

**BRASSY MINNOW IN COLORADO PLAINS STREAMS:
IDENTIFICATION, HISTORICAL DISTRIBUTION, AND
HABITAT REQUIREMENTS AT MULTIPLE SCALES**

by

Julie A. Scheurer and Kurt D. Fausch



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**Colorado
State
University**

**Brassy Minnow in Colorado Plains Streams:
Identification, Historical Distribution, and Habitat
Requirements at Multiple Scales**

Julie A. Scheurer

and

Kurt D. Fausch
Principal Investigator

Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins, CO 80523

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EXECUTIVE SUMMARY

BRASSY MINNOW IN COLORADO PLAINS STREAMS: IDENTIFICATION, HISTORICAL DISTRIBUTION, AND HABITAT REQUIREMENTS AT MULTIPLE SCALES

The brassy minnow (*Hybognathus hankinsoni*) has apparently declined in distribution and abundance in Colorado since the 1970s and was one of three plains fish species to be listed as threatened or endangered by the State of Colorado in 1998. ***Our research objectives were to determine the historic distribution and critical habitat requirements of brassy minnow.*** This information will aid fishery managers in efforts to locate suitable habitat and potentially restore the species to more of its native range, thereby precluding need for further listing.

Understanding the native range of brassy minnow is complicated because it is difficult to distinguish from a closely related species that also occurs in the region, the plains minnow (*H. placitus*). In addition, both species were originally classified as a different species in the same genus (Mississippi silvery minnow, *H. nuchalis*) before they were first described in 1929 (brassy minnow) and 1962 (plains minnow). As a result, many early collections were still classified as Mississippi silvery minnow, even though this species does not occur in Colorado, and many later collections were misclassified as the wrong species due to their similarity. In Chapter I of this final report, we detail a method for distinguishing brassy minnow from plains minnow. We developed logistic regression models from 12 candidate morphometric measurements to predict species identity of *Hybognathus* collections from Colorado and adjacent counties ($n=1154$ specimens in 134 lots). The best model included orbit diameter, standard length, and eye position, and correctly predicted 98% of the individuals and 100% of the museum lots. ***In***

general, brassy minnow have larger eyes with centers even with the tip of the snout, whereas plains minnow have smaller eyes centered above the tip of the snout. We emphasize that model predictions should be verified with the supplemental qualitative characteristics such as fin shape, pigmentation, and maximum body size that are described in the final report. Collection locality and habitat type are also useful for verifying model predictions. Two characteristics used in earlier keys, the number of scale radii and the shape of the basioccipital process, proved to be unreliable and should not be used for identification. Reference collections of these species are housed at the Colorado State University Larval Fish Laboratory.

By correctly identifying the 134 museum collections of Hybognathus, we were able to clarify the historic distributions of the two species in Colorado and vicinity. The two species were historically sympatric (i.e., found together) in the lower South Platte, North Platte, Republican, and Smoky Hill river basins, whereas plains minnow was allopatric (alone) in the Arkansas River basin. Brassy minnow was allopatric in the Transition Zone tributaries of the upper South Platte and North Platte rivers and Lodgepole Creek.

In Chapter II, we report on the ecological requirements of brassy minnow in an intermittent Great Plains stream in eastern Colorado, the Arikaree River. In 1999, the first year of this study, we sampled locations throughout eastern Colorado where brassy minnow had most recently been collected to locate populations for further study. We selected the Arikaree River because it presented a unique opportunity to study brassy minnow population dynamics at three spatial scales (habitat unit, segment, basin) across a gradient of stream intermittency (i.e., drying). This allowed us to determine their thresholds of tolerance and assess how much perennial water is necessary to sustain populations. A total of 99 habitat units (pools, backwater pools, and runs) in three 4-mile (6.4 km) long segments ranging from perennial to seasonally dry

were sampled during five surveys in 2000 and 2001, the two driest summers on record. On each survey, we measured habitat variables in each unit, mapped flow connections between habitat units, and sampled each unit using two-pass depletion seining to determine the presence or absence of brassy minnow. Basin scale flow connectivity was also mapped three times by aerial flights along the 66-mile (106 km) mainstem of the Arikaree River in Colorado.

At the basin scale, total habitat for brassy minnow was restricted to about 47 miles (75 km) of the mainstem Arikaree River upstream from the confluence, but during early summer 2001 only a 16-mile (26 km) stretch that contained our upstream segment had continuous flow. At the segment scale, drying occurred in all segments each summer, but was most pronounced in the downstream segment. The middle segment was intermediate in its degree of drying and the upstream segment had the most perennial habitat. ***The amount of available habitat, number of habitat units occupied by brassy minnow, persistence of brassy minnow through summer drying, and extent of recolonization after the channel rewetted were highest in the upstream segment and lowest in the downstream segment, corresponding to the gradient of flow intermittency.*** Of the 86 pools sampled across the three segments in 2000, brassy minnow were present in 65 during at least one survey. They persisted through summer 2000 in about half of the pools where they were ever present (n=30, 46%), were extirpated by drying from 17 pools (26%) and emigrated to adjacent habitat units or were extirpated from the other 18 pools (28%) that remained wet. We first identified factors that predicted brassy minnow persistence in pools that remained wet through the summer drought, and then predicted which pools would persist through summer drying.

Models of brassy minnow persistence through August 2000 were developed using variables measured at both the pool and segment scales in August. Then, because drying was

apparently the dominant mechanism extirpating brassy minnow, models of pool persistence through August 2000 were developed based on variables measured in June. ***Logistic regression showed that brassy minnow were more likely to persist through the summer in deeper pools connected to other habitats, and more likely to persist in pools in the upstream segment. The main cause of extirpation was by pool drying, which logistic regression showed was more likely in shallower pools in the drier segments.*** For example, a pool with a maximum depth in June of 0.5 m would have only a 50% probability of persistence in the downstream segment, but a 77% probability of persistence in the middle segment and a 95% probability in the upstream segment. Thus, shallower pools were more likely to persist in the upstream segment and more likely to dry in the downstream and middle segments. Brassy minnow were highly tolerant of physicochemical extremes such as maximum summer temperatures as high as 36°C and minimum dissolved oxygen as low as 0.01 mg/L. Given this high tolerance of harsh conditions, most adult brassy minnow were probably extirpated by pool drying or predation by terrestrial vertebrates when the fish are restricted to shallow drying pools. Overall, the patterns of stream drying at the segment scale were more important predictors of brassy minnow population persistence than water chemistry or habitat features measured at the local or pool scale.

In addition to persistence of brassy minnow and their habitat, we compared several measures of brassy minnow population performance among segments, including survival, growth, and reproductive success. ***Brassy minnow survived to older ages and were larger at older ages in the most perennial segment compared to the others. However, despite poor adult survival in the drier segments, brassy minnow larvae were present in all three segments in both years indicating that they are capable of reproduction and rapid recolonization when water is available.*** Brassy minnow spawned from mid-April to mid-May and larvae appeared

from mid-May through mid-June. The beginning of larval hatching coincided with the onset of pumping for irrigation and rapid dewatering of the driest segment, which killed most larvae.

Brassy minnow in the Arikaree River showed evidence of metapopulation dynamics because persistence was related to patch size (depth) and isolation, with extinctions more likely in shallow, disconnected pools. Moreover, some suitable habitats were empty, there were asynchronous local dynamics among pools, and the species persisted at the segment (regional) scale despite population turnover. The dynamic nature of plains streams, differences in flow regimes among segments, and the large scales over which brassy minnow fulfill their life history requires management at the ‘intermediate’ segment scale for effective conservation.

To improve habitat conditions in the Arikaree River and enhance brassy minnow populations we recommend several measures:

- ***Increase spring flows to prevent early drying of the downstream segment to improve survival and recruitment of brassy minnow larvae.***
- ***Maintain riparian and stream processes that create deep pools which provide critical refuges for brassy minnow during summer drying.*** Intact riparian vegetation binds stream banks and allows deep pools to be carved by periodic floods from summer thunderstorms. In addition, beaver dams often create deep pools that persist through summer.
- ***Maintain the native fish community and prevent invasion of exotic predators or competitors.*** Although most nonnative fishes apparently cannot withstand the harsh physicochemical conditions of plains streams, off-channel ponds supplied by groundwater can provide refuges that harbor nonnative predators like

largemouth bass. These fishes can emigrate and decimate native fishes in adjacent stream habitats.

- ***Investigate the effects of irrigation on groundwater hydrology that maintains stream flow and permanent refuge pools.*** These pools and backwaters are critical for brassy minnow larval and adult survival during periods of summer drying and winter freezing. A better understanding of the linkages between land and water use and plains fish populations at segment scales will be needed for effective conservation of these fishes.

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CHAPTER I

**RESOLVING TAXONOMY AND HISTORIC DISTRIBUTION FOR
CONSERVATION OF RARE GREAT PLAINS FISHES: *HYBOGNATHUS*
(TELEOSTEI: CYPRINIDAE) IN EASTERN COLORADO BASINS**

To be submitted to Copeia

ABSTRACT

Conservation of declining Great Plains fishes is often hampered by a limited understanding of their taxonomy and historic distribution. For example, the similar morphology and confused historical taxonomy of *Hybognathus hankinsoni* (brassy minnow) and *H. placitus* (plains minnow) have made determinations of their historic distributions and conservation status unclear in eastern Colorado basins. We developed logistic regression models from morphometric measurements to predict species identity of *Hybognathus* collections from Colorado and adjacent counties ($n=1154$ specimens in 134 lots). A model based on orbit diameter, standard length, and eye position correctly predicted 98% of the specimens examined and 100% of the museum lots. *Hybognathus hankinsoni* have larger eyes with centers even with the tip of the snout, whereas *H. placitus* have smaller eyes centered above the tip of the snout. The two species were historically sympatric in the Platte, Republican, and Smoky Hill river basins, whereas *H. placitus* was allopatric in the Arkansas River Basin. The taxonomic characters defined here will allow accurate identification of future collections to determine the status of these native fishes.

Native fishes of the Great Plains are well known for their tolerance of harsh physicochemical conditions, including floods, droughts, high water temperatures, and low dissolved oxygen concentrations (Matthews, 1988). Despite this tolerance, distributions of a large number of taxa have declined in recent decades. Four fish species endemic to the Great Plains region are listed as threatened or endangered under the Endangered Species Act (*Notropis girardi*, *N. topeka*, *Noturus placidus*, *Scaphirhynchus albus*) and one is a candidate for federal listing (*Etheostoma cragini*). Many other wide-ranging native fishes of the Great Plains have been extirpated or are in decline throughout much of the western part of their range (Rabeni, 1996; Fausch and Bestgen, 1997). For example, in Colorado, 6 of 38 native plains species are known to have been extirpated since the first fish collections were made in the late 1800s (*Anguilla rostrata*, *Nocomis biguttatus*, *Notropis heterolepis*, *N. girardi*, *Macrhybopsis tetranema*, *Stizostedion* sp.), and an additional 13 species are listed by the state as endangered, threatened, or of special concern (Nesler et al., 1997, 1999). Therefore, half of the native taxa have declined or been lost.

Conservation efforts to restore declining species are often hampered by two problems. First, there are few early collections available to determine historic distributions. Most were made after habitat was already altered, some native species were extirpated, and other nonnative species introduced. For example, fish were collected from only 12 locations before 1900 in the Great Plains portion of eastern Colorado (Fausch and Bestgen, 1997), yet diversion of water for irrigation was well developed by the 1860s. As a result, the historic distributions of fishes described only in early reports, such as walleye or sauger (*Stizostedion* sp.) from the South Platte River and speckled chub (*M. tetranema*; formerly *M. aestivalis tetranemus*) from the Arkansas River are unknown. Even their identity cannot be verified because no museum specimens were

preserved before these species were extirpated from the state (Fausch and Bestgen, 1997; Eisenhour, 1999; Luttrell et al., 1999).

A second problem is that identification of some taxa is difficult, resulting in inaccurate field surveys, or the historical taxonomy is confused so that the identity of museum specimens is unclear. Consequently, the historic distributions and current conservation status of some taxa are uncertain. Good examples of this are minnows in the genus *Hybognathus* in basins of eastern Colorado. Fishes in this taxon are similar morphologically, resulting in considerable taxonomic confusion and revision of the genus over the past 150 years (Cook et al., 1992; Bestgen and Propst, 1996). At least 15 species and subspecies have been described (Bestgen and Propst, 1996) of which 7 are currently recognized (Robbins et al. 1991). In the western Great Plains, three forms, later recognized as *Hybognathus hankinsoni* (brassy minnow), *H. placitus* (plains minnow), and *H. argyritis* (western silvery minnow), were all originally considered variants of *H. nuchalis* (Mississippi silvery minnow; Ellis, 1914). Based on current classification, *H. argyritis* and *H. nuchalis* do not occur in Colorado (Lee et al., 1980). *Hybognathus hankinsoni* was not described until 1929 (Hubbs in Jordan, 1929; Bailey, 1954), *H. placitus* was not separated from *H. nuchalis* until 1962 (Niazi and Moore, 1962; Al-Rawi and Cross, 1964), and *H. argyritis* was not accorded full specific status until 1971 (Pflieger, 1971). As a result, many historic museum collections from the Great Plains (e.g., Ellis, 1914) are still classified as *H. nuchalis*, even though this species does not occur in the region.

Surveys during the past 20 years have suggested that the two *Hybognathus* species in Colorado are in decline (Propst and Carlson, 1986), prompting a listing of *H. hankinsoni* as threatened, and *H. placitus* as endangered in Colorado in 1998 (Nesler et al., 1997, 1999). However, because of the relatively recent taxonomic clarifications, unreliable taxonomic keys,

and lack of museum specimens to confirm many published records, the historic and current distributions of *H. hankinsoni* and *H. placitus* at the western extent of their range in Colorado are unclear (Fausch and Bestgen, 1997). For example, Ellis (1914) recognized small- and large-eyed forms of *H. nuchalis* throughout warm water reaches of the South Platte River, but the identity of these early collections and many other extant specimens remains undetermined. More recent field collections may also have been misidentified because existing keys are inadequate to distinguish the two species. Therefore, before managers can propose conservation measures, better taxonomic characteristics are needed to accurately identify museum specimens and determine historic and current distributions of these taxa.

Our goal was to first develop a quantitative model based on taxonomic characteristics to distinguish *H. hankinsoni* from *H. placitus*. The model and additional qualitative characteristics were then used to identify all available museum specimens of *Hybognathus* from Colorado and adjacent counties in neighboring states, which allowed clarification of the historic distributions of *H. hankinsoni* and *H. placitus* in Colorado basins. This work, coupled with ongoing sampling and accurate identification, will help managers determine how much of their historic range in Colorado these two species currently occupy, and where to focus restoration and conservation efforts.

Materials and Methods

To select taxonomic characters that separate *H. hankinsoni* from *H. placitus*, material was obtained from locations in states where the species are allopatric ('knowns' hereafter). A suite of characters suggested by earlier keys and studies (Hubbs and Lagler 1964; Bestgen and Propst 1996) was measured. Measurements of specimens of *H. placitus* from the Canadian River, New Mexico (see Material Examined; n=51) and *H. hankinsoni* from four locations in Michigan (n=81) were used to develop a quantitative model to separate the two species. The lectotype of *H. hankinsoni* and four syntypes of *H. placitus* were also measured to test and verify the model.

We obtained all available museum collections of *Hybognathus* from Colorado and adjacent counties in neighboring states, totaling 1753 fish in 134 lots (see Material Examined; Scheurer, 2002) for examination and reidentification. Specimens included those from the earliest collections in the state by Jordan (1891) and Juday (1904). All these lots were considered *Hybognathus* of unknown species identity for the analysis ('unknowns', hereafter). The quantitative model was used to predict the identity of unknowns, and additional qualitative characters were used to verify model predictions.

Morphometric analysis

Nine quantitative and three qualitative characters were measured from the 132 known specimens to develop the key, and from 1154 unknown fish to analyze their identity (some lots were subsampled). When collections contained many individuals, a subsample of at least 30 fish of all sizes represented was measured. Damaged, deformed, or poorly preserved fish were excluded. Standard length, head length, pectoral fin length, snout length, orbit diameter, body depth, body width, caudal peduncle depth, and gape width were measured following Hubbs and Lagler (1964). Qualitative characters included snout shape, dorsal fin shape, and eye position. Snout shape and dorsal fin shape were categorized as either rounded or pointed. Eye position referred to the location of the center of the eye relative to a horizontal line through the anterior most tip of the snout, and was categorized as either even or above (Figure 1.1). Quantitative characters were measured to the nearest 0.01 mm using digital calipers.

Model Development and Testing

Logistic regression (SAS/STAT[®], 2000, PROC LOGISTIC) was used to develop a model for separating the two species, based on the morphometric independent variables measured from the known specimens. Model selection followed Burnham and Anderson (1998) using Akaike's Information Criterion (AIC) to select the top candidate models. This model selection procedure is based on an information-theoretic approach that is superior to traditional hypothesis testing for observational data such as these because it allows comparison of more than two models at once and balances precision and bias (Burnham and Anderson, 1998; Franklin et al., 2000).

Species identity (*H. hankinsoni* or *H. placitus*) was first modeled as a function of each of the eight quantitative characters (not including standard length), their ratios with standard length, and each of the three qualitative characters. Additional candidate models were developed using each quantitative character and standard length, the three variables considered *a priori* to be most diagnostic (orbit diameter, eye position, standard length), and these three variables with various combinations of their two-way interactions. The value of AIC_c (AIC corrected for small-sample bias), and Akaike weights were calculated and used to rank models (Burnham and Anderson, 1998). Models with the lowest AIC_c and highest Akaike weight were given the most consideration. An added criterion for selecting the best model was the percentage of known specimens that it classified as the correct species (Hosmer and Lemeshow, 2000).

Once the diagnostic model was developed using known specimens, measurements from the unknown *Hybognathus* from Colorado were entered in the model to predict their identity. These predictions were verified by the second author using supplemental characters to evaluate the efficacy of the model. With the exception of two large museum lots (UMMZ 135130 and

32241) for which only 30 specimens each could be obtained, all fish in each lot, including those not measured, were examined to ensure that no additional species were present.

The model developed from the known specimens proved only moderately useful for separating all individuals of the two species, so the two best candidate models were refit using the 1154 verified *Hybognathus* from Colorado to improve predictions. The identity of the type specimens was predicted to validate each model. These models were also tested using cross-validation (Hosmer and Lemeshow, 2000; p.186). The data were randomly ordered and divided into 10 equal sets. Ten separate models were fit using 9 of the 10 data sets, leaving out a different set each time. The data excluded were then used to test each model. The average percentage of the specimens classified correctly was used as a criterion to judge each model. Historic distributions of the two species were determined using only specimens we examined and verified. Other unsubstantiated records were not used because of potential taxonomic difficulties.

Scale radii analysis

The number of scale radii has often been cited as a useful characteristic to distinguish *H. hankinsoni* from *H. placitus* (e.g., Beckman, 1952; Baxter and Simon, 1970; Pflieger, 1975). *Hybognathus hankinsoni* is most often described as having about 20 faint or weak scale radii of varying lengths (except 17-19 in Bailey, 1954). In contrast, *H. placitus* is most often reported to have 10-15 strong radii (except <20 in Eddy and Underhill, 1969). No published account describes criteria to distinguish faint, weak, or strong radii.

The number of radii on 82 scales from 60 fish, 30 of each species, were counted to determine the utility of these characteristics for separating the species. Scales were removed from the right

side of the fish, posterior the pectoral fin base and above the lateral line (DeVries and Frie, 1996). Scales were cleaned, mounted on glass slides, and viewed under a compound microscope at 30X and 100X. Distances from the focus to the scale margin were measured at three angles, 45, 90, and 135 degrees from a horizontal line through the focus (Figure 1.2). Radii were categorized as faint, incomplete, or complete by comparing them to the nearest measured distance. Faint radii were less than 30% of the nearest measured distance from focus to scale margin, incomplete radii were 31-67%, and complete radii were greater than 67% the distance. In addition, to determine variation in scale radii counts within individuals, two scales were read from each of 22 fish, 11 of each species.

Results

Model Based on Known Specimens

Logistic regression analysis revealed that the best single quantitative variable for distinguishing between the known *H. hankinsoni* and *H. placitus* was orbit diameter. *Hybognathus hankinsoni* of a given length had a larger orbit diameter than *H. placitus*, and orbit diameter also increased allometrically with standard length for both species ($P < 0.001$ for both; Figure 1.3). The model based on these two characteristics had the lowest AIC_c value (41.73), accounted for a high proportion of the Akaike weight of the 27 models with valid parameter estimates (0.69; weights sum to 1.0), and correctly classified 96% of the known specimens. In fact, only one other model, standard length, orbit diameter, and their interaction, received any support ($AIC_c = 43.35$) and accounted for nearly all the remainder of the Akaike weight (0.31). Therefore, there was no support for including any of the other variables and the model based on orbit diameter and standard length was selected as the best model for predictions (Table 1.1).

The model was validated with the type specimens, and correctly predicted the identities of the lectotype of *H. hankinsoni* (UMMZ 84266) and 4 syntypes of *H. placitus* (USNM 89 (n=3), MCZ 1789 (n=1)).

The two-variable equation developed from the knowns for predicting species identity is:

$$P(H. hankinsoni) = \frac{\exp(-16.8465 - 0.8123SL + 18.8391OD)}{1 + \exp(-16.8465 - 0.8123SL + 18.8391OD)}$$

where P = probability of an unknown fish being *H. hankinsoni*, SL = standard length (mm), and OD = orbit diameter (mm). If $P > 0.50$ the fish is predicted to be *H. hankinsoni*, whereas if $P < 0.50$ the fish is predicted to be *H. placitus* (Figure 1.4).

Eye position was also a useful qualitative variable for distinguishing the two species. All of the known *H. hankinsoni* had the even eye position, whereas 88% of the known *H. placitus* had the above eye position (Figure 1.1). However, this variable could not be included in models because there was no variation in eye position of the known *H. hankinsoni* so valid maximum likelihood parameter estimates could not be calculated.

Predictions of Unknown Specimens, and Additional Models

Of 1154 unknown fish measured and verified, 78% were predicted by the model to be the correct species. Of the 212 *H. placitus*, species identities of 210 (99%) were correctly predicted, but species identities of only 73% of the 942 *H. hankinsoni* were predicted correctly. Of the 257 incorrectly predicted specimens, 255 were *H. hankinsoni* with smaller relative orbit diameters than the known specimens from Michigan used to build the model (Figure 1.4). This model is not useful in Colorado because it predicted that these fish were *H. placitus*, which would lead managers to overestimate the distribution and abundance of the rarer of the two species. Because

of this potential bias, we elected to refit the model using all 1154 verified specimens from the region.

This new two-variable model based on orbit diameter and standard length correctly predicted the identity of 88% of the *H. placitus* and 99% of the *H. hankinsoni* verified unknowns (Table 1.1, Figure 1.4). This larger sample included seven *H. hankinsoni* with the ‘above’ eye position, so we also fit a three-variable model including this variable. This model correctly predicted 91% of the *H. placitus* and 99% of the *H. hankinsoni* verified unknowns. The parameters for intercept, orbit diameter, and standard length were similar between these two- and three-variable models, so the $P=0.50$ decision line for predicting species identity was nearly identical for fish with the even eye position. In contrast, the added parameter for eye position allowed more accurate predictions for specimens with the above eye position. The three-variable model correctly predicted the identity of the most fish and had a lower AIC_c than the two-variable model (168.98 vs. 229.92), so it was selected as the best model. For each model, cross validation resulted in identical estimates for the average percentage of fish correctly classified as those presented above because of the large sample size. Both models correctly classified all the type specimens.

The best predictive model, developed from the 1154 Colorado specimens, included standard length, orbit diameter, and eye position (Table 1):

$$P(H. hankinsoni) = \frac{\exp(-11.3796 - 0.8009SL + 18.5823OD - 5.3898EP)}{1 + \exp(-11.3796 - 0.8009SL + 18.5823OD - 5.3898EP)}$$

where P = probability of an unknown fish being *H. hankinsoni*, SL = standard length (mm), OD = orbit diameter (mm), and EP = eye position ($EP=0$ for ‘even’, $EP= 1$ for ‘above’). If $P > 0.50$ the fish is predicted to be *H. hankinsoni*, whereas if $P < 0.50$ the fish is predicted to be *H. placitus*. For example, the model predicts that a fish with standard length of 50 mm, orbit

diameter of 3.25 mm, and even eye position has nearly a 100% probability of being *H. hankinsoni*, whereas a fish with an orbit diameter of 2.75 mm, the same standard length, and the above eye position has <1% probability of being *H. hankinsoni* (Figure 1.4). Therefore, the smaller-eyed fish is predicted to be *H. placitus*.

Overall, all but 25 of the 1154 unknown specimens (2%) were correctly classified by the final model. Moreover, in all lots the majority ($\geq 67\%$) of fish were predicted to be the correct species. Eight lots were not measured due to the poor condition of all specimens (range: 1-16 specimens each), but species identity was verified from supplemental characters. Of the 134 lots of unknown *Hybognathus*, 33 (25%) were misidentified or cataloged as species that no longer exist or have been revised. Three of these were mixed lots of *H. hankinsoni* and *H. placitus*, three lots contained *Hybognathus* mixed with other taxa, and two lots originally cataloged as *H. nuchalis* contained no *Hybognathus*.

Taxonomic Characteristics of H. hankinsoni and H. placitus

Hybognathus hankinsoni Hubbs was first proposed by Hubbs and Greene (1926) but was not described until Jordan (1929). Bailey (1954) elaborated on this description and designated a lectotype (UMMZ 84266) from the Dead River, a tributary of Lake Superior in Marquette County, Michigan. Earlier names used for *H. hankinsoni* and under which specimens may still be catalogued, include:

H. nuchalis nuchalis Agassiz (in part), 1855; Hendricks, 1950.

H. nuchalis Agassiz (in part), 1855; Jordan, 1891; Juday, 1904, 1905; Cockerell, 1908; Ellis, 1914.

H. nubilum (in part), Call, 1887; Meek, 1891; Evermann and Cox, 1896.

H. nuchale evansi (in part), Eigenmann, 1894; Evermann and Cox, 1896.

Researchers should refer to Eschmeyer (1998) for a more thorough etymology of this species.

Descriptive characters:

Head: Eye large relative to *H. placitus* and about equal to snout length (Figure 1.1; mean orbit diameter/snout length = 0.93, range 0.70-1.38, n=503 Colorado fish). Horizontal line drawn through the anterior most tip of snout intersects the center of eye. Mouth terminal and slightly oblique. Head with upturned ventral profile. Basioccipital process peg shaped, shorter than in *H. placitus*. Fleshy snout not visible ventrally. Snout rounded.

Body: Average adult body size 50-70 mm total length (TL). Maximum size <100 mm TL.

Dorsal, anal, and pectoral fins rounded (Figure 1.5). First ray of dorsal fin shorter than second, giving rounded appearance. Prominent, dark, lateral and predorsal bands of pigment. Margins of scales outlined, especially dorsally. Scales large and prominent. Pectoral fins smaller than in *H. placitus*. Males golden during breeding season.

Regional accounts of fishes, such as Scott and Crossman (1973) and Becker (1983), provide more detail on descriptive characteristics for *H. hankinsoni*.

Hybognathus placitus Girard was first described by Girard (1856). The name *H. evansi* has line priority over *H. placitus* but the first revision by Jordan and Gilbert (1882) used the name *H. placitus* (Al-Rawi and Cross, 1964). Girard designated five syntypes, USNM 89 (3), MCZ 1789 (1), ANSP 5065 (1), from the Arkansas River near Dodge City, Ford County, Kansas collected in

1858. Earlier names used for *H. placitus* and under which specimens may still be catalogued, include:

H. nuchalis nuchalis Agassiz (in part), 1855; Hendricks, 1950.

H. nuchalis Agassiz (in part), 1855; Hay, 1887; Ellis, 1914.

H. evansi Cope, 1865; Girard, 1856, 1858 *nomen nudum*.

H. placita Girard; Graham, 1885; Personius and Eddy, 1955.

H. nubilum (in part), Call, 1887; Meek, 1891; Everman and Cox, 1896.

H. nuchalis placita, Jordan, 1891; Evermann, 1893.

H. nuchale, Meek, 1894.

H. nuchale evansi (in part), Eigenmann, 1894; Everman and Cox, 1896.

H. churchilli Hildebrand, 1932.

H. placitus placitus, Johnson, 1942.

H. placita placita, Beckman, 1952.

Researchers should refer to Eschmeyer (1998) for a more thorough etymology of this species.

Descriptive characters:

Head: Eye smaller than in *H. hankinsoni* and notably less than snout length (Figure 1.1; mean orbit diameter/snout length = 0.69, range 0.52-1.03, n= 66 Colorado fish). Horizontal line through anterior most tip of snout generally crosses below the center of the eye resulting in a decurved anterior dorsal profile. Mouth subterminal and horizontal. Head with flat ventral profile. Peg-shaped basioccipital process, longer than in *H. hankinsoni*. Fleshy snout visible ventrally. Snout relatively pointed.

Body: Average adult body size 50-90 mm TL. Maximum size 130 mm TL. Dorsal, anal, and pectoral fins pointed (Figure 1.5). First ray of dorsal fin usually longer than second, creating a falcate posterior fin margin. Lateral and predorsal bands of pigment present, but not as prominent as in *H. hankinsoni*. Scales more embedded than in *H. hankinsoni*. Dorsal scales not darkly outlined. Pectoral fins large relative to *H. hankinsoni*.

