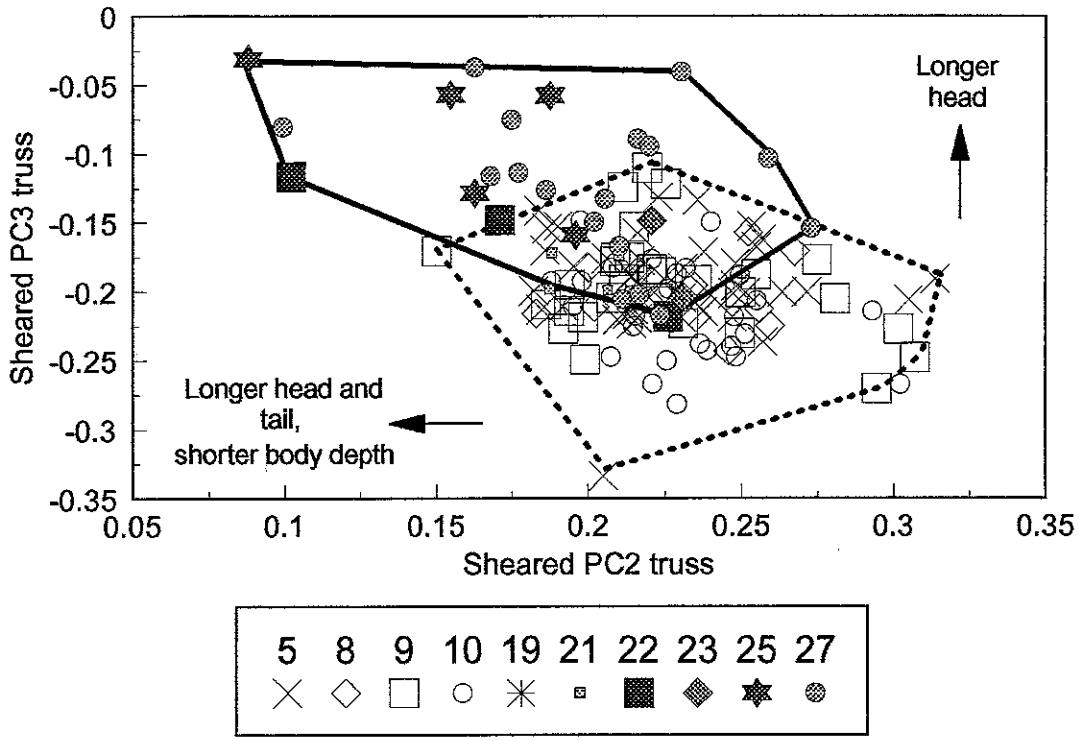


Figure 2-14. Scatter plot of individual sheared PC2 truss scores plotted against individual sheared PC3 truss scores from sicklefin chubs collected in ten Missouri and lower Yellowstone river study segments in 1996 and 1997. Interpretation of sheared PC2 and PC3 truss axes based on loadings in Table 2-4. Lines connecting polygons encompass all segment populations in the upper (dashed line, Montana and North Dakota, segments 5, 8, 9, 10) and lower (solid line, Nebraska, Iowa, Kansas, and Missouri, segments 19, 21, 22, 23, 25, 27) river areas.

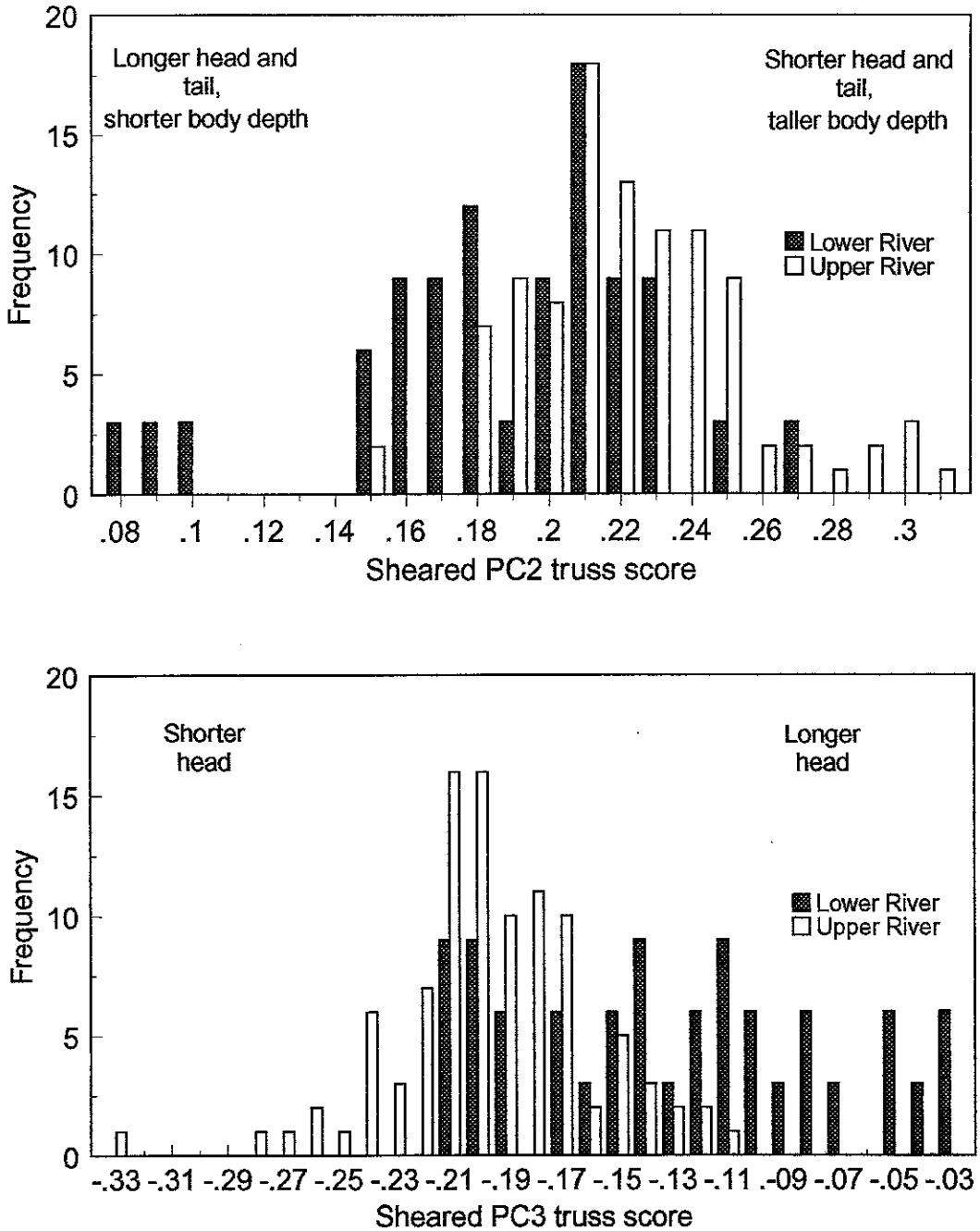


Figure 2-15. Frequency histograms of sheared PC2 (top) and PC3 (bottom) truss scores from sicklefin chubs plotted for two study areas. The upper river area includes study segments on the Missouri River in Montana and North Dakota and one study segment on the lower Yellowstone River (segments 5, 8, 9, 10). The lower river area includes study segments on the Missouri River in southern Nebraska, southern Iowa, Kansas, and Missouri (segments 19, 21, 22, 23, 25, 27). Interpretation of sheared PC2 and PC3 truss axes based on loadings in Table 2-7. Sicklefin chubs were collected in 1996 and 1997.

gene flow, clines etc.). However, some of these mechanisms that could explain the observed phenotypic similarity here can be omitted as plausible explanations based on current knowledge.

Genetic Mechanisms

Genetic factors maintaining similar phenotypes include gene flow among populations and homeostasis in genetic regulation of phenotypic traits. The current fragmented distribution of sicklefin chubs suggests that gene flow among all populations is minimal. Recent surveys conducted in riverine areas in the Missouri River have failed to collect individuals from the impounded middle third of the river (Mizzi 1994, Dieterman et al. 1996, Everett and Scarnecchia 1996, Young et al. 1997). The large dams lack upstream fish passage facilities and thus prevent upstream movement. Water can pass downstream, but dam outflows originate near mid-water in reservoirs (depths about 7-34 m) and pass through hydropower generators (Sveum 1988). The benthic nature of sicklefin chubs coupled with extensive lentic environments in the reservoirs likely precludes downstream movement.

Homeostasis in the genetic regulation of phenotypic traits may also result in minimal interpopulation variation (Riddell and Leggett 1981). This means that the genotypic range of selected phenotypic expressions has been reduced over time and may explain some of the similarities I observed. Populations with substantial homeostasis typically exhibit little variation in phenotypic or genotypic traits (Riddell and Leggett 1981). Although I did not examine genotypes, the substantial intra-segment variation in

phenotypic traits, which overwhelmed any inter-segment differences, argues against homeostasis as an explanation. However, genetic studies are still necessary to verify this conjecture.

Environmental Mechanisms

Similar phenotypes may also indicate that environmental differences among populations either exert little selective pressure or selective pressures have not operated for sufficient time to induce phenotypic differences. The former hypothesis may be true, but cannot be verified until the latter has been refuted. Evidence suggesting a long time requirement is seen in the many populations of fishes in northern North America that exhibit phenotypic differences after being isolated for 10,000 - 20,000 years following Pleistocene glaciation (e.g., *Coregonus* spp., Ihssen et al. 1981; *Gasterosteus* sp., Schluter and McPhail 1992, Foster and Baker 1995; *Osmerus* sp., Taylor and Bentzen 1993; *Phoxinus* sp., Toline and Baker 1993). Alternatively, phenotypes can change rapidly as gill raker morphology in Great Lakes *Coregonus* spp. changed after only 20 years in probable response to competition from the exotic alewife, *Alosa pseudoharengus* (Crowder 1986, Phillips and Ehlinger 1995). In an extreme example, body morphology of crucian carp, *(Carassius carassius*) changed in response to predation pressure in just 12 weeks (Bronmark and Miner 1992). Clearly, no universal time frame is necessary to induce phenotypic differences.

Although phenotypically distinct populations were not apparent, there was some indication that body morphologies may be diverging between upper and lower river

sicklefin chub populations (Figures 2-14, 2-15), suggesting that selective pressures do exist. The most likely selective pressure influencing this divergence of body morphology is current velocity.

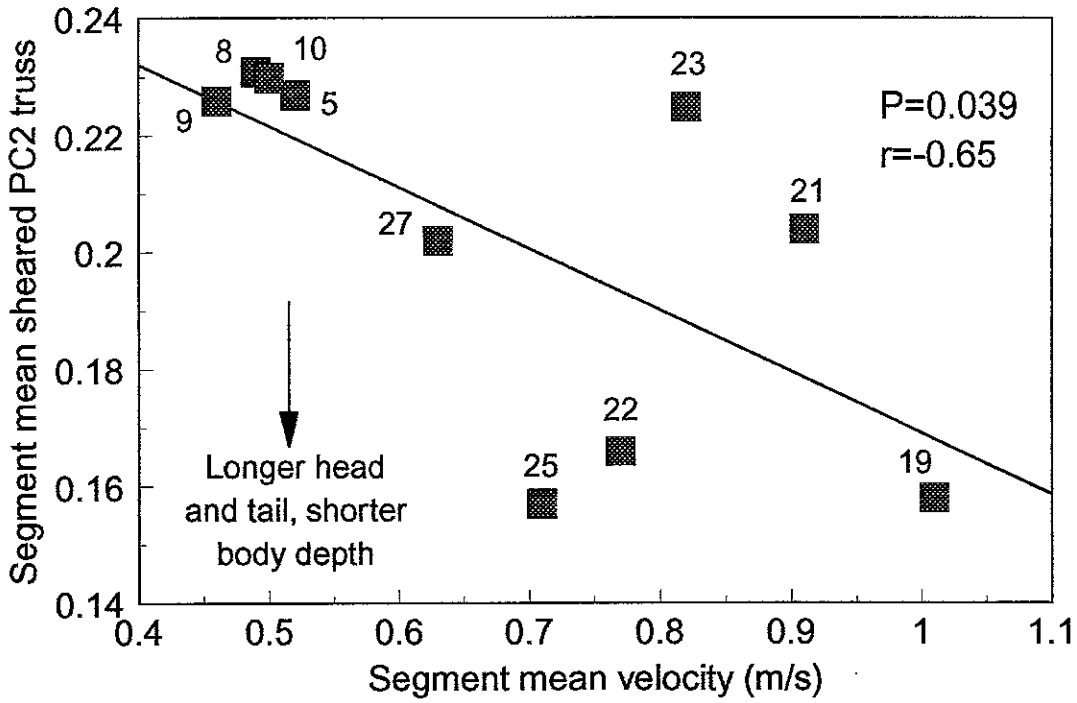
Body morphology has been shown to be functionally important in foraging, migration, and station holding behaviors in many fishes (Webb 1975, 1984). Optimal body morphologies characteristic of fishes inhabiting flowing waters or foraging on widely distributed food items, and termed *body/caudal fin periodic propulsion fishes*, include a relatively stiff streamlined anterior body, a narrow caudal peduncle, and a large anterior body depth (Webb 1984). These characteristics should either maximize thrust and/or minimize drag forces. Drag forces are likely more important to sicklefin chubs because maximal thrust is most often associated with the ability of large piscivores to capture fish prey (Webb 1984).

Matthews (1998) summarized much of the available literature on body morphology and ability of fishes to reduce drag and maintain their position in lotic environments. Drag forces acting on a fish include friction drag, a force acting along the body of a fish due to a gradient between slow velocity water molecules near the fish's surface and faster moving water molecules at progressive distances from the fish's surface, and pressure drag, a force that results when turbulent eddies are established along and behind a fish's body. Fishes reduce pressure drag with a long, thin body, because this form moves the point of flow separation with subsequent turbulent eddies, to a more posterior point along the fish's body. However, the long body increases surface area which results in increased friction drag. Friction drag is reduced with a thick, short body which reduces surface area,

however, a thick body results in high pressure drag as the flow separation point would be more anterior. To minimize the effect of both friction and pressure drag forces, a fish should have a smooth body, a gradually tapering and elongate caudal peduncle, and the greatest body depth about 1/3 of the distance toward the tail (Matthews 1998).

Body morphology patterns of sicklefin chubs may signify the beginnings of local adaptation for individuals inhabiting faster current velocities in the channelized river. Sicklefin chubs were more streamlined in the channelized river as evidenced by low sheared PC2 and high sheared PC3 scores (i.e., individuals in upper left corner of Figure 2-14) meaning that chubs had longer heads (truss distances A-J, A-B, B-J), shorter bodies (distance C-J), and longer caudal trunks (distances E-F, E-G) (Table 2-3, Figure 2-13) there. Current velocity data collected in conjunction with sicklefin chubs (Sappington et al. 1996, Dieterman et al. 1996, Young et al. 1997) permits further assessment of this environmental mechanism at the segment level.

Body shape, as quantified by sheared PC2 scores (head distance A-J, body height distance C-J, caudal distances E-F, E-G), was significantly correlated with the mean velocity measured in each segment during fish collection (Figure 2-16). Similar streamlined body morphologies have been associated with station holding and migratory behavior patterns of populations of various salmon species inhabiting higher flow velocities (e.g., *Oncorhynchus* spp., Beacham 1985, Taylor and McPhail 1985, Fleming and Gross 1989, Swain et al. 1991; *Salmo* sp. Riddell and Leggett 1981). Similarly, the fish community of a small Iowa stream exhibited more streamlined forms in a



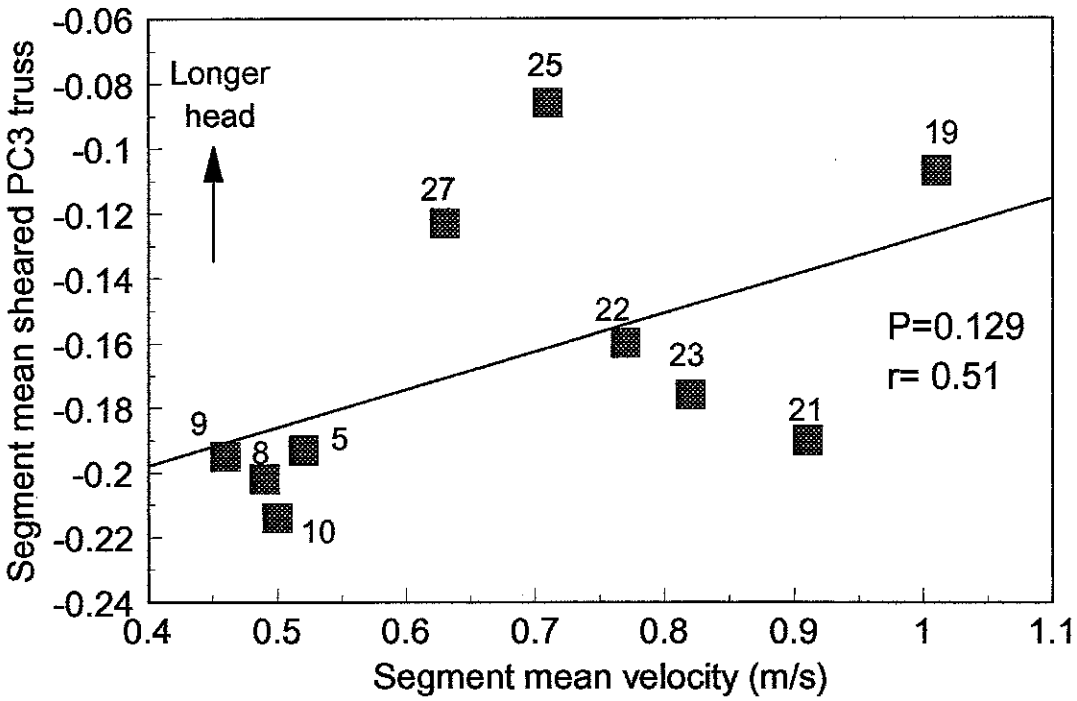


Figure 2-16. Correlations between body morphologies of sicklefin chubs as quantified by mean sheared principal component truss scores, and mean water velocity measured in ten Missouri and lower Yellowstone river study segments in 1996 and 1997. Interpretation of sheared PC2 and PC3 truss axes based on loadings in Table 2-7.

channelized stream reach than in a nearby unchannelized reach (Scarnecchia 1988). Absence of refugium from current velocities in the channelized Iowa stream reach was speculated as the probable mechanism for body form differences.

Body shape, as quantified by sheared PC3 (head lengths A-J, A-B, and B-J), was not significantly correlated with mean segment velocities collected in conjunction with sicklefin chubs (Figure 2-16). In both correlations, data points for upper river segments 5, 8, 9, and 10 were clustered together, possibly suggesting less variation in current velocity and associated body morphologies (Figure 2-16). Whereas, lower river segments 19-27 exhibited high variability in both segment mean velocities and sheared PC-scores. The greater variability may be due to smaller fish sample sizes in the lower river (Appendix 2B, Table 2B.2), greater variability in velocity patterns there, or it may further indicate the temporal variability of selection pressures, meaning that populations are still adapting to the altered habitat.

Anthropogenic alteration of aquatic habitat in the Missouri River has been ongoing for about 150 years beginning with snag removal operations in the 1830's (Galat et al. 1996). However, alterations that could directly influence the phenotypic traits I examined have only been completed recently. Channelization began in 1912 but proved ineffective as many early structures were destroyed by floods. Modern channelization projects to narrow and deepen the river channel were begun in the 1930s under authorization of the Missouri River Bank Stabilization and Navigation Project (Ferrell 1996). These efforts reduced diversity of instream habitats such as side channels and sand bars, changed physical substrate, and increased water depth and current velocity in the main channel

(Galat et al. 1996). However, these alterations were not considered complete until 1981 (Hesse et al. 1989). The first mainstem impoundment was closed in 1937 and the last, Big Bend Dam, SD, was closed in 1963. Drought slowed reservoir system filling and it was not until 1967 that operating levels were achieved (Sveum 1988). Pflieger and Grace (1987) examined the effect of impoundment upon turbidity and described three temporal periods; preimpoundment (1930-1952), transition (1952-1965), and postimpoundment (1965-current). Thus, modern channelization effects span about 65 years while turbidity and water temperature alterations span about 40 years. Complete adaptation to these selection pressures may require more time.

Diverging body morphology patterns observed here could also be due to selection pressures not associated with river regulation. Sicklefin chubs in the lower river may always have exhibited more variability in body morphology than upstream conspecifics or diverging patterns may simply reflect an adaptive cline. Clinal patterns are gradual changes in phenotypic characters typically associated with ecological gradients such as temperature, moisture, or light (Endler 1977). Principal component scores of meristic, morphologic, and truss characters did not exhibit gradual upstream to downstream changes (Figures 2-3, 2-7, 2-8). Meristic and morphologic PC-scores varied widely within segments but not among them. Truss PC-scores showed some differences between upstream (segments 5-10) and downstream (segments 19-27) segments but no gradual patterns within these groupings (Figure 2-14). This suggests that diverging patterns are unrelated to traditional ecological gradients of temperature or light (Endler 1977) and are

more likely related to contemporary selection pressures such as flow velocity caused by channelization activities.

Historical information on body morphologies of Missouri River fishes is scant for most species and until the present study, absent for sicklefin chubs. Olund and Cross (1961) examined geographic variation in a related species, the flathead chub (*Platygobio gracilis*). They described two body forms, a streamlined form with a more wedge shaped head and larger body size and a chubbier form with a less depressed head and generally smaller. The more streamlined form was typical of large rivers including the lower Missouri River. However, upper Missouri River specimens were either represented by streamlined individuals also, or were considered intergrades between the two body forms. The chubbier form was generally associated with small tributary streams in the western Missouri Basin. Metcalf (1966) described variation in body shape, mouth pattern, eye size, and features of scales for many fishes inhabiting the Kansas River basin. Variation in these features was discussed in relation to zoogeography of fishes of the Great Plains region. Many features followed a northeast-southwest pattern with chubbier body forms and small eyes found in conspecifics in southwestern areas. Few phenotypic differences were noted along the northwest-southeast Missouri River trajectory. Metcalf (1966) speculated that the repeated advance and retreat of glaciers with continual alteration of drainage patterns (e.g., deflection of historic Missouri River from a northeasterly course to the southeast) across the plain like topography likely provided little opportunity for extended periods of isolation necessary for speciation, but rather promoted continual

intermingling of stocks. This was probably especially true of the north-south flowing Missouri River.

Summary and Management Implications

Although intra-segment variation of sicklefin chub phenotypic traits currently exceeds inter-segment variation, there is some evidence that body morphologies may be diverging possibly in response to increased current velocities from river channelization. Diverging body morphology patterns do not resemble adaptive clines and appear to be recent changes with potentially adaptive benefits. The relatively short time river-regulation structures have been in place suggests that more time may be necessary to fully evaluate the adaptive significance of the patterns emerging here. Assessing phenotypic variation associated with these river regulation activities could have benefited from examination of historical specimens. However, sicklefin chubs were first collected in upper river segments 5, 8, 9, and 10 in the late 1970s precluding a more system-wide temporal evaluation. Also, differences in collection and preservation activities could artificially introduce unknown biases into data analyses.

Nevertheless, these data are of value because they demonstrate some potential for evolutionary flexibility, indicate which phenotypic traits are beginning to diverge, and provide a "benchmark" for future studies to use for continual monitoring of these local adaptations of sicklefin chubs. In particular, body morphologies and possibly compound tastebuds are traits that should be monitored in the future. If sicklefin chubs continue to diverge, localized stocks requiring unique management or protection, may develop.

Stocks could then be used in re-introduction programs in particular habitats. Alternatively, continued body divergence may aid natural recolonization into the most highly channelized segments in Iowa and Nebraska. Others have suggested that these dams and impoundments serve as mechanisms isolating populations of other Missouri River fishes (Werdon 1993, Keenlyne et al. 1994, Epifanio et al. 1996), but this study provides the first river-wide examination of phenotypic variation in an archetypical large-river fish within the altered Missouri River hydrosystem.

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Appendix 2A. *Principal Components Analysis*

A brief summary of PCA is provided here but more detailed information can be found in Johnson and Wichern (1992), Hatcher and Stepanski (1994), and Manley (1994). Principal components analysis takes multiple variables, such as morphometric and meristic traits, and combines them into groups such that variables within groups are typically highly correlated with each other but that the groups themselves, are usually uncorrelated (Manley 1994). Also, PCA orders the groups so that the first group accounts for the largest amount of variation in the data, the second group accounts for the second largest amount of variation, and so on. These variable groups are called principal components (PC-s). The interpretation of variables comprising a principal component is based on their eigenvector (also called a coefficient or PC-loading). Eigenvectors can range from 0 to 1 and can be either positive or negative. Each variable has an associated eigenvector with each principal component. Variables with a high positive or negative eigenvector (generally > 0.20), are considered important in explaining what that principal component represents. A score for each fish is determined for each principal component by multiplying the eigenvectors of each variable by the original measurement value of the variable for that individual. Summing these values provides a score for each individual. Populations are then determined by examining bivariate plots of individual scores along two or three principal components and looking for spatially aggregated groups of individuals. If population groups are discerned, subsequent analyses such as multivariate analysis of variance can be performed to further examine trait differences.

Body size variation among populations can interfere with their identification because many trait measurements are positively correlated with body size (e.g., eye diameter, body depth, inter-orbital width etc.). Thus, multivariate techniques such as PCA which produce scores that maximize the variation in a set of correlated traits, may show differences among individuals that are primarily a function of overall body size differences rather than trait differences. Because fish body size varied among individuals, we used the "shear" procedure of Humphries et al. (1981) and Bookstein et al. (1985) to remove body size variation from PCA (Appendix 2C). Removal of body size variation from PCA was assessed by first examining eigenvectors of the analysis. If all variables loaded nearly even and high on the first principal component (PC1), then this component was interpreted as a general measure of fish body size (Bookstein et al. 1985). A plot of PC1 scores against a surrogate measure of fish body size, such as standard length, that displayed a relationship, confirmed that PC1 reflected body size. After the "shear" procedure, subsequent sheared principal components were considered independent of size if plots of sheared PC-scores against standard length exhibited no relationship (Humphries et al. 1981).

Appendix 2B.--Summary tables of meristic and morphometric traits of sicklefin chubs collected from ten study segments on the Missouri and Lower Yellowstone rivers in 1996 and 1997.

Table 2B.1. Meristic characters of sicklefin chubs (*Macrhybopsis meeki*) collected from 10 study segments in the Missouri and lower Yellowstone rivers in 1996 and 1997. Segment 9 is the Yellowstone River. All other segments are on the Missouri River. River kilometer (rkm) is the approximate mid-point distance of each study segment from the mouth.

	Anal fin rays				Dorsal fin rays				Pelvic fin rays			
Segment (state, rkm)	N	Mode	Freq.	Min-Max	N	Mode	Freq.	Min-Max	N	Mode	Freq.	Min-Max
5 (MT, rkm 3085)	55	8	98	8-9	55	8	98	7-8	56	8	96	8-10
8 (MT, rkm 2642)	22	8	100	8	22	8	100	8	22	8	100	8
9 (MT, rkm 57)	36	8	100	8	36	8	97	7-8	36	8	92	8-9
10 (ND, rkm 2522)	31	8	97	8-9	31	8	100	8	31	8	100	8
19 (NE/IA, rkm 915)	1	8	100	8	1	8	100	8	1	8	100	8
21 (KS/MO, rkm 755)	5	8	100	8	5	8	100	8	5	8	100	8
22 (KS/MO, rkm 650)	3	8	100	8	3	8	100	8	3	8	100	8
23 (MO, rkm 498)	2	8	100	8	2	8	100	8	2	8	100	8
25 (MO, rkm 282)	7	8	100	8	7	8	100	8	7	8	100	8
27 (MO, rkm 40)	13	8	100	8	13	8	100	8	13	8	100	8

	Lateral line scales				Scale rows above lateral line				Scale rows below lateral line			
Segment (state, rkm)	N	Mode	Freq.	Min-Max	N	Mode	Freq.	Min-Max	N	Mode	Freq.	Min-Max
5 (MT, rkm 3085)	54	42	15	40-52	55	7	71	6-8	54	6	78	5-7
8 (MT, rkm 2642)	22	48,50	23	43-50	22	7	86	6-8	22	6	73	5-7
9 (MT, rkm 57)	35	48	34	42-59	36	7	75	6-8	36	6	61	5-7
10 (ND, rkm 2522)	31	48	23	42-53	31	7	71	6-8	31	6	81	3-7
19 (NE/IA, rkm 915)	1	46	100	46	1	7	100	7	1	7	100	7
21 (KS/MO, rkm 755)	4	49	75	47-49	5	7	60	7-8	5	6	80	6-7
22 (KS/MO, rkm 650)	3	*	100	46-50	3	7	67	7-8	3	6	100	6
23 (MO, rkm 498)	2	42,49	100	42-49	2	7	100	7	2	6,7	100	6-7
25 (MO, rkm 282)	6	44	33	42-50	6	7	67	5-7	6	6	100	6
27 (MO, rkm 40)	11	44	36	42-50	11	7	45	6-8	11	6	45	5-7

*three fish each with 46, 47, and 50 lateral line scales, respectively.

Table 2B.2. Morphometric characters of sicklefin chubs (*Macrhybopsis meeki*) collected from 10 study segments in the Missouri and lower Yellowstone rivers in 1996 and 1997. Segment 9 is the Yellowstone River. All other segments are on the Missouri River. River kilometer (rkm) is the approximate mid-point distance from the mouth for each study segment. All measurements except standard length are expressed as percent of standard length.

		Standard length (mm)		Eye diameter		Barbel length		Inter-orbital width		Head length	
Segment (state, rkm)	N	Mean	SD(Min-Max)	Mean	SD(Min-Max)	Mean	SD(Min-Max)	Mean	SD(Min-Max)	Mean	SD(Min-Max)
5 (MT, rkm 3085)	57	55.6	11.7(31.4-91.5)	4.0	0.5(3.0-6.0)	2.8	0.3(2.1-3.8)	8.1	0.4(6.3-8.7)	22.7	1.1(19.1-24.6)
8 (MT, rkm 2642)	22	67.6	9.2(54.1-86.8)	3.6	0.3(3.0-4.3)	2.8	0.5(2.1-4.1)	8.6	0.4(7.9-9.6)	22.9	2.8(10.4-24.7)
9 (MT, rkm 57)	36	71.5	9.3(46.8-86.2)	3.4	0.4(2.4-4.1)	2.5	0.4(1.4-3.7)	8.4	0.4(7.0-9.1)	22.6	2.3 (9.3-24.9)
10 (ND, rkm 2522)	31	61.8	9.4(47.4-95.6)	3.5	0.5(2.6-4.9)	3.0	0.4(2.3-4.0)	8.6	0.4(7.7-9.7)	22.4	1.0(20.3-23.8)
19 (NE/IA, rkm 915)	1	89.1		2.6		4.0		8.4		23.4	
21 (KS/MO, rkm 755)	5	38.5	7.0(33.0-50.4)	4.7	0.5(3.9-5.2)	3.1	0.5(2.3-3.8)	7.9	0.5(7.2-8.4)	25.7	1.7(23.6-28.5)
22 (KS/MO, rkm 650)	3	52.8	14.4(37.5-66.3)	4.1	0.7(3.6-5.0)	2.7	0.4(2.2-3.2)	8.6	0.7(8.0-9.5)	24.8	2.0(22.5-26.1)
23 (MO, rkm 498)	3	40.9	16.0(30.1-59.4)	5.0	1.0(3.8-6.0)	3.3	0.8(2.5-4.3)	5.7	4.0(1.3-9.3)	25.1	1.6(23.4-26.7)
25 (MO, rkm 282)	7	64.6	12.3(41.7-76.0)	3.7	1.0(2.6-5.9)	3.3	0.8(2.4-5.0)	9.3	0.3(8.8-9.6)	24.8	1.3(23.1-26.8)
27 (MO, rkm 40)	17	39.0	13.9(20.8-70.0)	4.9	0.9(2.7-6.7)	3.2	0.8(2.2-5.2)	8.0	1.1(5.3-9.6)	25.5	1.5(22.5-27.7)

Table 2B.2. Continued.

Segment (state, rkm)	N	Anal-fin base length Mean	Anal-fin base length SD(Min-Max)	Dorsal-fin base length Mean	Dorsal-fin base length SD(Min-Max)	Longest dorsal ray len. Mean	Longest dorsal ray len. SD(Min-Max)	Longest pectoral ray len. Mean	Longest pectoral ray len. SD(Min-Max)	Longest pelvic ray len. Mean	Longest pelvic ray len. SD(Min-Max)
5 (MT, rkm 3085)	57	11.9	0.6(10.8-13.8)	13.3	0.6(12.1-14.7)	25.2	2.0(17.3-30.0)	27.5	2.0(23.6-34.0)	17.4	1.1(15.0-21.7)
8 (MT, rkm 2642)	22	11.9	0.6(10.9-13.0)	13.6	0.6(12.6-15.4)	26.3	2.2(18.4-29.6)	28.4	2.4(23.8-34.0)	18.0	1.0(16.3-20.3)
9 (MT, rkm 57)	36	11.8	0.7(9.9-13.2)	13.9	0.8(11.8-15.5)	26.0	1.8(22.4-30.9)	28.9	2.3(24.5-37.0)	18.1	0.8(16.5-19.9)
10 (ND, rkm 2522)	31	12.4	0.8(10.9-14.2)	14.2	0.7(12.7-15.8)	26.7	1.1(24.5-30.0)	27.8	2.0(24.4-33.6)	17.9	1.5(14.4-21.5)
19 (NE/IA, rkm 915)	1	12.0		14.1		25.8		31.5		19.0	
21 (KS/MO, rkm 755)	5	11.9	0.5(11.1-12.6)	14.3	0.7(13.0-15.2)	25.0	2.1(21.8-27.6)	27.0	2.2(24.5-30.0)	16.8	1.0(15.2-17.9)
22 (KS/MO, rkm 650)	3	13.7	1.5(12.6-15.4)	13.9	1.6(12.5-15.7)	25.0	2.6(22.0-26.6)	29.1	1.3(28.0-30.6)	18.1	0.3(17.7-18.4)
23 (MO, rkm 498)	3	12.8	0.8(11.9-13.4)	13.8	1.9(11.6-15.3)	24.7	2.9(21.5-27.2)	27.8	2.9(24.5-30.1)	17.6	1.2(16.2-18.8)
25 (MO, rkm 282)	7	12.6	0.7(11.5-13.4)	14.6	0.9(13.5-15.9)	27.8	1.6(25.6-30.4)	30.5	3.3(24.8-33.3)	19.3	1.5(17.2-21.9)
27 (MO, rkm 40)	17*	12.3	1.3(10.5-15.6)	14.4	0.9(13.0-16.3)	24.6	4.2(11.3-29.3)	25.8	3.5(19.7-33.1)	16.9	1.5(14.4-19.9)

Segment (state, rkm)	N	Body depth Mean	Body depth SD(Min-Max)	Caudal peduncle depth Mean	Caudal peduncle depth SD(Min-Max)	Snout length Mean	Snout length SD(Min-Max)	Pectoral fin taste buds Mean	Pectoral fin taste buds SD(Min-Max)	Pelvic fin taste buds Mean	Pelvic fin taste buds SD(Min-Max)
5 (MT, rkm 3085)	57	18.4	1.0(16.0-20.8)	8.2	0.4 (7.0-9.0)	8.6	0.9(6.9-10.7)	192	28(149-334)	122	17 (70-153)
8 (MT, rkm 2642)	22	19.9	1.0(17.9-22.0)	8.2	0.4 (7.4-9.1)	9.8	0.7(8.4-10.9)	211	32(151-269)	134	19 (96-162)
9 (MT, rkm 57)	36	19.2	0.8(17.6-21.1)	8.2	0.4 (7.3-9.3)	9.0	0.6(7.6-10.3)	213	30(123-270)	144	15(101-166)
10 (ND, rkm 2522)	31	20.0	0.9(18.2-21.9)	8.8	0.5 (7.5-9.8)	8.1	1.2(4.8-10.0)	201	25(152-247)	136	14(112-172)
19 (NE/IA, rkm 915)	1	22.6		8.4		10.5		191		101	
21 (KS/MO, rkm 755)	5	19.1	0.9(18.2-20.2)	8.8	0.3 (8.4-9.4)	9.6	0.6(8.9-10.3)	154	38(125-208)	74	24 (46-109)
22 (KS/MO, rkm 650)	3	19.0	0.3(18.8-19.4)	8.9	0.5 (8.4-9.5)	10.3	0.6(9.6-10.8)	184	23(157-200)	133	11(120-141)
23 (MO, rkm 498)	3	18.4	1.8(16.2-19.5)	8.5	0.9 (7.6-9.6)	8.3	1.6(7.3-10.2)	177	115 (46-265)	104	58 (46-163)
25 (MO, rkm 282)	7	19.2	0.9(17.8-20.4)	8.7	0.4 (7.9-9.2)	9.6	1.0(8.4-11.0)	203	43(142-284)	135	16(114-166)
27 (MO, rkm 40)	17	18.4	0.8(16.1-19.7)	8.6	0.6(7.0-10.0)	8.5	0.8(7.1-10.6)	156	53 (21-224)	98	43 (27-174)

*Anal-fin base length was only measured on 16 specimens in segment 27.

Table 2B.3. Number of sicklefin chubs (*Macrhybopsis meeki*) observed with counts of lateral line scales shown below. Sicklefin chubs were collected from the Missouri and Lower Yellowstone rivers in 1996 and 1997. Segment 9 is on the lower Yellowstone River. Other segments are on the Missouri River. See Figure 2-1 for spatial location of all river segments.

	Number of lateral line scales																			
Segment	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
5	3		8	2	3	7	4	4	5	5	4	5	4							
8				2		2	4	3	5	1	5									
9			1		1	6	4	2	12	5	3									1
10			1		4	1	2	2	7	4	4	4		2						
19							1													
21								1		3										
22							1	1			1									
23			1							1										
25			1		2		1		1		1									
27			1		4		1	1	2	1	1									

Table 2B.4. Number of sicklefin chubs (*Macrhybopsis meeki*) observed with counts of scale rows above and below the lateral line shown below. Sicklefin chubs were collected from the Missouri and Lower Yellowstone rivers in 1996 and 1997. Segment 9 is on the Lower Yellowstone River. Other segments are on the Missouri River. See Figure 2-1 for spatial location of all river segments.

	Number of scale rows					
Segment	3	4	5	6	7	8
			Above lateral line			
5				15	39	1
8				2	19	1
9				6	27	3
10				6	22	3
19					1	
21					3	2
22					2	1
23					2	
25			1	1	4	
27				4	5	2
			Below lateral line			
5			7	42	5	
8			2	16	4	
9			3	22	11	
10	1		1	25	4	
19					1	
21				4	1	
22				3		
23				1	1	
25				6		
27			3	5	3	