Al-Rawi and Cross (1964), and Niazi and Moore (1962) provide detailed descriptive characteristics of *H. placitus*.

Scale radii

Scale radii were not useful for distinguishing between *H. placitus* and *H. hankinsoni*. Several sources stated that *H. hankinsoni* have about 20 weak radii, which we assumed included either complete plus incomplete radii or the total of all three categories. However, the mean number of total radii for *H. hankinsoni* from this analysis was 17 (range 8-27). More than half of the 30 fish analyzed would be misidentified as *H. placitus* based on the most conservative criterion for *H. hankinsoni* of having 17 or more total radii (Bailey, 1954; Figure 1.6) and more than 75% would be misidentified based on the most common criterion of 20 or more total radii (Figure 1.6). Even higher proportions would be misidentified based on complete plus incomplete radii. In contrast, although *H. placitus* averaged 10 total radii (range 4-20), 4 of 30 would be misidentified as *H. hankinsoni* based on the most common criterion of 15 or fewer total radii (e.g., Baxter and Simon, 1970). In addition to often misidentifying the two species, the number of scale radii increased with standard length for both ($P < 0.001$). As a result, only *H. hankinsoni* >60 mm and *H. placitus* <55 mm would be consistently identified correctly.

The number of scale radii also differed between scales from the same fish, further confounding use of this characteristic. Five of 11 *H. placitus* and 10 of 11 *H. hankinsoni* had different numbers of total radii on two scales. Three of 11 *H. hankinsoni* would have been identified as *H. hankinsoni* based on one scale but as *H. placitus* (or intermediate between, with 16 total radii) based on the other, using a criterion of 17 or more total radii for *H. hankinsoni*. Five of 11 had 16 or fewer radii on both scales and would have been misidentified, leaving only 3 of 11 correctly identified as *H. hankinsoni*. Similarly, 2 of 11 *H. placitus* would have been misidentified based on one of two scales, using a criterion of 15 or fewer total radii. Two others would have been misidentified as *H. hankinsoni* based on both scales, leaving only 7 of 11 correctly identified as *H. placitus*.

Historic Distribution

The correct identification of museum specimens allowed a clear determination of the historical distribution of these two *Hybognathus* species in Colorado and surrounding states (Figure 1.7). *Hybognathus hankinsoni* was distributed throughout the main stem of the South Platte River, in one of its major plains tributaries in southwestern Nebraska (Lodgepole Creek), and west to its transition-zone tributaries in the foothills of the Rocky Mountains. In the Republican River Basin its distribution extended into the headwater plains tributaries in eastern Colorado. The southwestern extent of its entire distribution was in the headwaters of the Smoky Hill River in the Kansas River Basin of western Kansas. *Hybognathus hankinsoni* has never been recorded or collected from the Arkansas River Basin. It was also widely distributed along the North Platte River in Nebraska and into the headwaters in Wyoming. In contrast, *H. placitus* was allopatric in the Arkansas River Basin. It occurred in sympatry with *H. hankinsoni* in the Smoky Hill and

Republican rivers near their headwaters, and in the lower main stems of the South Platte and North Platte rivers on the plains.

Discussion

The logistic regression model with the independent variables orbit diameter, standard length, and eye position fit to the 1154 measured and verified specimens from Colorado and adjacent counties reliably distinguished most *H. hankinsoni* from *H. placitus*. This model correctly predicted species identities for 98% of all individuals, and 100% of the lots based on predictions for the majority of individuals in each lot. When this model is used in conjunction with the recommended supplemental characteristics, all but the most unusual individuals should be correctly identified. This analysis clarified the identities of all museum specimens of *Hybognathus* collected from the region known to us, 25% of which were previously misclassified. The proper identification of extant specimens allowed accurate description of the historic distributions of these species in eastern Colorado river basins.

This model will also be a useful diagnostic tool for reliably distinguishing *H. placitus* from *H. hankinsoni* in new collections, and allow their current distribution and status to be determined. The model is based on precise measurements, so proper identification will require preserving voucher specimens for laboratory analysis and comparing them with other verified collections. Eventually, field biologists may become familiar with the differences between these species allowing identification without using the model. A small percentage of individuals will not fit the key due to individual or clinal variation. Extra care must be taken with small fish because measurement errors will have a proportionately larger effect on the model predictions. All model predictions should be verified using supplemental characteristics such as the shape of

the snout, shape of dorsal and anal fins, mouth position, maximum body size, and coloration patterns. This is especially important when identifying fish collected from areas of sympatry and when the model yields borderline predictions (i.e., $P \approx 0.50$). This key will be especially helpful for collections from northern Kansas and Missouri northwest to Montana and North Dakota where *H. hankinsoni* and *H. placitus* are sympatric in the upper Missouri, Platte, Republican, and upper Kansas river basins (Burr, 1980; Gilbert, 1980).

Hybognathus hankinsoni in eastern Colorado basins had smaller eyes than those from near the center of their distribution in Michigan. Wells (1978) identified two morphological groups of *H. hankinsoni*, a Great Lakes form and a Missouri River form, that he believed evolved in separate glacial refugia during the Wisconsin glaciation. The Great Lakes form is described as having a larger eye than the Missouri River form, but Wells (1978) did not think taxonomic distinction of the two forms was warranted. According to his hypothesis, the original model based on fish from Michigan describes the Great Lakes form, whereas the final model based on the Colorado fish describes the Missouri River form. Overall, the final model is most useful, because it can be used to separate the two species where they are sympatric in western Great Plains basins.

Two commonly used characters, the number of scale radii and the shape of the basioccipital process, should not be used to separate *H. hankinsoni* and *H. placitus*. We do not recommend the continued use of scale radii counts because of the strong overlap in ranges of scale radii between the two species, the increase in scale radii with standard length, and variation among scales from the same fish. The basioccipital process of both *H. hankinsoni* and *H. placitus* is narrow and peg-like (Schmidt, 1994; Bestgen and Propst, 1996). Although they differ in relative lengths, the similarity in shape of the basioccipital process between these two species

makes it a difficult characteristic to use by itself. Measuring orbit diameter, standard length, and eye position is not only more reliable for distinguishing the two species, but is faster and easier than mounting and reading scales or comparing relative lengths of the basioccipital process which requires partial dissection.

The different morphologies of *H. hankinsoni* and *H. placitus* are consistent with adaptations for their preferred habitats. *Hybognathus hankinsoni* prefer small, clear streams with low velocity (Copes, 1975). These conditions favor larger eyes, more prominent scales, and a more upturned ventral profile. A preference for smaller streams may also limit the maximum body size and low flow velocity precludes the need for large pectoral fins. In contrast, *H. placitus* prefer medium to large plains rivers (Cross, 1967). Their smaller eyes and more embedded scales may be adapted to turbid water environments. The larger pectoral fins, flatter ventral profile, and larger maximum body size of *H. placitus* also better suit them to the flow conditions encountered in larger streams. The differences in form between *H. hankinsoni* and *H. placitus* also match the patterns of form in relation to zoogeographic dispersal pathways described by Metcalf (1966). He identified a typical body form for fish of northeastern origin, such as *H. hankinsoni*, characterized by a more fusiform body outline, nearly terminal and oblique mouth, and larger eyes. *Hybognathus placitus*, on the other hand, have a southwestern origin characterized by a decurved anterior dorsal surface, flat ventral surface, inferior, horizontal mouth, and smaller eyes and scales. These patterns fit our observations about the differences between the two species.

The current distribution of these species is believed to be contracting from the western edge of their former range (e.g., Nesler et al., 1997, 1999; Patton, 1997). However, it is impossible to verify many recent accounts because no voucher specimens exist and the species

may have been misidentified in the field. We stress the importance of collecting and preserving voucher specimens for laboratory identification so that precise measurements and comparative assessments of supplemental characters can be obtained. Additionally, properly curated museum specimens are critical for ecologists attempting to determine changes in distribution (Shaffer et al., 1998) and taxonomists resolving future taxonomic conundrums of fishes like *Hybognathus* in Colorado and surrounding states.

Material Examined

Museum lots are listed below according to their current museum classification.

Institutional abbreviations are as listed in Leviton et al. (1985). Museum lots from the Biological Surveys Division of the U.S. Department of the Interior (BSFC) are deposited in the Biological Surveys Collections in the Museum of Southwestern Biology, Albuquerque, New Mexico.

Hybognathus hankinsoni,

Colorado (CO): South Platte R.; CAS 100903 (n=5); LFL uncataloged (n=84), KU 4795 (n=3), KU 4668 (n=3); UMMZ 86895 (n=1), BSFC 906 (n=1), BSFC 1015 (n=1), BSFC 1125 (n=1), BSFC 1923 (n=2), BSFC 2176 (n=12), BSFC 2311 (n=2), BSFC 2420 (n=6), BSFC 2888 (n=13), BSFC 2897 (n=2), BSFC 2903 (n=8), BSFC 2919 (n=12), BSFC 2929 (n=11), BSFC 2940 (n=15), BSFC 2959 (n=5), BSFC 2986 (n=4), BSFC 2999 (n=1), BSFC 3009 (n=6), BSFC 3032 (n=2), BSFC 3086 (n=2), BSFC 3106 (n=1), BSFC 3256 (n=169), BSFC 3292 (N=53), BSFC 3400 (n=6), BSFC 3705 (n=6), BSFC 3707 (n=5), ; Lodgepole Ck.; UMMZ 66155 (n=4); Lonetree Ck.; BSFC 3409 (n=17); Cache la Poudre R.; BSFC 955 (n=11), KU 4782 (n=32), KU 5565 (n=27); Spottlewood Ck.; BSFC 2617 (n=1); Larimer-Weld Canal; MSB 4647 (n=3); MSB 4806 (n=33); St. Vrain Ck.; BSFC 853 (n=5), BSFC 2114 (n=6), BSFC 2395 (n=1), BSFC 2409

(n=1), BSFC 2754 (n=5), BSFC 3410 (n=10); Boulder Ck.; BSFC 1072 (n=1), MSB 1164 (n=1); UMMZ 66159 (n=5); Buffalo Ck.; MSB 1112 (n=1); Republican R.; UMMZ 66144 (n=5); Kansas (KS): Republican R.; KU 17283 (n=6), KU 4043 (n=1); Smoky Hill R.; KU 3788 (n=4); USNM 38237 (n=2); South Fk. Smoky Hill R.; UMMZ 160450 (n=1); Turtle Ck.; UMMZ 160462 (n=1); Michigan (MI): Dead R.; UMMZ 84266 (n=1); Rifle R.; UMMZ 229833 (n=28); Tamarack Ck.; UMMZ 23280 (n=15); Carp Lake R.; UMMZ 234967 (n=22); Railroad Ck.; UMMZ 234993 (n=16); Nebraska (NE): North Platte R.; KU 4848 (n=21); ZM 2445 (n=6); ZM 2446 (n=4); ZM 2503 (n=1); ZM 2627 (n=5); ZM 5387 (n=1); ZM 5993 (n=1); ZM 6108 (n=6); ZM 6114 (n=88); ZM 6155 (n=38); ZM 6164 (n=1); ZM 7015 (n=9); ZM 7120 (n=2); UMMZ 134430 (n=1); UMMZ 134452 (n=4); Lonergran Ck.; UMMZ 134398 (n=7); South Platte R.; UMMZ 134390 (n=4); Lodgepole Ck.; KU 2013 (n=153); ZM 6438 (n=3); UMMZ 132241 (n=30 of 319); UMMZ 135161 (n=41); Republican R.; UMMZ 134361 (n=7); Arikaree R.; KU 2680 (n=5); Wyoming (WY): South Platte R.; UMMZ 114653 (n=9); Muddy Ck.; UMMZ 162348 (n=8); North Platte R.; BSFC 1218 (n=10), UMMZ 104079 (n=3); UMMZ 113500 (n=2); UMMZ 134811 (n=5); UMMZ 169127 (n=16); Rawhide Ck.; UMMZ 104069 (n=5); UMMZ 115020 (n=4); Laramie R.; KU 4821 (n=3), KU 4808 (n=3).

Hybognathus placitus,

Colorado (CO): South Platte R.; BSFC 3255 (n=5), BSFC 3708 (n=1); Republican R.; Arikaree R.; UMMZ 66144 (n=2); Purgatoire R.; KU 4744 (n=2); Arkansas R.; KU 4735 (n=31); UMMZ 94934 (n=16); Kansas (KS): Republican R.; UMMZ 122120 (n=1); Smoky Hill R.; UMMZ 122144 (n=1); UMMZ 160466 (n=9); Arkansas R.; USNM 89 (n=3); MCZ 1789 (n=1); UMMZ 160439 (n=8); Nebraska (NE): South Platte R.; UMMZ 134389 (n=7); Republican R.; ZM 9311

(n=2); ZM 9452 (n=7); ZM 9578 (n=2); UMMZ 134349 (n=32); UMMZ 134360 (n=2); UMMZ 134370 (n=1); Red Willow Ck.; UMMZ 135109 (n=1); Frenchman Ck.; UMMZ 135119 (n=57); North Fork Republican R.; ZM 8699 (n=2); Arikaree R.; UMMZ 135130 (n=30 of 374); UMMZ 145017 (n= 37); North Platte R.; UMMZ 135249 (n=1); New Mexico (NM): Canadian R.; LFL 43030 (n=51); Wyoming (WY): North Platte R.; UMMZ 104061 (n=3); UMMZ 134812 (n=2).

Hybognathus nuchalis,

Colorado (CO): South Platte R.; UCM 342 (n=9); USNM 41721 (n=3); Lodgepole Ck.; UCM 343 (n=34); Saint Vrain R.; UCM 17 (n=1); Boulder Ck.; CAS 68226 (n=3); UCM 24 (n=3); UCM 344 (n=27); UCM 6266 (n=68); UCM 6278 (n=38); UCM 6878 (n=1); Rock Ck.; UCM 6324 (n=7); Bear Ck.; CAS 72788 (n=10); North Fork Republican R.; UCM 345 (n=127); Arikaree R.; UCM 6212 (n=38); Black Wolf Ck.; UCM 6224 (n=1); Arkansas R.; UCM 347 (n=2); USNM 41708 (n=1); Kansas (KS): Republican R.; USNM 249860 (n=1).

Hybognathus argyritis,

Colorado (CO): South Platte R.; BSFC 3180 (n=2).

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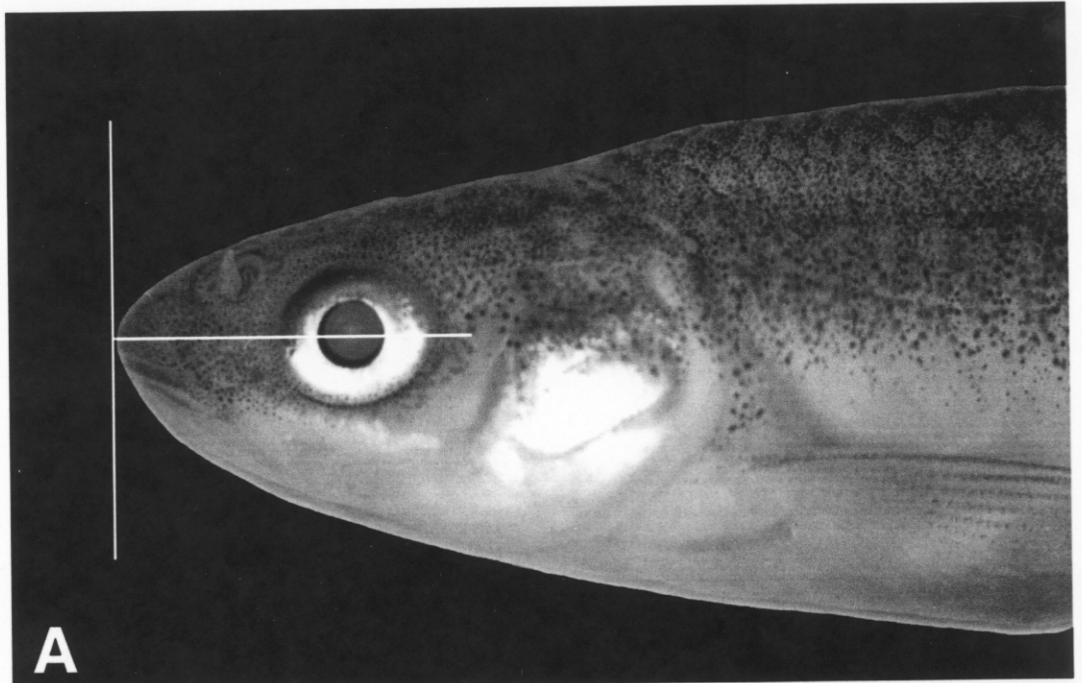
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Table 1.1. Maximum likelihood estimates of intercept and slope parameters from logistic regression for the best model based on the 132 known specimens and the two candidate models based on the 1154 unknown specimens to predict *Hybognathus* species identity. Models predict the probability that an unknown specimen is *H. hankinsoni*. Coefficients for the eye position parameter are 0 for even and 1 for above. Standard errors of parameters are in parentheses.

Model	Intercept	Standard Length	Orbit Diameter	Eye Position
<i>Model based on 132 known specimens</i>				
Standard length, orbit diameter	-16.8465 (4.0462)	-0.8123 (0.1690)	18.8391 (3.8075)	---
<i>Model based on 1154 unknown specimens</i>				
Standard length, orbit diameter	-11.8900 (1.7387)	-0.8222 (0.0740)	18.9196 (1.7511)	---
Standard length, orbit diameter, eye position	-11.3796 (2.0969)	-0.8009 (0.0839)	18.5823 (2.0224)	-5.3898 (1.0643)

Figure 1.1 Eye position characteristic for *H. hankinsoni* (A) and *H. placitus* (B). *H. hankinsoni* typically have larger eyes with the centers even with a horizontal line drawn back from the anteriormost tip of the snout. *H. placitus* have smaller eyes with the centers often above this line. Images are by R. E. Zuellig, with permission.



A



B

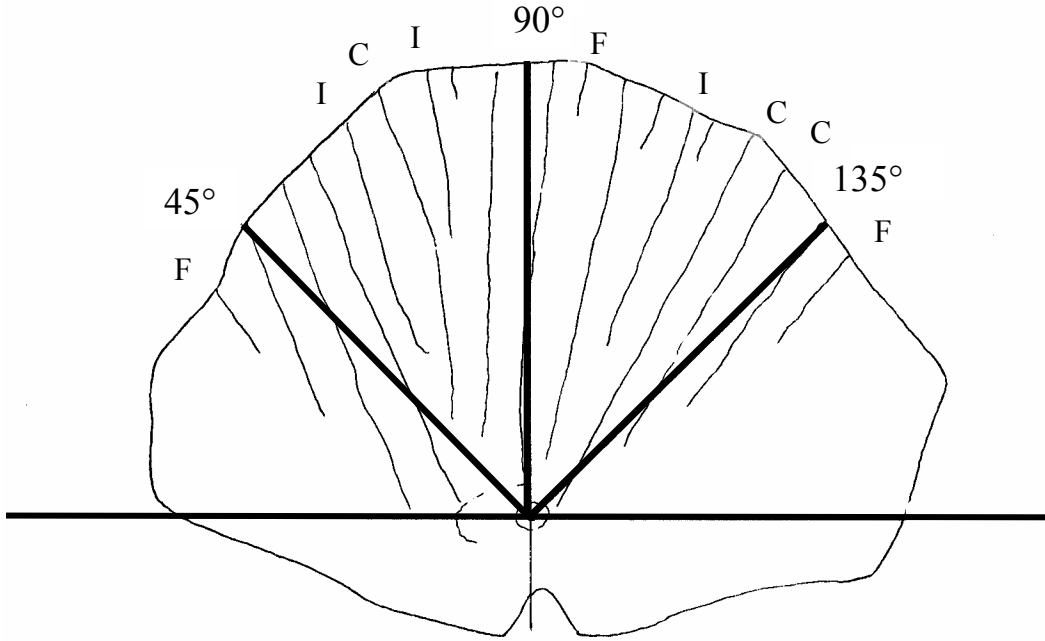


Figure 1.2. Diagram of a typical brassy minnow scale showing three angles from the horizontal line through the focus along which distances were measured to the scale margin for comparison with radii lengths. Radii were compared to the nearest measured distance and categorized as faint (F, <30%), incomplete (I, 30-67%), or complete (C, >67%). Examples of radii category designations are shown.

Figure 1.3. Orbit diameter as a function of standard length for the 132 known specimens. Solid lines show regression lines for *H. hankinsoni* (squares; $r^2=0.88$, $P<0.001$) and *H. placitus* (circles; $r^2=0.86$, $P<0.001$). Dashed line is the 50% probability line predicted from logistic regression. Fish represented by points above the line are predicted to be *H. hankinsoni*, whereas those below are predicted to be *H. placitus*. The equation for the 50% probability line is $y = 0.0431x + 0.8951$.

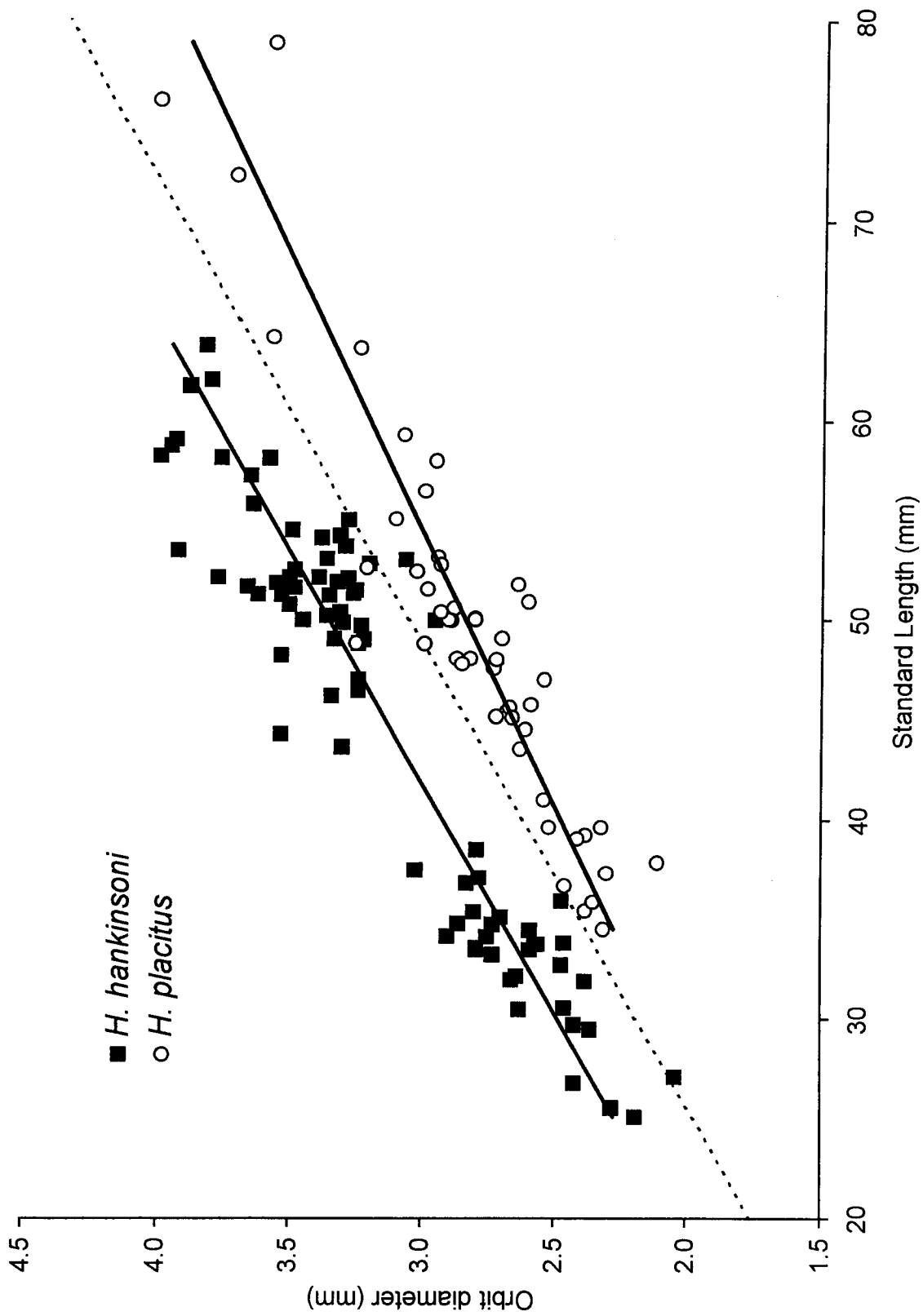
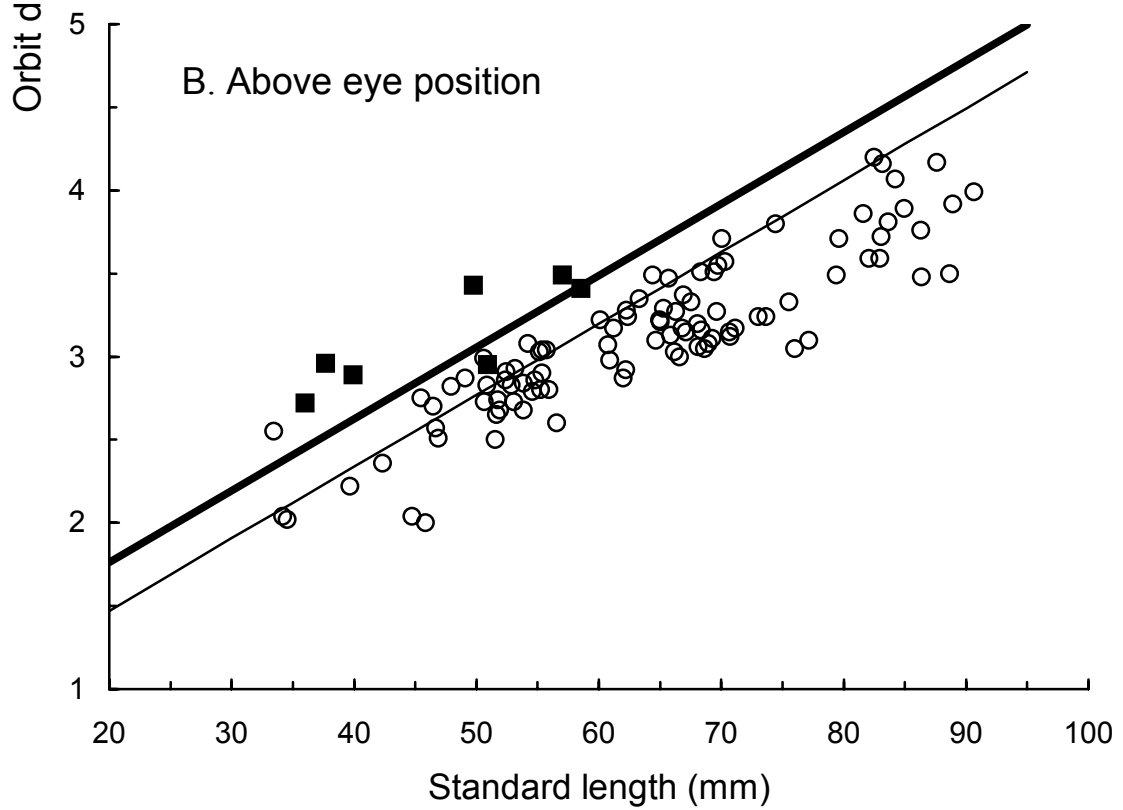
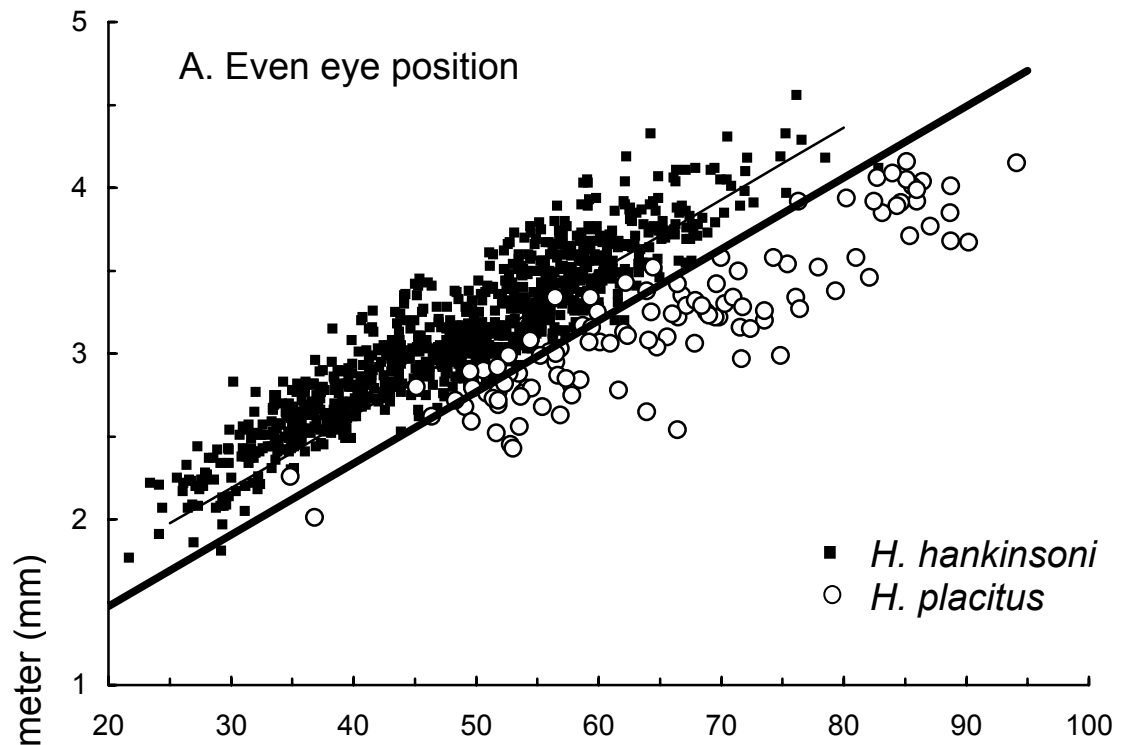


Figure 1.4. Orbit diameter as a function of standard length for the 1154 unknown specimens with even eye position (A) and above eye position (B). Filled squares show *H. hankinsoni* and open circles show *H. placitus*. Decision lines show where the probability of a specimen being *H. hankinsoni* is predicted to be 50%. In A the thin line shows the prediction for the original two-variable model based on the 132 known specimens (see Fig. 1.3) and the thick line shows the prediction for fish with the even eye position for the final three-variable model based on 1154 verified unknowns. In B the thick line shows the prediction from the final three-variable model for fish with the above eye position, whereas the thin line show the prediction for fish with the even eye position for comparison (same as thin line in Fig. 1.4A). The 50% decision line for the final three-variable model for the even eye position is $y = 0.0431x + 0.6119$, and for the above eye position the decision line is $y = 0.0431x + 0.9019$.