Appendix 2C.--Statistical Analysis Systems (SAS) codes used to perform the sheared principal components analysis of Humphries et al. (1981) and Bookstein et al. (1985). The codes used to analyze the truss data are presented here as an example.

```
filename csvin 'c:/office/wpwin/wpdocs/chub/morphmet/trussan2.csv';
data csv;
infile csvin missover dsd;

input tracking : segment : habitat $ : sl : AB : AC : AJ : BC : BJ : CD : CI : CJ : DE :
DH : DI : DJ : EF : EG : EH : EI : FG : FH : GH : HI : IJ :;

data truss1; set csv;

        /*these are notes I recorded for myself as I went through the shear procedure,
          this method follows the example in the red Bookstein book (1985) pages
          105-109*/

        /* Page 105, step 1 is to get the data as above, step 2 is to log 10 transform the
           data */

LGAB=LOG10(AB);
LGAC=LOG10(AC);
LGAJ=LOG10(AJ);
LGBC=LOG10(BC);
LGBJ=LOG10(BJ);
LGCD=LOG10(CD);
LGCI=LOG10(CI);
LGCJ=LOG10(CJ);
LGDE=LOG10(DE);
LGDH=LOG10(DH);
LGDI=LOG10(DI);
LGDJ=LOG10(DJ);
LGEF=LOG10(EF);
LGEG=LOG10(EG);
LGEH=LOG10(EH);
LGEI=LOG10(EI);
LGFG=LOG10(FG);
LGFH=LOG10(FH);
LGGH=LOG10(GH);
LGHI=LOG10(HI);
LGIJ=LOG10(IJ);

        /*Page 106, step 3-the first PCA but need to subsequently get the corrected
        component scores as SAS's scores are mean adjusted. This means that the scores
        that SAS typically presents are modified. SAS takes the original scores then gets
        an overall mean value for them and then subtracts this mean value from each
        score, thus some of SAS's typical scores are negative while others are positive*/
```

```
/*We correct this problem by asking SAS to create a normal SAS OUTPUT, in
this case OUT=X but also ask for an OUTSTAT dataset which is Q here. This
OUTSTAT dataset lists the eigenvectors called scores which must be subsequently
multiplied by the variables to produce the original component scores that are not
mean adjusted.*/

PROC PRINCOMP DATA=TRUSS1
        COV
        N=21
        NOPRINT
        OUT=X
        OUTSTAT=Q;
 VAR  LGAB LGAC LGAJ LGBC LGBJ LGCD LGCI LGCJ LGDE LGDH LGDI
        LGDJ LGEF LGEG LGEH LGEI LGFG LGFH LGGH LGHI LGIJ;

DATA P; SET X;
DOUG=1;

DATA Q2; SET Q;
IF _TYPE_ = 'SCORE';
DROP _TYPE_ _NAME_;

PROC TRANSPOSE DATA=Q2 OUT=Q3;

PROC SORT DATA=Q3; BY _NAME_;
PROC TRANSPOSE DATA=Q3 OUT=Q4; BY _NAME_;

PROC TRANSPOSE DATA=Q4 OUT=Q10 PREFIX=V;

DATA Q5; SET Q10;
DOUG=1;

PROC SORT DATA=P; BY DOUG;
PROC SORT DATA=Q5; BY DOUG;

DATA Q6; MERGE P Q5; BY DOUG; DROP _NAME_;
```

```
/*Now I am telling SAS to calculate component scores that are not mean
  centered*/

DATA Q7; SET Q6;

PC1=(LGAB*V1)+(LGAC*V2)+(LGAJ*V3)+(LGBC*V4)+(LGBJ*V5)+(LGCD*V6)+
(LGCI*V7)+(LGCJ*V8)+(LGDE*V9)+(LGDH*V10)+(LGDI*V11)+(LGDJ*V12)+
(LGEF*V13)+(LGEG*V14)+(LGEH*V15)+(LGEI*V16)+(LGFG*V17)+(LGFH*V18)+
(LGGH*V19)+(LGHI*V20)+(LGIJ*V21);

PC2=(LGAB*V22)+(LGAC*V23)+(LGAJ*V24)+(LGBC*V25)+(LGBJ*V26)+
(LGCD*V27)+(LGCI*V28)+(LGCJ*V29)+(LGDE*V30)+(LGDH*V31)+(LGDI*V32)+
(LGDJ*V33)+(LGEF*V34)+(LGEG*V35)+(LGEH*V36)+(LGEI*V37)+(LGFG*V38)+
(LGFH*V39)+(LGGH*V40)+(LGHI*V41)+(LGIJ*V42);

PC3=(LGAB*V43)+(LGAC*V44)+(LGAJ*V45)+(LGBC*V46)+(LGBJ*V47)+
(LGCD*V48)+(LGCI*V49)+(LGCJ*V50)+(LGDE*V51)+(LGDH*V52)+(LGDI*V53)+
(LGDJ*V54)+(LGEF*V55)+(LGEG*V56)+(LGEH*V57)+(LGEI*V58)+(LGFG*V59)+
(LGFH*V60)+(LGGH*V61)+(LGHI*V62)+(LGIJ*V63);

PC4=(LGAB*V64)+(LGAC*V65)+(LGAJ*V66)+(LGBC*V67)+(LGBJ*V68)+
(LGCD*V69)+(LGCI*V70)+(LGCJ*V71)+(LGDE*V72)+(LGDH*V73)+(LGDI*V74)+
(LGDJ*V75)+(LGEF*V76)+(LGEG*V77)+(LGEH*V78)+(LGEI*V79)+(LGFG*V80)+
(LGFH*V81)+(LGGH*V82)+(LGHI*V83)+(LGIJ*V84);

PC5=(LGAB*V85)+(LGAC*V86)+(LGAJ*V87)+(LGBC*V88)+(LGBJ*V89)+
(LGCD*V90)+(LGCI*V91)+(LGCJ*V92)+(LGDE*V93)+(LGDH*V94)+(LGDI*V95)+
(LGDJ*V96)+(LGEF*V97)+(LGEG*V98)+(LGEH*V99)+(LGEI*V100)+
(LGFG*V101)+(LGFH*V102)+(LGGH*V103)+(LGHI*V104)+(LGIJ*V105);

PC6=(LGAB*V106)+(LGAC*V107)+(LGAJ*V108)+(LGBC*V109)+(LGBJ*V110)+
(LGCD*V111)+(LGCI*V112)+(LGCJ*V113)+(LGDE*V114)+(LGDH*V115)+
(LGDI*V116)+(LGDJ*V117)+(LGEF*V118)+(LGEG*V119)+(LGEH*V120)+
(LGEI*V121)+(LGFG*V122)+(LGFH*V123)+(LGGH*V124)+(LGHI*V125)+
(LGIJ*V126);

PC7=(LGAB*V127)+(LGAC*V128)+(LGAJ*V129)+(LGBC*V130)+(LGBJ*V140)+
(LGCD*V141)+(LGCI*V142)+(LGCJ*V143)+(LGDE*V144)+(LGDH*V145)+
(LGDI*V146)+(LGDJ*V147)+(LGEF*V148)+(LGEG*V149)+(LGEH*V150)+
(LGEI*V151)+(LGFG*V152)+(LGFH*V153)+(LGGH*V154)+(LGHI*V155)+
(LGIJ*V156);
```

```
PC8=(LGAB*V157)+(LGAC*V158)+(LGAJ*V159)+(LGBC*V160)+(LGBJ*V161)+
(LGCD*V162)+(LGCI*V163)+(LGCJ*V164)+(LGDE*V165)+(LGDH*V166)+
(LGDI*V167)+(LGDJ*V168)+(LGEF*V169)+(LGEG*V170)+(LGEH*V171)+
(LGEI*V172)+(LGFG*V173)+(LGFH*V174)+(LGGH*V175)+(LGHI*V176)+
(LGIJ*V177);

PC9=(LGAB*V178)+(LGAC*V179)+(LGAJ*V180)+(LGBC*V181)+(LGBJ*V182)+
(LGCD*V183)+(LGCI*V184)+(LGCJ*V185)+(LGDE*V186)+(LGDH*V187)+
(LGDI*V188)+(LGDJ*V189)+(LGEF*V190)+(LGEG*V191)+(LGEH*V192)+
(LGEI*V193)+(LGFG*V194)+(LGFH*V195)+(LGGH*V196)+(LGHI*V197)+
(LGIJ*V198);

PC10=(LGAB*V199)+(LGAC*V200)+(LGAJ*V201)+(LGBC*V202)+(LGBJ*V203)+
(LGCD*V204)+(LGCI*V205)+(LGCJ*V206)+(LGDE*V207)+(LGDH*V208)+
(LGDI*V209)+(LGDJ*V210)+(LGEF*V211)+(LGEG*V212)+(LGEH*V213)+
(LGEI*V214)+(LGFG*V215)+(LGFH*V216)+(LGGH*V217)+(LGHI*V218)+
(LGIJ*V219);

    /*And continue the above procedure until you reach PC21, for example PC21
      would be as follows*/

PC21=(LGAB*V421)+(LGAC*V422)+(LGAJ*V423)+(LGBC*V424)+(LGBJ*V425)+
(LGCD*V426)+(LGCI*V427)+(LGCJ*V428)+(LGDE*V429)+(LGDH*V430)+
(LGDI*V431)+(LGDJ*V432)+(LGEF*V433)+(LGEG*V434)+(LGEH*V435)+
(LGEI*V436)+(LGFG*V437)+(LGFH*V438)+(LGGH*V439)+(LGHI*V440)+
(LGIJ*V441);


    /*Now I am mean-centering the log data by group as outlined on Page 107, step 7,
      in the red Bookstein book*/

PROC SORT DATA=Q7; BY GROUP;
PROC MEANS DATA=Q7 NOPRINT; BY GROUP;
VAR LGAB LGAC LGAJ LGBC LGBJ LGCD LGCI LGCJ LGDE LGDH LGDI LGDJ
    LGEF LGEG LGEH LGEI LGFG LGFH LGGH LGHI LGIJ;
OUTPUT OUT=QP2 MEAN = MNLGAB MNLGAC MNLGAJ MNLGBC MNLGBJ
      MNLGCD MNLGCI MNLGCJ MNLGDE MNLGDH MNLGDI MNLGDJ
      MNLGEF MNLGEG MNLGEH MNLGEI MNLGFG MNLGFH MNLGGH
      MNLGHI MNLGIJ;

PROC SORT DATA=Q7; BY GROUP;
PROC SORT DATA=QP2; BY GROUP;
```

```
DATA QP3; MERGE Q7 QP2; BY GROUP; DROP _TYPE_ _FREQ_;

DATA QP4; SET QP3;

QPLGAB=LGAB-MNLGAB;
QPLGAC=LGAC-MNLGAC;
QPLGAJ=LGAJ-MNLGAJ;
QPLGBC=LGBC-MNLGBC;
QPLGBJ=LGBJ-MNLGBJ;
QPLGCD=LGCD-MNLGCD;
QPLGCI=LGCI-MNLGCI;
QPLGCJ=LGCJ-MNLGCJ;
QPLGDE=LGDE-MNLGDE;
QPLGDH=LGDH-MNLGDH;
QPLGDI=LGDI-MNLGDI;
QPLGDJ=LGDJ-MNLGDJ;
QPLGEF=LGEF-MNLGEF;
QPLGEG=LGEG-MNLGEG;
QPLGEH=LGEH-MNLGEH;
QPLGEI=LGEI-MNLGEI;
QPLGFG=LGFG-MNLGFG;
QPLGFH=LGFH-MNLGFH;
QPLGGH=LGGH-MNLGGH;
QPLGHI=LGHI-MNLGHI;
QPLGIJ=LGIJ-MNLGIJ;

        /*Now we do a PCA on these mean centered data to get the covariance matrix
          Q-prime on page 107, step 7, middle of page, the first principal component of
          Q-prime data is the within group size factor S, hence my use of the PREFIX=S
          below*/

PROC PRINCOMP DATA=QP4
        COV
        N=2
        PREFIX=S
        NOPRINT
        OUT=QP5;
 VAR QPLGAB QPLGAC QPLGAJ QPLGBC QPLGBJ QPLGCD QPLGCI QPLGCJ
        QPLGDE QPLGDH QPLGDI QPLGDJ QPLGEF QPLGEG QPLGEH QPLGEI
        QPLGFG QPLGFH QPLGGH QPLGHI QPLGIJ;
```

```
/*Now I am on page 108, step 8 which has two tasks, task 1 is to mean center the
PC-scores from the first PCA, which I had to manually program SAS to do above.
These original scores are mean centered by group. Note that you only have to
calculate these mean centered scores for PC1 and PC2, not for all 21 scres above.
At this step you also mean center scores for PC1 and PC3 to get sheared PC3
scores for analysis*/

PROC SORT DATA=Q7; BY GROUP;
PROC MEANS DATA=Q7 NOPRINT; BY GROUP; VAR PC1 PC2 PC3;
OUTPUT OUT=PCZ MEAN=MNPC1 MNPC2 MNPC3;

PROC SORT DATA=Q7; BY GROUP;
PROC SORT DATA=PCZ; BY GROUP;

DATA PCZ2; MERGE Q7 PCZ; BY GROUP; DROP _TYPE_ _FREQ_;

DATA PCZ3; SET PCZ2;

/*These are now the mean centered scores*/

DFPCIZ=PC1-MNPC1;
DFPCIIZ=PC2-MNPC2;
DFPC3Z=PC3-MNPC3;

/*Now task 2 under step 8, page 108, specifies merging two datasets so that we
can calculate the regression equations to get our coefficients for H2 or H3 sheared
values*/

PROC SORT DATA=QP5; BY TRACKING;
PROC SORT DATA=PCZ3; BY TRACKING;

DATA STEP8; MERGE QP5 PCZ3; BY TRACKING;

/*Task 2 on page 108, step 8-getting regression equations to shear PC2*/

PROC REG DATA=STEP8;
MODEL DFPCIIZ=S1;
TITLE 'THE SLOPE FROM THIS REGRESSION IS ALPHA ON PAGE 108';

PROC REG DATA=STEP8;
MODEL S1=DFPCIZ DFPCIIZ;
TITLE 'DFPCIZ SLOPE IS BETA1 AND DFPCIIZ SLOPE IS BETA2 ON PAGE 108';
```

```
/*Same as above but now getting regression equations to shear PC3*/

PROC REG DATA=STEP8;
MODEL DFPC3Z=S1;
TITLE 'THE SLOPE FROM THIS REGRESSION IS ALPHA ON PAGE 108';

PROC REG DATA=STEP8;
MODEL S1=DFPCIZ DFPC3Z;
TITLE 'DFPCIZ SLOPE IS BETA1 AND DFPC3Z SLOPE IS BETA2 ON P. 108';

/*Now we are calculating sheared PC-scores*/

DATA SHEARED; SET STEP8;

H2 = PC2 - (alpha * ((Beta1 * PC1) + (Beta2 * PC2)));
H3 = PC3 - (alpha * ((Beta1 * PC1) + (Beta2 * PC3)));

/*Note alpha and Beta1 and Beta2 numbers are from the previous regressions*/

/*Sheared PC2 and PC3 scores (i.e., H2 and H3 scores) would then be plotted
against each other and individuals from specific populations and/or geographic
locations could be uniquely identified to see if any populations/locations are
phenotypically distinct from others*/
```

Chapter 3. **Factors associated with the distribution of sicklefin chubs (*Macrhybopsis meeki*) at two spatial scales in the Missouri and lower Yellowstone Rivers**

Introduction

Conservation, management, and recovery of rare or imperiled fishes necessitates knowledge of their distribution, abundance, habitat requirements, and interactions with other species, including man (e.g., overharvest, environmental contamination) (Caughley and Gumm 1996, Rahel et al. 1999). Changes in distribution and abundance are necessary to identify declines and if possible, aid protection. Knowledge of habitat requirements and community interactions are necessary to identify reasons for declines and to aid formulation of management alternatives. Although species introductions, hybridization, and overharvest have contributed to declines and extinctions of North American fishes, habitat alteration has been the most frequently cited factor (Miller et al. 1989, Richter et al. 1997, Ricciardi and Rasmussen 1999). Thus, identification of habitat requirements is often a fundamental step in imperiled species conservation and recovery efforts.

The 3,768 km long Missouri River is a large North American river with extensive modifications and rare and imperiled fishes (Hesse et al. 1989, Galat et al. 1996). The lower third of the river has been channelized to support navigation and much of the floodplain has been isolated from the river by levees for agriculture and flood protection (Funk and Robinson 1974, Hallberg et al. 1979). These activities have modified physical habitat by: 1) reducing the area and number of sand bars, islands, side channels, and off-channel habitats such as backwaters; 2) reducing overall habitat diversity; 3) increasing

water depth and velocity in the main channel; 4) altering channel geomorphology by reducing channel width and sinuosity; and 5) reducing availability of floodplain habitats (Funk and Robinson 1974, Pflieger and Grace 1987, Hesse et al. 1989, Galat et al. 1996). The middle third of the river has been impounded by six large dams for purposes of flood control, irrigation, hydropower, water supply, and recreation. Impoundment has reduced sediment load and turbidity and altered natural thermal and hydrologic regimes (Morris et al. 1968, Whitley and Campbell 1974, Pflieger and Grace 1987, Hesse et al. 1989, Galat et al. 1996, Galat et al. 1998, Galat and Lipkin 2000). Altered habitat associated with reservoir development, such as establishment of coldwater zones and reduced turbidity, prompted enhancement of recreational fishing opportunities through introduction and supplemental stocking of many non-native and native predatory fishes such as chinook salmon (*Oncorhynchus tshawytscha*) and walleye (*Stizostedion vitreum*) (Hesse et al. 1989). Together, these abiotic and biotic modifications of the Missouri River have been qualitatively implicated in the decline of many native fish species (Cross and Moss 1987, Pflieger and Grace 1987, Hesse et al. 1989, Hesse 1994a, Hesse 1994b, Everett 1999, Galat and Lipkin 2000).

One native Missouri River fish species considered imperiled and globally classified by The Nature Conservancy as rare (i.e., G3 global rank), is the sicklefin chub, *Macrhybopsis meeki*. Sicklefin chub are an obligate riverine fish, primarily restricted to the mainstem Missouri River, the Lower Yellowstone River, and portions of the Mississippi River downstream of the Missouri confluence (Bailey and Allum 1962, Jenkins 1980, Werdon 1993). Few are collected below the mouth of the Ohio River. Concern for

the status of sicklefin chubs and requests from conservation groups to afford it federal protection prompted recent surveys to assess its distribution (Stasiak 1990, Werdon 1992, Gelwicks et al. 1996, Grisak 1996, Grady and Milligan 1998, Everett 1999). The U. S. Fish and Wildlife Service (USFWS) began work on a listing package in December 1994 (USFWS 1995), but was interrupted by a Congressional moratorium on new listings that lasted until May 1996. Currently, the listing package has been updated with new information through 1998 and is being reviewed internally by the USFWS. The current listing package under review indicates that the sicklefin chub presently occupies only 25% of its former range. Its reduced range, potential federal listing, and designation as rare by The Nature Conservancy, indicates that information on habitat requirements and community interactions is critically important. Specifically, quantitative associations between sicklefin chub distribution and aspects of physical habitat, water quality, flow regime, and predator communities in the Missouri River would aid identification of reasons for decline and formulation of management options.

Abiotic characteristics of rivers and habitat requirements of their biota can be examined at multiple hierarchically nested spatiotemporal scales (Allan 1995, Matthews 1998). While habitat in the Missouri River has been modified at all spatial scales, two of these, segment and site, are amenable to evaluation and management in a large river. River segments are defined by geomorphic, hydrologic and constructed features (e.g., major tributaries, dams), and range from about 10 to 200 km long.

Within segments, macrohabitats define specific geomorphic features such as riffles, pools, and glides (Frissell et al. 1986). This spatial scale is often examined in fish habitat

studies of streams where fishes are collected with traditional fish sampling gears from most of a macrohabitat ranging from 1 to 100 m in length (Allan 1995)(e.g., Sowa and Rabeni 1995, Rabeni and Sowa 1996). However, analogous macrohabitats in a large river (e.g., inside bend, outside bend) are much larger, ranging from 500 to 5,000 m, and deployment of individual gears may therefore yield only a representative sample of the entire macrohabitat. Fishes and physical habitat in large rivers are more commonly sampled from "sites" within macrohabitats, at a scale of 10 to 300 meters. The specific scale is dependent on the area sampled by a particular gear. I adopt this site spatial scale here as it most accurately reflects how habitat use is generally quantified in a large river. A higher resolution scale, "microhabitat," is generally applied to the exact location of a fish. An example of an associated habitat measurement made at this scale would be focal velocity (Baltz 1990). It is not currently possible to identify habitat use of small fishes in large, deep rivers at the microhabitat scale. Thus, the site scale is currently the most appropriate small, high resolution, spatial scale practical for assessing habitat use of small fishes in large rivers.

Most previously cited status surveys contributed information on distribution, abundance, and habitat use patterns of sicklefin chubs at the site scale. However, these surveys were often conducted in selected segments of the Missouri River known to harbor populations. In some instances, survey sites were located at pre-determined locations where historical surveys had been conducted (e.g., Grady and Milligan 1998). Habitats sampled were often restricted to specific types known to be used by sicklefin chubs, such as sandbars. Information on where a species is absent may be equally important to

presence information because environmental conditions associated with absent locations may help define the range of conditions it will use (sensu Shelford's Law of Tolerance 1913; Allen and Hoekstra 1992). Also, site-scale habitat use patterns are known to differ among life stages for many fishes in response to food availability, foraging habits, and predation risk (Werner and Gilliam 1984, Aadland 1993). Differences in site-scale habitat use patterns between adults and juveniles were not identified in previous status surveys because they were primarily concerned with discerning distribution and abundance patterns. Finally, quantitative analyses identifying the importance of larger scale variables such as flow regime have never been reported for sicklefin chubs.

Fish habitat-use patterns have commonly been identified with traditional linear and multiple linear regression techniques (e.g., Fausch et al. 1988, Hubert and Rahel 1989, Sowa and Rabeni 1995, Rabeni and Sowa 1996). However, rare and infrequently collected species, such as sicklefin chubs, and non-linear relationships between abundance and habitat characteristics, often preclude identification of habitat use patterns with these traditional approaches. In these instances, logistic regression has become an appealing method (e.g., Hayes and Jowett 1994, Watson and Hillman 1997, Allen et al. 1998, Porter et al. 2000). Presence/absence (P/A) is typically the dependent variable in logistic regression models associating rare species with habitat variables. In addition, logistic regression has been shown to be valuable for identifying a range of optimum habitat requirements when data over a sufficient range of environmental conditions have been collected (Peeters and Gardeniers 1998).

My objectives were to: 1) identify selected physical habitat, water quality, flow regime, and predation variables that are most highly associated with sicklefin chub P/A in the Missouri River at segment and site scales using logistic regression; 2) describe sicklefin chub frequency-of-use patterns for these variables; 3) compare site-scale habitat measurements between sites used by adults and juveniles; 4) define a range of optimum habitat conditions predicted from site-scale univariate logistic models, and; 5) identify the relative importance of multiple combinations of these variables that best predicts sicklefin chub P/A in the Missouri River at segment and site scales.

Methods

Sampling Design

Sicklefin chub P/A, physical habitat, water quality, flow regime, and predation data were gathered from two sources, field collections and existing sources. All site-scale and selected segment-scale data were gathered from field collections conducted by the Missouri River Benthic Fish Consortium, in conjunction with their study examining habitat use and population structure of benthic fishes in the Missouri and Lower Yellowstone Rivers (Dieterman et al. 1996, Young et al. 1997). Remaining segment- scale data were compiled from existing sources such as U.S. Geological Survey topographic maps and hydrology data. Segment-scale data were compiled from various combinations of both sources to provide the most accurate characterization of segment-scale features given the best available data.

Segments.--Twenty-seven segments, ranging in length from 16.1 to 191.6 km, were identified in riverine portions of the Missouri River to facilitate field sampling (Table 3-1). A subset of segments, 17 in 1996 and 14 in 1997, were sampled to ensure that data could be collected over a short time period so that seasonal variability in habitat use was minimized. Segments were sampled in midsummer-early autumn, approximately mid-July through mid-October, because water levels are typically low and stable. Segments selected for sampling included the full range of segment-scale lotic conditions. Segments were not censussed completely, therefore, sampling within segments may have yielded an absent designation when sicklefin chub populations were extremely low. Low fish catches in 1996 prompted increased sampling effort within segments in 1997 (detailed below), which resulted in deleting three segments sampled in 1996 (Table 3-1).

Macrohabitats.--Segments were partitioned into six macrohabitat strata to ensure the diversity of site-scale abiotic conditions was evaluated and to provide a method for maintaining standardized data collection across segments. Macrohabitat strata included were: channel cross-over, outside bend, non-connected secondary channel, inside bend, tributary mouth, and connected secondary channel (Table 3-2, Appendix 3B). The channel cross-over area was defined as the inflection point of the thalweg (i.e., location where the thalweg crosses over from one concave side of the river to the other concave side; Leopold et al. 1964, Leopold and Langbein 1966). Outside bends were defined as the concave side of a river bend extending from the apparent shoreline to the thalweg. Non-connected secondary channels were aquatic areas typically associated with old river channels that maintained a downstream hydrologic connection with the main channel that

Table 3-1. Deliniation of Missouri and lower Yellowstone river study segments, location by river kilometer, total length (km), years sampled and name and location of associated U.S. Geological Survey gaging stations used to calculate 31 intra-annual hydrologic variables.

Segment	Location	Length (km)	1996	1997	USGS gaging station (station number)	Gage location (rkm)
01	Loma Ferry-Rattlesnake Coulee (rkm 3305.6-3257.8)	47.8				
02	Rattlesnake Coulee-Arrow Creek (rkm 3257.8-3219.6)	38.2				
03	Arrow Creek-Birch Creek (rkm 3219.6-3189.3)	30.3				
04	Birch Creek-Sturgeon Island (rkm 3189.3-3143.6)	45.7				
05	Sturgeon Island-Beauchamp Coulee (3143.6-3031.7)	111.9	X	X	Landusky, MT (06115200)	3095
	Fort Peck Reservoir (rkm 3031.7-2850.2)					
06	Fort Peck Dam-Milk River (rkm 2850.2-2834.1)	16.1	X		Fort Peck Dam, MT (06132000)	2850
07	Milk River-Hwy 13 bridge (Wolf Point) (rkm 2834.1-2739.1)	95.0	X	X	Wolf Point, MT (06177000)	2737
08	Wolf Point-Yellowstone River (rkm 3739.1-2547.5)	191.6	X	X	Culbertson, MT (06185500)	2610
09	Lower Yellowstone River (Intake Diversion dam-mouth)(rkm 114.3-0.0)	114.3	X	X	Sidney, MT (06329500)	46
10	Yellowstone River-Lake Sakakawea Headwaters (rkm 2547.5-2499.1)	48.3	X	X	No gage available[a]	
11	Lake Sakakawea Headwaters-Lake Sakakawea (rkm 2499.1-2471.8)	27.3				
	Lake Sakakawea (rkm 2471.8-2236.7)					

Table 3-1. con't.

Segment	Location	Length (km)	1996	1997	USGS gaging station (station number)	Gage location (rkm)
12	Garrison Dam-Lake Oahe Headwaters (rkm 2236.7-2099.8)	136.8	X	X	Bismarck, ND (06342500)	2114
13	Lake Oahe Headwaters to Lake Oahe (rkm 2099.8-2053.1)	46.6				
	Lakes Oahe, Sharpe, and Francis Case (rkm 2053.1-1417.0)					
14	Fort Randall Dam-Lewis and Clark Lake (rkm 1417.0-1344.6)	72.4	X	X	No gage available	
	Lewis and Clark Lake (rkm 1344.6-1304.3)					
15	Gavins Point Dam-Ponca, Nebraska (rkm 1304.3-1212.5)	91.7	X	X	No gage available[b]	
16	Ponca, Nebraska-Big Sioux River (rkm 1212.5-1191.6)	20.9				
17	Big Sioux River-Little Sioux River (rkm 1191.6-1077.6)	114.0	X	X	Sioux City, IA.(06486000)	1191
18	Little Sioux River-Platte River (rkm 1077.6-958.9)	118.6	X		Omaha, NE (06610000)	990
19	Platte River-Nishnabotna River (rkm 958.9-872.7)	86.1	X	X	Nebraska City, NE (06807000)	904
20	Nishnabotna River-Rulo, Nebraska (rkm 872.7-801.9)	70.8				
21	Rulo, Nebraska-St. Joseph, Missouri (rkm 801.9-708.5)	93.3	X		Rulo, NE (06813500)	801
22	St. Joseph, Missouri-Kansas River (rkm 708.5-591.7)	116.7	X	X	St. Joseph, MO (06818000)	721

Table 3-1. con't.

Segment	Location	Length (km)	1996	1997	USGS gaging station (station number)	Gage location (rkm)
23	Kansas River-Grand River (rkm 591.7-402.5)	189.2	X	X	Waverly, MO (06895500)	473
24	Grand River-Glasgow, Missouri (rkm 402.5-354.2)	48.3				
25	Glasgow, Missouri-Osage River (rkm 354.2-209.9)	144.2	X	X	Boonville, MO (06909000)	317
26	Osage River-Mississippi River valley (rkm 209.9-80.5)	129.4				
27	River kilometer 80.5-Mississippi River Confluence (rkm 80.5-0.0)	80.5	X	X	Hermann, MO (06934500)	157

[a] Discharge estimated by adding data at gages 06185500 + 06329500

[b] Discharge estimated by subtracting Big Sioux River (gage 06485500) discharge data from gage 06486000

Table 3-2. Macro- and meso-habitat strata, site locations within them, and gears (DTN=drifting trammel net, BT=benthic trawl, EF=electrofishing, BS=bag seine, SGN=stationary gill net) used to sample benthic fishes and habitat variables in Missouri and lower Yellowstone river study segments in 1996 and 1997. Sicklefin chubs were collected by gears in **bold**. Number of replicates is the number proposed for sampling, but the actual number depended on presence of each strata within segments, in each year.

Strata		Number of replicates			
Macrohabitat	Mesohabitat	1996	1997	Gears	Site locations
Channel cross-over		5	5	DTN, **BT**	40% and 60% of channel width[a]
Outside bend		5	5	DTN, **BT**	25% and 75% of the longitudinal distance[b]
				EF	shorelines at lower, mid-, and upper boundary points
Inside bend		5			
	Channel border		5	DTN, **BT**	25% and 75% of the longitudinal distance[b]
	Bars		5	**BS**	shorelines at lower, mid-, and upper boundary points
	Steep shoreline		5	EF	three adjacent sites located at the bend mid-point
	Pools		5	SGN	2 pools, 1 each at 25% and 75% of bend distance
Non-connected secondary channels		5	5	**BS**	shorelines at lower, mid-, and upper boundary points
				SGN	one third the distance of macrohabitat length
Tributary mouths		5			
	Large		5	DTN, **BT**	40% and 60% of channel width[a]
				EF	2 sites, 1 along each shoreline
	Small		5	SGN	1 site, 30 m upstream from confluence
				EF	2 sites, 1 along each shoreline
Connected secondary channels		5			
	Deep		5	DTN, **BT**	25% and 75% of the longitudinal distance[b]
				EF	2 sites, 1 along each shoreline
				BS	shorelines at lower, mid-, and upper boundary points
	Shallow		5	**BS**	shorelines at lower, mid-, and upper boundary points

[a] Additional site added in segments 5-15 in 1997 with sites repositioned to the left, middle, and right one third of channel width.
[b] Additional site added in segments 5-15 in 1997 with sites repositioned to the top, middle, and bottom one third of the longitudinal distance.

allowed fish access. The upstream connection was typically closed off by river training structures. Site-scale abiotic conditions were particularly complex within inside bends, tributary mouths, and connected secondary channels. Therefore, these macrohabitats were further partitioned into mesohabitats.

Inside bends were the area on the convex side of a river bend extending from the apparent shoreline to the thalweg and were partitioned into channel border, bar, steep shoreline, and pool mesohabitats. Inside-bend bars were the area along shorelines, extending from the apparent shoreline to the approximate location of the 1.2 m depth interval (i.e., about chest deep). Inside-bend bar areas could be either shorelines along river banks or along in-channel sand bars or islands. Inside-bend channel borders were areas extending approximately from the 1.2 m depth interval to the thalweg. Inside-bend pools were areas associated with current deflectors that resulted in a deep-water area usually scoured deeper than the main channel. Inside-bend pools were commonly associated with wing dikes in channelized segments and with sand bars in non-channelized segments. Inside-bend steep shorelines were shorelines where water depth exceeded 1.2 m within 5 m of the bank.

Tributary mouths were the lowest 200 m of tributaries and were partitioned into large and small mesohabitat classes. Large tributary mouths were tributaries with average annual discharges > 20 m^3/s and/or drainage areas > 2,600 km^2. Small tributary mouths were those not meeting the large tributary mouth definition.

Connected secondary channels were channels carrying less flow than the main channel and were partitioned into deep and shallow mesohabitat classes. Deep connected

secondary channels had maximum depths frequently exceeding 1.2 m. Shallow secondary connected channels were channels with maximum depths rarely exceeding 1.2 m.

Five replicates of each macrohabitat type, if present, were randomly selected for sampling in 1996. Within segment sampling was partially increased in 1997 (discussed previously) by sampling five replicates of both macro- and meso-habitats if present (Table 3-2). For example, two channel border and three bar mesohabitats would have constituted five inside-bend macrohabitat replicates in 1996. Whereas, five of each mesohabitat type within the inside-bend macrohabitat type (i.e., channel border, bars, steep shoreline, pool), were sampled in 1997.

Sites.--Sites were specific locations within each macro- or meso-habitat type (Table 3-2) where a fish sampling gear was deployed. Environmental conditions at each site such as depth and presence of current, dictated gear type used to collect fishes (Table 3-2).

Variables

Sicklefin chub P/A.-- Sicklefin chub P/A was the dependent variable in all logistic regression models. Sicklefin chub were considered present at a site or segment if at least one chub was collected there. Sicklefin chub P/A was assessed at shallow-water (i.e., < 1.2 m) sites with a bag seine (10.7-m long x 1.8-m high with 5-mm mesh and a 1.8 x 1.8 x 1.8-m center bag) and at deep-water sites with a benthic trawl (2-m wide x 0.5-m high with a 3.2-mm inner-mesh net) (Table 3-2). The bag seine was deployed in a 180-degree arc adjacent to shore in a downstream direction. The bag seine was extended fully if

depths never exceeded 1.2 m or else extended only to the 1.2 m depth contour. A fully extended bag seine sampled an area of 179.8 m^2. Sites sampled by the benthic trawl were designated by a 300 m rope attached to buoys marking known distance increments set parallel to current. A trawl sample was considered complete if it traveled at least 75 m. Thus, the trawl sampled an area from 150 to 600 m^2. If the trawl became snagged prior to 75 m, the sample was abandoned and a new sample taken. Most trawl samples were $\geq$ 150 m.

A representative sample of sicklefin chubs was retained for age determination so that age 0 and age 1+ sicklefin chubs could be separated for comparison of site-scale habitat differences. Ages were assigned based on examination of scales (Sappington et al. 1998). An age-length key was developed and applied to chubs released in the field. Age 0 sicklefin chubs were considered juveniles and age 1+ chubs adults.

Physical habitat.-- Twenty-one physical habitat variables were examined at segment and site scales (Appendix Table 3A.1). River channelization and snagging have altered these variables from historical conditions and all are considered to potentially influence sicklefin chub P/A (Werdon 1993). Sixteen of these 21 variables were measured or enumerated at the segment scale from existing data sources. The other five were measured during field sampling at the site scale.

The 16 segment-scale physical habitat variables were measured or enumerated from one or all of the following sources: USGS 1:24,000 and 1:100,000 scale topographical maps, aerial photos (USACE 1981a, 1981b, 1982, 1983, 1990, 1993), navigation charts (USACE 1994a, 1994b), and consultations with river biologists. Eight

segment-scale variables were simply enumerated and seven of these standardized to a common distance (i.e., #/1.609 km). A macrohabitat diversity index was calculated from counts of five macrohabitat types (Appendix Table 3A.1). A generic, "distance to upstream impoundment" variable was also measured because it integrates a longer temporal scale and wider variety of riverine disruptions caused by dams (sensu, the Serial Discontinuity Concept, Ward and Stanford 1983; 1995).

Finally, six other segment-scale physical habitat variables were measured or classified from 1:100,000 scale maps: mean channel width (km), channel sinuosity, channel width to length ratio, channel slope (m/km), floodplain availability (km) and channel pattern. Methods followed Gordon et al. (1992) and included visual determination of maps for some variables (e.g., channel slope, channel pattern) and calculations from direct measurements made with a ruler and map wheel (i.e., opisometer) (e.g., channel width, floodplain availability).

Five descriptors of physical habitat requirements for riverine fishes were evaluated at the site scale: water depth (m), water column velocity (m/s), and three categories of substrate: percent silt, sand, and gravel (Gorman and Karr 1978, Baltz 1990) (Appendix Table 3A.1). Depth was measured with a standard wading rod at sites < 1.2 m deep and with sonar at sites > 1.2 m deep. Column velocity was measured with either a Marsh-McBirney Flow-mate model 2000 large river flow meter or a USGS "AA" type Price meter following standard methods (McMahon et al. 1996). Substrate was either sampled by hand or by dragging a 610 mm long pipe with a 102 mm diameter opening along the bottom. Substrate percentages were visually estimated (Gordon et al. 1992).

Water quality.-- Two water quality variables affected by mainstem impoundment (Morris et al. 1968, Whitley and Campbell 1974) that influence sicklefin chubs (Bailey and Allum 1962, Werdon 1993, Hesse 1994a), were measured: water temperature (°C) and turbidity (NTUs) (Appendix Table 3A.1). Water temperature was measured with a YSI 30 water temperature/conductivity meter and turbidity with a Hach Model 2100P turbidimeter. Surface measurements of both were made at the midpoint distance of each site. Segment-scale indices were calculated from site scale daily measurements. Segment-scale calculations only used measurements made in main channel habitats (i.e., channel cross-over, inside bend, outside bend) because off-channel habitats such as large tributary mouths made up a relatively small proportion of total available aquatic habitat based on surface area and measurements often differed substantially from main channel habitats. Therefore, inclusion of measurements made in these habitats would have resulted in an inaccurate characterization of predominant segment-scale conditions.

Flow regime.-- Richter et al's. (1996) Indicators of Hydrologic Alteration, including 31 intra- and 4 inter-annual flow regime variables (Appendix Table 3A.1), were tested as ecologically relevant indicators of sicklefin chub P/A. However, percent of total annual flow in each month (Haines et al. 1988) was substituted for their values of monthly magnitude. Intra-annual flow statistics were calculated independently for each year (i.e., 1996 and 1997) from daily mean discharge data collected at U. S. Geological Survey river gages (Table 3-1). Data were obtained or estimated for 16 of the 17 segments sampled for sicklefin chubs.

Four inter-annual flow statistics were modeled to provide a more temporally integrative segment-scale characterization of flow regime. These indices were calculated from a 29 year time period (1967-1996) considered representative of post-impoundment conditions (Galat and Lipkin 2000). Nineteen-ninety-six and 1997 were unusually high water years and intra-annual statistics calculated from them may not have been representative of normal conditions. The 29 year time scale provides a different assessment of flow regime that sicklefin chubs may respond to. Inter-annual flow statistics were gathered from existing sources (Galat and Lipkin 1999, Mark Pegg, Illinois Natural History Survey, personal communication).

Predation.--Two groups of piscivorous fishes were identified, all piscivores and a subset of introduced and/or commonly stocked sight feeders. The all piscivore group included 27 fish taxa (Table 3-3) classified as piscivores based on references (Harlan et al. 1987, Cross and Collins 1995, Pflieger 1997, Goldstein and Simon 1999), conversations with river biologists, and personal knowledge. A subset of these 27, composing a group of 15 taxa (Table 3-3), were classified as introduced and/or commonly stocked sight feeders based on: known stocking record (e.g., northern pike and walleye); probable stocking and/or introduction indicated in the literature (Bailey and Allum 1962, Pflieger and Grace 1987, Hesse et al. 1989, White and Bramblett 1993); a reported optical mode of food location (Harlan et al. 1987, Cross and Collins 1995, Pflieger 1997, Goldstein and Simon 1999); and historical absence, so contemporary presence indicates introduction (e.g., muskellunge and chinook salmon). Relative abundance of these two groups was calculated at the segment scale, based on Missouri River Benthic Fish Consortium field

Table 3-3. Two groups of piscivorous fishes collected from the Missouri and lower Yellowstone rivers in 1996 and 1997 and examined for association with sicklefin chub presence/absence. The all piscivore fishes group includes the entire list, whereas an * indicates a subset group, classified as introduced and/or commonly stocked.

Scientific name	Common name
Scaphirhynchus albus	Pallid sturgeon
Lepisosteus oculatus	Spotted gar
Lepisosteus osseus	Longnose gar
Lepisosteus platostomus	Shortnose gar
Amia calva	Bowfin
Alosa chrysochloris	Skipjack herring
Ictalurus furcatus	Blue catfish
Pylodictis olivaris	Flathead catfish
Esox americanus	Grass pickerel
Esox lucius	Northern pike*
Esox masquinongy	Muskellunge*
Oncorhynchus tshawytscha	Chinook salmon*
Lota lota	Burbot
Morone chrysops	White bass*
Morone mississippiensis	Yellow bass
Morone saxatilis	Striped bass*
Morone saxatilis x *M. chrysops*	Hybrid-Wiper*
Ambloplites rupestris	Rock bass*
Micropterus dolomieu	Smallmouth bass*
Micropterus punctulatus	Spotted bass*
Micropterus salmoides	Largemouth bass*
Pomoxis annularis	White crappie*
Pomoxis nigromaculatus	Black crappie*
Perca flavescens	Yellow perch*
Stizostedion canadense	Sauger*
Stizostedion vitreum	Walleye*
Stizostedion canadense x *S. vitreum*	Hybrid-Saugeye

collections with bag seines and stationary gill nets (Dieterman et al. 1996, Young et al. 1997, Sappington et al. 1998). Four indices of piscivore relative abundance (i.e., catch-per-unit-effort (CPUE)) were calculated: CPUE of all piscivores collected in bag seines, CPUE of all piscivores collected in stationary gill nets, CPUE of introduced and/or commonly stocked sight feeding piscivores in bag seines, and CPUE of introduced and/or commonly stocked sight feeding piscivores in stationary gill nets. Bag seines were as previously described. Stationary gill nets were 30.5 m long x 1.8 m high with four 7.6 m panels composed of 19.0, 38.1, 50.8, and 76.2 mm square mesh, respectively. Sampling with stationary gill nets was conducted in a standardized fashion similar to bag seines but in different macro- and meso-habitats (Table 3-2, Sappington et al. 1997).

Statistical Analyses

Segment and site scales were analyzed independently. Each segment sampled in each year was considered a separate observation. Years were kept separate so yearly differences in hydrology and associated habitat availability could be examined. Each individual sampling site, irrespective of year, was considered a separate observation at the site scale. The level of significance for acceptance of all statistical tests was 0.05 (but see below for multiple test exceptions).

Logistic regression.--Univariate and multiple logistic regression models were developed to identify components of physical habitat, water quality, flow regime, and predation that most highly predicted sicklefin chub P/A at segment and site spatial scales. Logistic regression tests for associations between predicted probabilities of presence and

independent variables. The form of the logistic function is:

$$P = e^u / 1 + e^u \quad (1)$$

where P = the estimated probability of presence, e = the inverse natural logarithm of 1, and u = the linear model; where the linear model is expressed in the form

$$u = a + b_1X_1 + b_2X_2 + \ldots + b_nX_m \quad (2)$$

where a = regression constant, b_n = regression coefficients, and X_m = independent variables. Statistical significance and model fit were evaluated for each univariate and multiple logistic regression model using multiple criteria.

Statistical significance was assessed with 1) a log-likelihood test for the overall model, 2) a log-likelihood test comparing one model to another (i.e., log-likelihood ratio test), and 3) a test of the significance of individual slope coefficients using a Wald chi-square statistic (Hosmer and Lemeshow 1989, Menard 1995). The **log-likelihood test for the overall model** tests the null hypothesis that all regression coefficients of the model are zero (Hosmer and Lemeshow 1989, SAS 1995). A significant difference ($p \leq 0.05$) indicates that at least one variable is causing the slope to differ from zero and thus, is affecting predicted probabilities of sicklefin chub P/A. The **log-likelihood ratio test** compares one model to another using log-likelihood values of each model with differing sets of variables. For example, this test compares a model with all variables to a reduced model with one or more variables omitted. A significant difference indicates that the omitted variable(s) significantly altered the overall slope of the first model (Hosmer and Lemeshow 1989, Menard 1995). Thus, models differ significantly and omitted variable(s) should be retained. The **Wald chi-square statistic** tests whether the individual slope

coefficients for the independent variable(s) differ significantly from zero (Hosmer and Lemeshow 1989, SAS 1995).

Model fit was examined with the **adjusted coefficient of determination** (Hosmer and Lemeshow 1989, Menard 1995, SAS 1995). The adjusted coefficient of determination (R^2) measures the proportional reduction in the absolute value of the log-likelihood measure (Menard 1995). It indicates how much inclusion of independent variables in the model improves fit over an intercept only model. This is similar to the reduction in the error sums of squares in linear regression and can be interpreted as the traditional proportion of variation explained (Nagelkerke 1991). The adjustment is made for the number of independent variables in the model (SAS 1995). Thus, models with differing numbers of independent variables can be simultaneously compared (Hosmer and Lemeshow 1989).

Spatial independence of observations is an assumption of most statistical methods including univariate and multiple logistic regression (Legendre and Fortin 1989, Menard 1995). Spatial independence was assessed at the segment scale with spatial autocorrelation (Griffith 1987, Legendre and Fortin 1989). Spatial autocorrelation occurs when data in one segment may be partly predicted by values at neighboring segments (Legendre 1993). Smith (1994) recommended assessment of spatial autocorrelation prior to development of logistic regression models and if present, include some measure of it in model development. Two spatial autocorrelation coefficients are commonly used, Moran's I and Geary's (c) (Griffith 1987, Legendre and Fortin 1989). A coefficient is calculated between biological response variables for various distances among localities

(i.e., a separate coefficient is calculated for each distance category). Coefficients are then displayed in the form of a correlogram and tested to determine if they differ significantly from zero. Two biological response variables can be used, simple counts of the number of presences in adjoining segments or the proportion of available sites containing presences in adjoining segments (Smith 1994). Segments are considered adjoining, and termed nearest neighbors, if they are within the distance category specified. The proportion of sites containing presences was selected because some segments may not have been bounded by both upstream and downstream study segments thus artificially reducing the possible number of present sites. For example, segment 27 exists between segment 25 upstream and the Mississippi River confluence downstream. Thus, only sites in segment 25 could be used. Whereas, segment 25 could count sites in segments 23 upstream and segment 27 downstream. Therefore, proportion of sites is a less biased descriptor where localities are bounded by areas that cannot be sampled (Smith 1994).

Spatial autocorrelation was assessed with Geary's (c) because this index is less sensitive to extreme values than Moran's I (Legendre and Fortin 1989). Geary's (c) was calculated for 0, 80.5, 160.9, 241.5, 322.0, and 402.5 km distances among segments. Distances greater than 402.5 km were not assessed because this distance would have considered segments separated by dams to be adjoining. Missouri River dams likely impede fish movement (Keenlyne et al. 1994, Galat et al. 1996). Geary's coefficient ranges between 0 and some indeterminate positive value which rarely exceeds 3 in most cases (Legendre and Fortin 1989). Values between 0 and 1 indicate positive autocorrelation (i.e., the percentage of sites with sicklefin chubs in a segment is most like

the percentage of sites with sicklefin chubs in nearby segments) while values greater than 1 correspond to negative autocorrelation. Significance of coefficients was tested following methods in Griffith (1987). An alpha level of 0.05 was set for acceptance of a coefficient differing significantly from zero. Coefficients were summarized with a correlogram showing the magnitude and direction of the association and significance of the coefficient. If spatial autocorrelation existed, the correlogram was used to determine the best nearest neighbor distance (e.g., 0, 80.5, . . . 402.5 km) to consider in logistic regression models (Legendre 1993, Smith 1994). Based on this distance, the percentage of sites in study segments, within this distance, having a sicklefin chub present was modeled.

Regression models are sometimes criticized for not considering the full range of environmental conditions a species' encounters throughout its range (Shirvell 1989, Rabeni and Sowa 1996). Consequently, many regression models are found to transfer poorly to other geographic areas (e.g., Bowlby and Roff 1986, Porter et al. 2000). Geographic transferability was minimized in this study because models were developed from data collected over nearly the entire native range of the sicklefin chub. Hence, nearly the full range of environmental conditions experienced by this species was incorporated in statistical analyses.

Univariate logistic regression models.--Model development was similar for segment and site scales and generally followed guidelines in Hosmer and Lemeshow (1989). First, individual independent variables most highly associated with sicklefin chub P/A were identified with univariate logistic regression models. Because 64 segment-scale and six site-scale univariate logistic models were run, some variables could be identified as

significantly associated with P/A based on chance alone. Therefore, a sequential Bonferroni technique (Holm 1979, Rice 1989) was used to correct for multiple tests. The sequential Bonferroni technique maintained the experiment-wise probability of Type-I error at 0.05. This test was applied to the P-value associated with the log-likelihood test for significance of the overall model.

Two sets of univariate logistic regression models were developed to ensure a correct relationship; a linear model and a model with a quadratic term added. The quadratic term was retained if it significantly altered the slope of the overall model ($P \leq 0.05$, assessed with the log-likelihood ratio test) and if it improved model fit. Linear plus quadratic models were converted to a single centered quadratic term only model because it is easier to subsequently build multiple models with a single term. For example, in a univariate model, a linear and quadratic term may have significant coefficients, as determined with the Wald X^2 statistic, but when combined with other variables, one coefficient may become non-significant. At this point a decision has to be made whether or not to include the entire variable. Quadratic terms were developed by first centering raw data and then squaring the new values. Only the new centered term was considered in subsequent multiple modeling steps.

Frequency-of-use patterns.--Frequency-of-use histograms were developed to illustrate relationships between sicklefin chub P/A and variables identified with univariate logistic regression. Frequency-of-use histograms were developed by dividing continuous variables into discrete groups of nearly equal size. Examination of univariate logistic

regression parameters, such as the sign and magnitude of estimated slope coefficients, also facilitated interpretation.

Habitat use of age-0 and age-1+ sicklefin chubs.--Age-0 and age-1+ sicklefin chub habitat use patterns were examined for differences prior to developing site-scale univariate models. Habitat variables were compared between sites with age-0 and age-1+ sicklefin chubs using t-tests after ensuring the normality assumption was met. Depth and turbidity were $\log_{10}$ transformed and percent silt, sand, and gravel were arc-sine square root transformed to meet this assumption. The arc-sine square root transformation is used to stabilize the variance of proportion data (Zar 1984). Six separate t-tests were run, one each for depth, velocity, three substrate types, and turbidity. Therefore, the sequential Bonferroni technique (Holm 1979, Rice 1989) was again used to correct for multiple tests. Age-0 and age-1+ sicklefin chubs were modeled separately if any variable differed significantly.

Range of optimum habitat conditions.--Univariate logistic regression models were used to describe a range of optimum habitat requirements for sicklefin chubs following methods outlined in Jongman et al. (1987) and Peeters and Gardeniers (1998). Logistic regression equations with linear plus quadratic terms have been shown to accurately describe the optimum range of habitat conditions of other aquatic biota (Peeters and Gardeniers 1998). However, this technique is only expected to succeed where large numbers of observations have been recorded over a sufficient gradient of environmental conditions. Only site-scale observations were considered to adequately meet this criterion

and only those variables where quadratic equations significantly improved models were examined.