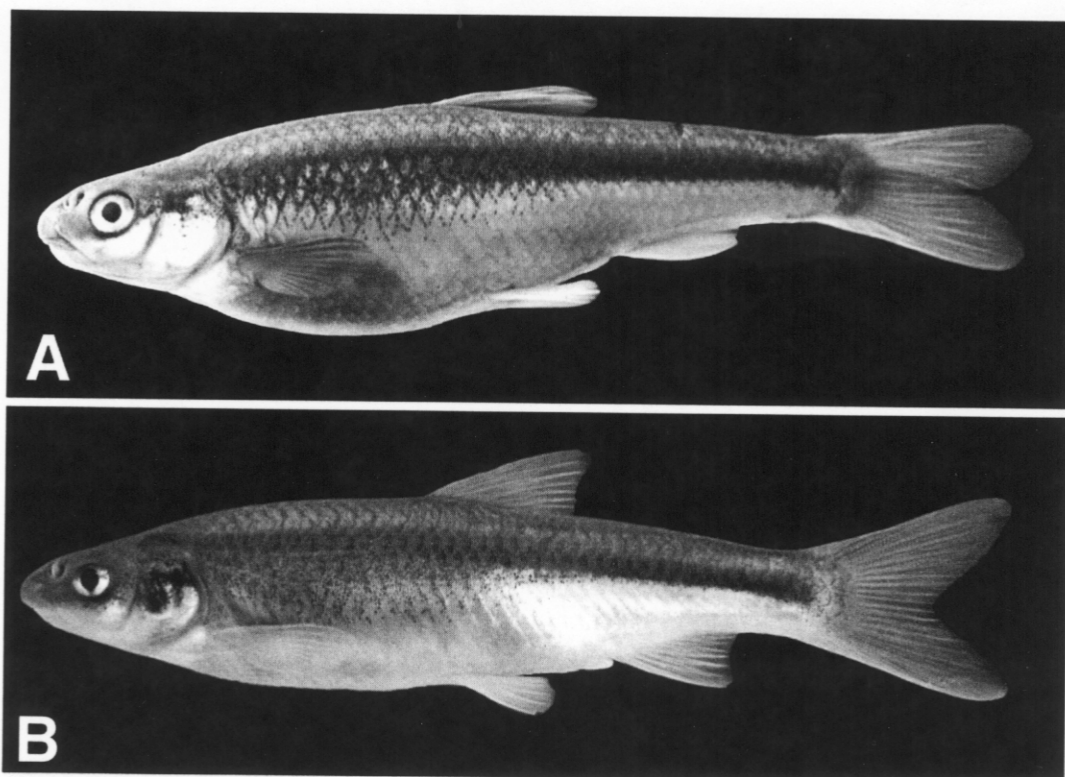


Figure 1.5. Lateral views of A. *Hybognathus hankinsoni* (brassy minnow) and B. *H. placitus* (plains minnow). Images are by R. E. Zuellig, with permission.

Figure 1.6. Total number of scale radii (faint, incomplete, and complete) as a function of standard length for *H. hankinsoni* (filled squares) and *H. placitus* (open circles).

Regression lines are shown for each species. Horizontal dashed lines indicate commonly used criteria for separating the two species. *Hybognathus hankinsoni* was reported to have 17 to 19 full radii in the original full description (Baily, 1954) and about 20 radii in subsequent keys. *Hybognathus placitus* was described as having 10 to 15 radii in most keys.

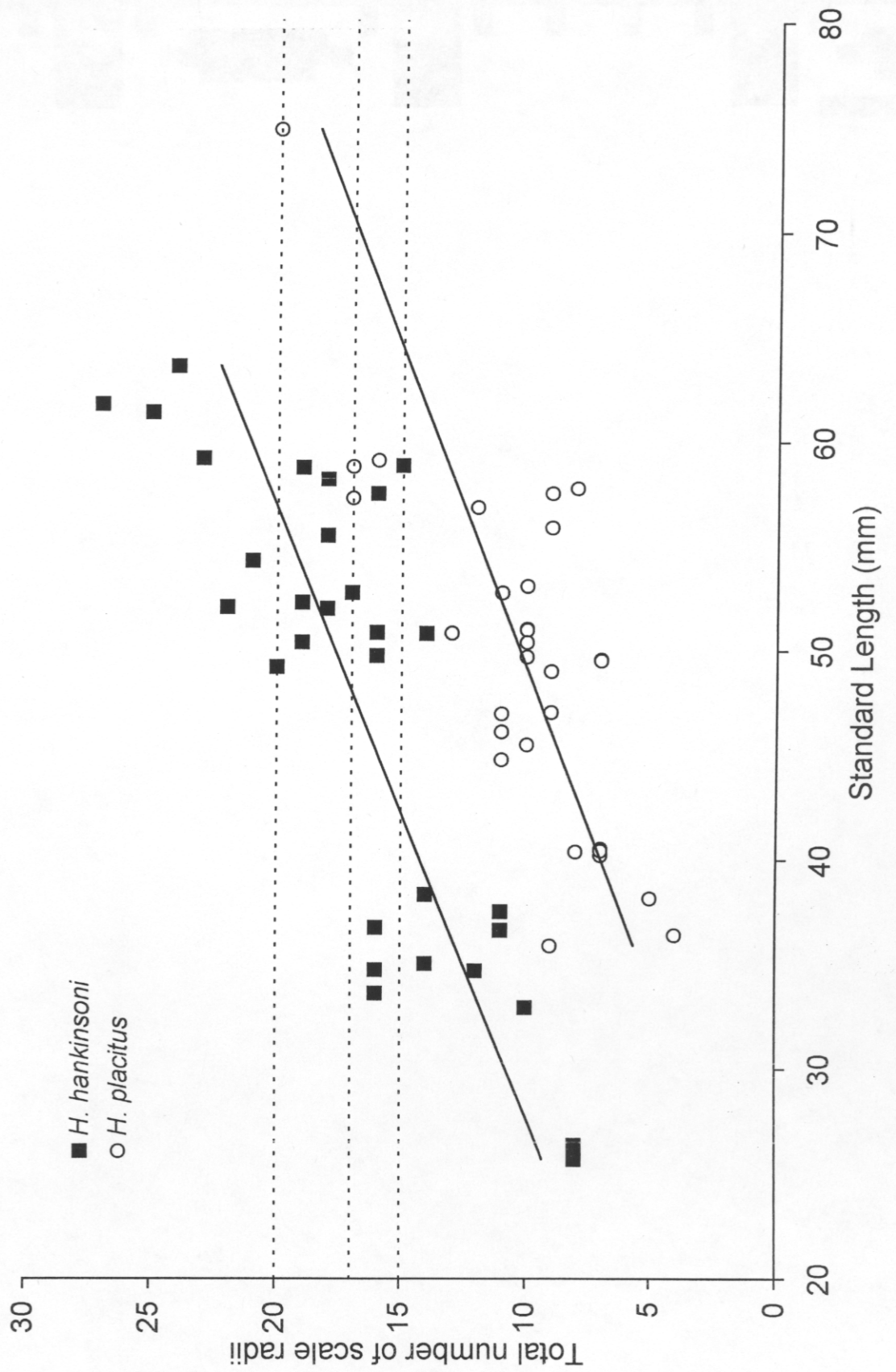
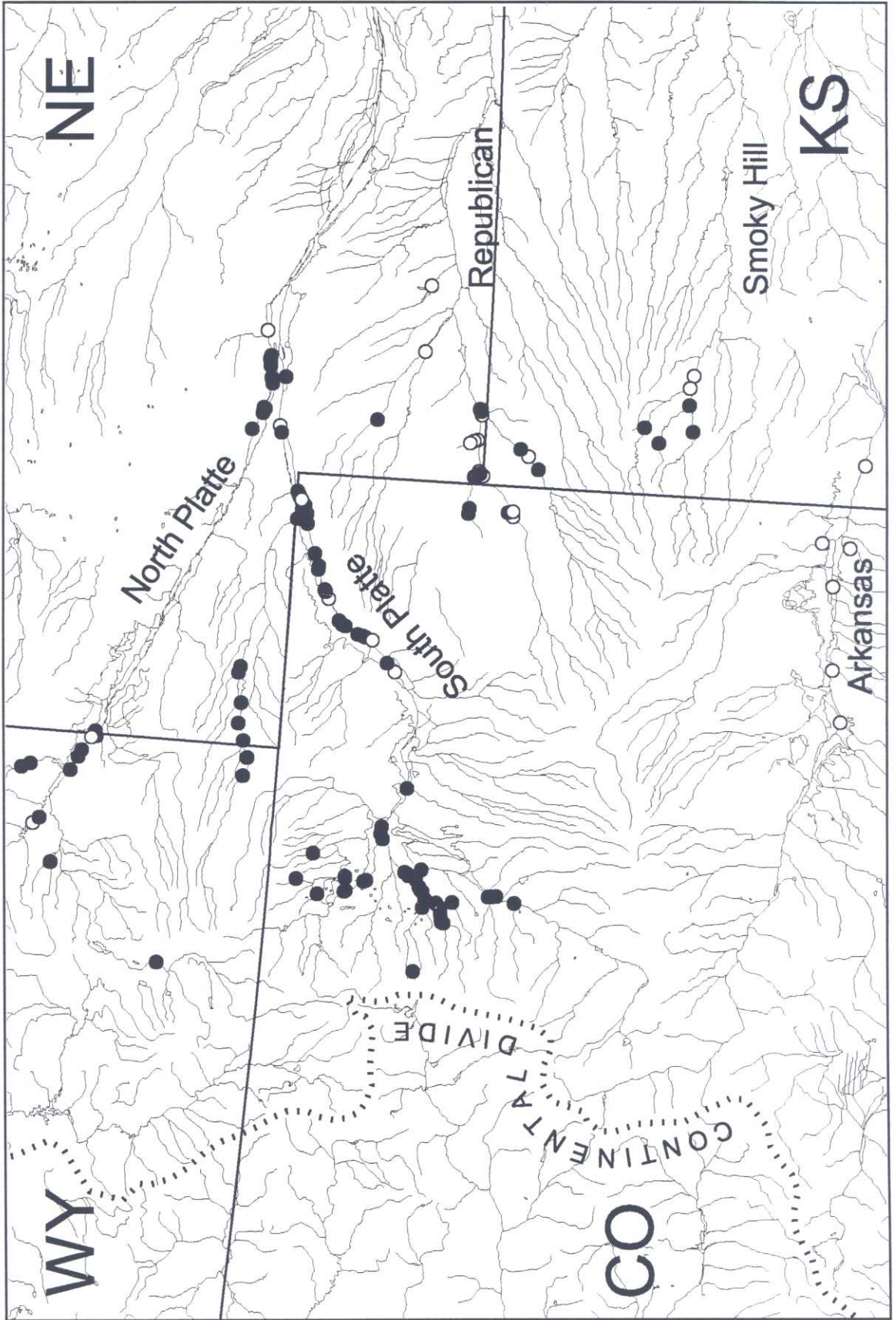


Figure 1.7. Historical distribution of *H. hankinsoni* and *H. placitus* in Colorado and adjacent counties in neighboring states based on verified museum collections (Appendix 1.1). Closed circles indicate *H. hankinsoni* and open circles *H. placitus*.



APPENDIX 1.1:

MODEL PREDICTIONS AND VERIFIED IDENTITIES OF EXAMINED MUSEUM
COLLECTIONS OF *HYBOGNATHUS* FROM COLORADO AND VICINITY

Appendix 1.1. Identities of museum collections of *Hybognathus* from Colorado and adjacent regions in neighboring states in order by verified species, then alphanumeric by museum collection. Collections of mixed species are listed at the end of the table. Institutional abbreviations are as listed in Leviton et al. (1985). Species identity was determined from logistic regression model predictions and verified using supplemental characters. Numbers in parentheses indicate the number of fish for which predictions were obtained. Large lots were sometimes subsampled and measurements from poorly preserved or damaged specimens were not included. With the exception of two large lots for which only 30 specimens each could be obtained, complete lots were examined to verify species identity. Species are coded as *hankinsoni* (*h.*), *placitus* (*p.*), *nuchalis* (*n.*), or *argyritis* (*a.*).

Museum collection	<i>Hybognathus</i> species identity	Original species designation	Year	State	County	River basin	Locality		Number in lot	Percent predicted	Percent predicted
							Site	Site		<i>placitus</i>	<i>hankinsoni</i>
BSFC 1015	<i>h.</i>	<i>h.</i>	1968	CO	Sedgwick	S. Platte	S. Platte R., S. of Ovid		1		100
BSFC 1072	<i>h.</i>	<i>h.</i>	1968	CO	Weld	S. Platte	St. Vrain and Boulder Cks. confl.		1		100
BSFC 1125	<i>h.</i>	<i>h.</i>	1968	CO	Larimer	S. Platte	spring near Waverly		1		100
BSFC 1218	<i>h.</i>	<i>h.</i>	1981	WY	Goshen	N. Platte	N. Platte R., Torrington		10		100
BSFC 1923	<i>h.</i>	<i>h.</i>	1980	CO	Sedgwick	S. Platte	S. Platte R., Julesburg		2		100
BSFC 2176	<i>h.</i>	<i>h.</i>	1980	CO	Logan	S. Platte	S. Platte R. slough, Tamarack		12		100
BSFC 2311	<i>h.</i>	<i>h.</i>	1980	CO	Weld	S. Platte	S. Platte R., Kersey		2		100
BSFC 2395	<i>h.</i>	<i>h.</i>	1980	CO	Weld	S. Platte	St. Vrain Ck., Gowanda		1 (0)	-- ^a	-- ^a
BSFC 2409	<i>h.</i>	<i>h.</i>	1980	CO	Weld	S. Platte	St. Vrain Ck., railroad tracks		1		100
BSFC 2420	<i>h.</i>	<i>h.</i>	1980	CO	Logan	S. Platte	S. Platte R., Ford		6		100
BSFC 2617	<i>h.</i>	<i>h.</i>	1979	CO	Larimer	S. Platte	Spottlewood Ck.		1		100
BSFC 2754	<i>h.</i>	<i>h.</i>	1979	CO	Weld	S. Platte	St. Vrain Ck., nuclear plant		5		100
BSFC 2888	<i>h.</i>	<i>h.</i>	1980	CO	Sedgwick	S. Platte	S. Platte R., Julesburg		13		100

Museum collection	<i>Hybognathus</i> species identity	Original species designation	Year	State	County	Locality		Number in lot	Percent predicted <i>placitus</i>	Percent predicted <i>hankinsoni</i>
						River basin	Site			
BSFC 2897	<i>h.</i>	<i>h.</i>	1980	CO	Sedgwick	S. Platte	S. Platte R., Julesburg	2		100
BSFC 2903	<i>h.</i>	<i>h.</i>	1980	CO	Sedgwick	S. Platte	S. Platte R. slough	8		100
BSFC 2919	<i>h.</i>	<i>h.</i>	1980	CO	Sedgwick	S. Platte	S. Platte R., Sedgwick	12 (1)		100
BSFC 2929	<i>h.</i>	<i>h.</i>	1980	CO	Logan	S. Platte	S. Platte R., Red Lion	11		100
BSFC 2940	<i>h.</i>	<i>h.</i>	1980	CO	Logan	S. Platte	S. Platte R. slough, Crook	15 (12)		100
BSFC 2959	<i>h.</i>	<i>h.</i>	1980	CO	Logan	S. Platte	S. Platte slough, Proctor	5		100
BSFC 2986	<i>h.</i>	<i>h.</i>	1980	CO	Logan	S. Platte	S. Platte R., Sterling	4		100
BSFC 2999	<i>h.</i>	<i>h.</i>	1980	CO	Washington	S. Platte	S. Platte R., Messer	1		100
BSFC 3009	<i>h.</i>	<i>h.</i>	1980	CO	Logan	S. Platte	S. Platte R. sidechannel, Atwood	6		100
BSFC 3086	<i>h.</i>	<i>h.</i>	1980	CO	Weld	S. Platte	S. Platte R. near Masters	2		100
BSFC 3106	<i>h.</i>	<i>h.</i>	1980	CO	Weld	S. Platte	S. Platte R., Greeley	1		100
BSFC 3180	<i>h.</i>	<i>a.</i>	1980	CO	Weld	S. Platte	S. Platte R., Platteville	2		100
BSFC 3255	<i>p.</i>	-- ^b	1983	CO	Logan	S. Platte	S. Platte R., S. of Proctor	5 (3)	67	33
BSFC 3256	<i>h.</i>	-- ^b	1983	CO	Logan	S. Platte	S. Platte R., S. of Proctor	169 (30)	3	97
BSFC 3292	<i>h.</i>	<i>h.</i>	-- ^c	CO	Sedgwick	S. Platte	S. Platte R., S. of Ovid	53 (30)	6	94
BSFC 3400	<i>h.</i>	<i>h.</i>	1983	CO	Logan	S. Platte	S. Platte R., Crook	6		100
BSFC 3409	<i>h.</i>	<i>h.</i>	1968	CO	Weld	S. Platte	Lonetree Ck., Hwy. 85	17		100
BSFC 3410	<i>h.</i>	<i>h.</i>	1967	CO	Weld	S. Platte	St. Vrain Ck., Hwy. 66	10		100
BSFC 3705	<i>h.</i>	<i>h.</i>	1980	CO	Sedgwick	S. Platte	S. Platte R.	6 (4)		100

Museum collection	<i>Hybognathus</i>		Locality				Number in lot	Percent predicted	
	species identity	Original species designation	State	County	River basin	Site		<i>placitus</i>	<i>hankinsoni</i>
BSFC 3707	<i>h.</i>	<i>h.</i>	CO	Sedgwick	S. Platte	S. Platte R., Sedgwick	5 (4)		100
BSFC 3708	<i>p.</i>	<i>p.</i>	CO	Washington	S. Platte	S. Platte R., Messer	1	100	
BSFC 853	<i>h.</i>	<i>h.</i>	CO	Weld	S. Platte	St. Vrain Ck., Gowanda	5		100
BSFC 906	<i>h.</i>	<i>h.</i>	CO	Logan	S. Platte	S. Platte R. NE of Ford	1		100
BSFC 955	<i>h.</i>	<i>h.</i>	CO	Larimer	S. Platte	Cache la Poudre R., Hwy. 392	11		100
CAS 100903	<i>h.</i>	<i>h.</i>	CO	-- ^d	S. Platte	S. Platte R. at Denver	5		100
CAS 68226	<i>h.</i>	<i>n.</i>	CO	Boulder	S. Platte	Boulder Ck. at Hwy. 287	3		100
KU 17283	<i>h.</i>	<i>h.</i>	KS	Cheyenne	Republican	S. Fk. Republican R.	6		100
KU 2013	<i>h.</i>	<i>h.</i>	NE	Kimball	S. Platte	Lodgepole Ck.	153 (50)		100
KU 2680	<i>h.</i>	<i>h.</i>	NE	Dundy	Republican	Arikaree R.	5		100
KU 3788	<i>h.</i>	<i>h.</i>	KS	Sherman	Smoky Hill	N. Br. Smoky Hill R.	4		100
KU 4043	<i>h.</i>	<i>h.</i>	KS	Cheyenne	Republican	Republican R.	1		100
KU 4668	<i>h.</i>	<i>h.</i>	CO	Logan	S. Platte	S. Platte R., Iliff	3		100
KU 4735	<i>p.</i>	<i>p.</i>	CO	Prowers	Arkansas	Arkansas R., Lamar	31 (30)	97	3
KU 4744	<i>p.</i>	<i>p.</i>	CO	Bent	Arkansas	Purgatoire R., Las Animas	2	100	
KU 4782	<i>h.</i>	<i>h.</i>	CO	Larimer	S. Platte	Cache la Poudre R.	32		100
KU 4795	<i>h.</i>	<i>h.</i>	CO	Weld	S. Platte	S. Platte R., Greeley	3		100
KU 4808	<i>h.</i>	<i>h.</i>	WY	Albany	N. Platte	Laramie R.	3		100
KU 4821	<i>h.</i>	<i>h.</i>	WY	Platte	N. Platte	N. Laramie R., Uva	3		100

Museum collection	<i>Hybognathus</i>		Original species designation	Year	State	County	Locality		Number in lot	Percent predicted	Percent predicted
	species identity	species designation					River basin	Site		<i>placitus</i>	<i>hankinsoni</i>
KU 4848	<i>h.</i>	<i>h.</i>	<i>h.</i>	1959	NE	Keith	N. Platte	N. Platte R., Keystone	21		100
KU 5565	<i>h.</i>	<i>h.</i>	<i>h.</i>	1960	CO	Larimer	S. Platte	Cache la Poudre R.	27		100
LFL uncat.	<i>h.</i>	<i>h.</i>	<i>h.</i>	1975	CO	Weld	S. Platte	S. Platte R., St. Vrain Ck.	84 (41)	2	98
MSB 1112	<i>p.</i>	<i>h.</i>	<i>h.</i>	-- ^c	CO	Prowers	Arkansas	Buffalo Ck.	1	100	
MSB 1164	<i>h.</i>	<i>h.</i>	<i>h.</i>	1950	CO	Boulder	S. Platte	Boulder Ck. near White Rocks	1		100
MSB 4647	<i>h.</i>	<i>h.</i>	<i>h.</i>	1987	CO	Larimer	S. Platte	Larimer-Weld Canal	3 (2)		100
MSB 4806	<i>h.</i>	<i>h.</i>	<i>h.</i>	1987	CO	Larimer	S. Platte	Larimer-Weld Canal	33	3	97
UCM 17	<i>h.</i>	<i>n.</i>	<i>n.</i>	1903	CO	Boulder	S. Platte	St Vrain R., Longmont	1		100
UCM 24	<i>h.</i>	<i>n.</i>	<i>n.</i>	1903	CO	Boulder	S. Platte	Boulder Ck.	3 (0)	-- ^a	-- ^a
UCM 342	<i>p.</i>	<i>n.</i>	<i>n.</i>	1912	CO	Sedgwick	S. Platte	S Platte R., Julesburg	9	89	11
UCM 343	<i>h.</i>	<i>n.</i>	<i>n.</i>	1912	CO	Sedgwick	S. Platte	Lodgepole Ck., Ovid	34 (32)		100
UCM 344	<i>h.</i>	<i>n.</i>	<i>n.</i>	1912	CO	Boulder	S. Platte	Boulder Ck, 6 mi. E. of Boulder	27		100
UCM 345	<i>h.</i>	<i>n.</i>	<i>n.</i>	1912	CO	Yuma	Republican	N. Fk. Republican, Wray	127 (30)		100
UCM 6224	<i>h.</i>	<i>n.</i>	<i>n.</i>	1915	CO	Yuma	Republican	Black Wolf Ck., May's Ranch	1		100
UCM 6266	<i>h.</i>	<i>n.</i>	<i>n.</i>	1916	CO	Boulder	S. Platte	Boulder Ck., slough trib.	68 (25)		100
UCM 6278	<i>h.</i>	<i>n.</i>	<i>n.</i>	1916	CO	Boulder	S. Platte	Boulder Ck., White Rock	38		100
UCM 6878	<i>h.</i>	<i>n.</i>	<i>n.</i>	1950	CO	Boulder	S. Platte	Boulder Ck., Hwy. US287	1		100
UMMZ 66124	<i>p.</i>	<i>p.</i>	<i>p.</i>	1915	CO	Yuma	Republican	Arikaree R., Beecher Is.	2	100	
UMMZ 66144	<i>h.</i>	<i>h.</i>	<i>h.</i>	-- ^c	CO	Yuma	Republican	N. Fk. Republican, Wray	5		100

Museum collection	<i>Hybognathus</i>		Original species designation	Year	State	County	Locality		Number in lot	Percent predicted	
	species identity	species designation					River basin	Site		<i>placitus</i>	<i>hankinsoni</i>
UMMZ 66155	<i>h.</i>	<i>h.</i>	<i>h.</i>	-- ^c	CO	Sedgewick	S. Platte	Lodgepole Ck. near Ovid	4		100
UMMZ 66159	<i>h.</i>	<i>h.</i>	<i>h.</i>	1916	CO	Boulder	S. Platte	Boulder Ck., White Rocks	5		100
UMMZ 86895	<i>h.</i>	<i>h.</i>	<i>h.</i>	1871	CO	-- ^d	S. Platte	Ditches near Denver	1		100
UMMZ 94934	<i>p.</i>	<i>p.</i>	<i>p.</i>	1926	CO	Prowers	Arkansas	Clay Ck.	16	100	
UMMZ 104061	<i>p.</i>	<i>p.</i>	<i>p.</i>	1937	WY	Platte	N. Platte	N. Platte R. below Guernsey Dam	3	100	
UMMZ 104069	<i>h.</i>	<i>h.</i>	<i>h.</i>	1937	WY	Goshen	N. Platte	Rawhide Ck. near Jay Em	5		100
UMMZ 104079	<i>h.</i>	<i>h.</i>	<i>h.</i>	1937	WY	Platte	N. Platte	N. Platte slough near Guernsey	3		100
UMMZ 113500	<i>h.</i>	<i>h.</i>	<i>h.</i>	1936	WY	Goshen	N. Platte	N. Platte R., Torrington	2		100
UMMZ 114653	<i>h.</i>	<i>h.</i>	<i>h.</i>	1936	WY	Laramie	S. Platte	Muddy Ck. near Cheyenne	9		100
UMMZ 115020	<i>h.</i>	<i>h.</i>	<i>h.</i>	1937	WY	Goshen	N. Platte	Rawhide Ck, Hwy. 85	4		100
UMMZ 122114	<i>p.</i>	<i>p.</i>	<i>p.</i>	1926	KS	Logan	Smoky Hill	Smoky Hill R., Russell Springs	1	100	
UMMZ 122120	<i>p.</i>	<i>p.</i>	<i>p.</i>	1926	KS	Cheyenne	Republican	Republican R., St. Francis	1	100	
UMMZ 132241	<i>h.</i>	<i>h.</i>	<i>h.</i>	1934	NE	Kimball	S. Platte	Lodgepole Ck. near Kimball	319 (30)	3	97
UMMZ 134349	<i>p.</i>	<i>p.</i>	<i>p.</i>	1939	NE	Dundy	Republican	Republican R. near Benkelman	32 (22)	91	9
UMMZ 134360	<i>p.</i>	<i>p.</i>	<i>p.</i>	1939	NE	Dundy	Republican	Rock Ck.	2	100	
UMMZ 134361	<i>p.</i>	<i>p.</i>	<i>h.</i>	1939	NE	Dundy	Republican	Rock Ck.	7 (4)	75	25
UMMZ 134370	<i>p.</i>	<i>p.</i>	<i>p.</i>	1939	NE	Dundy	Republican	Rock Ck.	1	100	
UMMZ 134389	<i>p.</i>	<i>p.</i>	<i>p.</i>	1939	NE	Keith	S. Platte	S. Platte R., Ogallala	7 (5)	100	
UMMZ 134390	<i>h.</i>	<i>h.</i>	<i>h.</i>	1939	NE	Keith	S. Platte	S. Platte R., Ogallala	4 (3)		100