Multiple logistic regression models.--The relative importance of multiple combinations of variables that best predicted sicklefin chub P/A was evaluated by building multiple logistic regression models from variables identified in univariate analyses. Spearman rank correlations were used prior to multiple model development to reduce problems of collinearity and further cull variables. Correlations were considered important if they were significant following corrections for multiple tests ($P \leq 0.05$) and demonstrated a strong relationship (generally $r_s \geq 0.40$). Variables were ordered from those most correlated with sicklefin chub presence to those least correlated. The first variable most highly correlated with sicklefin chub presence (VAR1) was retained and any subsequent variables significantly correlated with it (i.e., VAR1) were removed (e.g., Watson and Hillman 1997). The next highest correlated variable with sicklefin chub presence (VAR2) that was not correlated with VAR1 was subsequently retained. All subsequent variables significantly correlated with VAR2 were removed. This process was repeated until a final list of variables that were the most highly correlated with sicklefin chub presence but not significantly correlated with each other was developed. Retained variables were considered in multiple model development.

Multiple models were developed by first fitting a model with all remaining terms. Various combinations of variables were then mechanically entered and removed until the best model, based on significance and fit, was developed. Interaction terms of main effects selected in the final model were also evaluated. Mechanical development of

models was chosen because variable culling usually reduced the number of variables to a manageable size where formal model building procedures such as stepwise and backward elimination proved unnecessary.

Results

Sicklefin chubs were present at 157 of 1,860 sites in 31 study segments (17 in 1996, 14 in 1997) over the two year study period. They were collected in segments 5, 8, 9, 10, 22, 23, 25, and 27 in both years and exclusively in 1996 in segments 15 and 19. They were also present in segment 21 in 1996, however, this segment was not sampled in 1997 (Table 3-1). Their presence in nearly the same segments in both years suggested spatial dependence at the segment scale.

Spatial dependence, as assessed with Geary's (c), almost always indicated positive spatial autocorrelation within the 402.5 km linear distances calculated (Figure 3-1). However, only one coefficient in 1996 and three coefficients in 1997 were significantly different from 0 (Table 3-4). In both years, the greatest positive autocorrelation, expressed as the smallest coefficient, was at a distance of 160.9 km. Coefficients for 0 and 80.5 km distances were greater (indicating less positive autocorrelation) and mostly non-significant. This was due to most study segments being isolated at these distances (e.g., non-adjacent segments could not be considered in calculations of autocorrelation at the 0 distance). The 160.9 km distance was the first realistic distance at which most segments could be considered adjoining. Thus, segments within a 160.9 km distance were

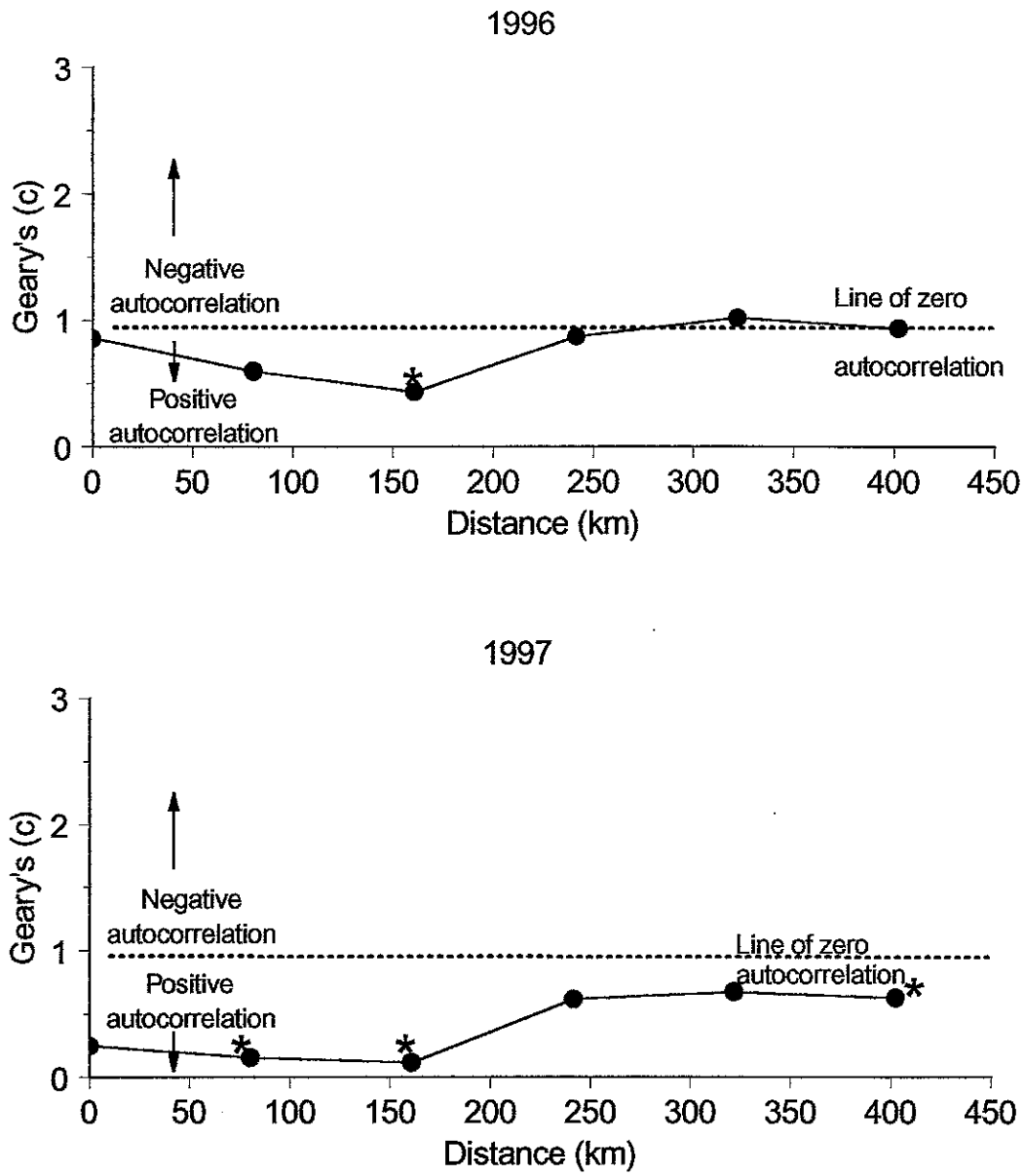

Figure 3-1. Correlogram showing spatial autocorrelation of the percent of sites within study segments having sicklefin chubs by 80.5 river kilometer distances in 1996 and 1997. Geary's (c) is the spatial autocorrelation coefficient. Coefficients significantly different from zero ($P \leq 0.05$) are indicated by an *. Positive autocorrelation indicates that the percentage of sites with sicklefin chubs in each segment is most like the percentage of sites in nearby segments (i.e., within the distance category specified). Negative autocorrelation indicates the percentage of sites with sicklefin chubs in each segment is different from the percentage of sites in segments within the distance category specified.

Table 3-4. Spatial autocorrelation coefficients and associated tests (z-statistic and P-value) of their significance for various distances among Missouri and lower Yellowstone River study segments sampled for sicklefin chubs in 1996 and 1997. Locations of study segments are in Table 3-1.

Distance (km)	Geary's (c) coefficient	Z-statistic	P
	1996		
0.0	0.856	0.3433	0.723
80.5	0.598	1.2915	0.196
160.9	0.437	2.1805	0.030
241.5	0.874	0.6003	0.543
322.0	1.021	-0.1378	0.882
402.5	0.938	0.4048	0.681
	1997		
0.0	0.245	1.4189	0.156
80.5	0.153	2.0047	0.045
160.9	0.114	2.6672	0.007
241.5	0.613	1.4649	0.143
322.0	0.671	1.7092	0.088
402.5	0.622	2.0787	0.039

considered nearest neighbors in development of an autocorrelation variable to model at the segment scale.

Segment scale

Univariate analysis.--Twenty-eight of 64 segment-scale variables were significantly associated with sicklefin chub P/A at an uncorrected probability level of 0.05 (Appendix Table 3A.2). However, only four variables were significant following correction for multiple tests: distance to upstream impoundment, flow constancy, mean segment turbidity, and percent of annual flow in August (Table 3-5, Appendix Table 3A.2). Frequency of occurrence of sicklefin chubs was highest when segments were > 301 km downstream from an impoundment; flow constancy was 0.56 or less, indicating an association with segments having more variable flow regimes; mean summer-early autumn turbidities were 80 NTUs or greater, and percent of the total annual flow in August was < 10% (Figures 3-2, 3-3).

Multiple logistic regression analysis.--Distance to upstream impoundment was the first variable retained for multiple model development because it exhibited the strongest correlation (r_s=0.70) with sicklefin chub P/A (Table 3-6) and was the most significantly associated variable with P/A in univariate logistic regressions (Table 3-5). Mean turbidity, percent of annual flow in August, and flow constancy were significantly correlated ($P \leq 0.05$) with distance to impoundment and therefore not considered further in development of the first multiple model. Thus, the first segment-scale model, termed model A, only included distance to upstream impoundment. However, distance to upstream impoundment may provide little in terms of management alternatives. Therefore, I

Table 3-5. Univariate logistic regression models associating sicklefin chub presence/absence with independent variables considered significant ($P \leq 0.05$, test of the overall model) following correction for multiple tests[a]. Data were measured in Missouri and lower Yellowstone river study segments in 1996 and 1997. The -2 log likelihood value and chi-square statistic tests for overall model signficance. The Wald chi-square statistic tests the significance of each coefficient in the model. The odds ratio is the multiplicative factor by which the odds of a segment having a sicklefin chub present changes when the independent variable increases by one unit. Models are listed in decreasing order of significance (i.e., increasing P-values).

	Tests of individual model parameters					Test of the overall model		
Model term	Coefficients	SE	Wald X^2	$P > X^2$	Odds ratio	-2 log Likelihood	-2 log L-X^2	P
			Distance to upstream impoundment (km)					
constant	-1.6215	0.7345	4.87	0.0273		21.544	19.837	0.0001
dist_imp	0.0096	0.0036	7.06	0.0079	1.010			
			Flow constancy					
constant	28.7255	12.8123	5.02	0.0250		23.005	12.589	0.0004
constncy	-0.4860	0.2178	4.97	0.0257	0.615			
			Average turbidity (NTUs)					
constant	-1.3154	0.7392	3.16	0.0751		29.106	12.275	0.0005
turb_ave	0.0314	0.0140	5.03	0.0248	1.032			
			Percent of annual flow in August					
constant	10.8767	4.6803	5.40	0.0201		26.074	11.289	0.0008
aug_perc	-1.0669	0.4708	5.13	0.0235	0.344			

[a] All univariate segment-scale models are in Appendix Table 3A.2.

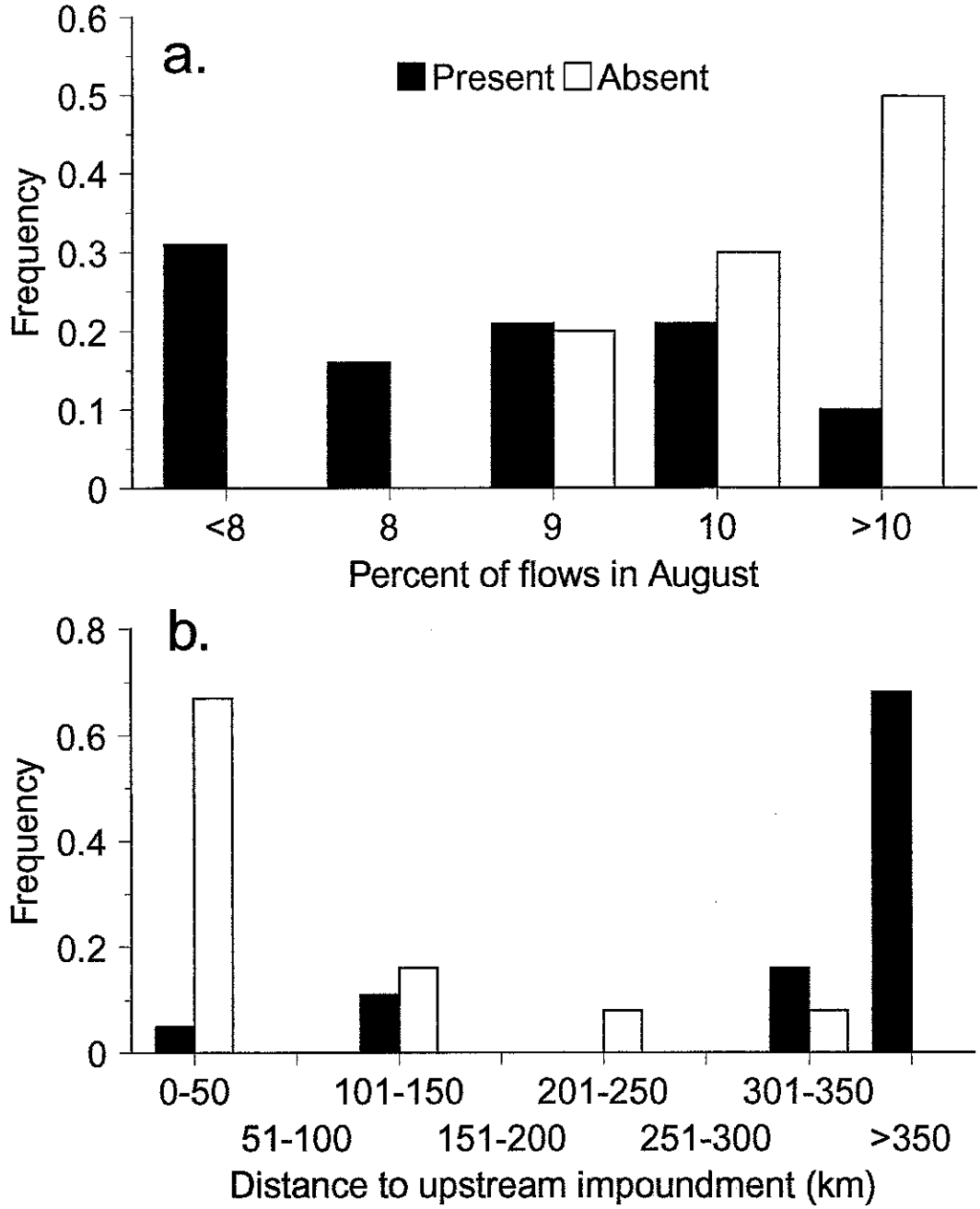

Figure 3-2. Relative frequency of (a) percent of annual flows in August and (b) distance to upstream impoundment categories for Missouri and lower Yellowstone river segments where sicklefin chubs were present (N=19) and absent (N=10 for (a) and N=12 for (b)) in late summer-early autumn, 1996 and 1997.

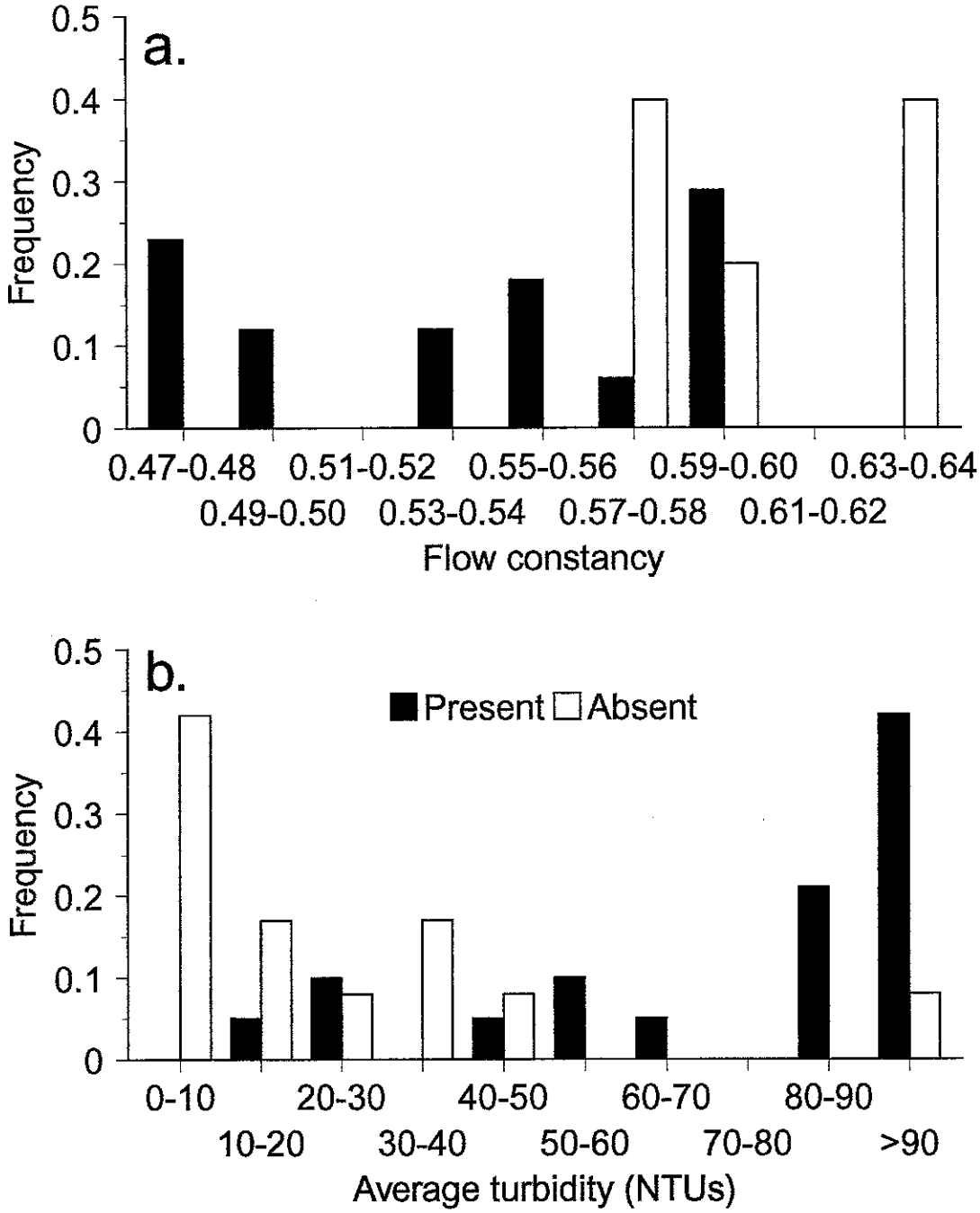

Figure 3-3. Relative frequency of (a) flow constancy and (b) mean turbidity categories for Missouri and Lower Yellowstone river segments where sicklefin chubs were present (N=17 for (a), N=19 for (b)) and absent (N=10 for (a); N=12 for (b)) in late summer-early autumn, 1996 and 1997.

Table 3-6. Spearman rank-order correlation matrix for segment scale variables considered significant following univariate logistic regression analyses. All data were measured from the Missouri and lower Yellowstone rivers in 1996 and 1997. Top numbers represent the probability that the correlation coefficient differs from zero; bottom numbers are the correlation coefficient (r_s). Sicklefin chub were coded as "0" for absent segments and "1" for present segments. Variables in the left column are ranked from the highest to least correlated with sicklefin chub presence/absence. Acceptance levels ($P \leq 0.05$) were corrected for multiple tests (Holm 1979, Rice 1989). Significant correlations following correction for multiple tests are indicated in **bold**.

Variable	Sicklefin chub	Distance to upstream impoundment	Mean turbidity	Percent of annual flow in August	Flow constancy
Sicklefin chub					
Distance to upstream impoundment	**0.0001** **0.70**				
Mean turbidity	**0.0001** **0.65**	**0.0001** **0.70**			
Percent of annual flow in August	**0.0018** **-0.55**	**0.0001** **-0.65**	0.4122 -0.15		
Flow constancy	**0.0040** **-0.53**	**0.0001** **-0.84**	**0.0001** **-0.68**	**0.0137** **0.46**	

developed a second segment-scale model (model B), by a-priori omitting distance to upstream impoundment. Based on correlations, model B began with terms mean turbidity and percent of annual flow in August. Mean turbidity and percent of annual flow in August were retained over flow constancy because they were more strongly correlated with sicklefin chub P/A (Table 3-6).

The relative importance of multiple variables was best described by these two unaltered models (Table 3-7). Model A could not be developed further because it contained only one term, distance to upstream impoundment. Distance to upstream impoundment provided a good fit to the data with $R^2 = 0.64$. Removal of percent of annual flow in August significantly altered model B (log-likelihood ratio test comparing models with and without percent of annual flow in August: -2 log L=15.013, $P < 0.001$) indicating that the two term model was best. This model also provided a good fit to the data with $R^2 = 0.76$. Inclusion of an interaction term did not significantly improve model B. In summary, sicklefin chub presence was most highly predicted in segments far downstream from reservoirs, where turbidity during the sampling period was high, and August flows were low.

Site scale

Habitat use age-0 and age-1+ sicklefin chubs.--Age-0 and age-1+ sicklefin chubs were collected at 20 and 135 sites, respectively, in 1996 and 1997. Three site-scale variables differed significantly between age-0 and age-1+ sicklefin chubs collection sites following corrections for multiple tests (Table 3-8). Sites where age-1+ sicklefin chubs

Table 3-7. Multiple logistic regression models to predict the occurrence of sicklefin chubs in selected Missouri and lower Yellowstone river segments based on data collected in 1996 and 1997. In model A, Distance to upstream impoundment is measured in km from the upstream most segment boundary to the impoundment. In model B, mean turbidity is measured in NTUs and is based on measurements made from late July through mid-October. The -2 log-likelihood statistic tests the significance of the overall model and the Wald X^2 statistic tests the significance of the individual coefficients. The odds ratio is the multiplicative factor by which the odds of a segment having a sicklefin chub present changes when the independent variable increases by one unit.

	Tests of individual model parameters					Test of the overall model		
Model term	Coefficients	SE	Wald X^2	$P > X^2$	Odds ratio	-2 log Likelihood	-2 log L-X^2	P
Segment-scale model A								
constant	-1.6215	0.7345	4.87	0.0273		21.544	19.837	0.0001
Distance to upstream impoundment	0.0096	0.0036	7.06	0.0079	1.010			
Segment-scale model B (distance to upstream impoundment omitted a-priori)								
constant	11.2617	5.8291	3.73	0.0534		14.093	23.270	0.0001
Mean turbidity	0.0496	0.0222	5.00	0.0253	1.051			
Percent of annual flow in August	-1.3990	0.6540	4.57	0.0324	0.247			

Table 3-8. Comparisons of site-scale habitat characteristics between sites used by age-1+ and age-0 sicklefin chubs in the Missouri and lower Yellowstone rivers from late July through mid-October in 1996 and 1997. Percent gravel, sand, and silt substrate were arc-sine square root transformed. Turbidity and depth were $\log_{10}$ transformed. Standard deviations (SD) are based on transformed data. Substrate, turbidity, and depth means are untransformed. T is the calculated *t*-test statistic. P-values in bold are significant ($P \leq 0.05$) following corrections for multiple tests (Holm 1979, Rice 1989).

	Age-1+ sites		Age-0 sites				
Variable	mean	SD	mean	SD	T	df	P
percent gravel substrate	15.76	0.47	0.07	0.06	8.67	152.9	**0.0001**
column velocity (m/s)	0.81	0.28	0.60	0.34	2.97	147.0	**0.0034**
percent silt substrate	0.14	0.11	23.00	0.66	-3.11	19.2	**0.0056**
turbidity (NTUs)	53.96	0.43	68.49	0.12	-0.96	152.0	0.3377
depth (m)	2.65	0.23	2.92	0.21	-0.76	147.0	0.4443
percent sand substrate	77.63	0.51	75.46	0.65	0.20	153.0	0.8410

were present were characterized by faster column velocities, a higher percentage of gravel, and a lower percentage of silt than sites where age-0 sicklefin chubs were present. Therefore, site-scale variables were modeled independently for age-1+ sicklefin chubs. The low numbers of sites where age-0 individuals were collected precluded development of logistic regression models for this life stage.

Univariate analysis.--Inclusion of a quadratic term significantly improved univariate logistic regression models for depth, velocity, and turbidity, based on log-likelihood ratio tests comparing models with and without the quadratic term. All individual site-scale variables were significantly associated with adult P/A following corrections for multiple tests, except turbidity and percent sand (Table 3-9). Therefore, turbidity and percent sand were dropped from further analysis. A centered quadratic term was used in lieu of the linear plus quadratic terms for depth and velocity in subsequent multiple model building steps for reasons mentioned previously.

Site scale habitat-use patterns of age-1+ sicklefin chubs were illustrated by frequency-of-use histograms and univariate logistic regression models. The positive linear and negative quadratic terms in univariate logistic models indicated that depth and velocity relationships followed a symmetrical bell-shaped curve (Figure 3-4, 3-5). A similar pattern was evident in frequency-of-use histograms. Age-1+ sicklefin chubs in midsummer-early autumn were present at depths between 0.2 and 7.6 m and velocities between 0.1 and 1.7 m/s (Figures 3-4, 3-5). However, *optimum* habitat conditions of adult sicklefin chubs ranged from 2.20 to 4.80 m for depth and 0.60-1.10 m/s for velocity, as determined by the Peeters and Gardeniers (1998) method. Wider optimum habitat

Table 3-9. Univariate logistic regression models associating age-1+ sicklefin chub presence/absence with site-scale habitat variables measured in the Missouri and lower Yellowstone rivers in 1996 and 1997. The -2 log-likelihood value and associated chi-square statistic tests for overall model signficance. The Wald chi-square statistic tests the significance of each coefficient in the model. The odds ratio is the multiplicative factor by which the odds of a site having a sicklefin chub present changes when the independent variable increases by one unit. Models are listed in decreasing order of significance (i.e., increasing P-values). P-values in bold are significant ($P \leq 0.05$) following corrections for multiple tests (Holm 1979, Rice 1989).

	Tests of individual model parameters					Test of the overall model		
Model term	Coefficients	SE	Wald X^2	$P > X^2$	Odds ratio	-2 log Likelihood	-2 log L-X^2	P
				Depth (m)				
constant	-3.7962	0.2610	211.53	0.0001		918.693	58.727	**0.0001**
depth	1.1512	0.1746	43.48	0.0001	3.162			
depth^2	-0.1656	0.0261	40.21	0.0001	0.847			
				Column velocity (m/s)				
constant	-5.3512	0.4421	146.50	0.0001		849.349	122.800	**0.0001**
velocity	8.7876	1.1340	60.05	0.0001	999.00			
velocity^2	-5.1306	0.7096	52.27	0.0001	0.006			
				Percent of substrate composed of gravel				
constant	-2.8160	0.1077	683.47	0.0001		942.458	35.882	**0.0001**
gravel	0.0180	0.0027	42.47	0.0001	1.018			
				Percent of substrate composed of silt				
constant	-2.2244	0.0926	577.32	0.0001		920.025	58.315	**0.0001**
silt	-0.0541	0.0140	14.95	0.0001	0.947			
				Turbidity (NTUs)				
constant	-2.7346	0.1308	436.99	0.0001		959.077	7.270	0.0264
turbidity	0.0041	0.0015	6.94	0.0084	1.004			
turbidity^2	-0.000004	0.000001	5.77	0.0163	1.000			
				Percent of substrate composed of sand				
constant	-2.6034	0.1915	184.75	0.0001		978.157	0.183	0.6692
sand	0.0010	0.0024	0.18	0.6708	1.001			

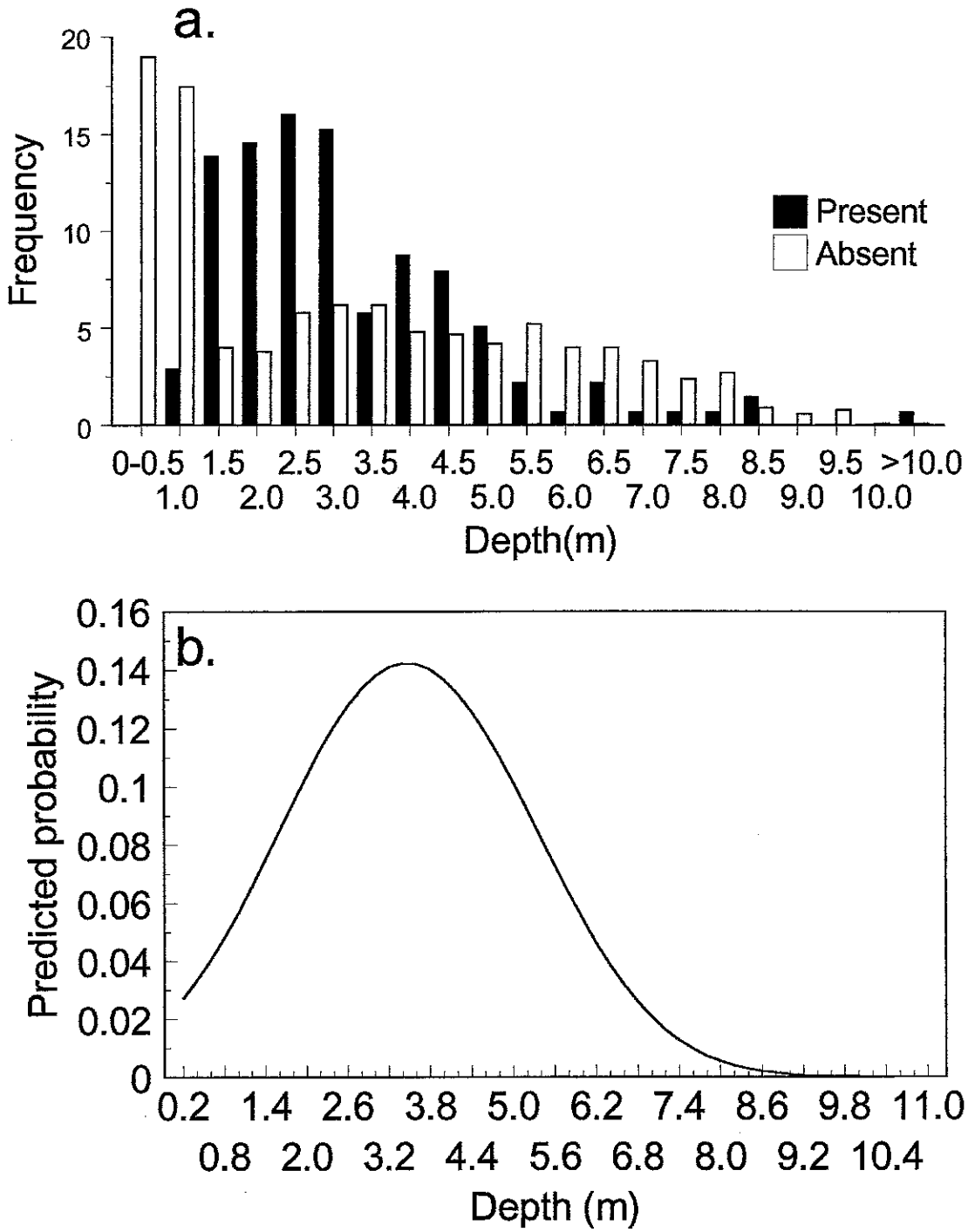

Figure 3-4. (a) Relative frequency of 0.5-m depth intervals at collection sites in the Missouri and lower Yellowstone rivers where adult sicklefin chubs were present (N=137) and absent (N=1717) in late summer-early autumn, 1996 and 1997. (b) Plot of predicted probabilities of occurrence of adult sicklefin chubs based on a logistic regression model developed from the data in (a).

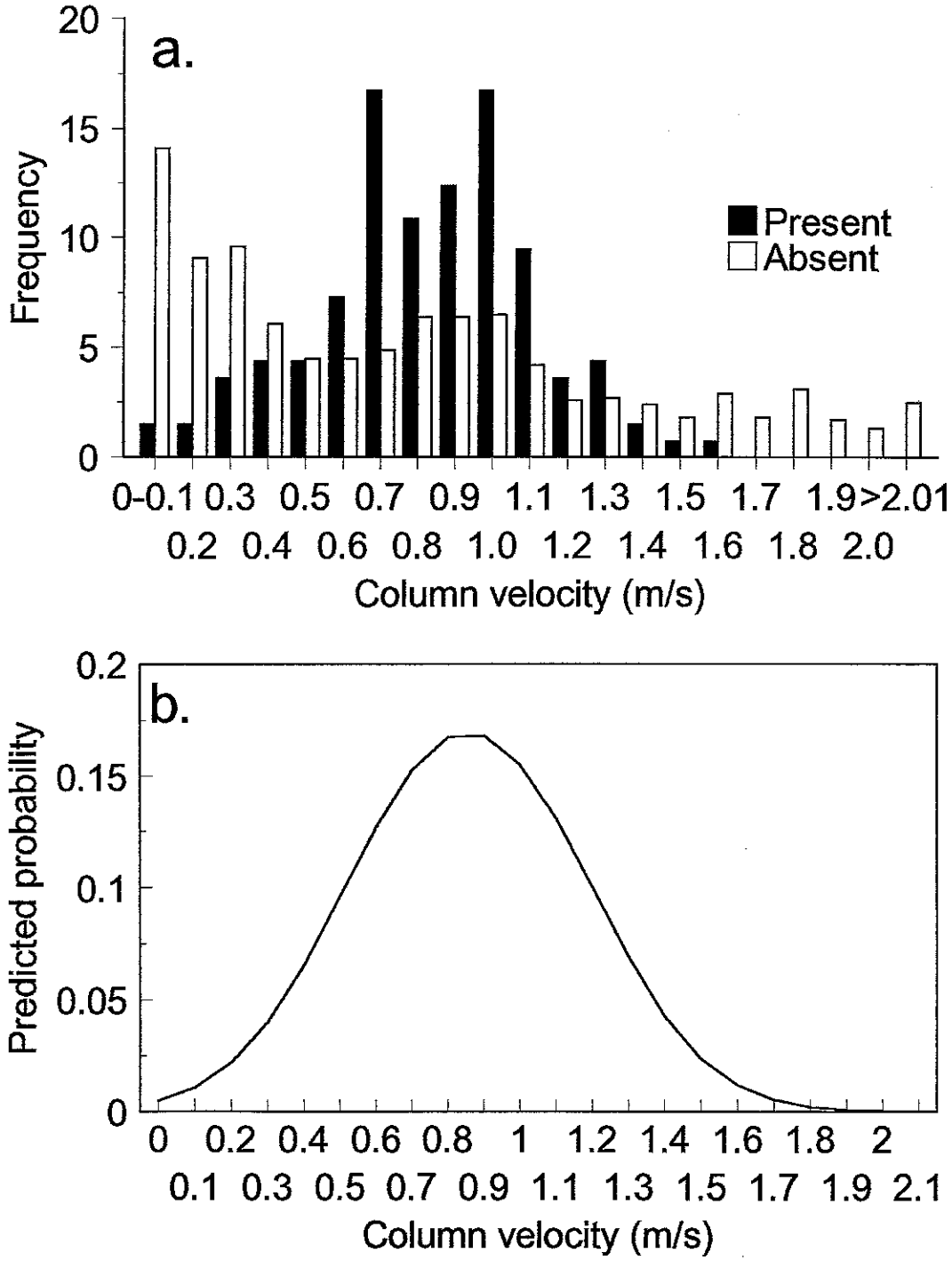

Figure 3-5. (a) Relative frequency of 0.1-m/s column velocity intervals at collection sites in the Missouri and lower Yellowstone rivers where adult sicklefin chubs were present (N=137) and absent (N=1683) in late summer-early autumn, 1996 and 1997. (b) Plot of predicted probabilities of occurrence of adult sicklefin chubs based on a logistic regression model developed from the data in (a).

ranges were predicted by the Jongman et al. (1987) method. Optimum depths ranged from 1.73 to 5.21 m, and velocity from 0.54 to 1.16 m/s with their method. The negative linear coefficient for silt indicated that the probability of age-1+ sicklefin chub presence increased as the percentage of the substrate composed of silt declined. Conversely, the positive linear coefficient for gravel indicated that the probability of age-1+ fish presence increased as percentage of gravel substrate increased. The smaller slope coefficient for gravel indicated that predicted probabilities changed less rapidly with changing gravel substrates than with changing silt substrates. Frequency of occurrence of age-1+ sicklefin chubs was highest when substrates contained < 10% silt (Figure 3-6a). Age-1+ sicklefin chubs were never present over substrates with > 50% silt. Although frequency of occurrence of age-1+ sicklefin chubs was also highest over substrates with < 10% gravel (Figure 3-6b), this was likely due to a low prevalence of gravel in most Missouri and lower Yellowstone river areas (Dieterman et al. 1996, Young et al. 1997). Excluding substrates with < 10% gravel, the frequency of occurrence of age-1+ sicklefin chubs was highest over substrates with > 80% gravel.

Multiple logistic regression analysis.--Most Spearman rank correlations were significant following corrections for multiple tests, but most only demonstrated weak association (i.e., $r_s < 0.40$) (Table 3-10). This was especially evident in correlations with sicklefin chub P/A and was likely due to the non-linear form of these relationships indicated in univariate logistic regressions. Therefore, significance and strength of correlation with sicklefin chub P/A could not be used as criteria for culling variables. Instead, the -2 log-likelihood X^2 and R^2 statistics from univariate logistic regressions

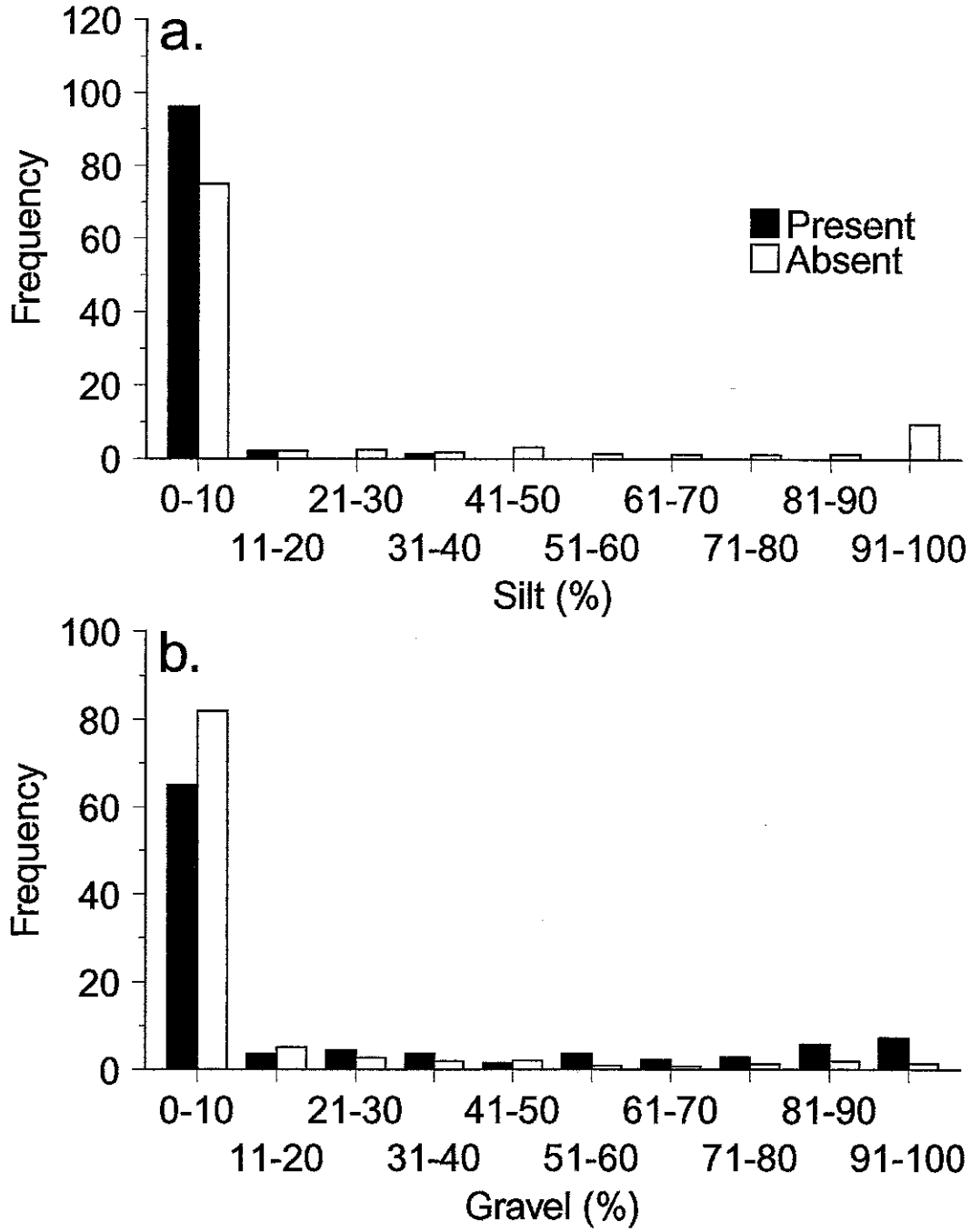

Figure 3-6. Relative frequency of 10% (a) silt and (b) gravel substrate intervals at Missouri and lower Yellowstone river collection sites where adult sicklefin chubs were present (N=137) and absent (N=1723) in late summer-early autumn, 1996 and 1997.

Table 3-10. Spearman rank-order correlation matrix for site-scale variables considered significant following univariate logistic regression analyses. All data were measured from the Missouri and lower Yellowstone rivers in 1996 and 1997. Top number of each pair is the probability that the correlation coefficient differs from zero; bottom number of each pair is the correlation coefficient (r_s). Sicklefin chub were coded as "0" for absent sites and "1" for present sites. Variables in the left column are ranked from the highest to least correlated with sicklefin chub presence/absence. Acceptance levels ($P \leq 0.05$) were corrected for multiple tests (Holm 1979, Rice 1989). Significant correlations following correction for multiple tests are indicated in **bold**.

Variable	Sicklefin chub	Silt	Gravel	Velocity	Depth
Sicklefin chub					
Silt	**0.0001** **-0.14**				
Gravel	**0.0001** **0.13**	**0.0001** **-0.30**			
Velocity	**0.0014** **0.07**	**0.0001** **-0.64**	**0.0001** **0.32**		
Depth	0.0384 0.04	**0.0001** **-0.49**	**0.0001** **0.22**	**0.0001** **0.80**	

(Table 3-9) were used to assess the strength of association between independent variables and adult sicklefin chub P/A. Three independent variables demonstrated significantly strong ($r_s > 0.40$) Spearman rank correlations among themselves: depth, velocity, and silt (Table 3-10). Only velocity was retained based on the new criteria.

The best site-scale multiple logistic regression model included the two remaining terms, velocity and percent gravel (Table 3-11). Removal of percent gravel resulted in a significant change in the log-likelihood ratio (-2 log L=133.45, $P < 0.001$), indicating that percent gravel was a significant predictor of sicklefin chub P/A. This model provided a good fit to the data but only explained 17.1% of the variation. Velocity was the most important of the two variables as its removal changed R^2 from 17.1 to 4.6%. Inclusion of an interaction term did not improve this model. In summary, age-1+ sicklefin chub presence was most highly predicted at sites with velocities between 0.6 and 1.1 m/s over gravel substrates in midsummer-early autumn.

Discussion

Segment Scale

Sicklefin chub distribution in the Missouri River was associated at large spatial scales with river impoundment, August flows and midsummer-early autumn turbidities. This result represents the first quantitative association between sicklefin chub distribution patterns and large-scale Missouri River features. These associations may mean that summer flow regime and turbidity patterns can influence success of sicklefin chub reproduction and survival at large spatial scales.

Table 3-11. Multiple logistic regression model to predict the probability of age-1+ sicklefin chub presence at sites in the Missouri and lower Yellowstone rivers based on data collected from late July through mid-October in 1996 and 1997. Velocity ("cenveloc" measured in m/s) was a mean centered quadratic term where original observations were first mean centered and then squared. Gravel was measured as a percentage. The -2 log likelihood value and associated chi-square statistic tests for overall model significance. The Wald chi-square statistic tests the significance of each coefficient in the model. The odds ratio is the multiplicative factor by which the odds of a site having a sicklefin chub present changes when the independent variable increases by one unit.

	Tests of individual model parameters					Test of the overall model		
Model term	Coefficients	SE	Wald X^2	$P > X^2$	Odds ratio	-2 log Likelihood	-2 log L-X^2	P
				Site-scale multiple model				
constant	-1.8786	0.1301	208.60	0.0001		814.330	126.690	0.0001
cenveloc	-4.7789	0.7283	43.05	0.0001	0.008			
gravel	0.0174	0.0030	34.16	0.0001	1.018			

Sicklefin chub are believed to spawn in either spring or summer depending on latitude. The lower Missouri River warms earlier in spring due to a more southerly latitude and warmer climate influenced primarily by air masses originating in the Gulf of Mexico (Hesse et al. 1989). Thus, sicklefin chubs are believed to spawn in May or June in the lower river (Pflieger 1997). Tibbs and Galat (1997) surmised peak spawning in the lower Missouri River in mid- to late June based on size of larval *Macrhybopsis* chubs collected in 1996. Alternatively, Grisak (1996) documented gravid female and ripe male sicklefin chubs between late July and mid-August at a more northerly latitude in Montana, which corresponded to my segment 5, in 1994 and 1995. Thus, low August flows may influence larval and juvenile chubs in lower river segments in Missouri or spawning adults and larvae in upper river segments in Montana.