Museum collection	<i>Hybognathus</i> species identity	Original species designation	Year	State	County	Locality		Number in lot	Percent predicted <i>placitus</i>	Percent predicted <i>hankinsoni</i>
						River basin	Site			
UMMZ 134398	<i>h.</i>	<i>h.</i>	1939	NE	Keith	N. Platte	Lonergran Ck. near Lemoyne	7 (0)	-- ^a	-- ^a
UMMZ 134430	<i>h.</i>	<i>h.</i>	1939	NE	Kimball	N. Platte	Lodgepole Ck. near Kimball	1		100
UMMZ 134452	<i>h.</i>	<i>h.</i>	1939	NE	Scotts Bluff	N. Platte	N. Platte R. near Henry	4 (0)	-- ^a	-- ^a
UMMZ 134811	<i>h.</i>	<i>h.</i>	1941	WY	Goshen	N. Platte	N. Platte R., state line	5		100
UMMZ 134812	<i>p.</i>	<i>p.</i>	1941	WY	Goshen	N. Platte	N. Platte R., state line	2	100	
UMMZ 135109	<i>p.</i>	<i>p.</i>	1940	NE	Red Willow	Republican	Red Willow Ck., county line	1	100	
UMMZ 135119	<i>p.</i>	<i>p.</i>	1940	NE	Hitchcock	Republican	Frenchman Ck., Beverly	57 (30)	87	13
UMMZ 135130	<i>p.</i>	<i>p.</i>	1940	NE	Dundy	Republican	Arikaree R. near Haigler	374 (30)	90	10
UMMZ 135161	<i>h.</i>	<i>h.</i>	1940	NE	Kimball	S. Platte	Lodgepole Ck. near WY state line	41		100
UMMZ 135249	<i>p.</i>	<i>p.</i>	1940	NE	Lincoln	N. Platte	Sutherland Res.	1	100	
UMMZ 160439	<i>p.</i>	<i>p.</i>	1950	KS	Hamilton	Arkansas	Arkansas R., Syracuse	8	100	
UMMZ 160450	<i>h.</i>	<i>h.</i>	1950	KS	Wallace	Smoky Hill	Rose Ck., S. Fk. Smoky Hill	1		100
UMMZ 160462	<i>h.</i>	<i>h.</i>	1950	KS	Wallace	Smoky Hill	Turtle Ck.	1		100
UMMZ 160466	<i>p.</i>	<i>p.</i>	1950	KS	Logan	Smoky Hill	S. Fk. Smoky Hill, Russell Springs	9	100	
UMMZ 162348	<i>h.</i>	<i>h.</i>	1937	WY	Laramie	S. Platte	Muddy Ck., Pine Bluffs	8		100
UMMZ 169127	<i>h.</i>	<i>h.</i>	1941	WY	Goshen	N. Platte	N. Platte R., Torrington	16 (0)	-- ^a	-- ^a
USNM 249860	<i>h.</i>	<i>n.</i>	1856	KS	-- ^d	Republican	Republican R. tributary	1		100
USNM 38237	<i>h.</i>	<i>h.</i>	1886	KS	Wallace	Kansas	Smoky Hill R.	2 (0)	-- ^a	-- ^a
USNM 41708	<i>p.</i>	<i>n.</i>	1889	CO	Pueblo	Arkansas	Arkansas R. near Pueblo	1	100	

Museum collection	<i>Hybognathus</i>		Original species designation	Year	State	County	Locality		Number in lot	Percent predicted	Percent predicted
	species identity	species designation					River basin	Site		<i>placitus</i>	<i>hankinsoni</i>
USNM 41721	<i>h.</i>	<i>n.</i>		1889	CO	-- ^d	S. Platte	S. Platte R. at Denver	3		100
ZM 2445	<i>h.</i>	<i>h.</i>		1979	NE	Keith	N. Platte	Bull Ditch, N. Platte R.	6		100
ZM 2446	<i>h.</i>	<i>h.</i>		1976	NE	Keith	N. Platte	Cedar Ck., N. Platte R.	4		100
ZM 2503	<i>h.</i>	<i>h.</i>		1983	NE	Chase	Republican	Spring Ck.	1 (0)	-- ^a	-- ^a
ZM 2627	<i>h.</i>	<i>h.</i>		1981	NE	Keith	N. Platte	Bull Ditch, N. Platte R.	5 (0)	-- ^a	-- ^a
ZM 5387	<i>h.</i>	<i>h.</i>		1979	NE	Keith	N. Platte	Bull Ditch, N. Platte R.	1		100
ZM 5993	<i>h.</i>	<i>h.</i>		1995	NE	Keith	N. Platte	N. Platte R. 0.6 mi. S. of Paxton	1		100
ZM 6108	<i>h.</i>	<i>h.</i>		1995	NE	Keith	N. Platte	backwater 0.5 mi. N. of Sarben	6		100
ZM 6114	<i>h.</i>	<i>h.</i>		1995	NE	Keith	N. Platte	0.5 mi. N. of Sarben	88 (51)		100
ZM 6155	<i>h.</i>	<i>h.</i>		1995	NE	Keith	N. Platte	0.7 mi. SW Keystone	38		100
ZM 6164	<i>h.</i>	<i>h.</i>		1995	NE	Keith	N. Platte	3.7 mi. N. of Paxton	1		100
ZM 6438	<i>h.</i>	<i>h.</i>		1993	NE	Kimball	S. Platte	Lodgepole Ck.	3		100
ZM 7015	<i>h.</i>	<i>h.</i>		1995	NE	Keith	N. Platte	N. Platte R., Keystone	9 (6)		100
ZM 7120	<i>h.</i>	<i>h.</i>		1995	NE	Keith	N. Platte	N. Platte R., Whitetail Ck.	2		100
ZM 8699	<i>h.</i>	<i>p.</i>		1995	NE	Dundy	Republican	N. Fk. Republican R.	2 (1)		100
ZM 9311	<i>h.</i>	<i>p.</i>		1995	NE	Dundy	Republican	Republican R., Benkelman	2		100
ZM 9452	<i>h.</i>	<i>p.</i>		1996	NE	Dundy	Republican	Republican R., Benkelman	7 (6)		100
ZM 9578	<i>h.</i>	<i>p.</i>		1996	NE	Dundy	Republican	Republican R., Benkelman	2		100
BSFC 2114 ^g	<i>h.</i>	<i>h.</i>		1979	CO	Weld	S. Platte	St. Vrain Ck., nuclear plant	6 (4)		100

Museum collection	<i>Hybognathus</i> species identity	Original species designation	Year	State	County	Locality		Number in lot	Percent predicted <i>placitus</i>	Percent predicted <i>hankinsoni</i>
						River basin	Site			
BSFC 3032 ^f	<i>h.</i>	<i>h.</i>	1980	CO	Logan	S. Platte	S. Platte R., Merino	1		100
BSFC 3032 ^f	<i>p.</i>	<i>h.</i>	1980	CO	Logan	S. Platte	S. Platte R., Merino	1	100	
CAS 72788 ^g	<i>h.</i>	<i>n.</i>	1889	CO	Denver	S. Platte	S. Platte R. at Bear Ck.	10 (7)		100
UCM 347	-- ^e	<i>n.</i>	1913	CO	Fremont	Arkansas	Sells Lake, Canon City	2 (0)		
UCM 6212 ^{f,g}	<i>h.</i>	<i>n.</i>	1915	CO	Yuma	Republican	Arikaree R.	12		100
UCM 6212 ^{f,g}	<i>p.</i>	<i>n.</i>	1915	CO	Yuma	Republican	Arikaree R.	25 (21)	76	24
UCM 6324	-- ^e	<i>n.</i>	1918	CO	Boulder	S. Platte	Rock Ck.	7 (0)		
UMMZ 145017 ^f	<i>p.</i>	<i>p.</i>	1947	NE	Dundy	Republican	Arikaree R., Kansas line	5	100	
UMMZ 145017 ^f	<i>h.</i>	<i>p.</i>	1947	NE	Dundy	Republican	Arikaree R., Kansas line	32 (31)		100

^a Specimens in poor condition so accurate measurements could not be made, but species identity verified.

^b Original *Hybognathus* species not determined

^c Collection date not available

^d County of collection information not available

^e No fish in museum lot were *Hybognathus*

^f Museum lot contained both *H. placitus* and *H. hankinsoni*.

^g Collection contained mixture of *Hybognathus* and other species

APPENDIX 1.2:
DESCRIPTIONS OF MORPHOMETRIC CHARACTERS MEASURED FOR MODEL
DEVELOPMENT

Appendix 1.2. Description of morphometric characters for analysis of systematics of brassy and plains minnow. Definitions of quantitative characters are from Hubbs and Lagler (1964).

Character	Description
<i>Quantitative (measured to nearest 0.01 mm)</i>	
Standard length	distance from tip of snout backward to end of vertebral column
Head length	distance from tip of snout to most distant point on opercular membrane
Body width	greatest width of body, not including fins
Body height	greatest depth of body, not including fins
Pectoral fin length	distance from extreme base of anteriormost ray to farthest tip of fin
Snout length	distance from tip of snout to the front margin of the eye orbit
Eye diameter	greatest distance between the free orbital rims
Gape width	greatest transverse distance across the opening of the mouth
Caudal peduncle depth	least depth of caudal peduncle
<i>Qualitative</i>	
Dorsal fin shape	rounded (R) or pointed (P)
Snout shape	rounded (R) or pointed (P)
Eye position	Middle of eye is even with (E), or above (A) the horizontal line drawn back from most anterior point of snout.

CHAPTER II

**BRASSY MINNOW METAPOPULATION PERSISTENCE IN AN
INTERMITTENT COLORADO PLAINS STREAM**

To be submitted to Transactions of the American Fisheries Society

ABSTRACT

Few studies have addressed whether stream fish are arranged as metapopulations, despite frequent reports of extinction and colonization in these patchy, seasonal environments. Fishes like the brassy minnow (*Hybognathus hankinsoni*; a threatened species in Colorado) in streams of the western Great Plains are likely candidates because they live in harsh, fluctuating environments where they are subject to frequent extirpations by processes like summer drying and winter freezing, yet persist in part due to adaptations for rapid dispersal and reproduction during the wet season. We studied brassy minnow populations at multiple scales in the Arikaree River Basin of eastern Colorado to determine whether they exhibited evidence of metapopulation dynamics that allow regional persistence, and if so, to determine the underlying mechanisms driving local extinction and colonization. Habitat units in three long segments, arrayed across a gradient of stream intermittency from perennial to seasonally dry, were sampled five times in 2000 and 2001, the two driest summers on record. Logistic regression showed that brassy minnow were more likely to persist through the summer in deeper pools connected to other habitat units, and more likely to persist in pools in the most perennial segment. The main cause of fish extirpation was pool drying, which logistic regression showed was more likely in shallower pools in the drier segments. Population turnover was high in all segments, but only in the wettest segment did colonizations outnumber extinctions. Despite poor adult survival in the drier segments, larval brassy minnow were present in all segments in early summer of both years, indicating substantial movement for recolonization. Brassy minnow in the Arikaree River showed evidence of metapopulation dynamics because persistence was related to patch size (depth) and isolation, with extinctions more likely in shallow, disconnected pools. Moreover, some suitable habitats were empty, there were asynchronous local dynamics among pools, and

the species persisted at the segment (regional) scale despite population turnover. The dynamic nature of plains streams, differences in flow regimes among segments, and the large spatial scales over which brassy minnow carry out their life history requires management at the 'intermediate' segment scale for effective conservation.

For many populations living in patchy environments, such as fish in streams, persistence at the regional scale depends on the balance between local extinction and colonization from adjacent patches that serve as refuges (Harrison and Taylor 1997). Many stream environments are seasonally intermittent, as in the southwestern United States and the tropics (John 1964; Chapman and Kramer 1991), with marked wet and dry periods, so extinction and recolonization are common. Extinction occurs primarily as streams dry, whereas recolonization is prevalent during the wet season. Understanding the processes that drive populations in such habitats requires examining the distribution of fishes at both local and regional scales, and during cycles of wetting and drying. Groups of subpopulations that persist in a network of patches despite such local extinctions are termed metapopulations (Levins 1970; Harrison and Taylor 1997), and theoretical models have been developed to predict conditions of colonization and extinction that promote regional persistence.

Only a few studies have addressed whether stream fish populations are arranged as metapopulations (Gagen et al. 1998; Gotelli and Taylor 1999; Rieman and Dunham 2000), despite the numerous studies of movement, extinction, and colonization patterns of fish (e.g., Larimore et al. 1959; Fausch and Bramblett 1991; Lonzarich et al. 1998). However, several studies provide good evidence that metapopulation processes are at work in stream fish populations. Schlosser (1995) described the role of movement from beaver pond ‘source’ habitats to adjacent stream ‘sink’ habitats in controlling fish distribution and density in a Minnesota headwater stream. Likewise, Labbe and Fausch (2000) found that fish apparently moved relatively long distances to recolonize pools where they had previously been extirpated by drought or freezing.

Even fewer studies have tested theoretical metapopulation models with empirical stream fish data. Gotelli and Taylor (1999) found that patterns of extinction and recolonization in an Oklahoma river failed to support the key predictions of the classic Levins metapopulation model, and recommended the use of spatially explicit models instead. Incidence Function Models are spatially realistic models fit to empirical data on patch occupancy that incorporate functions describing colonization and extinction and can be used to predict probabilities of metapopulation persistence (Hanski 1999). However, the underlying assumptions of these models, namely that rates of extinction and colonization are at equilibrium (Hanski 1999) and that habitat patches do not change in area, make them difficult, if not impossible, to apply to stream fish populations in dynamic seasonal environments. Before metapopulation models with more realistic assumptions can be developed for stream fish, it must first be determined whether populations exhibit metapopulation dynamics and the underlying mechanisms driving local extinction and colonization. Hanski (1999) cites 12 types of evidence from field studies that support the notion that metapopulation level processes are important in population dynamics, of which 9 types are germane to single species populations (Table 2.1).

If any stream fish are likely to show metapopulation processes, fishes of the Great Plains are good candidates. Plains streams are harsh environments that fluctuate drastically in both physical and chemical properties due to flash floods that rearrange habitat, seasonal drying, and winter freezing (Matthews 1988; Fausch and Bestgen 1997). The extreme conditions created by these natural processes are often exacerbated by anthropogenic land and water use (Eschner et al. 1983; Matthews and Zimmerman 1990; Strange et al. 1999). Plains fishes are tolerant of physicochemical extremes (Matthews and Maness 1979; Matthews and Zimmerman 1990) and many have life histories that allow rapid dispersal (Fausch and Bramblett 1991). The dynamic

nature of Great Plains streams makes most local fish populations vulnerable to extinction, but the species persist in long segments or subwatersheds due to a balance between stochastic extinction and colonization events at the regional scale (Fausch and Bestgen 1997; Lohr and Fausch 1997).

Brassy minnow (*Hybognathus hankinsoni*) populations in Great Plains rivers of eastern Colorado are potentially good subjects for evaluating metapopulation dynamics and the underlying mechanisms allowing persistence. Little is known about the habitat requirements or population dynamics of brassy minnow, which was designated as a threatened species by the State of Colorado in 1998. Both Copes (1975) and Goldowitz and Whiles (1999) reported that brassy minnow use seasonally flooded habitats for spawning, recruitment, and growth. Labbe and Fausch (2000) found that another rare plains fish species, the Arkansas darter (*Etheostoma cragini*) also used seasonally flooded habitats and required deep stable pools as refuges from summer drying and winter freezing, a requirement likely shared by other plains species. Because brassy minnow use temporary habitats during certain life stages, live in dynamic streams where habitats ebb and flow through time and space, and inhabit an ecosystem where uncertainty is the norm, populations are at considerable risk of stochastic local extinction. Therefore, persistence at the regional scale requires fish movement to recolonize these vacant habitats. The presence of empty habitat, and regional persistence despite population turnover, are two types of evidence supporting metapopulation dynamics (Hanski 1999; Table 2.1).

Understanding the role of metapopulation processes in sustaining rare and declining species is important for managers because their goal is to achieve regional persistence of these species and their habitats. To be effective, managers must determine not only the critical habitats needed to sustain each life stage of the target species at the local scale, but also the entire range of spatial and temporal scales over which fish live out their life history and the processes

that create and maintain the critical habitats at these multiple scales (Fausch et al. *in press*). Therefore, we chose to study the distribution of different life stages of brassy minnow and their habitats through time at three scales, basin, segment, and habitat unit, in a dynamic intermittent plains stream in eastern Colorado. Our main goals were to determine mechanisms driving local population and habitat persistence in individual habitat units (i.e., pools, backwaters, runs), and to assess whether metapopulation processes at the segment scale influenced regional persistence. We suspected that the degree of stream drying would strongly influence the persistence of habitat and fish in pools, so we selected three long segments of the Arikaree River arrayed across a gradient of stream intermittency to address how stream drying influences persistence of brassy minnow populations at the basin scale. We used several measures of population performance for comparison across this gradient, including persistence in local habitats, survival to older ages, growth, and reproduction.

Study Area and Sampling Units at Three Spatial Scales

Arikaree River Basin

The Arikaree River is a major tributary of the Republican River in the Kansas River Basin in eastern Colorado (Figure 2.1). The Arikaree River Basin covers 4,477 km² in the Western High Plains ecoregion (Omernik 1987), a semi-arid grassland due to its mid-continental location in the rain shadow of the Rocky Mountains (Cross and Moss 1987). The region is fairly flat (stream gradient averages 1%), reminiscent of the vast shallow sea that covered it during the Cretaceous. Sand and gravel eroded from the eastern slope of the Rocky Mountains as they uplifted in the late Cretaceous and Miocene, creating large alluvial fans that buried ancestral drainages and formed the Ogallala aquifer (Cross et al. 1986). The headwaters of the Arikaree River lie on the plains so stream flow is derived mostly from groundwater from the Ogallala

aquifer, punctuated by infrequent, intense floods caused by thunderstorms during May through September. For example, during the 69-year record of flows at the river mouth (U.S. Geological Survey [USGS] gauge 06821500; <http://water.usgs.gov/nwis>), there were eight floods greater than 200 m³/s during these months. However, no such floods occurred during the study period (May 2000-June 2001). Mean monthly flows during the study were below the 95% confidence limits for the 69-year average and were among the lowest ever recorded (Figure 2.2).

Study segments

We selected three 6.4-km segments for study where populations of brassy minnow had been found during pilot sampling in 1999 (Figure 2.1). The segments were arrayed along a gradient of intermittency, from perennial to seasonally intermittent. The upstream segment had the most perennial flow and the most pools (Table 2.2). The channel was narrow and sinuous with alternating pools and runs, all with predominantly silt and some sand substrates. Riparian vegetation consisted of dense grasses, willow, and cottonwood gallery forest. Several beaver dam complexes created deep, persistent pools. The primary land use was cattle grazing, which was seasonally rotated.

The middle segment was intermediate in its degree of drying. The channel varied from narrow with perennial flow to wide with shifting sand substrate and intermittent flow. Riparian vegetation was grasses along the downstream reaches and cottonwoods upstream. The few deep permanent pools were created by high flows, but gradually filled with sand during low flow. Cattle grazing caused bank erosion throughout the segment, and some pools used by cattle had low dissolved oxygen during summer.

The downstream segment was the driest. Flow was intermittent and the channel was wide and sandy with few pools. The segment is bordered by privately owned pasture and cottonwood gallery forest in the floodplain, and dry land and irrigated agriculture in the uplands (Figure 2.1). Most riparian areas are managed as conservation easements by the Colorado Division of Wildlife. Groundwater pumping for irrigation may have contributed to channel drying during summer. A perennial tributary, Black Wolf Creek, may provide refuge for fish during dry periods.

Habitat units

Discrete channel units, pools, backwaters, and runs (Hawkins et al. 1993), were selected for sampling in each segment. Each segment was divided into 800-m reaches (Table 2.2). Some pools filled with sand during the study and others were created by high flows so the number of habitat units sampled per survey varied slightly. Pools were abundant in the upstream segment (Table 2.2) and so were selected by stratified random sampling. Pools were stratified as either shallow (<40 cm residual depth; Lisle 1987) or deep (>40 cm residual depth). Two pools in each stratum were randomly selected from each reach. Nine pools >1.5 m deep were not included because they could not be sampled effectively. Five runs and six backwaters were also selected at random from throughout the segment. Thirty-nine habitat units were sampled in 2000 and 38 in 2001.

In the middle segment, most pools were shallow and were stratified as either channel spanning or lateral scour (Hawkins et al. 1993). All pools in the six downstream reaches were surveyed. Pools were abundant in the two upstream reaches in 2000, so every other channel spanning and every third lateral scour pool was systematically selected for sampling. Eight runs

and 11 backwaters were also randomly selected from throughout the segment, totaling 51 channel units sampled in 2000 (Table 2.2). Many pools filled with sand during winter 2000 so only 36 habitat units were sampled in 2001.

The downstream segment dried rapidly each spring, so we sampled all the remaining pools and backwaters. New habitats were sampled as they were created. We also sampled a reference section of Black Wolf Creek near its mouth that included a slow deep run and a deep vegetated pool. Nine habitat units were sampled in the downstream segment (Table 2.2) in 2000, excluding the Black Wolf Creek site. In 2001, 5 runs were added, and 13 pools and backwaters were sampled.

Methods

Basin and Segment Scale

The presence of water and flow connectivity was surveyed throughout the Arikaree River Basin three times, during December 2000, March 2001, and June 2001. The lower 106 km of stream channel from Cope, Colorado to its mouth near Haigler, Nebraska was flown at low elevation and flow connectivity was estimated on 7.5 minute USGS topographic maps and recorded using a global positioning system (GPS). To measure habitat persistence at the segment scale, we traversed each of the three segments on foot five times, during June, August, and November 2000, and May and June 2001. We recorded on maps the presence of water in each habitat unit and flow connectivity among them. A Geographic Information System (GIS) using ArcView 3.2 (ESRI, Inc. 1999) was used to map patterns of flow connectivity at the basin and segment scales.

Habitat Unit Scale

Habitat and Water Chemistry

Seven habitat characteristics were measured at each habitat unit on each survey, including total length, wetted width, maximum depth, substrate composition, aquatic vegetation, riparian vegetation, and flow connectivity. Length was measured along the channel midline, and wetted width was measured at 0.25, 0.50, and 0.75 of the habitat unit length. Bankfull width was not measured because banks were often indistinct. Percentage composition by area was estimated visually for channel substrate, aquatic vegetation, and riparian vegetation. Substrate was categorized after Wolman (1954), aquatic vegetation was categorized as algae or rooted aquatic macrophytes, and riparian vegetation was categorized as grasses, shrubs, trees, or absent. Flow connectivity was defined as connected (flowing on at least one end) or isolated.

Five physicochemical characteristics were measured in each channel unit including temperature, dissolved oxygen, specific conductance, salinity, and pH. Temperature was measured using a digital thermometer (Atkins Model 39658-K) at the surface and near the substrate in the deepest part of each unit. The pH was measured with an Orion Model 210A meter. Dissolved oxygen, specific conductance, and salinity were measured using a Yellow Springs Instruments multimeter (Model 85). Maximum summer water temperatures were measured in all habitat units during 8-15 August 2000 between 1100-1700 hours. Minimum dissolved oxygen was also measured on the same dates, before sunrise when nighttime plant respiration had depleted the oxygen to a minimum. Ten thermographs (Onset Corp. StowAway[®] TidBit[®]) were installed throughout the segments in shallow (n=4) and deep (n=4) pools and backwaters (n=2, 1 deep, 1 shallow) to measure daily and seasonal temperature fluctuations.

Eight additional thermographs were installed in habitats where gravid brassy minnow or fish larvae were captured in May 2001 to record temperatures in spawning and rearing habitats.

Fish Sampling

Fish were sampled in each habitat unit on each survey. Habitats were blocked at the downstream end and seined in a downstream direction using a 1.2-m by 3.0-m seine with 5-mm mesh. Dipnetting (5-mm mesh) was used in areas with dense aquatic vegetation or other structure. Minimum sampling effort required to capture all fish species present was determined by depletion sampling at two sites in July 1999. One site consisted of a riffle, run, and pool (24 m x 1.5 m average width) that had little physical structure. It was sampled using four seine passes and 1157 fish were captured. The other site consisted of a densely vegetated riffle and run, and a pool and backwater with physical structure (52 m x 2.2 m). It was sampled using two passes of dipnetting followed by one pass with a backpack electrofishing unit (Coffelt Model BP-10, 150 V, 50 Hz) and 1159 fish were captured. At both sites, all seven fish species captured in all passes were caught on the first pass, so one seine pass or two persons dipnetting throughout the habitat unit was determined to be sufficient to capture all fish species present.

Based on these results, in subsequent sampling, if brassy minnow were collected in the first pass no additional sampling was conducted, but if brassy minnow were absent in the first pass a second pass was conducted to confirm their absence. In large or complex habitats, we conducted three or more passes for greater confidence in determining the absence of brassy minnow. All brassy minnow captured were counted and fork lengths measured (nearest mm). When fewer than 200 fish of all species were captured, all fish were counted and identified. When more were captured, random subsamples of 200-300 fish were counted by species to

estimate relative abundances, but all fish were examined to determine species richness. Fish were processed immediately after sampling and returned to the water. Nearly all fish were identified to the species level in the field, but any unknown specimens were preserved for laboratory verification by Dr. Kevin Bestgen (Colorado State University Larval Fish Laboratory). Voucher collections are curated at the Colorado State University Larval Fish Laboratory. A sample of 98 brassy minnow representing the range of lengths captured in each segment were collected between 31 July and 17 August 2000 and preserved in 70% ethanol for aging. Otoliths proved difficult to age because of indistinct annuli, so scales were removed, manually cleaned of excess tissue, and examined at 32X and 100X to count annuli (DeVries and Frie 1996).

Larval fish were collected from the regularly sampled habitat units in the three segments during three surveys from May to July 2000 and two surveys from May through June 2001 to identify locations where brassy minnow reared. In 2001, larvae were collected from additional habitat units as they were encountered during regular surveys and in the weeks between surveys. Larvae were collected with a 1.6-mm-mesh seine or small aquarium dipnets from early May to June and 5-mm-mesh dipnets during late June and July. Samples were preserved in 3% formalin for laboratory identification and measurement. Dr. Kevin Bestgen identified or verified identifications of larval fish. Standard lengths of brassy minnow larvae were measured to the nearest 0.1 mm using digital calipers under a dissecting microscope.

Statistical analysis

Logistic regression (SAS/STAT[®] 2000, PROC LOGISTIC) was used to model the persistence of brassy minnow and their primary habitat types, pools and backwaters, during the

summer 2000 drying period (June through August) as functions of factors measured at the habitat unit (pool) scale. Only pools and backwaters were included because few brassy minnow inhabited runs as segments dried (see *Results*). We divided the units into those where juvenile or adult brassy minnow persisted through August (including those colonized during summer), and those where juvenile or adult brassy minnow disappeared during summer (including those habitat units that dried). We developed models of brassy minnow persistence as a function of August 2000 measurements of six of the physical habitat and physicochemical variables (area, depth, aquatic vegetation, connectivity, maximum temperature, minimum dissolved oxygen). We also included as variables the minimum distance to the next habitat unit ever occupied by brassy minnow estimated from an ArcView GIS coverage of flow connectivity to measure the opportunity for colonization, and the presence or absence of fish predators (creek chub *Semotilus atromaculatus*, green sunfish *Lepomis cyanellus*, and black bullhead *Ameiurus melas*). We also modeled persistence of pools and backwaters through summer 2000 as a function of June measurements of physical habitat and connectivity. There was little variation in four physicochemical variables (substrate composition, pH, salinity, specific conductance) so they were not included. Area, depth, temperature, and dissolved oxygen were transformed using natural logarithms (ln) to normalize skewed distributions. We also fit both sets of models with and without segment as a categorical variable to determine if persistence could be predicted solely from variables measured at the local (habitat unit) scale or if the landscape context of segment was important.

Models for predicting persistence of brassy minnow and their habitat were ranked using Akaike's Information Criterion (AIC). This procedure compares multiple models simultaneously to select the most parsimonious model consistent with the data while balancing

precision and bias (Burnham and Anderson 1998; Franklin et al. 2000), and is well suited for selecting models based on observational data. Models were ranked using AIC_c (corrected for small sample size) and Akaike weights (w_i) were calculated to compare competing models. Models with the lowest AIC_c and highest weights are considered the “best approximating” models. We considered only models with five or fewer parameters (not including the intercept) due to modest sample size, and eliminated models with quasi-complete separation of data because parameters could not be estimated using logistic regression (P. Chapman, Dept. of Statistics, Colorado State Univ., pers. comm.).

Results

Fish community

Twelve fish species were captured in the three segments in 2000 and 2001 including central stoneroller (*Campostoma anomalum*), red shiner (*Cyprinella lutrensis*), brassy minnow, sand shiner (*Notropis stramineus*), fathead minnow (*Pimephales promelas*), creek chub, white sucker (*Catostomus commersoni*), black bullhead, plains killifish (*Fundulus zebrinus*), green sunfish, largemouth bass (*Micropterus salmoides*), and orangethroat darter (*Etheostoma spectabile*). Three species previously reported from the Arikaree River (Cancalosi 1980), plains minnow (*H. placitus*), river shiner (*N. blennioides*), and suckermouth minnow (*Phenacobius mirabilis*), were not collected. Largemouth bass was the only nonnative species present and was only collected in the first survey in June 2000 from three locations in the middle segment. We believe largemouth bass were flushed from an upstream farm pond into the main channel during a spate in September 1999 and were subsequently extirpated from the segment during summer 2000 when conditions became harsh. White sucker were collected primarily in the upstream

segment and only once in the middle segment. Sand shiner were relatively abundant in the middle and downstream segments, but were rarely collected from the upstream segment. Central stoneroller, fathead minnow, creek chub, and plains killifish were the most abundant species. Red shiner were abundant in 2000, but less common in 2001.