August flows may influence drifting eggs and larvae in both areas. Egg type and spawning behavior of sicklefin chubs are unknown but the related speckled chub (*Macrhybopsis aestivalis*) is a pelagic-broadcast spawner that produces nonadhesive, semi-buoyant eggs (Bottrell et al. 1964, Platania and Altenbach 1998). Eggs and larvae of speckled chub take from 3-5 days, depending on water temperature, to develop to a stage where horizontal movement of larvae is possible (Bottrell et al. 1964, Platania and Altenbach 1998).

If sicklefin chub spawn similarly, then high August flows may transport developing eggs and larvae out of riverine areas and into reservoirs in the upper Missouri River or transport them into the middle Mississippi River from lower Missouri River segments. Channelization of the lower river may have exacerbated the problem by increasing mid-

channel velocities (Hesse et al. 1989). For example, a current velocity of 1.2 m/s (i.e., 4.3 km/hr) is a conservative estimate of mid-channel velocity in the channelized lower river (Slizeski et al. 1982). If the 3-5 day developmental period from egg to horizontally mobile larvae is representative and eggs and larvae remain in mid-channel currents, then eggs and larvae could be transported from 311 to 518 km. These distances are approximately from Glasgow, MO (354 rkms) or Kansas City, MO (592 rkms) to the mouth. Evidence supporting downstream transport include: no age-0 sicklefin chubs collected in the lower river upstream from segment 23 (i.e., Kansas City), most age-0 sicklefin chubs were collected near the Missouri River's mouth, age-0 chubs are collected in the middle Mississippi River and are speculated to be washouts from the lower Missouri River (Werdon 1993), and sicklefin chubs in general increased in abundance downstream from Glasgow, MO (Gelwicks et al. 1996, Pflieger 1997, Grady and Milligan 1998). Mid-channel current velocities are less in segments in Montana and North Dakota, about 0.7 m/s (i.e., 2.5 km/hr, Dieterman et al. 1996, Young et al. 1997), but distances between impoundments are shorter. Eggs and larvae would need about 180 to 300 km of uninterrupted river in Montana and North Dakota given a mid-channel current velocity of 2.5 km/hr and a 3-5 day development period. Distances of riverine habitat between Missouri River impoundments averages 128 km and ranges from 378 to 0 km (Galat et al. 1996). Only the Missouri River between Ft. Peck Dam, MT and Lake Sakakawea, ND would provide sufficient riverine distances to allow eggs and larvae to properly develop given these estimates. Eggs and larvae transported into Missouri River reservoirs may perish due to starvation, lack of resources, or predation by other biota. Similar inferences

were speculated to have led to declines of speckled chubs in the Rio Grande River (Platania and Altenbach 1998).

Alternatively, an association with August flows may mean that these flows can effect availability of nursery habitat for sicklefin chub larvae and age-0 individuals. Most sicklefin chubs in other studies were collected along shallow shorelines associated with sand bars in the lower river and most were likely age-0 based on length distributions (Grace and Pflieger 1985, Gelwicks et al. 1996, Grady and Milligan 1998). Shallow shorelines with gradually sloping banks are important nursery habitats for many rheophilic fishes in rivers because they provide areas with reduced velocity, shallow depths, greater light penetration than deeper waters, higher water temperatures and increased primary productivity, thus facilitating faster growth rates (Bain et al. 1988, Schiemer et al. 1991, Schiemer and Zalewski 1992, Schiemer et al. 1995, Travnichek and Maceina 1994, Scheidegger and Bain 1995, Platania and Altenbach 1998). Shallow shorelines also provide refugia from larger aquatic predators (Power 1987). High flows during critical periods, such as August, may inundate these areas and reduce their importance as nursery habitat (Schiemer and Zalewski 1992, Scheidegger and Bain 1995, Galat et al. 1998). Historically, Missouri River flows were characterized by an extended period of low discharge beginning in August (Galat and Lipkin 2000). Low summer flow patterns were eliminated in the lower river following establishment of mainstem impoundments, but vary spatially in upper segments (Galat and Lipkin 2000).

Probability of sicklefin chub presence in segments was positively associated with turbidity measured during midsummer-early autumn and may reflect a response to inter-

specific competition and predation. Late summer-early autumn is an important time for fish feeding and growth as water temperatures are usually warm and food resources abundant (Matthews 1998). Acquisition and storage of energy during this time is critical to over-winter survival of many fishes (MacKinnon 1972, Diana 1995, Lyons 1997).

Sicklefin chubs have adaptations promoting prey detection and capture, and predator avoidance in turbid waters, but consequences of these adaptations may affect survival in clear waters. Sicklefin chubs exhibit greater development of sensory structures associated with smell and taste, including numerous external and internal taste buds, enlarged vagal brain lobes, and abundant lateral-line neuromasts than most other fishes (Moore 1950, Davis and Miller 1967, Reno 1969). However, sicklefin chubs have sacrificed development of structures associated with visual senses: eye size is reduced, eyes are often partially or wholly covered by skin, and optic brain lobe size is reduced. Water clarity increases following mainstem impoundment led to increased numbers of sight-feeding fishes such as gizzard shad and emerald shiner (Cross and Moss 1987, Pflieger and Grace 1987). Sicklefin chubs may be out-competed for food resources by these sight-feeding fishes in less turbid segments. Also, reduced visual senses may make sicklefin chubs more vulnerable to predation by introduced sight-feeding piscivores, such as walleye (Everett 1999). However, sicklefin chub P/A was not significantly associated with relative abundance of two piscivore groups in this study, but the disparity might be due to some other aspect of predation not accounted for in our index.

Data availability was limited to piscivore catches in bag seines and stationary gill nets. A half-arc seine haul adjacent to shore may not have captured large, mobile,

predatory fishes. Stationary gill nets are an effective gear for sampling large, mobile fishes (Hubert 1996), but were often used in non-flowing, off-channel macrohabitats such as tributary mouths and non-connected secondary channels (Table 3-2). Thus, they may not have adequately represented piscivores in macrohabitats used by sicklefin chubs.

Surprisingly, physical habitat variables, such as sand bars, islands, and channel pattern, were not significantly associated with sicklefin chub presence/absence at the segment scale. Some segments below dams (e.g., segments 12, 14, 15) remain unchannelized and still retain semi-natural physical habitat conditions, including an abundance of sand bars and islands (Morris et al. 1968, Kallemeyn and Novotny 1977, Modde and Schmulbach 1977, Schmulbach et al. 1992, Mestl and Hesse 1993). However, only one sicklefin chub was collected in one of these segments in one year (i.e., segment 15 in 1996). This collection represented the first documented occurrence of a sicklefin chub in South Dakota since establishment of mainstem impoundments (Stukel and Backlund 1997). The almost total absence of sicklefin chubs in these segments with semi-natural physical habitat conditions further indicates impoundment modifications on flow regime and turbidity as likely mechanisms regulating sicklefin chub distribution.

The negative association with distance to upstream impoundment may reflect a more integrative assessment of flow regime and water quality modifications influencing sicklefin chub P/A. Impoundments alter many aspects of flow, sediment, and thermal regimes (e.g., Morris et al. 1968, Ricther et al. 1996, Poff et al. 1997, Galat and Lipkin 2000, Pegg 2000) including those variables examined here as well as other measures, such as dissolved oxygen, invertebrate and zooplankton drift, and distribution of benthos

(Morris et al. 1968). Twenty-four other segment-scale variables were significantly associated with sicklefin chub P/A *prior* to corrections for multiple tests (Appendix Table 3A.2). Seventeen of these reflected some other aspect of flow regime and two others were different measures of turbidity. Although these variables cannot be completely omitted from consideration, my objective was to identify the *most* important variables and was necessarily conservative owing to the large number of variables examined and a low sample size at the segment scale. Considerable longitudinal distances are needed to overcome the effects of impoundments (Ward and Stanford 1983, 1995) and other taxa have shown similar longitudinal responses to river impoundment, including other fishes (Gore and Bryant 1986, Kinsolving and Bain 1993), freshwater mussels (Miller et al. 1984, Vaughn and Taylor 1999) and invertebrates (Gore and Bryant 1986, Voeltz and Ward 1991).

Presence/absence data were used in this study because of the rarity of sicklefin chubs in collections. However, presence data should be interpreted with care as individuals may be collected in undesirable habitats either because they were simply moving through it or because they were forced out of optimum habitat areas by dominant individuals (e.g., source/sink habitats, Pulliam 1988). Alternatively, some indicator of population performance, such as a measure of reproductive success or population growth, may be a better parameter to model when such data are available.

Site Scale

Sites where age-0 sicklefin chubs were collected were characterized by slower water-column velocities and a greater percentage of silt substrate than sites where age-1+ fish were collected. Two mechanisms could explain these ontogenic differences. If sicklefin chubs are pelagic broadcast spawners with semi-buoyant eggs like the related speckled chub (Platania and Altenbach 1998), then eggs and larvae could have drifted into low-velocity areas, settled out, and age-0 individuals remained in these habitats through midsummer-early autumn when our sampling was conducted. Alternatively, age-0 fish could have actively searched for these habitats following a swim-up period. Age-0 individuals of other rheophilic fishes in large rivers actively search for low velocity areas associated with shallow shorelines (Schiemer et al. 1991, Schiemer and Zalewski 1992). Other studies in the lower Missouri River documented use of shallow shorelines along sand bars by sicklefin chubs that were likely age-0 fish based on length distributions (Grace and Pflieger 1985, Gelwicks et al. 1996, Grady and Milligan 1998). However, depths of age-0 sicklefin chub sites were not significantly different than sites with age-1+ individuals in the present study, which incorporated nearly all riverine areas in the Missouri River (Table 3-8). This indicates that velocity is the primary factor influencing age-0 sicklefin chubs and suggests the importance of maintaining and enhancing low velocity habitats.

Presence of age-1+ sicklefin chubs at sites was most highly associated with water column velocity and percentage of substrate composed of gravel. Velocity was the most important variable with optimum velocities ranging from 0.6 to 1.1 m/s. Sicklefin chubs

have hydrodynamic adaptations characteristic of species inhabiting strong currents (e.g., fusiform body shape and large flat pectoral fins, Webb 1975, 1984, see also chapter 2). However, no sicklefin chubs were collected at sites with velocities > 1.7 m/s (Figure 3-5), perhaps indicating an upper threshold. Age-1+ associations with moderate velocities and characterization of age-0 sites by slower velocities shows the complex nature of habitat needs for this species and indicates the importance of maintaining a diverse habitat with areas varying in current velocity.

A significant positive association of age-1+ sicklefin chubs with percent gravel differs from observations reported in other studies. Sand has been suggested as the most important substrate used by sicklefin chubs (Bailey and Allum 1962, Hesse 1994a, Grisak 1996, Everett 1999), although other authors included fine gravel (Pflieger and Grace 1987, Gelwicks et al. 1996, Pflieger 1997). However, few of these studies quantitatively assessed this relationship and all indicated that sand was the most common substrate in their studies. Sand was not significantly associated with sicklefin chub P/A in the present study because it was the most common substrate sampled. Grady and Milligan (1998) found the greatest percentage of sicklefin chubs (46.7%) over organic matter (Table 1-5), but most of these were likely age-0 fish. The present study represents the first demonstration of an association between gravel substrates and age-1+ sicklefin chubs. Davis and Miller (1967) found more taste buds in the pharyngeal cavity of sicklefin chubs than in sturgeon chubs (*Macrhybopsis gelida*) and speculated that this enabled sicklefin chubs to feed over detrital and sand substrates, as food items could be sorted internally.

However, the present study suggests more research is needed to ascertain the benefits of gravel substrates to age-1+ sicklefin chubs.

The site-scale multiple logistic regression model only explained 17% of the variation in these data. Three reasons could account for this low percentage. First, one measurement of velocity and substrate was recorded at, and expected to represent, each site. This coarse level of measurement may not have been adequate to characterize conditions used by an individual sicklefin chub and/or to account for the wide range of velocity and substrate conditions present at the site-scale. This implies a need for methods of higher resolution measurement in large rivers. Second, other factors not measured at the site scale, such as presence of a piscivore or absence of food resources, could have a greater influence on sicklefin chub P/A. Lastly, low variation explained may indicate that sicklefin chub densities are not large enough to have saturated available sites with optimum velocities and substrates. This would suggest other demographic problems, such as poor reproduction (e.g., Freeman and Freeman 1994).

Summary and Management Implications

The results of this study indicated associations between sicklefin chub presence and selected variables. If it is shown that these associations reflect causal relationships than the distribution of sicklefin chubs in the Missouri and lower Yellowstone rivers can be maintained and increased by providing low summer flows, increasing turbidity, and preserving sites with adequate velocities over sand and gravel substrates.

Controlled water releases are a viable management tool for the Missouri River because of the presence of mainstem impoundments (Hesse et al. 1988, Hesse et al. 1989). The U. S. Army Corps of Engineers (Corps) is the primary agency managing Missouri River flow and habitat (Werdon 1993). The Corps extensively monitors hydrologic inputs to the Missouri River to identify appropriate reservoir releases based on a Water Control Manual (Sveum 1988). Their forecasts could be used to determine what reservoir discharges would provide < 10% of the total annual flow in August for each segment. Low summer flows in general have been hypothesized to be important for other riverine fishes, birds, and turtles (Galat et al. 1998, Galat and Lipkin 2000) and are the subject of debate in development of a new Missouri River Water Control Manual for the Corps of Engineers (USACE 1998a, Galat 1999).

Turbidity could be increased by routing sediment around reservoirs via side channels and/or pipes following suggestions in Hesse et al. (1989) and Singh and Durgunoglu (1991). These data did not indicate a maximum limit to the amount of turbidity needed (i.e., no quadratic function was indicated in Figure 3-3b), but summer-fall averages should at least exceed 80 NTUs.

Velocity distributions can be modeled and predicted given differing flow and channel morphologies (e.g., Bovee 1982, Stalnaker et al. 1989, Nestler et al. 1993, Bult et al. 1998, Lamouroux et al. 1998). The data presented here (Figures 3-4, 3-5, 3-6 and ranges of optimum habitat conditions in text) can be used in models, such as RCHARC or the Instream Flow Incremental Methodology, to help evaluate flow regime alternatives

(e.g., Latka et al. 1993, USACE 1998b) and habitat restoration and mitigation projects (e.g., Harberg et al. 1993, Gore and Shields 1995, Milhous 1998).

These recommendations should be tested in an adaptive management framework and in the most cost-effective order. Adaptive management is characterized by implementation of management plans followed by continual monitoring of indicators that measure progress toward goals (Meffe and Carroll 1997, Krueger and Decker 1999). Plans are revised and revisions implemented following evaluations until goals are achieved. Sicklefin chub presence in a segment would be an indicator of success, but this would require development of a standardized monitoring program. Regarding these data, reducing August flows may be the easiest, most cost-effective recommendation to be implemented and evaluated. A revised plan modifying in-channel habitat to provide areas of optimal velocity could be implemented in conjunction with August flow reductions if no sicklefin chubs were initially collected. If sicklefin chubs remain absent, then other potentially more costly plans, such as augmenting turbidity levels, could subsequently be initiated until a final goal of age-0 and age-1+ sicklefin chub presence is achieved.

Alternatively, these data suggest testable hypotheses that future research could address and which might help explain mechanisms of sicklefin chub absence. Benefits of low August flows could be evaluated best with field experiments, perhaps using the adaptive management framework discussed above. Moderation of competition or predation by turbidity manipulation could be evaluated by bringing sicklefin chubs into a laboratory and placing them in tanks with differing turbidity levels. Predators and competitors could then be placed into these tanks and sicklefin chub feeding or predator

evasion behaviors monitored. These data suggest a significant difference in either or both situations at a turbidity level of 80 NTUs. Similar experiments could be conducted in flow tunnels with sicklefin chub, competitor, and predator responses to differing current velocities being evaluated. These data suggest that sicklefin chubs, but not competitors or predators, could maintain their positions longer in current velocities between 0.6 and 1.1 m/s.

In summary, sicklefin chub presence in large-scale, geomorphically defined, segments was most highly associated with large distances downstream of impoundments, where summer-autumn turbidities exceeded 80 NTUs and August flows were low, being generally < 10% of the total annual flow. Smaller-scale sites where age-1+ sicklefin chub were present were characterized by faster column velocities, a higher percentage of gravel, and a lower percentage of silt than sites where age-0 individuals were present. Age-1+ sicklefin chub presence at sites was most highly associated with current velocity and gravel substrates. These patterns may have been related to conditions necessary for reproduction and successful recruitment and to moderation of predation and competition impacts. These patterns also suggest avenues of future research, such as implementation of plans within an adaptive management framework and laboratory studies. Although others have qualitatively implicated large-scale factors in the decline of native fishes in the Missouri River system (Morris et al. 1968, Hesse et al. 1989, Hesse 1994a, Everett 1999), these data represent the first quantitative assessment of these factors influencing the distribution of a native fish and of ontogenic differences in its habitat use.

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Appendix 3A. Tables of variable descriptions and segment-scale univariate logistic regression models.

Table 3A.1. Segment and site scale variables evaluated for association with sicklefin chub presence/absence with logistic regression models developed from data gathered from the Missouri and lower Yellowstone rivers in 1996 and 1997. FS-data gathered from field sampling, ES-data gathered from existing sources.

Scale	Variable	Description
	Physical Habitat	
Segment		
	Channel width (km) (ES)	Mean channel width of each segment calculated from channel widths, indicated on USGS 1:24,000 scale maps, measured every 1.609 km within each segment.
	Sandbar density (# /1.609 km) (ES)	Sand bars identified on USGS 1:24,000 topographic maps as areas of land surrounded by water with no evidence of vegetation (i.e., no green color)
	Island density (# /1.609 km) (ES)	Islands identified on USGS 1:24,000 topographic maps as areas of land surrounded by water with vegetation present (i.e., with green color)
	Sandbar and/or island density (#/1.609 km) (ES)	Number of sandbars and islands, as previously defined, within a segment combined
	Channel sinuosity (ES)	Channel thalweg distance within a segment divided by the shortest downvalley distance for that segment
	Channel pattern (ES)	Classified as either meandering or braided based on descriptions in Gordon et al. (1992)
	Channel width to length ratio (ES)	Channel width divided by segment length
	Stream slope (m/0.1 km) (ES)	Elevation at the upstream segment boundary minus the elevation at the downstream segment boundary divided by segment length
	Floodplain availability (km) (ES)	Mean channel width in each segment subtracted from the mean width of the area between levees where present or valley walls where levees were absent. Valley and levee widths measured from transects spaced every 2.4 km along the main river
	Deep secondary connected channel density (#/160.9 km) (ES)	Deep secondary connected channels as defined in text
	Non-connected secondary channel density (#/160.9 km) (ES)	Non-connected secondary channels as defined in text
	Small tributary mouth density (#/160.9 km) (ES)	Small tributary mouths as defined in text
	Large tributary mouth density (ES)	Large tributary mouths as defined in text
	River bend density (#/160.9 km) (ES)	River bends defined as a bend encompassing an outside and inside bend between two channel cross-overs

Table 3A.1. continued.

Scale	Variable	Description
		Physical Habitat (con't)
Segment (con't)		
	Macrohabitat diversity index (ES)	Shannon-Weiner index following Ney (1999) based on counts of five macrohabitat types; river bend, large tributary mouth, small tributary mouth, deep secondary connected channel, and backwater. Backwaters included non-connected secondary channels, oxbow lakes, scour holes, and vegetated bays. Counts of all macrohabitat types except large tributaries were standardized to the # / 160.9 km
	Distance to upstream impoundment (km) (ES)	Distance from upstream segment boundary to closest upstream impoundment. Canyon Ferry dam used for segment 5. The greatest distance between a study segment and the nearest upstream impoundment (i.e., 1223 km) was used for the Yellowstone River which has no upstream impoundment.
Site		
	Depth (m) (FS)	Measured at three points at sites sampled by the bag seine; 2 m, 6 m, and the greatest distance reached by the seine. A mean of the three points represented depth for that site. One depth measurement was taken at the midpoint of benthic trawl tows and represented these sites.
	Column velocity (m/s) (FS)	Measured at the same sites and in conjunction with depth
	Substrate percentages (silt, sand, gravel) (FS)	Visually assessed from either a hand sample at bag seine sites or by dragging a pipe along the bottom at trawl tow sites
		Water Quality
Segment		
	Water Temperature (^{0}C):	
	Mean water temperature (FS)	Mean of site scale daily measurements
	Minimum daily water temperature (FS)	Minimum daily water temperature measured
	Maximum daily water temperature (FS)	Maximum daily water temperature measured
	Range of daily water temperatures (FS)	Range of daily water temperature measured
	Coefficient of variation (CV) (FS)	CV of daily water temperatures recorded
	Turbidity (NTUs):	
	Mean turbidity (FS)	Mean of site scale daily measurements
	Minimum daily turbidity (FS)	Minimum daily turbidity recorded
	Maximum daily turbidity (FS)	Maximum daily turbidity recorded
Site		
	Turbidity (NTUs) (FS)	One surface measurement at midpoint of site

Table 3A.1. continued.

Scale	Variable	Description
	Flow Regime	
Segment		
	Inter-annual flow statistics	As defined in Colwell (1974) and Resh et al. (1988)
	Constancy (ES)	
	Contingency (ES)	
	Predictability (ES)	
	Constancy/Predictability (ES)	
	Intra-annual flow statistics	As defined in Richter et al. (1996) or Haines et al. (1988)
	CV of daily mean flows within each month (January-December) (ES)	
	Percent of total annual flow present in each month (January-December) (ES)	
	CV of 1-day (i.e., daily) flows for each year (ES)	
	CV of 3-day flows for each year (ES)	
	CV of 7-day (weekly) flows for each year (ES)	
	CV of 30-day (monthly) flows for each year (ES)	
	CV of 90-day (seasonal) flows for each year (ES)	
	Julian date of the 1-day annual minimum flow (ES)	
	Julian date of the 1-day annual maximum flow (ES)	
	Predation	
Segment		
	Catch-per-unit-effort (CPUE-#/haul) of all piscivores collected in bag seine samples (FS)	
	CPUE of all piscivores collected in stationary gill nets (#/1000 hr) (FS)	
	CPUE of introduced and/or commonly stocked sight feeding piscivores in bag seine samples (#/haul) (FS)	
	CPUE of introduced and/or commonly stocked sight feeding piscivores in stationary gill nets (#/1000 hr) (FS)	

Table 3A.2. Univariate logistic regression models associating sicklefin chub presence/absence with independent variables measured in Missouri and lower Yellowstone river study segments in 1996 and 1997. The Wald chi-square statistic tests the significance of each coefficient in the model. The odds ratio is the multiplicative factor by which the odds of a segment having a sicklefin chub present changes when the independent variable increases by one unit. The -2 log-likelihood value and chi-square statistic tests for overall model signficance. Models are listed in decreasing order of significance (i.e., increasing P-values). Models in bold are significant ($P \leq 0.05$) after correction for multiple tests.

	Tests of individual model parameters					Test of the overall model		
Model term	Coefficients	SE	Wald X^2	$P > X^2$	Odds ratio	-2 log Likelihood	-2 log L-X^2	P
			Distance to upstream impoundment (km)					
constant	-1.6215	0.7345	4.87	0.0273		21.544	19.837	0.0001
dist_imp	0.0096	0.0036	7.06	0.0079	1.010			
			Flow constancy					
constant	28.7255	12.8123	5.02	0.0250		23.005	12.589	0.0004
constncy	-0.4860	0.2178	4.97	0.0257	0.615			
			Average turbidity (NTUs)					
constant	-1.3154	0.7392	3.16	0.0751		29.106	12.275	0.0005
turb_ave	0.0314	0.0140	5.03	0.0248	1.032			
			Percent of annual flow in August					
constant	10.8767	4.6803	5.40	0.0201		26.074	11.289	0.0008
aug_perc	-1.0669	0.4708	5.13	0.0235	0.344			
			CV of July daily flows					
constant	-1.6671	0.9216	3.27	0.0705		26.573	10.789	0.0010
jul_cv	0.1878	0.0715	6.89	0.0087	1.207			
			Minimum daily turbidity (NTUs)					
constant	-1.2788	0.7360	3.01	0.0823		30.533	10.848	0.0010
turb_min	0.0785	0.0329	5.68	0.0171	1.082			
			Percent of annual flow in September					
constant	8.7061	3.4839	6.24	0.0125		26.647	10.716	0.0011
sep_perc	-0.9395	0.3902	5.79	0.0161	0.391			
			Percent of annual flow in October					
constant	7.1856	2.7767	6.69	0.0097		28.267	9.096	0.0026
oct_perc	-0.7343	0.3001	5.98	0.0144	0.480			
			CV of annual 1-day flows					
constant	-3.5171	1.9473	3.26	0.0709		28.764	8.598	0.0034
day1_cv	0.1193	0.0582	4.20	0.0404	1.127			

Table 3A.2. continued.

Model term	Tests of individual model parameters: Coefficients	SE	Wald X^2	$P > X^2$	Odds ratio	Test of the overall model: -2 log Likelihood	-2 log L-X^2	P
				CV of September daily flows				
constant	-1.8109	1.1777	2.3600	0.1241		29.159	8.203	0.0042
sep_cv	0.5465	0.2744	3.9653	0.0464	1.727			
				CV of annual 3-day flows				
constant	-3.3110	1.8724	3.12	0.0770		29.172	8.191	0.0042
day3_cv	0.1146	0.0566	4.09	0.0430	1.121			
				CV of October daily flows				
constant	-1.5524	1.0093	2.36	0.1240		29.638	7.725	0.0054
oct_cv	0.5198	0.2499	4.32	0.0375	1.682			
				Flow predictability				
constant	23.0002	10.1649	5.11	0.0237		27.895	7.699	0.0055
predicta	-0.3373	0.1513	4.9716	0.0258	0.714			
				CV of annual 7-day flows				
constant	-2.9682	1.7701	2.81	0.0936		29.887	7.476	0.0063
day7_cv	0.1076	0.0550	3.83	0.0503	1.114			
				CV of January daily flows				
constant	-1.9386	1.1530	2.82	0.0927		29.901	7.462	0.0063
jan_cv	0.2753	0.1239	4.93	0.0263	1.317			
				Percent of annual flow in June				
constant	-3.0341	1.9261	2.48	0.1152		30.578	6.785	0.0092
jun_perc	0.3161	0.1776	3.16	0.0750	1.372			
				CV of annual 30-day flows				
constant	-2.1336	1.4799	2.07	0.1494		31.432	5.930	0.0149
day30_cv	0.0957	0.0531	3.24	0.0717	1.100			
				Maximum daily turbidity (NTUs)				
constant	-0.3949	0.5322	0.55	0.4581		35.475	5.906	0.0151
turb_max	0.0037	0.0020	3.14	0.0762	1.004			
				CV of February daily flows				
constant	-1.0382	0.9062	1.31	0.2519		31.715	5.648	0.0175
feb_cv	0.0901	0.0486	3.43	0.0637	1.094			
				CV of May daily flows				
constant	-0.7851	0.7404	1.12	0.2889		31.734	5.628	0.0177
may_cv	0.0750	0.0364	4.23	0.0395	1.078			

Table 3A.2. continued.

Model term	Tests of individual model parameters: Coefficients	SE	Wald X^2	$P > X^2$	Odds ratio	Test of the overall model: -2 log Likelihood	-2 log L-X^2	P
				Percent of annual flow in January				
constant	3.8003	1.5515	5.99	0.0143		31.790	5.573	0.0182
jan_perc	-0.6090	0.2836	4.61	0.0318	0.544			
				CV of annual 90-day flows				
constant	-1.5261	1.1561	1.74	0.1868		32.185	5.178	0.0229
day90_cv	0.1046	0.0568	3.39	0.0655	1.110			
				Channel width:length ratio				
constant	1.1203	0.5395	4.31	0.0378		36.242	5.139	0.0234
chwid_le	-0.1157	0.0859	1.81	0.1780	0.891			
				Spatial autocorrelation				
constant	-0.3616	0.5374	0.45	0.5013		36.490	4.891	0.0270
autocorr	0.1892	0.1015	3.47	0.0623	1.208			
				Number of large tributaries				
constant	-0.2630	0.5021	0.27	0.6005		36.521	4.860	0.0275
trm_lrge	1.2109	0.6313	3.67	0.0551	3.357			
				CV of June daily flows				
constant	-0.9054	0.8385	1.16	0.2803		32.691	4.671	0.0307
jun_cv	0.1190	0.0601	3.91	0.0479	1.126			
				Floodplain availability (km)				
constant	1.4082	0.6405	4.83	0.0279		36.818	4.563	0.0327
floodavl	-0.2087	0.1186	3.09	0.0785	0.812			
				Maximum daily temperature(^{0}C)				
constant	-4.2512	2.4494	3.01	0.0826		36.849	4.531	0.0333
temp_max	0.1894	0.0970	3.81	0.0508	1.209			
				Flow constancy/predictability				
constant	14.1566	8.0184	3.11	0.0775		32.078	3.516	0.0608
con_pred	-1.5742	0.9201	2.92	0.0871	0.207			
				Percent of annual flow in November				
constant	3.5655	1.8598	3.67	0.0552		34.080	3.283	0.0700
nov_perc	-0.3418	0.2058	2.75	0.0967	0.711			
				Mean daily temperature(^{0}C)				
constant	-2.7182	1.9026	2.04	0.1531		38.215	3.166	0.0752
temp_ave	0.1470	0.0863	2.89	0.0886	1.158			

Table 3A.2. continued.

Model term	Tests of individual model parameters: Coefficients	SE	Wald X^2	$P > X^2$	Odds ratio	Test of the overall model: -2 log Likelihood	-2 log L-X^2	P
				CV of August daily flows				
constant	-0.1553	0.6294	0.06	0.8051		34.663	2.700	0.1004
aug_cv	0.1052	0.0721	2.12	0.1449	1.111			
				Channel pattern				
constant	1.0986	0.5774	3.62	0.0571		38.722	2.658	0.1030
chan_pat	-1.2321	0.7754	2.52	0.1120	0.292			
				Percent of annual flow in December				
constant	4.4254	2.9179	2.30	0.1294		35.265	2.098	0.1475
dec_perc	-0.6160	0.4629	1.77	0.1833	0.540			
				Number of sandbars/160.9 km				
constant	1.2095	0.6732	3.22	0.0724		39.307	2.073	0.1499
sandbar	-1.0020	0.7117	1.98	0.1591	0.367			
				Bag seine catch-per-unit-effort of introduced/commonly stocked sight feeding piscivores (#/haul)				
constant	0.7273	0.4116	3.12	0.0773		37.517	1.913	0.1666
bs_see	-0.0007	0.0008	0.82	0.3630	0.999			
				CV of November daily flows				
constant	-0.1807	0.7246	0.06	0.8030		35.573	1.789	0.1810
nov_cv	0.0848	0.0661	1.64	0.1994	1.088			
				Gill net catch-per-unit-effort of all piscivores (#/1000 hr)				
constant	-0.1143	0.5702	0.04	0.8411		39.623	1.758	0.1848
pred_sgn	0.0043	0.0034	1.54	0.2143	1.004			
				Number of small tributaries/160.9 km				
constant	1.1239	0.6582	2.91	0.0877		39.690	1.691	0.1935
trm_smll	-0.0707	0.0556	1.61	0.2036	0.932			
				Channel sinuosity				
constant	-3.6116	3.3279	1.17	0.2778		39.756	1.624	0.2025
sinuosty	3.2796	2.6860	1.49	0.2221	26.565			
				Bag seine catch-per-unit-effort of all piscivores (#/haul)				
constant	0.6183	0.3971	2.42	0.1194		39.765	1.616	0.2037
pred_bs	-0.0006	0.0007	0.80	0.3694	0.999			
				Percent of annual flow in May				
constant	-1.6174	1.8821	0.73	0.3901		35.761	1.602	0.2056
may_perc	0.2169	0.1780	1.48	0.2230	1.242			

Table 3A.2. continued.

Model term	Tests of individual model parameters: Coefficients	SE	Wald X^2	$P > X^2$	Odds ratio	Test of the overall model: -2 log Likelihood	-2 log L-X^2	P
				Minimum daily temperature (^{0}C)				
constant	-1.2574	1.4801	0.72	0.3956		39.919	1.462	0.2266
temp_min	0.0925	0.0779	1.41	0.2348	1.097			
				Flow contingency				
constant	-0.7170	1.1389	0.39	0.5290		34.175	1.419	0.2335
contingy	0.1385	0.1214	1.30	0.2539	1.149			
				Channel slope (m/0.1 km)				
constant	-0.9116	1.3263	0.47	0.4918		40.070	1.310	0.2523
slope	0.7397	0.7064	1.09	0.2950	2.095			
				Range of daily temperatures				
constant	-0.4317	0.8776	0.24	0.6228		40.083	1.297	0.2547
temp_ran	0.1462	0.1338	1.19	0.2747	1.157			
				Number of sand bars &/or islands per 160.9 km				
constant	0.9945	0.6728	2.18	0.1393		40.393	0.988	0.3202
sand_isl	-0.5733	0.5830	0.96	0.3255	0.564			
				Number of secondary connected channels per 160.9 km				
constant	0.1383	0.4930	0.07	0.7791		40.449	0.932	0.3343
scc_s	0.0163	0.0174	0.87	0.3501	1.016			
				Channel width (km)				
constant	1.3248	1.0230	1.67	0.1953		40.529	0.852	0.3560
chan_wid	-2.3640	2.5784	0.84	0.3592	0.094			
				CV of March daily flows				
constant	0.0639	0.8288	0.01	0.9386		36.702	0.661	0.4161
mar_cv	0.0349	0.0458	0.57	0.4465	1.035			
				Julian date of the minimum flow				
constant	0.3993	0.4946	0.65	0.4194		36.762	0.601	0.4382
date_min	0.0023	0.0031	0.56	0.4531	1.002			
				Number of islands per 160.9 km				
constant	0.1466	0.5488	0.07	0.7893		40.781	0.600	0.4386
islands	1.7123	2.3148	0.54	0.4595	5.542			
				Gill net catch-per-unit-effort of introduced/commonly stocked sight feeding piscivores (#/1000 hr)				
constant	0.2286	0.4800	0.22	0.6338		40.825	0.555	0.4561
see_sgn	0.0023	0.0033	0.51	0.4745	1.002			

Table 3A.2. continued.

Model term	Tests of individual model parameters: Coefficients	SE	Wald X^2	$P > X^2$	Odds ratio	Test of the overall model: -2 log Likelihood	-2 log L-X^2	P
				CV of December daily flows				
constant	0.1565	0.7600	0.04	0.8369		36.825	0.538	0.4634
dec_cv	0.0234	0.0321	0.52	0.4667	1.024			
				Macrohabitat diversity index				
constant	-1.1969	2.4478	0.23	0.6249		40.912	0.469	0.4933
diversty	1.5091	2.2128	0.46	0.4952	4.523			
				Percent of annual flow in July				
constant	2.0330	2.1842	0.86	0.3520		36.930	0.433	0.5104
jul_perc	-0.1344	0.2061	0.42	0.5144	0.874			
				CV of April daily flows				
constant	0.9239	0.5939	2.42	0.1198		36.942	0.421	0.5166
apr_cv	-0.0168	0.0258	0.42	0.5159	0.983			
				Number of river bends per 160.9 km				
constant	-0.0746	0.9523	0.01	0.9376		41.010	0.371	0.5425
rv_bends	0.0135	0.0224	0.36	0.5475	1.014			
				Percent of annual flow in March				
constant	-0.2626	1.8290	0.02	0.8859		37.106	0.257	0.6121
mar_perc	0.1341	0.2667	0.25	0.6151	1.143			
				Julian date of the maximum flow				
constant	1.2061	1.2346	0.95	0.3286		37.128	0.235	0.6279
date_max	-0.0034	0.0071	0.23	0.6273	0.997			
				CV of daily water temperatures				
constant	0.6976	0.6309	1.22	0.2689		41.160	0.221	0.6382
temp_cv	-0.0287	0.0611	0.22	0.6384	0.972			
				Percent of annual flow in February				
constant	1.3074	1.9999	0.42	0.5133		37.247	0.116	0.7331
feb_perc	-0.1124	0.3299	0.11	0.7333	0.894			
				Percent of annual flow in April				
constant	0.4832	1.3153	0.13	0.7133		37.347	0.016	0.8995
apr_perc	0.0185	0.1470	0.01	0.8997	1.019			
				Number of non-connected secondary channels per 160.9 km				
constant	0.4428	0.5565	0.63	0.4262		41.379	0.002	0.9680
scn_s	0.0013	0.0346	0.01	0.9681	1.001			

Appendix 3B. Figures illustrating conceptual locations of in-channel macrohabitat strata.

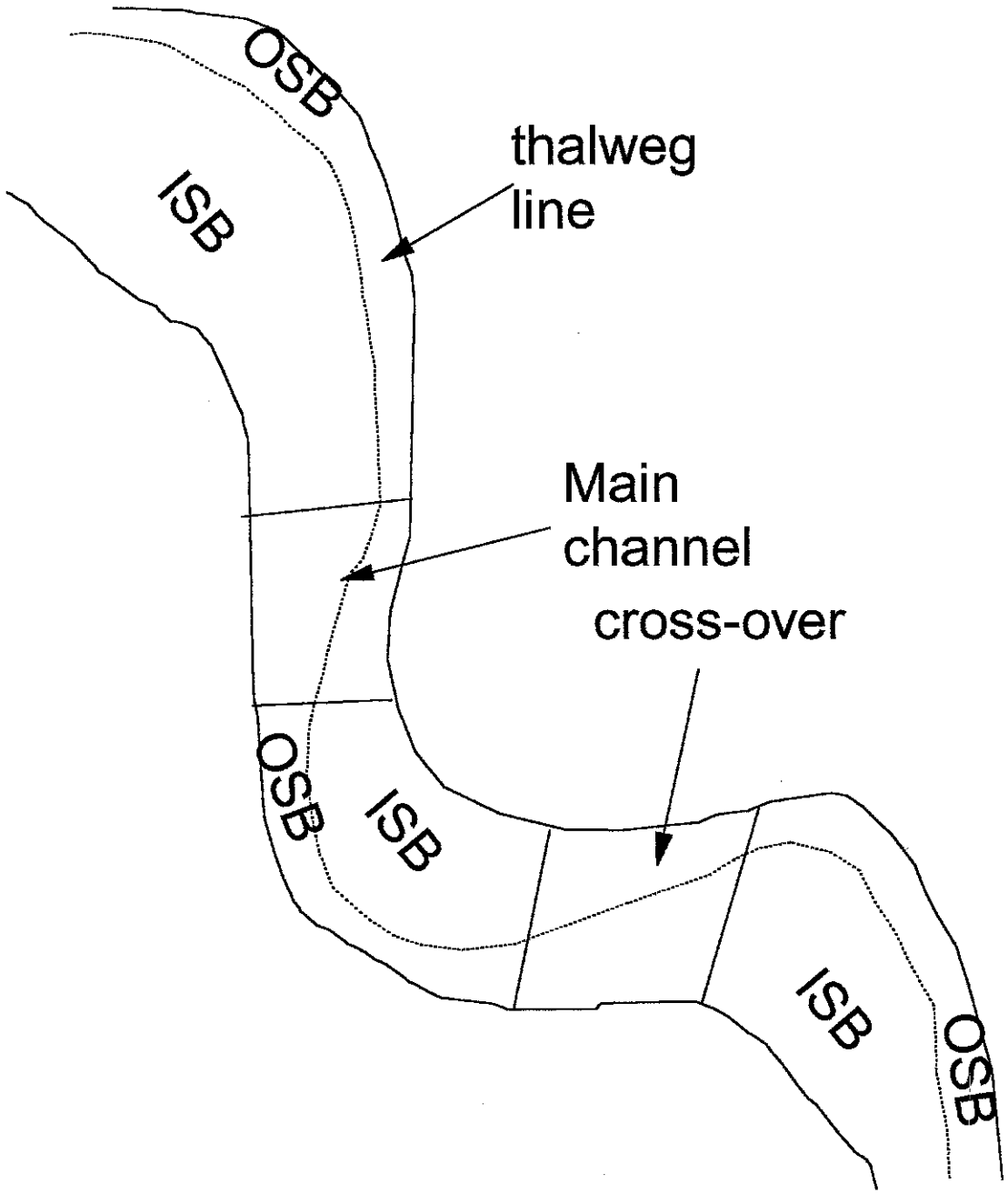

Figure 3B.1. Hypothetical map of the Missouri or lower Yellowstone river showing boundaries of macrohabitats: main channel crossover, outside bends (OSB) and inside bends (ISB).

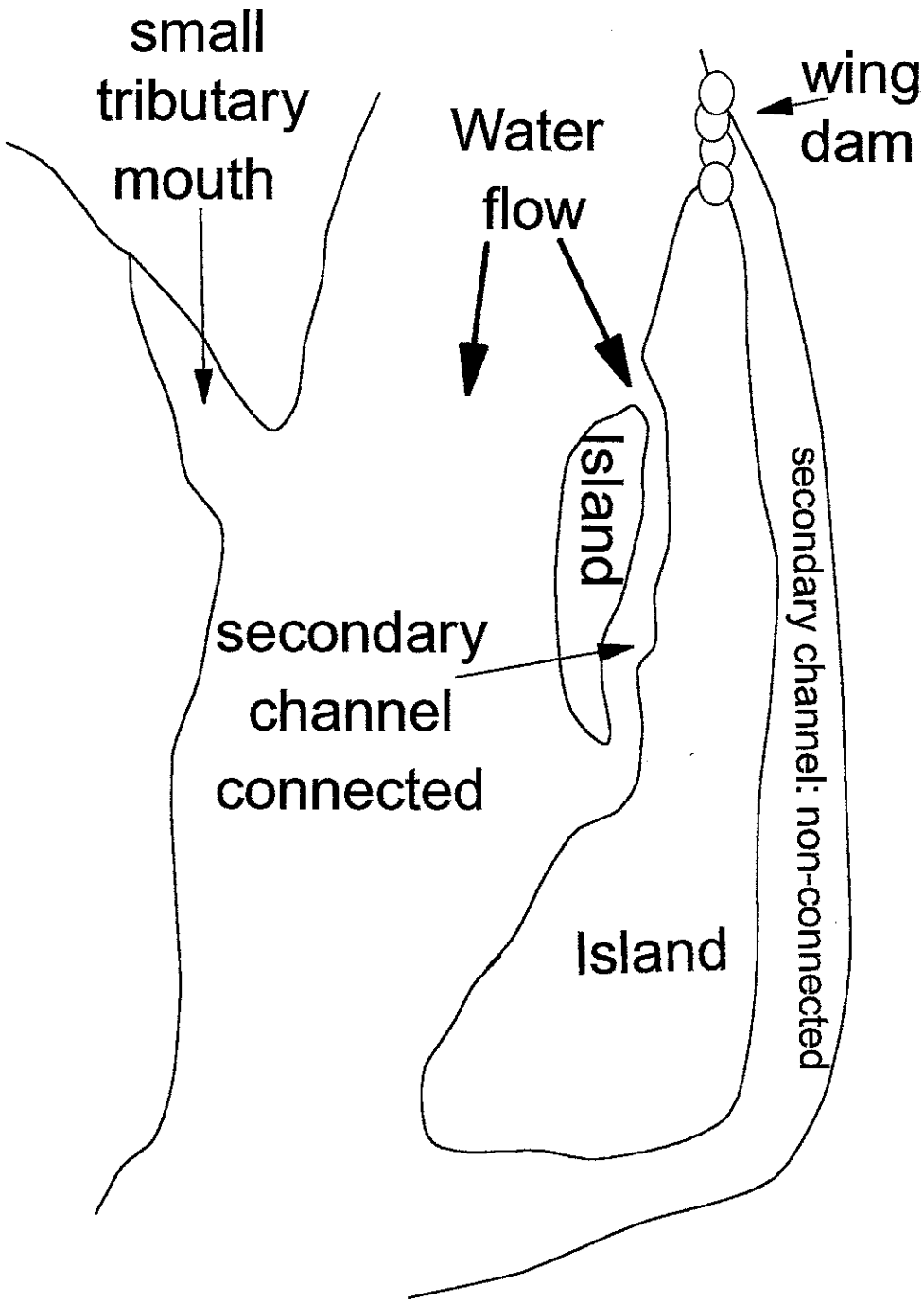

Figure 3B.2. Hypothetical map of the Missouri or lower Yellowstone river showing boundaries of macrohabitats: secondary channel connected, secondary channel non-connected, and tributary mouth.

VITA

Douglas Joseph Dieterman was born 22 January 1970 in the Upper Mississippi River town of Winona, Minnesota. He grew up there and graduated from Cotter High School in 1988. He attended St. Mary's University in his hometown and graduated in 1992 with a B. A. in Environmental Biology. He earned an M. S. Degree in Wildlife and Fisheries Sciences from South Dakota State University (1995) in Brookings. While there, he studied prairie stream fish communities. The Ph.D. degree in Fisheries and Wildlife was awarded in December 2000 by the University of Missouri-Columbia. Doug is currently employed by the Minnesota Department of Natural Resources, Section of Fisheries. He is married to the former Terrie Lynn Morey of Stockton, Minnesota and has two wonderful girls, Felicia Ashley and Wren Renee. He and his family enjoy hiking, fishing, hunting, and other outdoor activities.