Habitat and Fish Persistence

Basin scale

Habitat for brassy minnow in the Arikaree River basin during the study was restricted to about 75 km upstream from the confluence (Figure 2.3). The three study segments were located in the most perennial stretch of river. Upstream and downstream from this stretch the channel was dry most of the year. In mid-December 2000, flow was continuous throughout most of the lower and middle segments and the entire upstream segment, with some frozen sections between segments. During a visit in November 2000, long reaches of the downstream segment consisting of shallow runs were completely frozen and thick surface ice had formed over the pools, so although water was present in the channel much of it was frozen, and not available as habitat for fish. By March 2001, flow was continuous throughout a 55-km stretch containing the three segments and was not frozen, allowing fish to move long distances to recolonize open habitats. By June 2001, flow had declined downstream, causing most of the downstream and middle segments to become intermittent or dry and restricting fish to refuge pools and Black Wolf Creek. In contrast, flow was continuous throughout a 26-km stretch that contained the upstream segment.

Segment scale

The amount of available habitat in each segment changed with seasonal drying, but corresponded to the gradient of flow intermittency. The downstream segment was the driest (Figure 2.4) and contained the fewest pools in both years (Table 2.2). By June 2000, about two-thirds of the segment was dry, so most shallow pools and runs were already eliminated and the maximum depths of the remaining pools was biased high (mean [SE]= 0.36 [0.07] m). The middle segment was intermediate in its degree of drying (Figure 2.5) and number of pools, most of which were shallow (mean [SE]= 0.34 [0.02] m). The upstream segment had the most persistent flow (Figure 2.6), the largest number of pools, and deeper maximum pool depths (mean [SE]= 0.51 [0.04] m), even though nine very deep pools (>1.5 m deep) were not included in those surveyed. Fewer habitat units persisted through the summer 2000 drying in the downstream segment (33%) than either the middle (53%) or upstream segments (87%). Overall, more runs dried in the three segments than pools or backwaters (46% vs. 32%).

Brassy minnow persisted through seasonal drying and rewetting in the fewest locations in the downstream segment and the most in the upstream segment (Figure 2.7), in concert with the degree of flow permanence. In June 2000, the majority of the downstream segment was already dry (Figure 2.4). Brassy minnow were present in 75% (6 of 8) of the habitat units sampled, and also in a large pool at the mouth of Black Wolf Creek. In contrast, flow was continuous throughout the other two segments, and brassy minnow were present in 56% (28 of 50) of the habitat units sampled in the middle segment and 36% (14 of 39) of those in the upstream segment.

By August 2000, flows had declined markedly, and long reaches in the middle and downstream segments had dried, extirpating fish from many habitat units. Brassy minnow remained in only one pool in the downstream segment and 17 habitat units (all pools and backwaters) in the middle segment. Brassy minnow were not captured in the August survey from Black Wolf Creek. A flash flood occurred in July that apparently reduced fish populations to low levels. Few brassy minnow were captured during sampling in July and none were captured during the August survey. Flow had become intermittent in about two-thirds of the upstream segment by August, but fish remained in 13 habitat units, only one less than the number occupied in June. However, brassy minnow were not always present in the same habitat units because connections apparently allowed them to move among units as drying progressed.

Flows increased in the fall when irrigation ended, plants became quiescent, and temperatures cooled. By November 2000, a few short reaches in the downstream and middle segments were partially reconnected and the upstream segment was entirely rewetted. In the downstream segment, brassy minnow recolonized one pool at the mouth of Black Wolf Creek, presumably from upstream reaches of that tributary, and were present in only two locations in total. Infilling of pools with sand in the middle segment extirpated brassy minnow from all but 10 habitat units and only one pool that had lost brassy minnow during the summer was recolonized. In contrast, recolonization in the upstream segment increased the number of habitat units occupied to 23 compared to 14 in June. Overall, population turnover was high in all segments during 2000 (Table 2.3). The extensive drying in the downstream and middle segments through August caused higher rates of extinction than colonization, whereas the extensive rewetting of the upstream segment by November caused the opposite pattern.

Overwinter survival of brassy minnow was apparently low in all segments because few fish were captured during May 2001. Flows were continuous throughout all segments, but brassy minnow were absent from all 18 habitat units sampled in the downstream segment and present in only 5 of 33 habitat units sampled in the middle segment and 10 of 36 sampled in the upstream segment. Stream drying was more extensive by June 2001 than June 2000. No adult brassy minnow were collected in the downstream segment, and only two habitat units in the middle segment and five of those sampled in the upstream segment held brassy minnow in June 2001. Moreover, many pools in the middle segment had filled in, reducing their number by 44% from June 2000. Density of all fish, including brassy minnow, declined drastically from 2000 to 2001. For example, in June 2000, 200 adult brassy minnow were captured from 97 habitat units (average 2 fish/unit) across the three segments (18.4 km), whereas only 18 adult brassy minnow were captured in the 79 habitat units sampled in June 2001 (average 0.23 fish/unit).

Seasonal temperature regimes were harsher in the middle and downstream segments than the upstream segment, and harsher in shallow than deep pools, which may have contributed to lower survival of brassy minnow in the harsher habitats. For example, long-term thermographs showed that maximum temperatures exceeded 38°C in two of three pools monitored throughout summer in the downstream and middle segments. Maximum temperatures measured at the streambed in the regularly sampled units in August 2000 were warmer in shallow versus deep pools across segments (shallow: mean [SE, range]= 28.5 [0.53, 19.8-35.5] °C, n=39; deep: mean [SE, range]= 26.6 [0.97, 19.9-34.2] °C, n=21; P=0.07 by ANOVA). Maximum bottom temperatures were also significantly warmer in pools in the downstream and middle versus upstream segments (downstream and middle: mean [SE, range]= 29.7 [0.52, 21.9-35.5], n=30; upstream: mean [SE, range]= 25.4 [0.80, 19.8-33.9] °C, n=30; P<0.0001; segment*depth

interaction not significant, $P=0.54$). Segment was more important than pool depth in controlling temperature maxima because even deep pools in the downstream and middle segments were as warm as shallow pools in the upstream segment (downstream and middle deep pools: mean [SE, range]= 28.5 [1.64, 21.9-34.2] °C, $n=5$; upstream shallow pools: mean [SE, range]= 26.0 [1.34, 19.8-33.9] °C, $n=14$; $P=0.16$ by least squares means). However, there were no significant differences in temperatures between deep and shallow pools within segments ($P \geq 0.13$). Diel fluctuations were also greatest in shallow pools in the spring, and were larger in the middle than upstream segment. Maximum fluctuations determined from thermographs averaged 17.2°C (range 12.2-21.0°C) in the five shallow pools (of which four were in the middle segment) and 9.6°C (range 7.8-10.6°C) in the four deep pools (all in upstream segment) for which these data were available. Shallow pools were more likely to freeze to the bottom in winter (4 of 5 froze) than deep pools (0 of 5 froze).

Habitat unit scale

Brassy minnow occurred in all types of habitat units in 2000, but were found more often in pools and backwaters than runs. Moreover, as segments dried during summer 2000, brassy minnow were captured in fewer of the runs that remained (14% in August versus 23% in June), but about the same proportion of pools and backwaters (39% vs. 41%). Adult brassy minnow were scarce in 2001. They were present in only 17% and 9% of the habitat units sampled in May and June, respectively, and were never captured in runs.

Given that juvenile and adult brassy minnow primarily inhabited pools and backwaters during the summer drying period, we focused our analysis of fish persistence during this period on these two types of habitat units, which we group as 'pools' hereafter. Of 86 pools sampled

during summer 2000, 65 contained brassy minnow during at least one of the three surveys. Brassy minnow persisted in about half of the pools where they were ever present (n=30, 46%), were extirpated by pool drying from 17 pools (26%), and emigrated or were apparently extirpated from the other 18 pools (28%) that remained wet. We first fit logistic regression models to identify factors that explained brassy minnow persistence in the 48 pools that remained wet. Then, because drying was a major cause of extirpation from pools, we fit models to predict the probabilities of pool persistence through summer drought.

When pools in all segments were combined, brassy minnow persistence was best predicted by the independent variables August depth and August connectivity. Fish were more likely to persist in pools that were deeper in August and connected to other habitat units on at least one end. This model had the lowest AIC_c and the highest Akaike weight of any model without segment included as a variable (Table 2.4), and both parameters were significant (P<0.02 by likelihood ratio test). Models that included presence of predator species all yielded positive estimates for this parameter, indicating that brassy minnow persistence was more likely when predators were present. The presence of any fish species in August, predators or otherwise, probably increased the chances of brassy minnow persistence because they indicated tolerable conditions as pools dried. These results were in the opposite direction expected, so only models without this biotic variable were considered further. The fish community of the Arikaree River is composed entirely of native species so predator and prey species have coevolved, allowing coexistence. Schlosser (1988) found that creek chub, the most common predator in our system, ate few brassy minnow and only weakly affected their habitat selection.

Other pool scale variables were not useful in predicting brassy minnow persistence. For example, there was no significant relationship between maximum water temperature and brassy

minnow presence or absence ($P=0.49$ by logistic regression). Fish persisted in pools with maximum bottom water temperatures as high as 35.5°C , indicating that high temperature was unlikely to limit survival. Likewise, there was little evidence that low early morning dissolved oxygen limited brassy minnow persistence ($P=0.57$ by logistic regression). Minimum dissolved oxygen levels were low in all pools with brassy minnow (mean [SE]= 1.52 [0.15] mg/L), and they persisted in pools with concentrations as low as 0.03 mg/L.

Stream segment was always an important predictor of brassy minnow persistence in conjunction with other habitat variables, because models with segment had AIC_c values 1.4 - 6.3 units lower than models without segment for the three highest ranked models (Table 2.4). The “best approximating” model selected by AIC predicted brassy minnow persistence as a function of segment, pool area, pool depth, and connectivity in August. However, the effect of area was negative and small compared to the effects of depth and connectivity. For example, the odds of brassy minnow persistence *decreased* only 13.5% for a 10% increase in pool area (i.e., increase in \ln pool area of 0.1 unit). In contrast, the odds of brassy minnow persistence increased 47.2% for a 10% increase in pool depth and increased 12.6 times if pools were connected on at least one end versus isolated. Therefore, we chose the model with segment, depth, and connectivity as the most parsimonious model for prediction (Table 2.5). This model showed that the probability of brassy minnow persistence was highest in deeper pools that were connected on at least one end in August compared to shallower isolated pools (Figure 2.8). In addition, fish were more likely to persist in pools of a given depth in the middle and upstream segments than in the downstream segment. Based on this model, fish were also more likely to persist in pools of a given depth in the middle segment than the upstream. Pools in the middle segment were generally shallow, wide, and disconnected, or had only very shallow connections that likely impeded fish

movement. Therefore, the higher persistence predicted for brassy minnow in pools of a given depth in this segment is a reflection of their tolerance. In contrast, pools in the upstream segment were deep, narrow, and more often connected. Fish could more easily move among pools in this segment, so the model is likely a reflection of habitat preference of brassy minnow.

Models of brassy minnow persistence as a function of physicochemical variables revealed that brassy minnow were tolerant of high temperature and low dissolved oxygen, but intolerant of drying, a main mechanism of extirpation at the pool scale. Therefore, we also fit models predicting pool persistence through the summer drying period until August from physical habitat characteristics measured in June. As for models of fish persistence, those including segment had AIC_c values 1.8-5.7 units lower for all but two of the top seven models (for which AIC_c were only 0.1 units less and 1.8 units greater, respectively; Table 2.4), indicating that segment was also an important predictor of habitat persistence. The best model for predicting habitat persistence included segment, June depth, and June connectivity (Table 2.4), but nearly complete separation of data in the parameter space resulted in invalid parameter estimates with large standard errors so this model could not be used for prediction. Therefore, we selected the next best model, with segment and June depth, as the most suitable for prediction (Table 2.5). Based on this model, pools of a given depth were more likely to persist through the summer in the upstream segment than the other segments (Figure 2.9). For example, a pool with a maximum depth in June of 0.5 m would have only a 50% probability of persistence in the downstream segment, but a 77% probability of persistence in the middle segment and a 95% probability in the upstream segment. Thus, shallower pools were more likely to persist in the upstream segment and more likely to dry in the downstream and middle segments.

Population Performance among Segments

Age structure and growth

Brassy minnow survived to older ages in the upstream segment compared to the middle or downstream segments (Figure 2.10). In the sample of 98 fish aged from August 2000, age-3 brassy minnow were found only in the upstream segment. Most fish in the three segments were age 2 or younger. When the length ranges of the aged fish were compared to the length-frequency histograms for August 2000, age-3 fish were most abundant in the upstream segment, but extremely rare in the middle segment and absent from the downstream segment. Aging by scale annuli also revealed that age-2 brassy minnow were longer in the upstream than the middle segment. Too few adults were captured in the downstream segment to analyze because survival was very low. Brassy minnow in the middle and upstream segments were similar in fork length (FL) at ages 0 and 1 (pooled means: 37.6 mm FL at age 0, 52.7 mm FL at age 1; $P \geq 0.22$ for both by least squares means after ANOVA). However, age 2 fish were longer in the upstream than middle segment (62.3 mm vs. 57.9 mm FL; $P = 0.0004$ by least squares means), and age 3 fish were found only upstream (73.9 mm FL). Overall, differences in brassy minnow lengths between the two sections depended on age (section $P = 0.77$, age $P < 0.0001$, section*age $P = 0.01$ by ANOVA).

Recruitment

Brassy minnow spawned during spring (April-May) and hatched in early summer (May-June) of both years, but apparently hatched earlier or grew faster in 2001 than 2000. Spawning,

as determined by the presence of gravid females or golden-colored males, was observed during a single period from mid-April through mid-May in both years. The earliest date that larvae appeared was earlier in 2001 (17 May; Figure 2.11) than in 2000 (5 June). Hatching occurred between mid-May and mid-June when water temperatures in spawning and rearing habitats were between 15.7 and 23.5°C in 2001 (mean of 5-d running means=18.4°C for eight habitat units from 17 May through 15 June 2001). The first larvae collected in June 2000 were 10.4 mm FL, compared to 12.5 mm FL in May 2001. Brassy minnow larvae appeared earlier and grew larger by the end of June in 2001 than in 2000 (2000: mean [SE]= 24.50 [1.16] mm FL, n=18; 2001: mean [SE]= 27.56 [0.24] mm FL, n=145; P=0.02 by t-test with Satterthwaite correction for unequal variances), even though the 2000 sample included fish collected on later dates than those collected in 2001.

Brassy minnow larvae were collected in all three segments in both years, sometimes in habitats or reaches that were dry most of the year and where adults were never captured (Figure 2.12). They were captured in all reaches of the middle and upstream segments and in four of the five upstream reaches of the downstream segment. Larvae were also present in a higher percentage of the regularly surveyed habitat units in June 2001 than June 2000 (49% vs. 18%, respectively). Larval brassy minnow were captured in runs more often than adults in both June 2000 (46% of runs held larvae vs. 23% held adults), and June 2001 (50% of runs held larvae vs. 0% held adults). In contrast, percentages were similar for use of pools and backwaters in June 2000 (35% held larvae vs. 41% for adults; too few adults were captured in June 2001 for comparison).

Discussion

Factors influencing brassy minnow persistence across scales

At the pool scale, brassy minnow persistence during summer drying was related to habitat size (depth) and isolation (connectivity). Deeper pools are more favorable because they are less likely to dry, undergo smaller temperature fluctuations, offer more protection from terrestrial predators (Power 1987), and are often structurally more complex, allowing the habitat to be partitioned among species or life stages. Persistence may have been higher in connected habitats because fish could temporarily move to other habitats for feeding or to escape predation. Fish could also emigrate from connected pools to find better habitats as pools dried and conditions became harsher. The relative influence of depth and connectivity on brassy minnow persistence varied among segments, likely due to differences in geomorphology, groundwater hydrology, and land use. Fish were more likely to persist in shallow, isolated pools in the upstream and middle segments than the downstream segment. It is difficult to make general predictions about persistence without the context of segment, so management planning needs to consider processes at this larger scale.

Brassy minnow were tolerant of very low dissolved oxygen in early morning and high afternoon stream temperatures so these factors did not appear to limit their persistence. Although brassy minnow can likely survive these extreme conditions for short periods, they may not be able to tolerate them for longer periods, or if they occurred at the same time of day. Matthews and Zimmerman (1990) found that many plains fish already exist near their critical thermal maxima, and in west to east flowing rivers such as the Arikaree, fish are not able to

migrate north to cooler habitats. Therefore, a prolonged drought or global warming, combined with an increasing demand for irrigation water that further reduces stream flows, could push brassy minnow beyond their tolerance limits. Several species are already missing from the Arikaree River Basin, including the plains minnow, suckermouth minnow, and river shiner (Cancalosi 1980), all species adapted to larger rivers (Pflieger 1997). Further increases in temperature and decreases in stream flow could result in a shift that favors only the hardiest species. On the other hand, the seasonally harsh conditions in the Arikaree River apparently excluded nonnative predators like largemouth bass, and may contribute to the long-term survival of native species in the basin. For example, Schlosser (1988) reported that smallmouth bass (*M. dolomieu*), which are nonnative to Colorado, have stronger effects as predators on brassy minnow than creek chub, with which brassy minnow coevolved.

Drying was the dominant mechanism controlling fish distribution and persistence in the middle and downstream segments. In contrast, other factors like emigration from pools and predation by terrestrial vertebrates were apparently more important in the upstream segment where few pools dried and many remained connected. Because drying was apparently the major process extirpating fish, models of pool persistence were useful for determining where brassy minnow could persist. The best model for predicting pool persistence included the variables segment and depth, again illustrating the importance of the landscape context. Labbe and Fausch (2000) found the same pattern of increased pool persistence with June depth for pools inhabited by Arkansas darter, another highly tolerant plains fish (Smith and Fausch 1997).

The apparently high rates of movement among habitat units within segments and seasonal use of some habitats suggest that segment is the appropriate scale for study and conservation of plains fish. Fish rapidly colonized new habitat when water flowed, spawned in flooded

vegetation on floodplains, and retreated to refuges or perished as segments dried. Populations in segments with more water persisted in more locations, survived to older ages, and grew larger than those in drier segments. Brassy minnow populations were able to survive in the downstream and middle segments after the relatively wet fall of 1999 and were abundant in our earliest surveys in 2000. However, populations did poorly in these segments during the subsequent 13-month period of our study, because little water persisted through the two dry summers.

Despite poor adult survival from 2000 to 2001, brassy minnow larvae were present both years in all segments. This, along with other indirect evidence, supports the hypothesis that fish must move long distances to repopulate segments when flow resumes. Juvenile brassy minnow were found in the leading edge of a front of water as it rewetted the channel in the downstream segment in September 1999. This observation, and the finding that larvae were present in more runs than adults, suggest that larvae and juveniles may be the life stages responsible for dispersal and colonization. Larvae were also found in habitats that were only seasonally inundated and later dried. In several instances, floodplain rearing habitats present in 2000 were not inundated in 2001. Because larvae use temporary habitats, and habitats can change considerably between years, management will need to focus on the larger-scale processes that create and maintain these features at the landscape (segment) rather than local (pool) scale. For example, the beginning of larval emergence coincided with the onset of irrigation in the downstream segment in mid-May 2001 (Figure 2.11). This segment dried quickly after irrigation began, stranding many fish before they could find refuge in deep pools or Black Wolf Creek. So, although larval fish appeared in the downstream segment each year, they may not be able to recruit to older ages in all but the wettest years in this segment.

Low-altitude flights at the basin scale provided the opportunity to assess landscape-scale patterns of flow connectivity and identify potential refuges for fish in this basin. Only about 75 km of the Arikaree River were perennial during the maximum extent of flow connectivity in spring 2001. Summer drying in this drought year reduced the length of continuous flow to about 25 km centered around the upstream segment. Seasonal flights could be a useful management tool for quickly surveying large areas to identify and prioritize the most perennial segments of river for conservation (Torgersen et al. 1999; Fausch et al. *in press*). However, reaches that flow only part of the year are also important corridors for movement of fish and colonization of vacant segments, and so should not be allowed to be channelized or otherwise degraded.

This research provides direct evidence for most of Hanksi's (1999) nine types of evidence for metapopulation processes (Table 2.1), and lends strong support for the view that brassy minnow populations like the one we studied are arranged as metapopulations. For instance, in support of his first point, our data suggest significant movement of brassy minnow that affected population size and density. Brassy minnow migrated to colonize vacant habitats as flow returned, and larvae were present in all segments in early summer despite the absence of adults in the downstream segment in 2001. Second, population density was affected by patch size (in this case, depth) and isolation (point 2), with fewer brassy minnow persisting in the downstream segment where pools were shallowest and most isolated. Third, brassy minnow were extirpated from some pools, but persisted in others in the same segment, providing evidence for asynchronous local dynamics (point 3) and persistence despite population turnover (points 4 and 6). For example, from June to November 2000 there were 85 extinction and colonization events across the three segments, yet brassy minnow larvae were present in all segments the following year. Fourth, brassy minnow were present in about 50% of the available

pools during 2000, and less than 20% of the available pools in 2001, so empty habitat patches were always available for colonization (point 5). Fifth, the best logistic regression model for predicting brassy minnow persistence showed that fish were more likely to persist in deeper pools, so extinction risk depended on patch size (point 7), although this size threshold depended on connectivity and landscape context (segment). Sixth, colonization rates were higher in the upstream segment where pools were more often connected (less isolated) and lowest in the downstream segment where pools were most isolated (point 8). Finally, the best logistic regression model also provided evidence that patch occupancy depended on patch size (depth) and isolation (connectivity) because brassy minnow persistence was higher in deeper, connected pools in each segment (point 9). Therefore, our data directly and indirectly provide strong evidence that brassy minnow populations in the Arikaree River are influenced by metapopulation processes occurring simultaneously at the local and regional scales.

Management implications

Given that brassy minnow in western Great Plains watersheds are likely arranged as metapopulations, management should occur at a segment scale and consider processes influencing the entire “population of populations.” Fausch et al. (*in press*) concluded that for many stream fishes, management should be focused at this ‘intermediate’ segment scale, which represents the nexus at which important fish life history processes occur. The basin scale is generally too coarse, except to identify perennial stretches of river encompassing potential refuge habitats. Likewise, the habitat unit scale is too fine because habitats change drastically both within seasons and between years, fish move among habitat units, and pool persistence varies by segment. Moreover, it may also be important to consider an ‘intermediate’ temporal scale for

management because population densities of brassy minnow likely fluctuate with long-term drought cycles. This study showed that brassy minnow were very tolerant of harsh conditions, moved relatively long distances to recolonize empty habitat, and produced offspring even during the driest years on record, suggesting that the declines observed from 2000 to 2001 could be offset by a series of wet years. However, a prolonged drought could extirpate brassy minnow from most of the basin and recolonization could take many years once favorable conditions returned.

We recommend several measures for the conservation and management of brassy minnow in western Great Plains basins like the Arikaree River. The processes that create and maintain deep pools that provide refuges through summer drought and winter freezing need to be sustained. For instance, beaver dams create deep pool complexes are used by many fish species. In dam-regulated systems, releases should mimic the natural flow regime (Poff et al. 1997) to inundate floodplain habitats during spring and early summer and provide bankfull flows that scour pools. In basins without large dams, increasing spring flows by restricting diversion and groundwater withdrawals will also prolong the period when fish can recolonize vacant habitats, increase the likelihood that fish can find summer refuges, and increase recruitment success of larvae. A better understanding of groundwater hydrology will allow quantifying the effects of irrigation on stream flow and provide insight into factors that regulate stream flow at the segment scale. Finally, maintaining the native fish community and preventing the invasion of exotic predators will help conserve rare fish like the brassy minnow that already exist near the limits of their tolerance in plains streams like the Arikaree River.

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Table 2.1. Evidence for metapopulation-level processes that pertain to single species populations (after Hanski 1999).

1. Population size or density is significantly affected by migration
 2. Population density is affected by patch area and isolation
 3. Local dynamics are asynchronous among habitat patches
 4. There is population turnover due to local extinctions and establishment of new populations by colonization
 5. Some suitable habitat is empty
 6. Metapopulations persist despite population turnover
 7. Extinction risk depends on patch area
 8. Colonization rate depends on patch isolation
 9. Patch occupancy depends on patch area and isolation
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Table 2.2. Characteristics of the three study segments in the Arikaree River, including the total number of pools and backwaters present, and the number sampled for fish and habitat attributes, during 2000 and 2001. Each segment was divided into 800-m reaches. Not all habitat units were sampled during each survey because some dried or filled in and others were newly formed. Mean channel widths were based on June 2000 data. Total pools refers to the total number of pools and backwaters present.

Segment (ownership)	Total length		Mean channel		Total pools		No. habitat units surveyed each year	
	(km; no. reaches)	width (m; SE)	Year	(pools/km)	pools	backwaters	runs	
Upstream	5.6 ^a (7)	2.32 (0.19)	2000	245 (44)	28	6	5	
(The Nature Conservancy)			2001	378 (68)	28	5	5	
Middle	6.4 (8)	2.01 (0.12)	2000	62 (10)	32	11	8	
(Colorado Division of Wildlife)			2001	41 (6.6)	18	11	7	
Downstream	6.4 (8)	2.07 (0.34)	2000	9 (<2) ^b	7 ^b	2	-- ^c	
(private)			2001	13 (2.3) ^b	7 ^b	6	5	

^a The eighth reach of this segment contained several human-made ponds that were not representative of the natural channel and too deep to sample, so it was not included in the study.

^b Includes one pool formed after the June 2000 sample, but not a reference section sampled in Black Wolf Creek.

^c No runs were sampled in this segment in 2000.

Table 2.3. Number of extinction and colonization events (i.e. population turnover) of brassy minnow in the three study segments of the Arikaree River during June through November 2000.

Segment	Extinctions	Colonizations
Downstream	6	1
Middle	30	6
Upstream	19	24

Table 2.4. Top logistic regression models as ranked by AIC with fewer than five variables (excluding intercept) for predicting fish and habitat persistence through the summer 2000 drying period. Depth and area were transformed using the natural logarithm. The AIC_c is the AIC corrected for small sample size, K is the number of parameters (including the intercept) in the fitted model, and ΔAIC_c is the difference between the candidate model and the model with the lowest AIC_c. Akaike weights (w_i) sum to 1.0. The models shown in bold are those selected as final predictive models.

Model Parameters	AIC _c	K	ΔAIC_c	w_i
<i>Brassy Minnow Persistence</i>				
segment, August area, August depth, connectivity ^a	50.26	6	0.00	0.68
segment, August depth, connectivity	52.68	5	2.42	0.20
segment, August depth, connectivity, depth*connectivity ^b	55.17	6	4.91	0.06
August depth, connectivity	55.22	3	4.96	0.06
<i>Habitat Persistence</i>				
segment, June depth, connectivity ^c	85.49	5	0.00	0.26
segment, June depth^d	86.72	4	1.23	0.14
June depth, connectivity	87.57	3	2.08	0.09
segment, June depth, riparian vegetation	87.58	5	2.09	0.09
segment, June area, June depth, connectivity ^e	87.64	6	2.15	0.09

Table 2.4. Concluded.

June depth, riparian vegetation segment, June depth, connectivity, depth*connectivity ^e	87.68	3	2.19	0.09
June area, June depth, riparian vegetation, aquatic vegetation, connectivity ^e	87.81	6	2.32	0.08
segment, June area, June depth ^f	88.75	6	3.26	0.05
June area, June depth, connectivity	88.76	5	3.27	0.05
June depth, connectivity, depth*connectivity	89.39	4	3.90	0.04
	89.77	4	4.28	0.03

^aModel without segment had K=4 parameters and AIC_c=56.54.

^bModel without segment had K=4 parameters and AIC_c=56.57.

^cNearly complete separation of data in the parameter space prevented calculating valid parameter estimates, so the model cannot be used for prediction.

^dModel without segment had K=2 parameters and AIC_c=92.41.

^eModel including segment and these variables had K=8 parameters and AIC_c=90.52

^fModel without segment had K=3 parameters and AIC_c=94.15.

Table 2.5. Parameter estimates and their 95% profile likelihood confidence intervals for the top candidate logistic regression models for brassy minnow and habitat persistence. Where confidence intervals were inestimable, standard errors are shown in parentheses. Coefficients for the variables Segment 1 and Segment 2 are (1, 0) for the downstream segment, (0, 1) for the middle segment, and (-1, -1) for the upstream segment. Depth and area measurements are transformed using the natural logarithm.

<i>Brassy Minnow Persistence Model</i>	Parameter Estimates (95% CI)						
	Intercept	Segment 1	Segment 2	August depth	Connectivity	August area	
segment, August area, August depth, connectivity	7.16 (1.90,14.36)	-3.18 (-6.49,-0.48)	3.07 (1.14,5.65)	3.87 (1.69,7.09)	2.53 (0.76,4.70)	-1.45 (-3.04,-0.17)	
segment, August depth, connectivity	1.85 (-0.27,4.38)	-2.16 (-4.63,0.20)	2.13 (0.53,4.04)	2.22 (0.84,4.13)	1.96 (0.38,3.80)	-	
<i>Habitat Persistence Model</i>	Intercept	Segment 1	Segment 2	June depth	Connectivity	Riparian Vegetation	
segment, June depth, connectivity ^a	-10.12 (364) ^b	-0.72 (-2.19,0.83)	-0.48 (-1.44,0.45)	2.15 (0.80,3.73)	13.29 (364) ^b	-	
segment, June depth	2.88 (1.39,4.65)	-1.36 (-2.66,-0.18)	-0.17 (-1.01,0.70)	2.18 (0.90,3.73)	-	-	
June depth, connectivity ^a	-10.35 (341) ^b	-	-	2.57 (1.26,4.16)	13.94 (341) ^b	-	

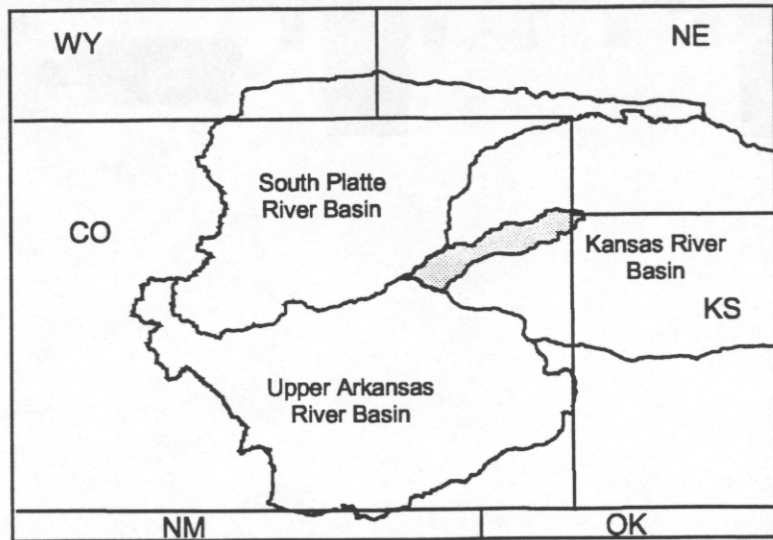
Table 2.5 Concluded.

segment, June depth, riparian vegetation	2.11 (0.28,4.26)	-0.97 (-2.41,0.36)	-0.22 (-1.08,0.66)	1.92 (0.62,3.50)	-	0.01 (0.00,0.03)
June depth, riparian vegetation	1.78 (0.15,3.69)	-	-	1.99 (0.83,3.40)	-	0.02 (0.00,0.03)

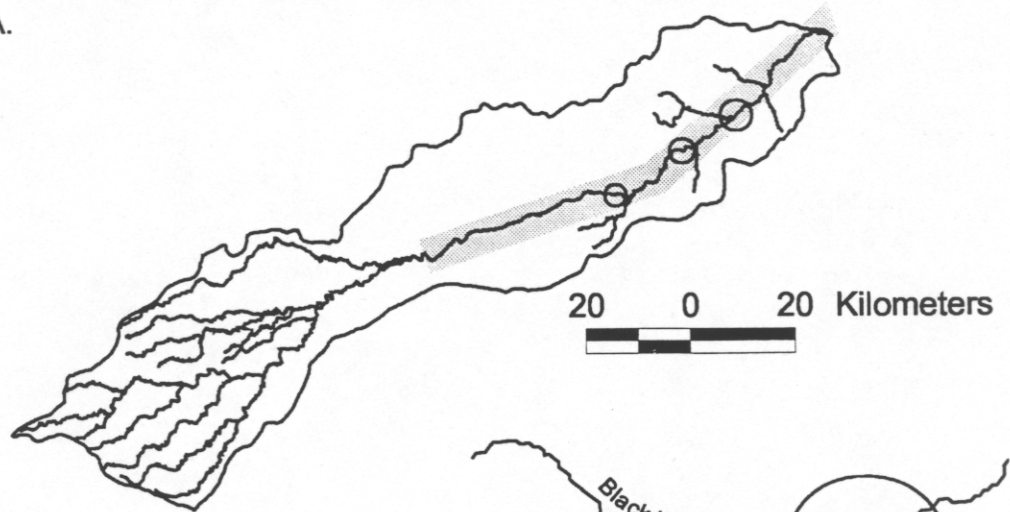
^a Nearly complete separation of data in the parameter space prevented calculating valid parameter estimates, so standard errors were large and the models cannot be used for prediction.

^b Standard error is shown because 95% profile likelihood confidence interval could not be estimated.

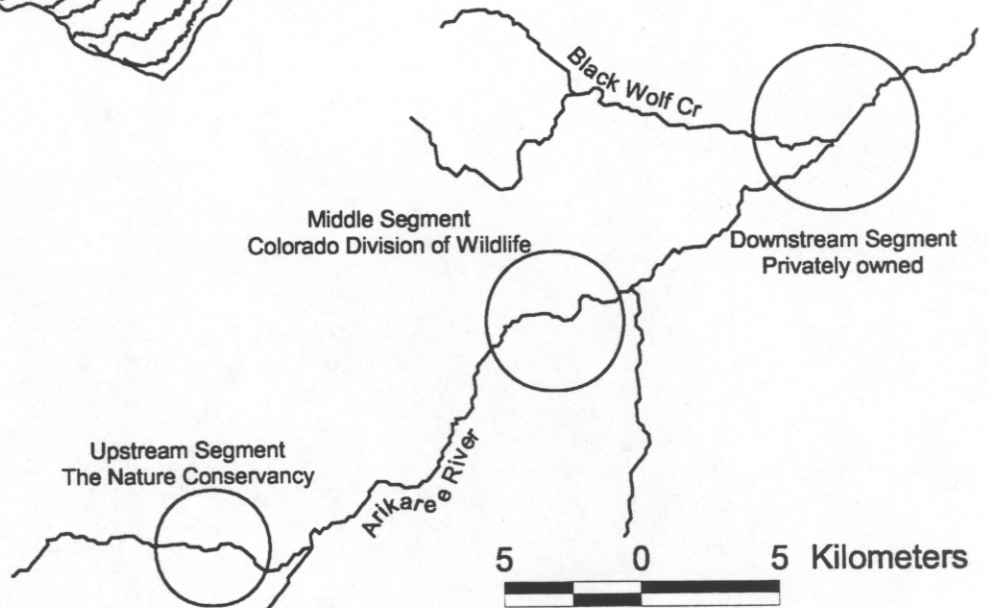
Figure 2.1. Location of the basin and study segments. A. Arikaree Basin (stippled) in the Kansas River Basin in eastern Colorado. B. Map of the basin, with the three study segments circled. Flight area for basin scale surveys is stippled. C. The three study segments showing ownership. The segments are arrayed across a gradient of intermittency from perennial (upstream) to seasonally intermittent (middle) to seasonally dry (downstream).



A.



B.



C.

Figure 2.2. Hydrograph of Arikaree River mean monthly flows ($\text{m}^3/\text{s} \pm \text{confidence intervals } [\pm 1.96 \text{ SE}]$) and minimum monthly flows for 69 years of record from USGS flow gauge 6821500 near the mouth at Haigler, Nebraska. Mean monthly flows for 2000, and direct discharge measurements for 2001 during the study (January to July) are also shown.

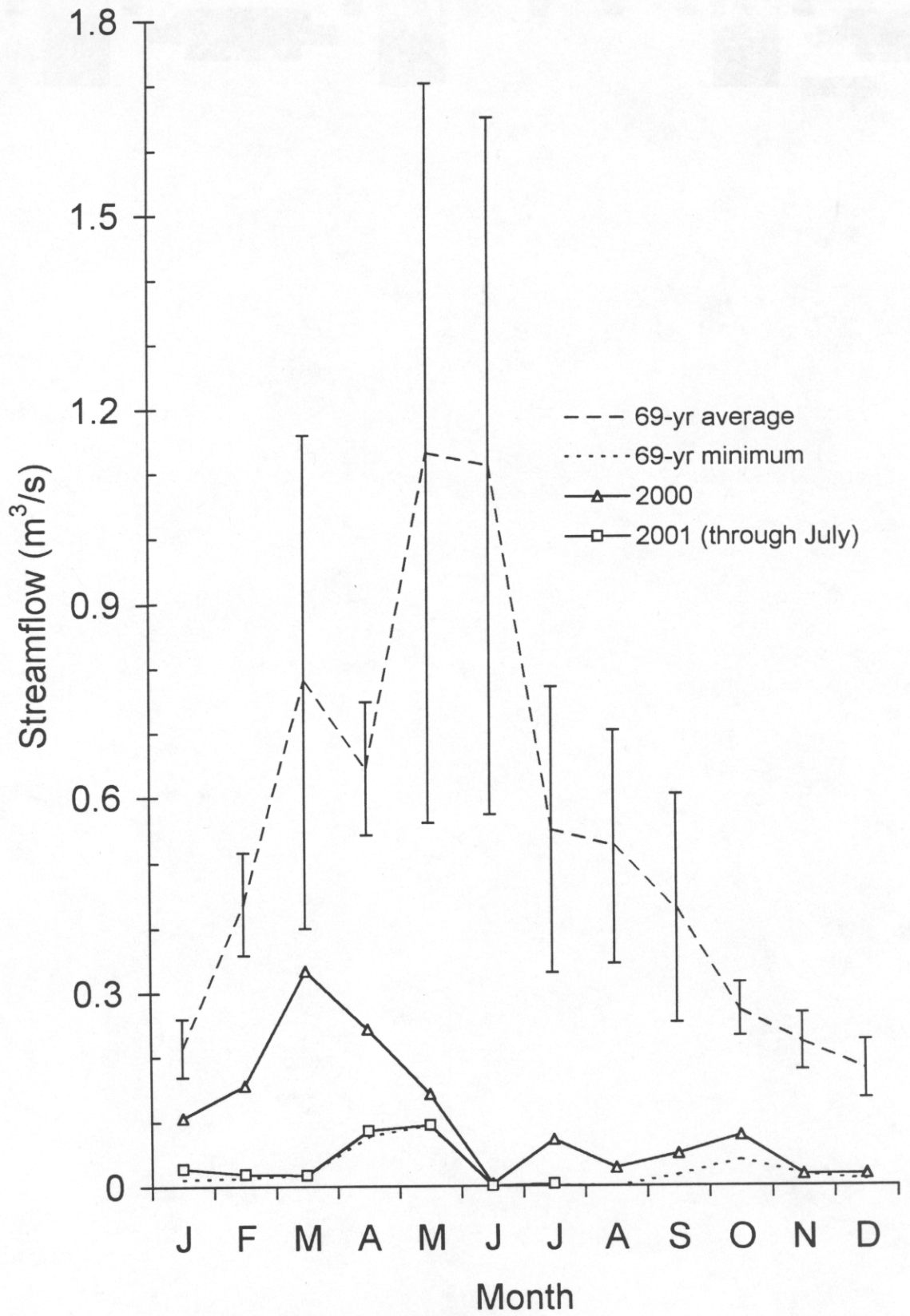


Figure 2.3. Flow connectivity in the Arikaree River basin during three surveys, determined by low altitude flights. Flow connectivity was mapped in the lower 95 km of the Arikaree River from Cope, Colorado to its mouth (see Figure 2.1). Except for a few isolated pools upstream, flows were restricted to the lower 75 km, shown here.

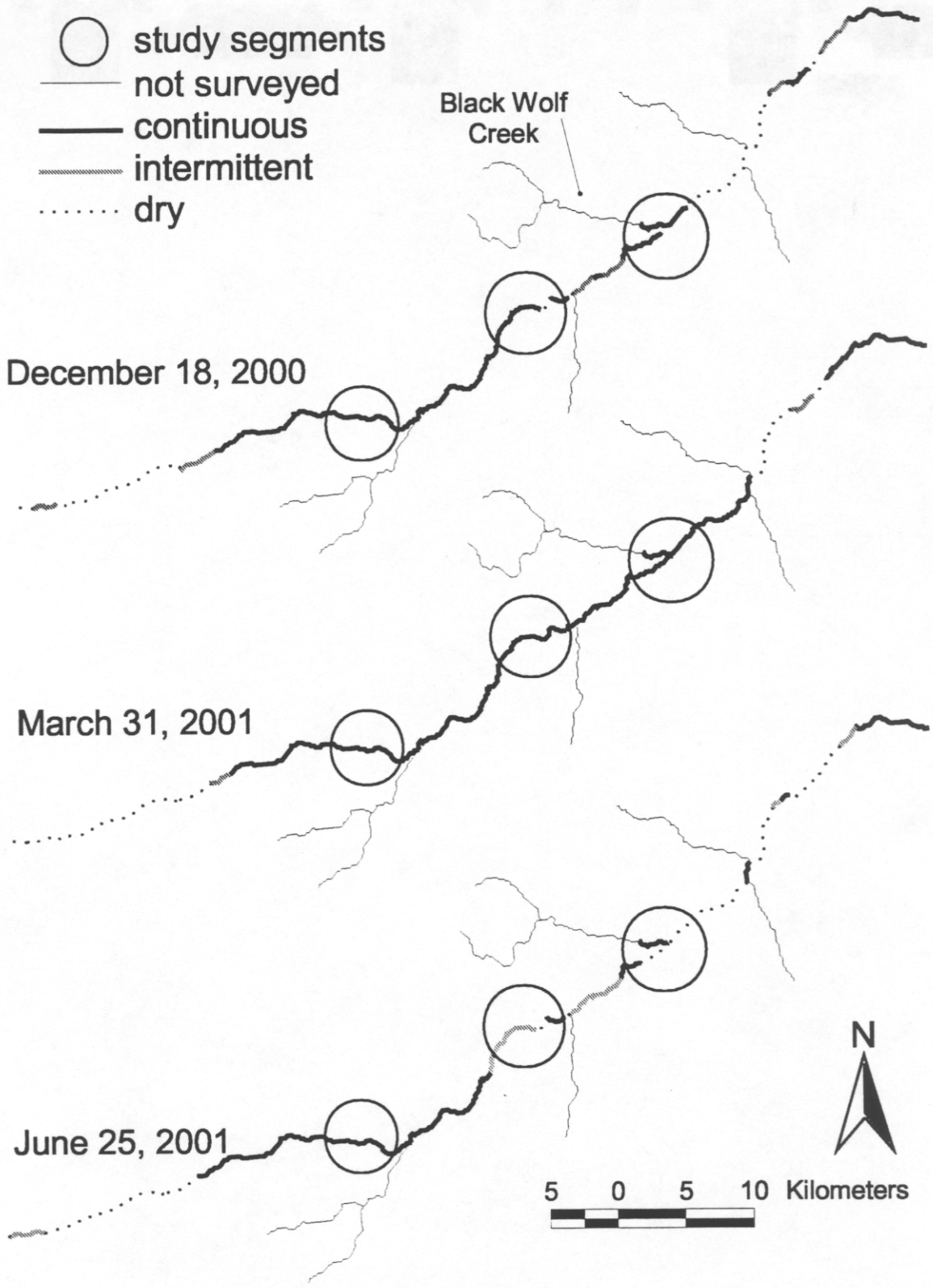


Figure 2.4. Flow connectivity and brassy minnow presence (filled circles) and absence (open circles) in habitat units in the Downstream Segment during four of the five surveys in 2000 and 2001. Triangles show thermograph locations. Ten habitat units (including Black Wolf Creek) were sampled in 2000, 19 in 2001, but only habitat units that contained brassy minnow during at least one survey are shown. No adults were captured in 2001. Flow is from left to right. The eight 800-m reaches are numbered at their upstream boundary.

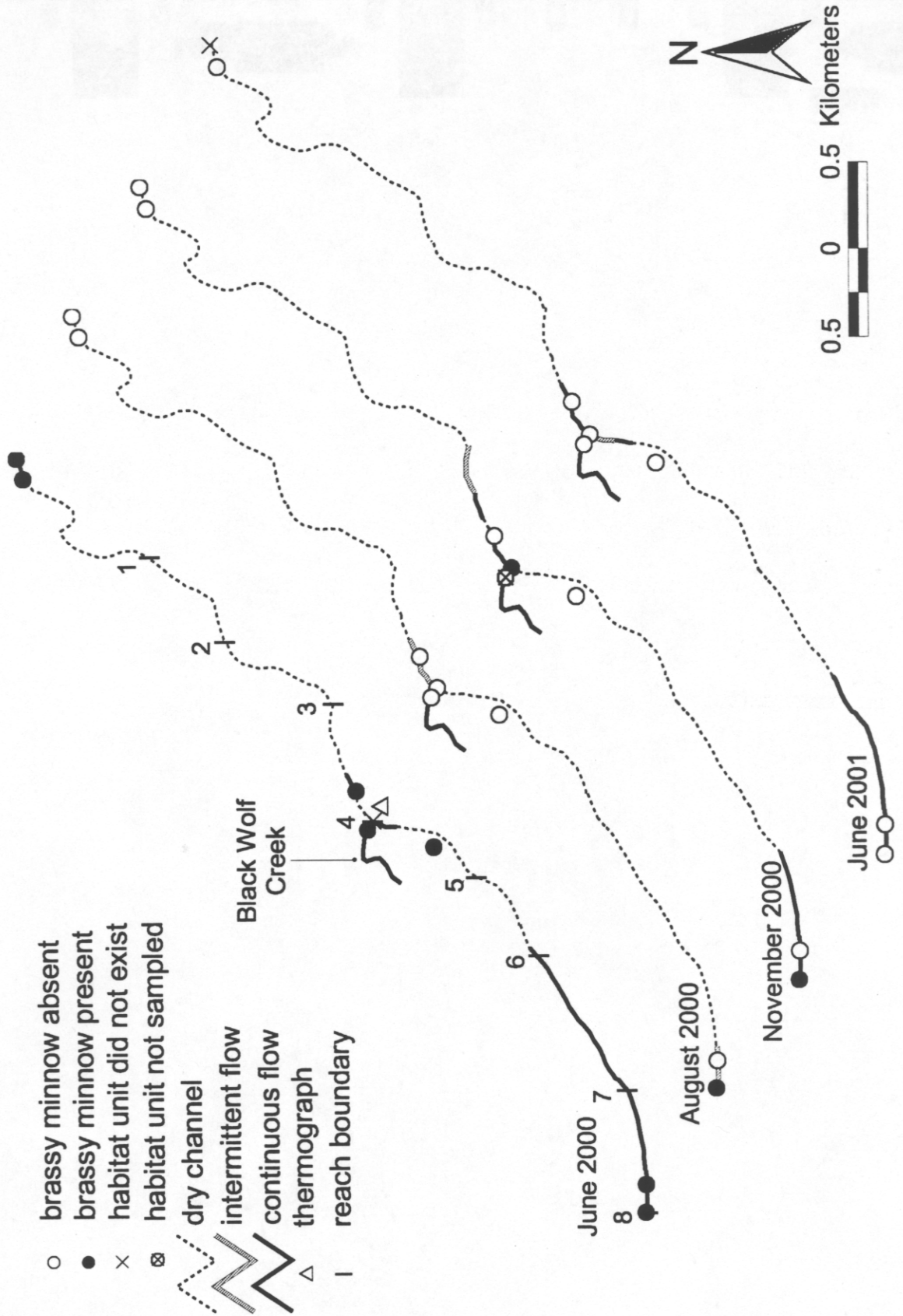


Figure 2.5. Flow connectivity and adult brassy minnow presence (filled circles) and absence (open circles) in habitat units in the Middle Segment during four of the five surveys in 2000 and 2001. Symbols are as in figure 2.4. Fifty-one habitat units were sampled in 2000, 36 in 2001, but only habitat units that contained brassy minnow during at least one survey are shown. Some pools with similar patterns of occupancy are combined for clarity. Flow is from left to right.

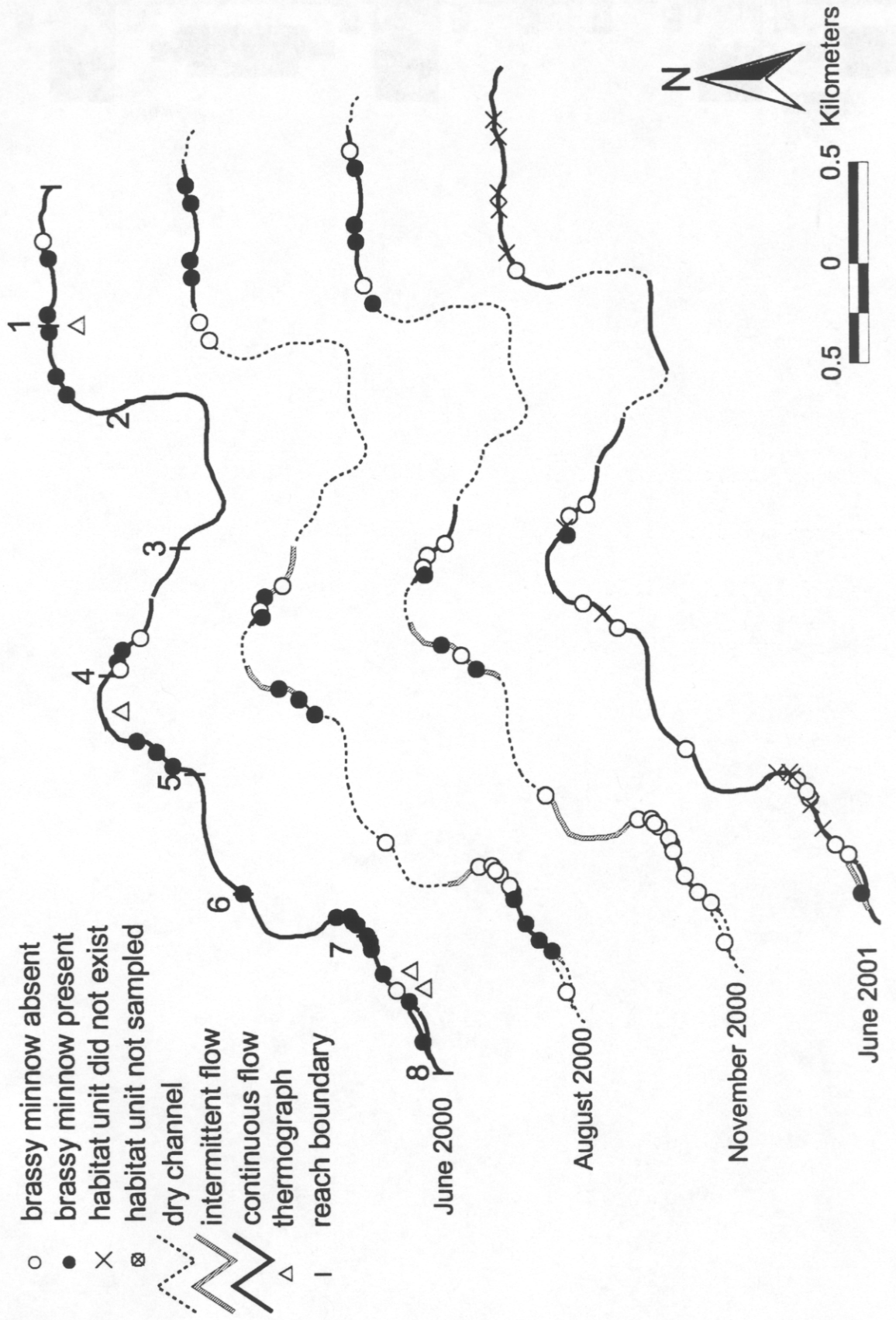


Figure 2.6. Flow connectivity and adult brassy minnow presence (filled circles) and absence (open circles) in habitat units in the Upstream Segment during four of the five surveys in 2000 and 2001. Symbols are as in Figure 2.4. Thirty-nine habitat units were sampled in 2000, 38 in 2001, but only habitat units that contained brassy minnow during at least one survey are shown. Some pools with similar patterns of occupancy are combined for clarity. Flow is from left to right.

- brassy minnow absent
- brassy minnow present
- × habitat unit did not exist
- ⊗ habitat unit not sampled

- ⋯ dry channel
- ▾ intermittent flow
- ▿ continuous flow
- △ thermograph
- | reach boundary

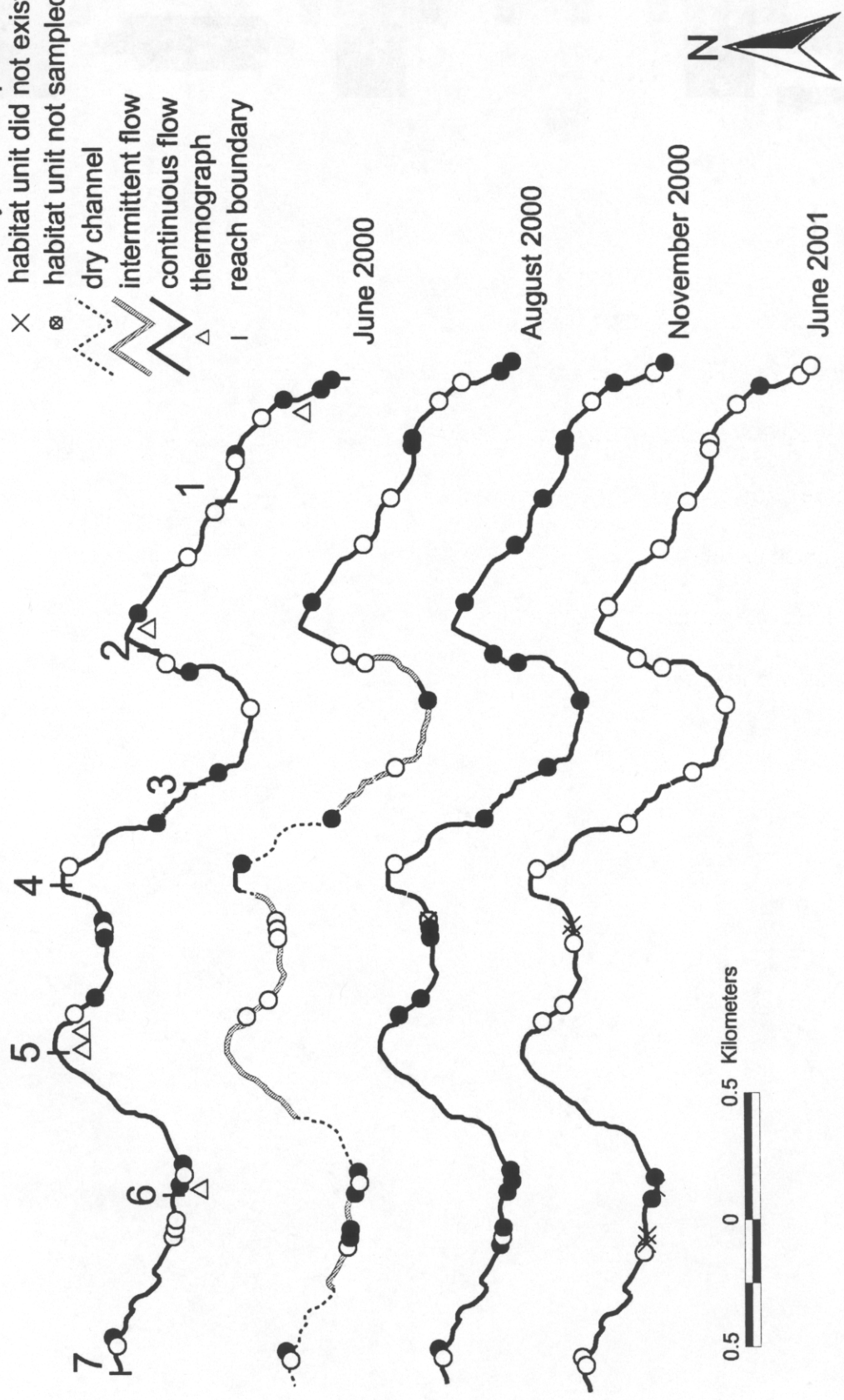


Figure 2.7. Number of habitat units occupied by brassy minnow in each segment by survey. The number of units occupied in the upstream segment was estimated from the proportion of randomly sampled units occupied. No adult brassy minnow were captured in the downstream segment in 2001.

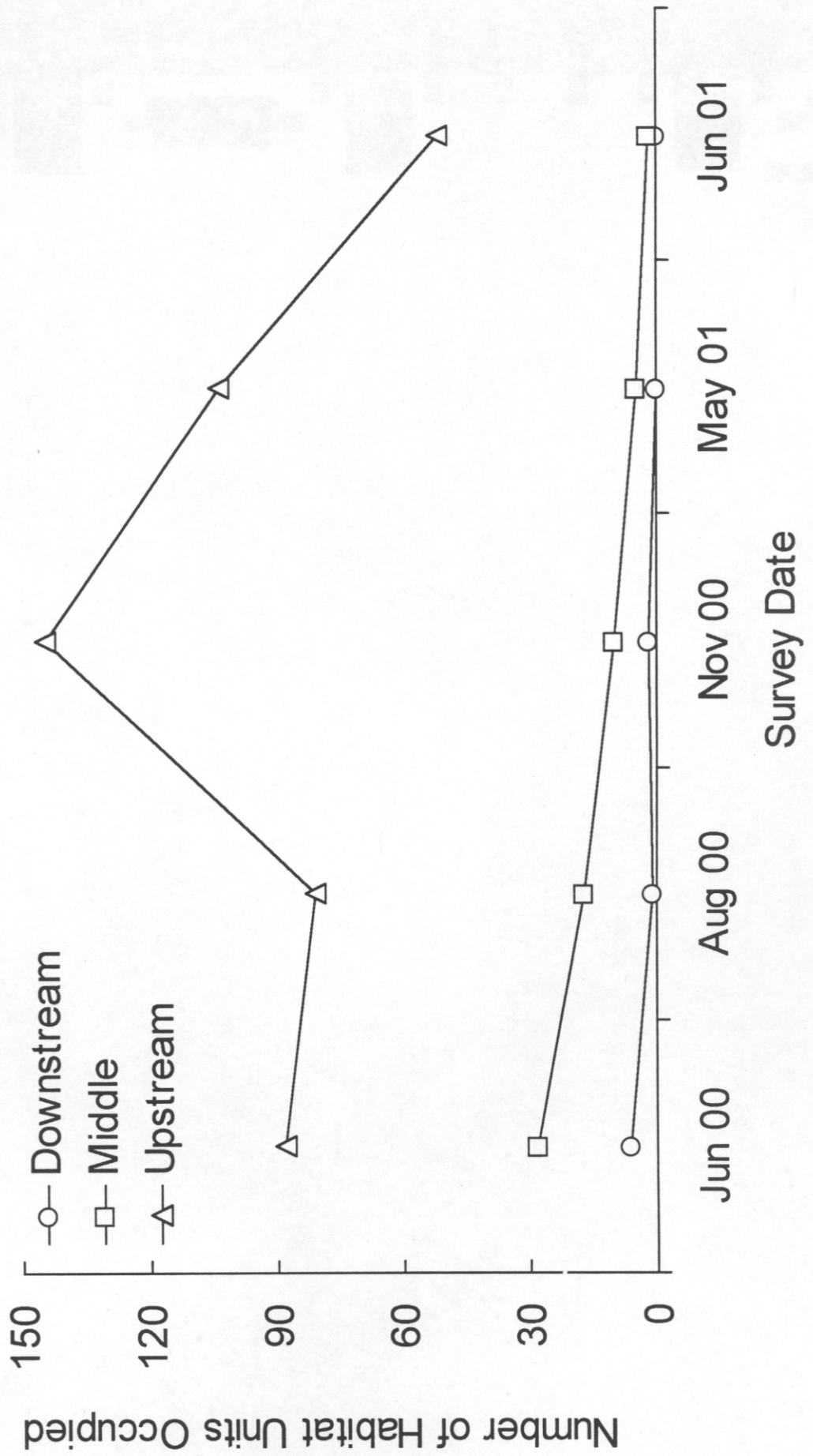


Figure 2.8. Logistic regression model predicting the probability of brassy minnow in pools through the summer drying period in 2000 as a function of segment, August depth, and August connectivity. The x -axis is in natural logarithm (\ln) units.

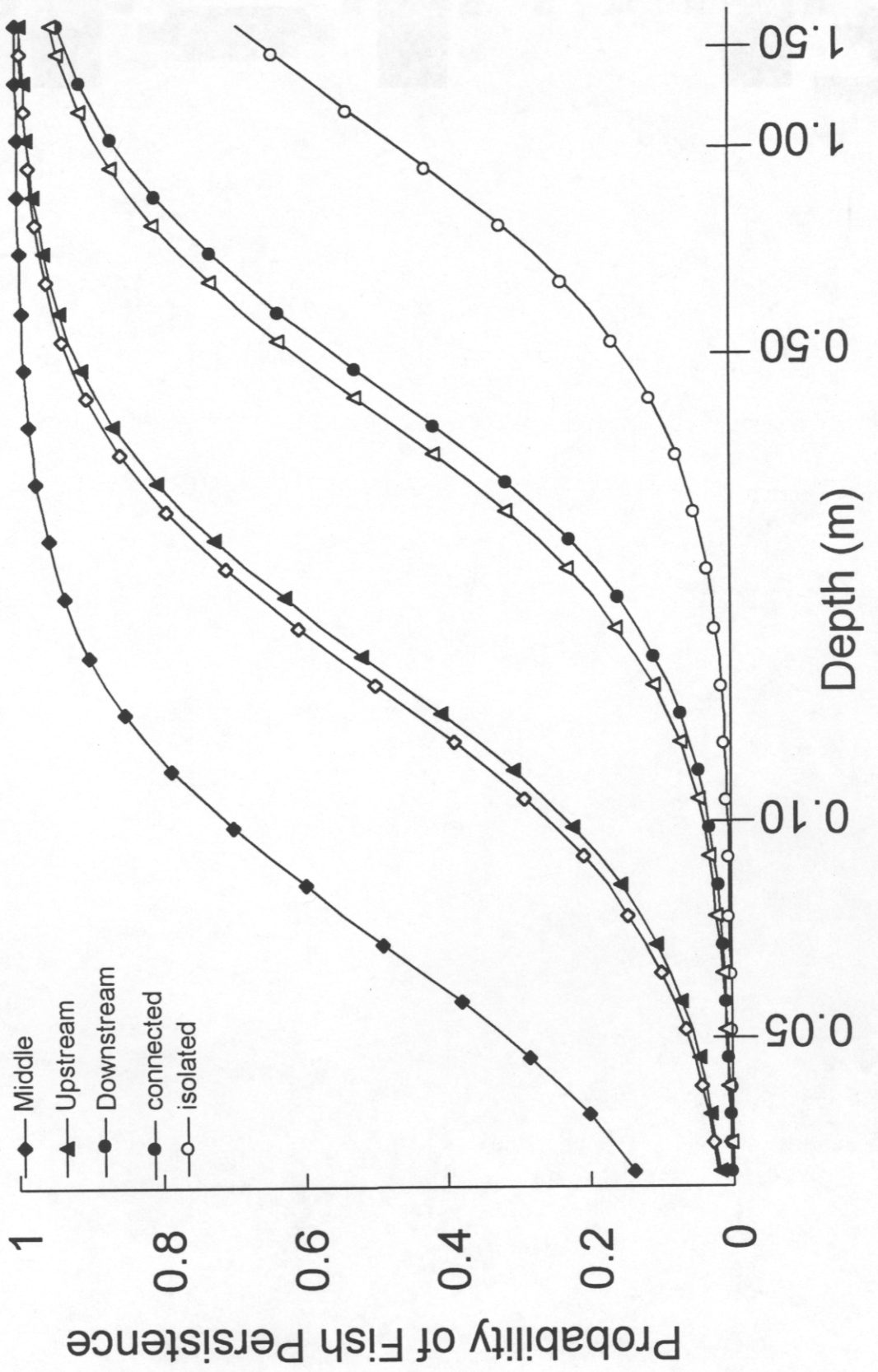


Figure 2.9. Logistic regression model predicting the probability of pool persistence through the summer drying period in 2000 as a function of segment and June depth. The x -axis is in natural logarithm (ln) units.

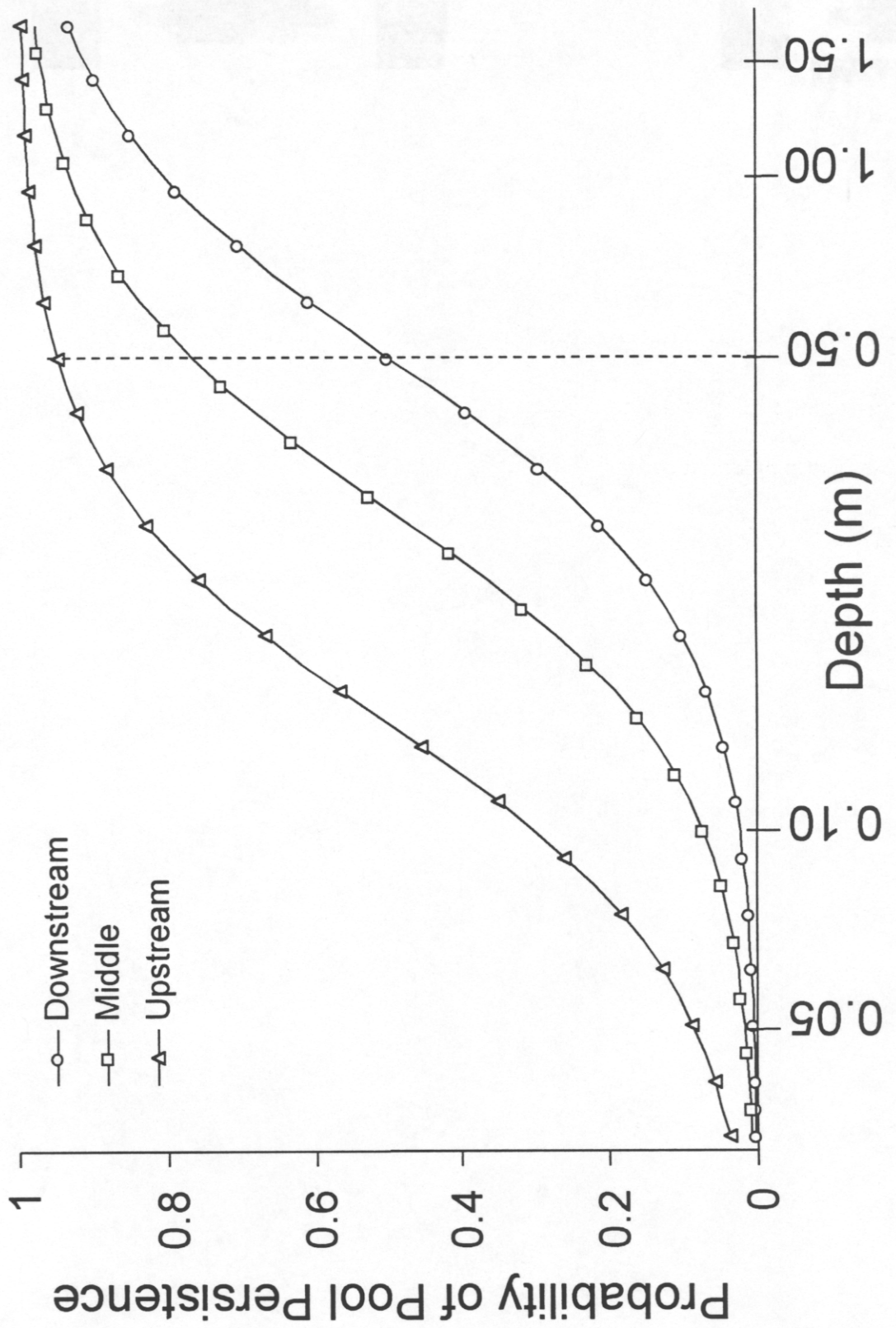


Figure 2.10. Length-frequency histogram for brassy minnow in all segments of the Arikaree River during surveys in June and August 2000. Bins are labeled with the upper value for length (e.g., bin labeled 35 mm included fish 31-35 mm fork length). The length ranges shown in the bottom panel are from 98 brassy minnow collected in August 2000 and aged using scale annuli.

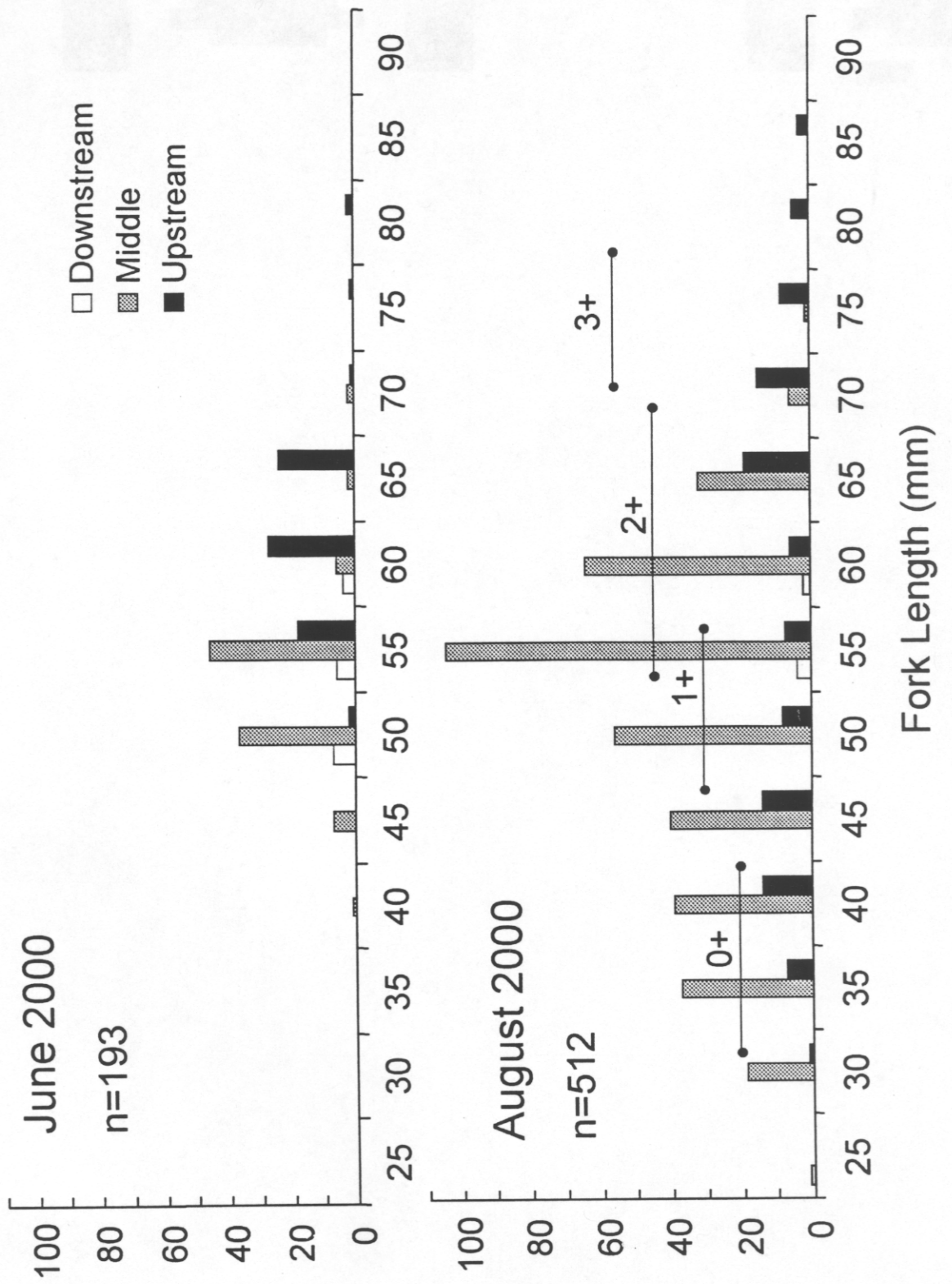


Figure 2.11. Mean fork lengths (mm; $\pm 95\%$ confidence intervals) by collection date for larval brassy minnow (pooled across segments), and the mean of 5-day running mean water temperatures in eight larval rearing habitats in the Arikaree River, Colorado during early summer 2000 and 2001. Spawning, inferred from the presence of gravid females and golden-colored males, occurred once yearly from mid-April through mid-May. Emergence occurred between mid-May and mid-June. The estimated date of the onset of irrigation is shown.

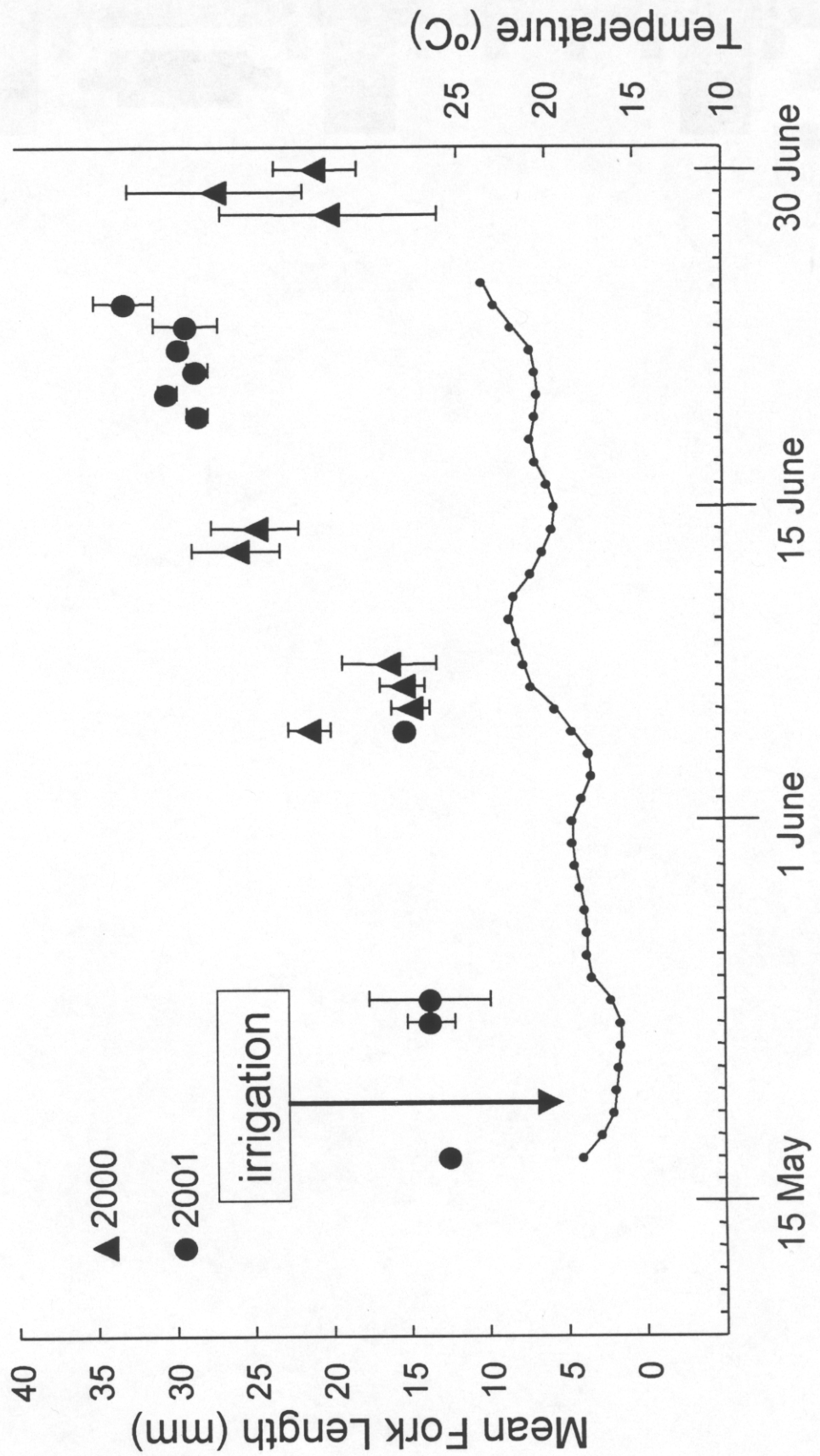
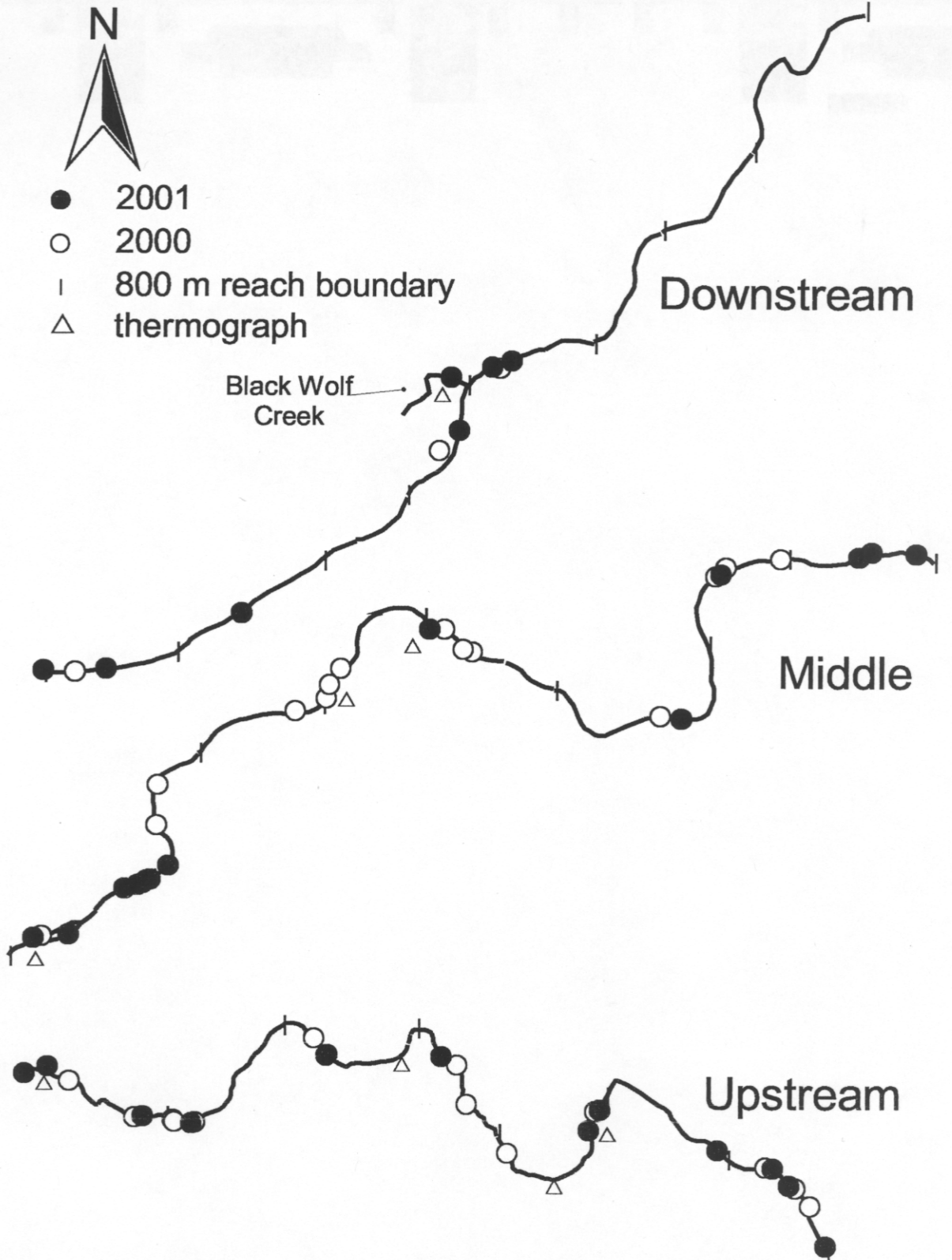
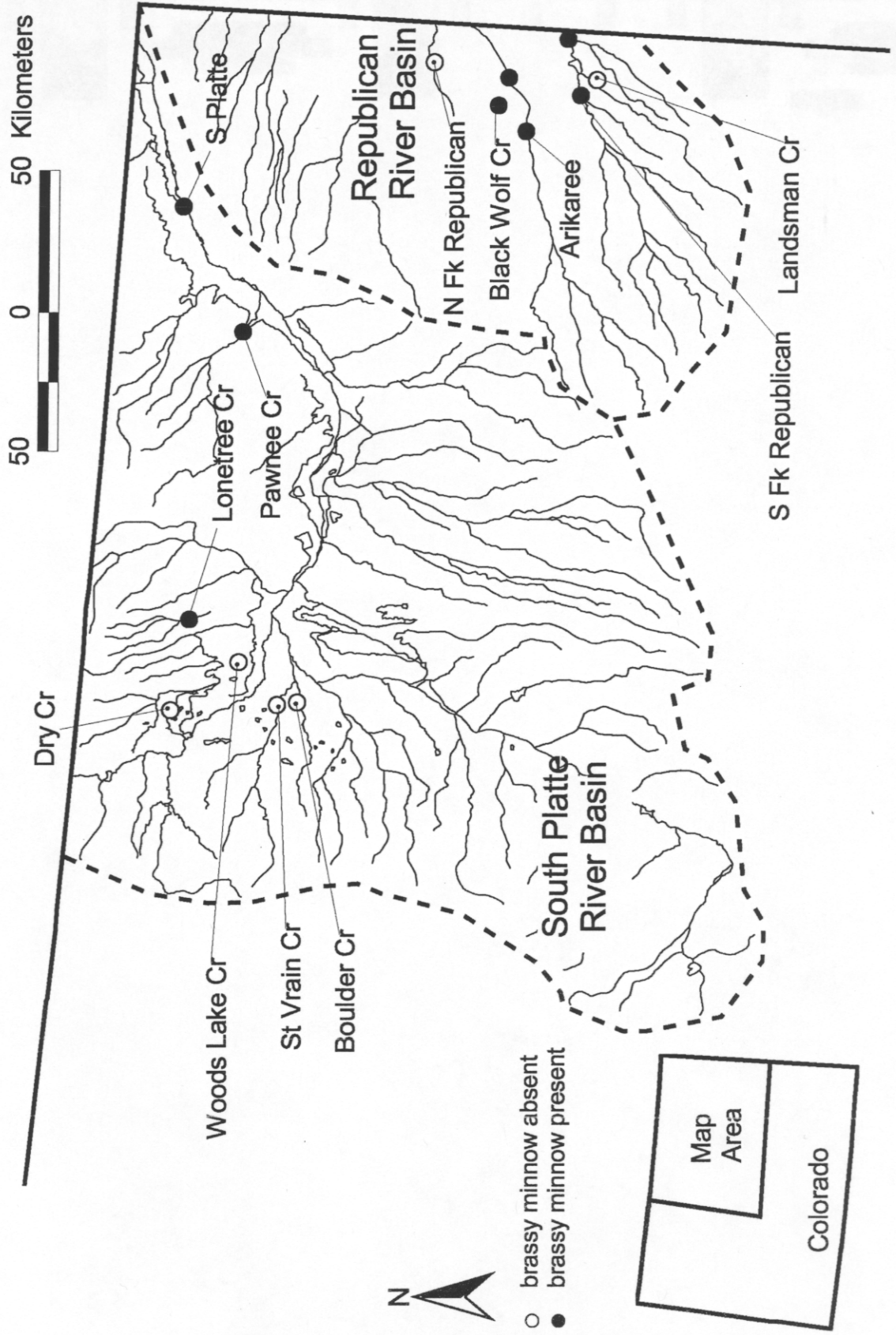


Figure 2.12. Distribution of larval brassy minnow in the three segments during 2000 (open circles) and 2001 (filled circles). Triangles indicate thermograph locations.



APPENDIX 2.1:

LOCATIONS SAMPLED IN 1999 TO LOCATE BRASSY MINNOW POPULATIONS
FOR STUDY



- brassy minnow absent
- brassy minnow present

APPENDIX 2.2:
DESCRIPTION OF PHYSICAL HABITAT VARIABLES MEASURED DURING
2000-2001 FIELD SURVEYS OF THE ARIKAREE RIVER, COLORADO.

Appendix 2.2. Physical habitat variables measured during surveys of the Arikaree River, Colorado, 2000-2001.

Variable (units of measurement)	Description
Total length (nearest 0.1 m)	Distance from farthest downstream point to farthest upstream point along the centerline of the unit
Wetted width (nearest 0.1 m)	Measured at $\frac{1}{4}$, $\frac{1}{2}$, and $\frac{3}{4}$ the unit length
Maximum depth (nearest 0.05 m)	Measured at deepest point of unit
Substrate composition (%)	Estimated percentages by area of sand, silt, gravel, cobble, boulder and bedrock
Aquatic vegetation (%)	Estimated percentages by area of total aquatic vegetation cover, percent algae, and percent vascular hydrophytes
Riparian vegetation (%)	Estimated percentages by area of bank that are bare ground, grass, shrub, or tree cover
Flow connectivity	Categorized as <u>C</u> onected (water flowing in or out of unit, or both) or <u>I</u> solated
Surface and bottom water temperature (°C)	Water temperature measured near substrate and near surface using digital thermometer (Atkins Model 39658-K) and water chemistry multimeter (YSI Model 85). Maximum temperatures measured in August 2000, between 1300 and 1700, the hottest part of the day.
Dissolved oxygen (mg/L)	Oxygen in percent of saturation measured using YSI multimeter in early morning (0400-0630), before sunrise, when dO is at a minimum
Specific conductance (µS/cm)	Conductivity compensated to 25°C measured with YSI multimeter.
Salinity (parts per thousand- ppt)	Dissolved salts in the water measured using YSI multimeter.
pH	Measured using Orion Model 210A pH meter compensated to 25°C.

APPENDIX 2.3:

FISH SPECIES COLLECTED BY SEGMENT AND REACH DURING 2000-2001 IN
THE THREE STUDY SEGMENTS OF THE ARIKAREE RIVER, COLORADO.

Appendix 2.3. Cumulative fish species present in six surveys of the three study segments by reach of the Arikaree River, Colorado. UTM coordinates designate the upstream boundary of each reach and the mouth of Black Wolf Creek. Fish species abbreviations are: BM-brassy minnow, CS-central stoneroller, RS-red shiner, SS-sand shiner, FM-fathead minnow, CC-creek chub, WS-white sucker, BB-black bullhead, PK-plains killifish, GS-green sunfish, LB-largemouth bass, OD-orangethroat darter.

Reach	UTM X	UTM Y	adult larval												
			BM	BM	CS	RS	SS	FM	CC	WS	BB	PK	GS	LB	OD
<i>Downstream segment</i>															
1	744908	4420463	X		X	X	X	X					X	X	X
2	744289	4419813				X		X					X		
3	743926	4419184													
4	743223	4418969	X	X		X	X	X				X	X		X
5	742791	4418140	X	X	X	X	X	X	X			X			X
6	742281	4417828													
7	741581	4417400		X	X										
8	740809	4417237	X	X	X	X	X	X	X			X	X		X
Black Wolf	743223	4418969	X	X	X	X	X	X	X			X	X	X	X
<i>Middle Segment</i>															
1	734322	4413042	X	X	X	X	X	X	X	X	X	X	X	X	X
2	733970	4412578	X	X	X	X	X	X	X			X	X	X	X
3	733440	4412175		X	X	X	X	X	X			X			X
4	732527	4412761	X	X	X	X	X	X	X	X	X	X	X	X	X
5	732071	4412287	X	X	X	X	X	X	X			X	X	X	X
6	731307	4411986	X	X	X	X		X				X	X	X	X
7	731041	4411323	X	X	X	X	X	X	X	X		X	X		X
8	730618	4411119	X	X	X	X	X	X	X	X		X	X		X
<i>Upstream Segment</i>															
1	721423	4403817	X	X	X	X		X	X	X		X	X		X
2	720679	4404189	X	X	X	X		X	X	X	X	X	X		X
3	720120	4404018	X	X	X	X		X	X	X	X	X	X		X
4	719716	4404380	X	X	X	X		X	X			X	X		X
5	719174	4404519	X	X	X	X		X	X	X	X	X	X		X
6	718571	4404078	X	X	X	X		X	X	X	X	X	X		X
7	718184	4404162	X	X	X	X	X	X	X			X	X	X	X

APPENDIX 2.4:

THERMOGRAPH DATA FROM 2000-2001.

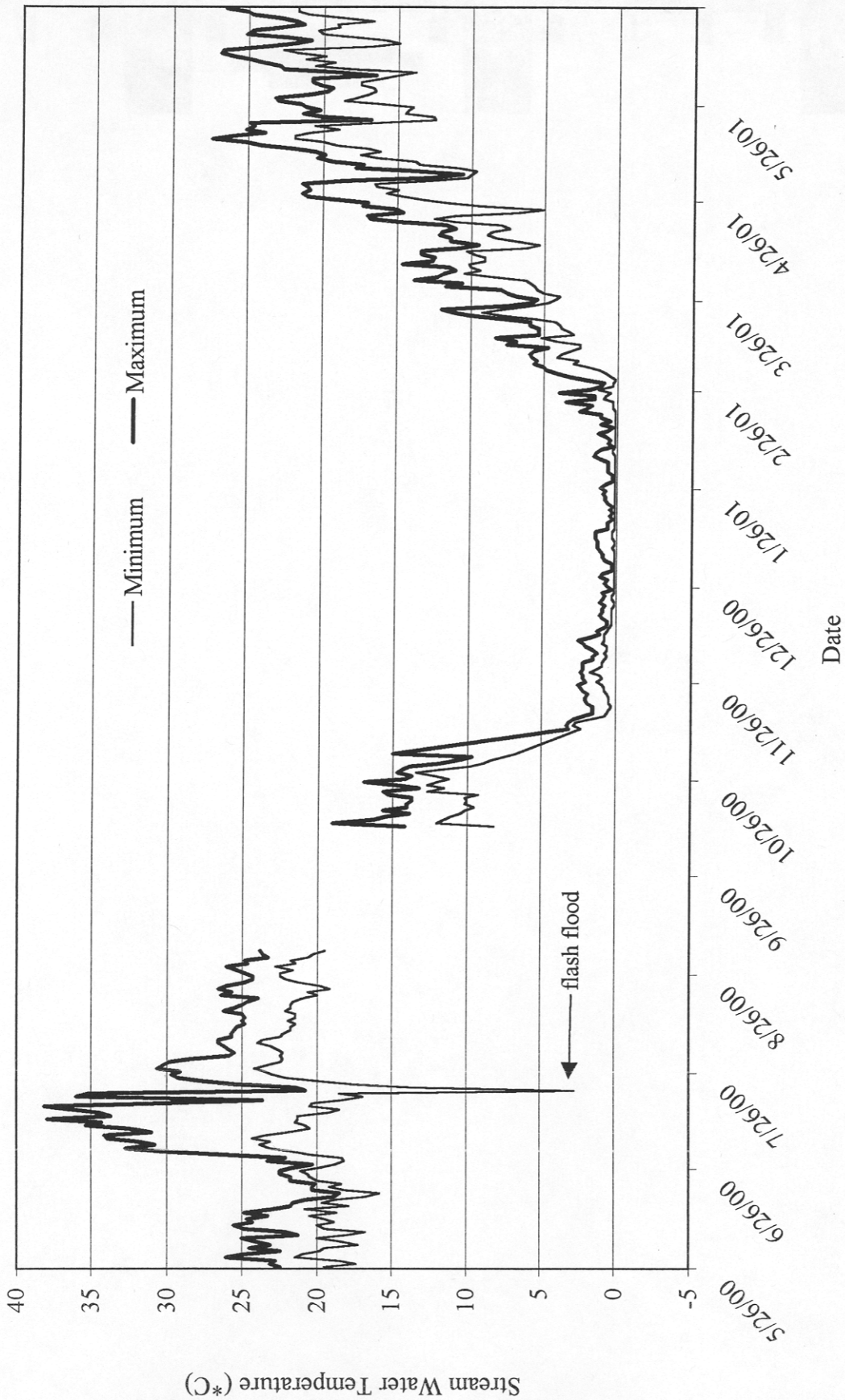


Figure A4-1. Maximum and minimum daily water temperatures in a deep pool at the mouth of Black Wolf Creek, tributary of the Arikaree River, in the Downstream Segment, 5/25/00 - 6/25/01, measured with an Onset StowAway(R) Tidbit(R) thermograph placed in a pool near the mouth of the stream.

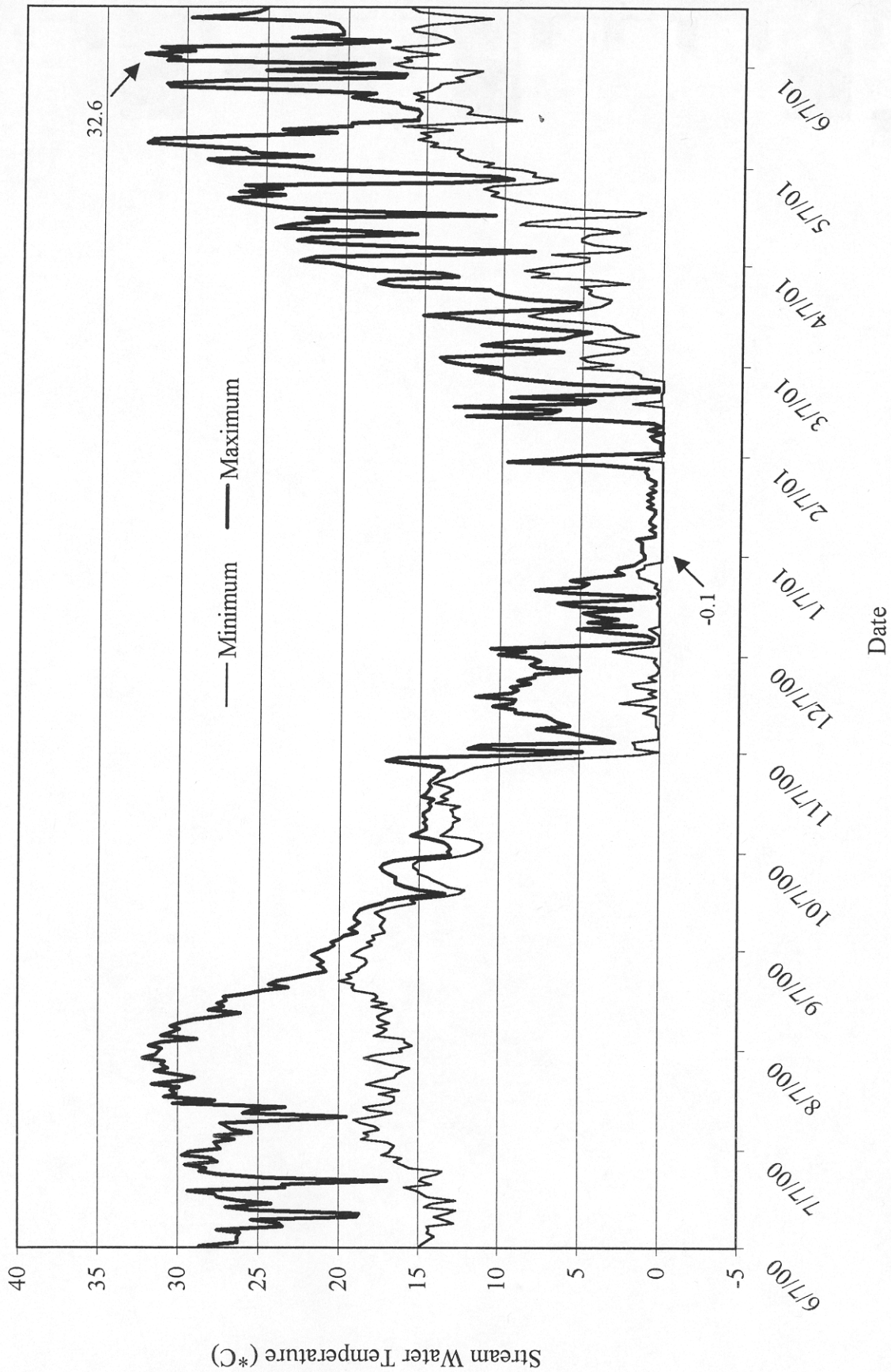


Figure A4-2. Maximum and minimum daily water temperatures in the Middle Segment, Reach 1, Pool 4, of the Arikaree River, 6/7/00 - 6/24/01, measured with an Onset StowAway(R) Tidbit(R) thermograph placed in the deepest part of the pool.

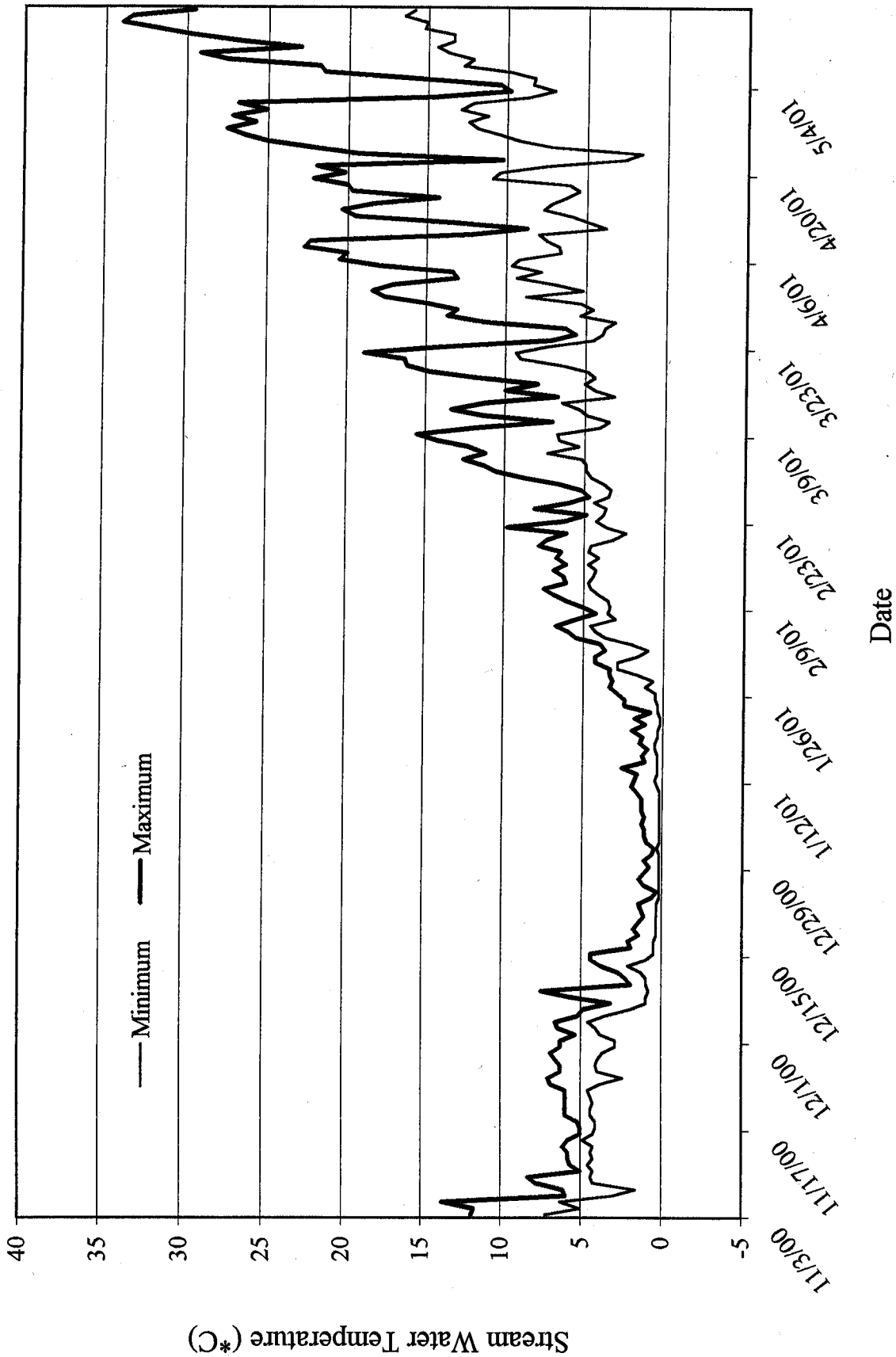


Figure A4-3. Maximum and minimum daily water temperatures in the Middle Segment, Reach 5, Backwater 1, in the Arkaree River, 11/3/00 - 5/15/01, measured with an Onset StowAway^(R) Tidbit^(R) thermograph placed in the deepest part of the pool.

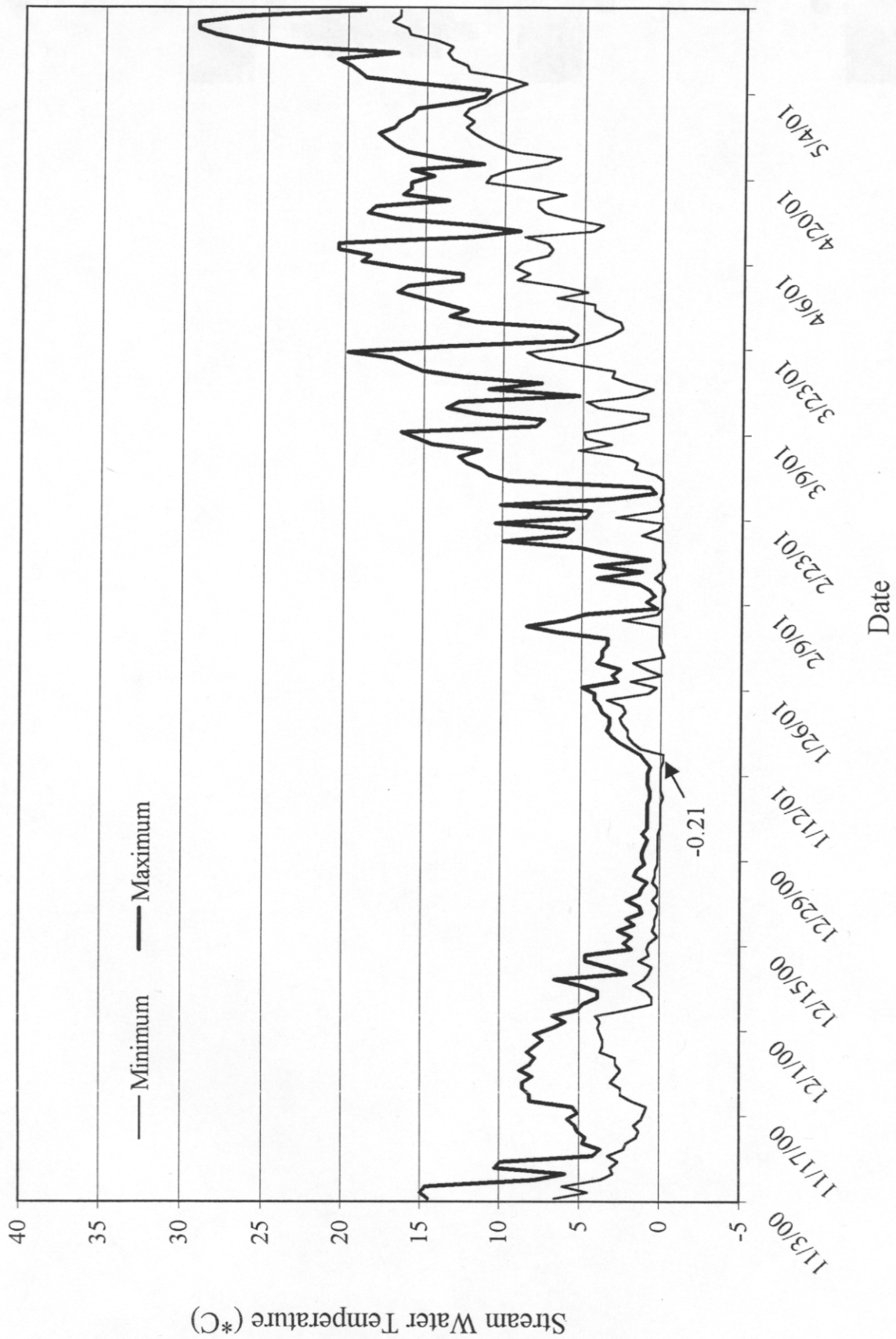


Figure A4-4. Maximum and minimum daily water temperatures in the Middle Segment, Reach 8, Lateral Scour Pool 1, of the Arikaree River, 11/3/00 - 5/17/01, measured with an Onset StowAway[®] Tidbit[®] thermograph placed in the deepest part of the pool.

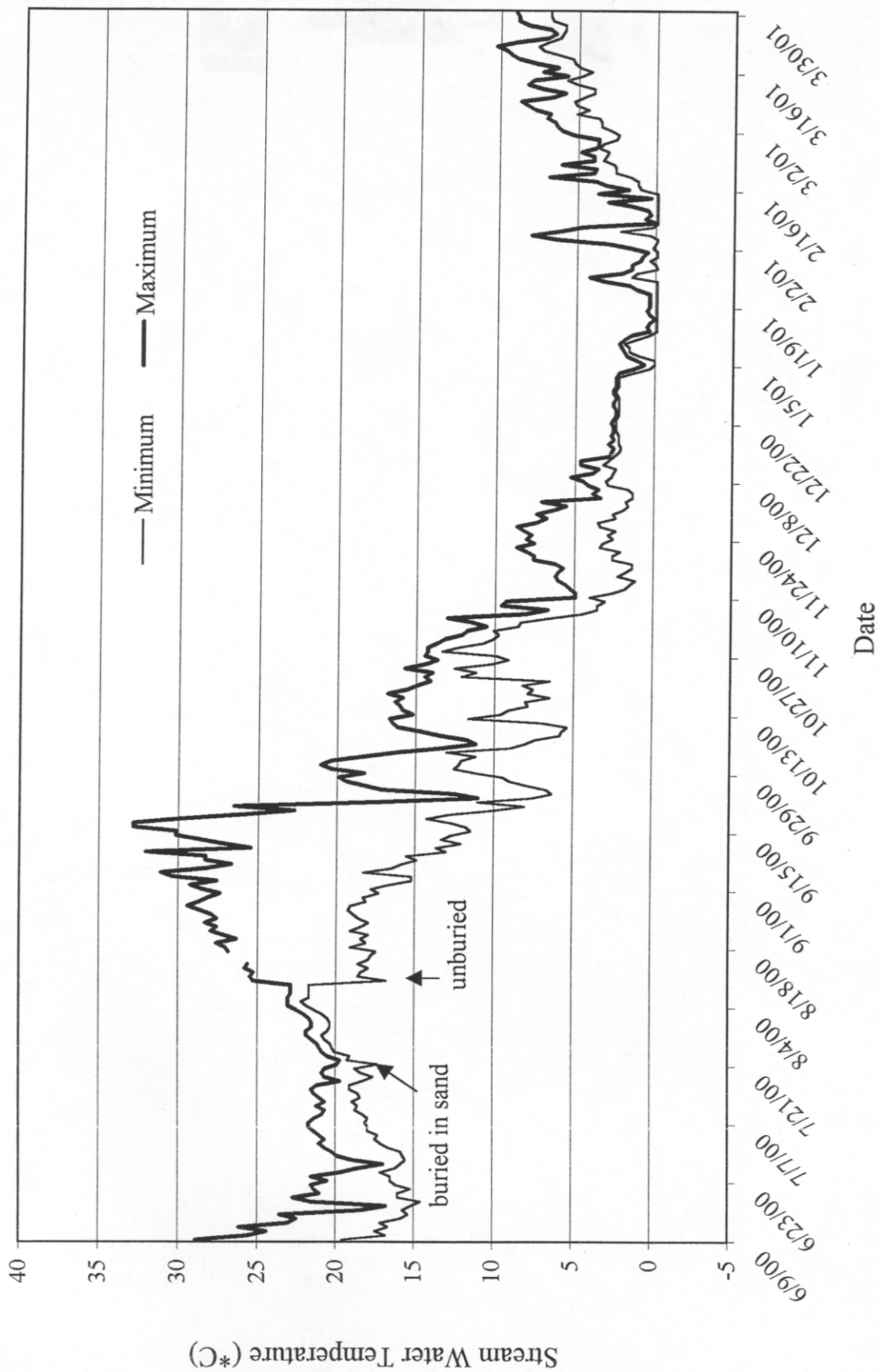


Figure A4-5. Maximum and minimum daily water temperatures in the Middle Segment, Reach 8, Pool 2, of the Arikaree River, 6/9/00 - 3/30/01, measured with an Onset StowAway® Tidbit® thermograph placed in the center of the pool.

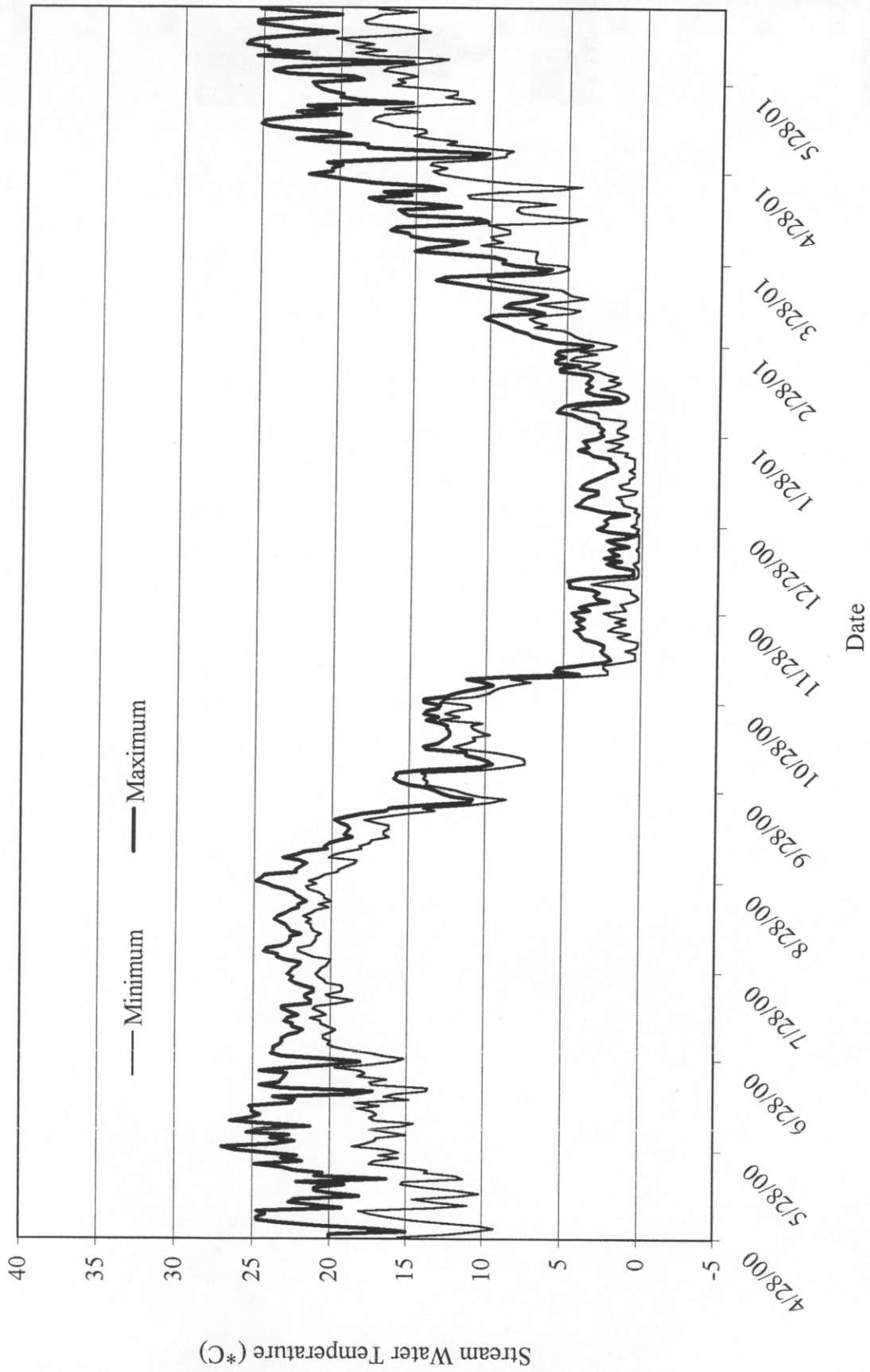


Figure A4-6. Maximum and minimum daily water temperatures in a deep pool at the downstream boundary of the Upstream Segment, of the Arikaree River, 4/28/00 - 6/25/01, measured with and Onset StowAway(R) Tidbit(R) thermograph placed in the center of the pool.

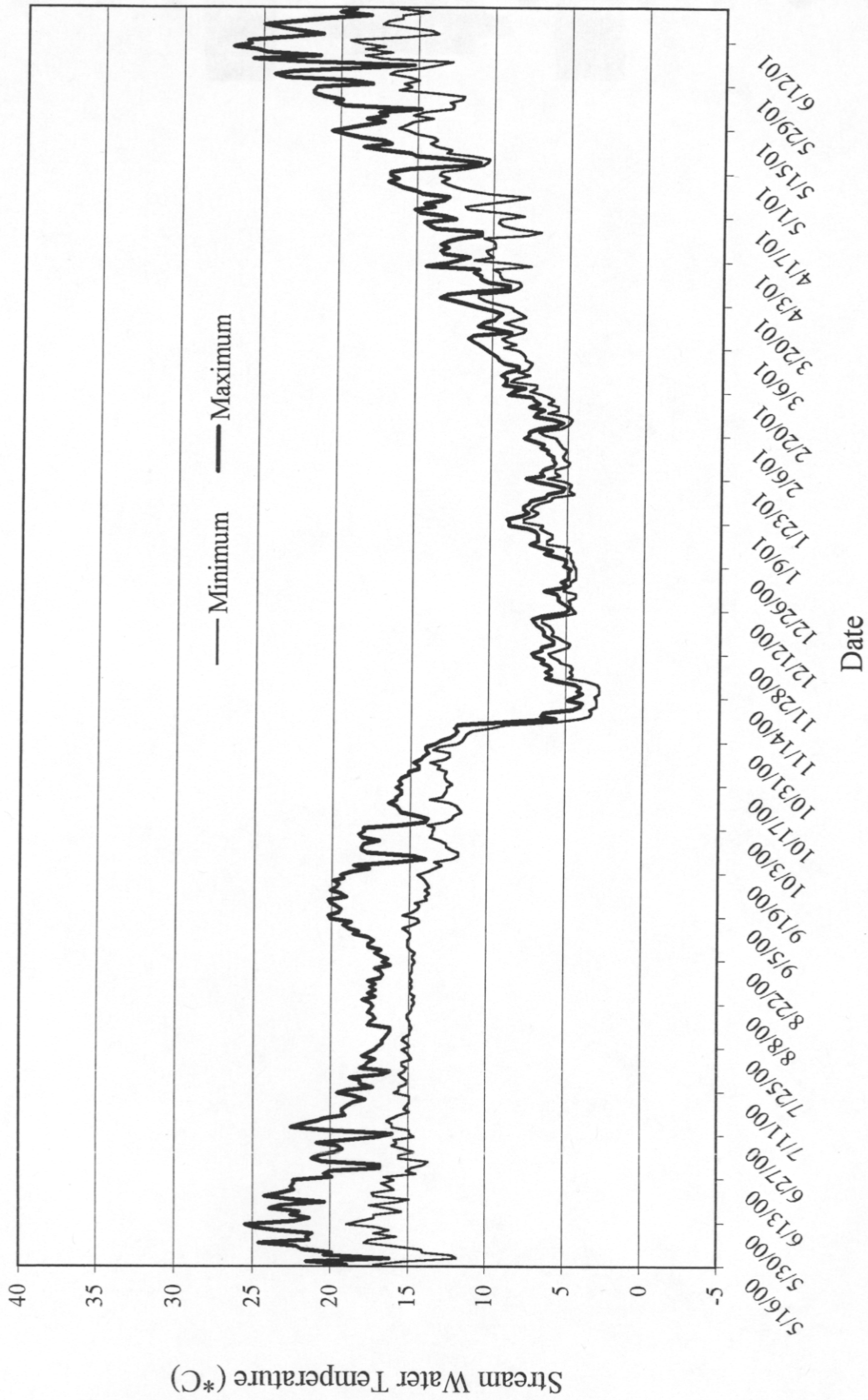


Figure A4-7. Maximum and minimum daily water temperatures in the Upstream Segment, deep pool at boundary between Reaches 2 and 3, of the Arikaree River, 5/16/00 - 6/23/01, measured with an Onset StowAway^(R) Tidbit^(R) thermograph placed in the center of the pool.

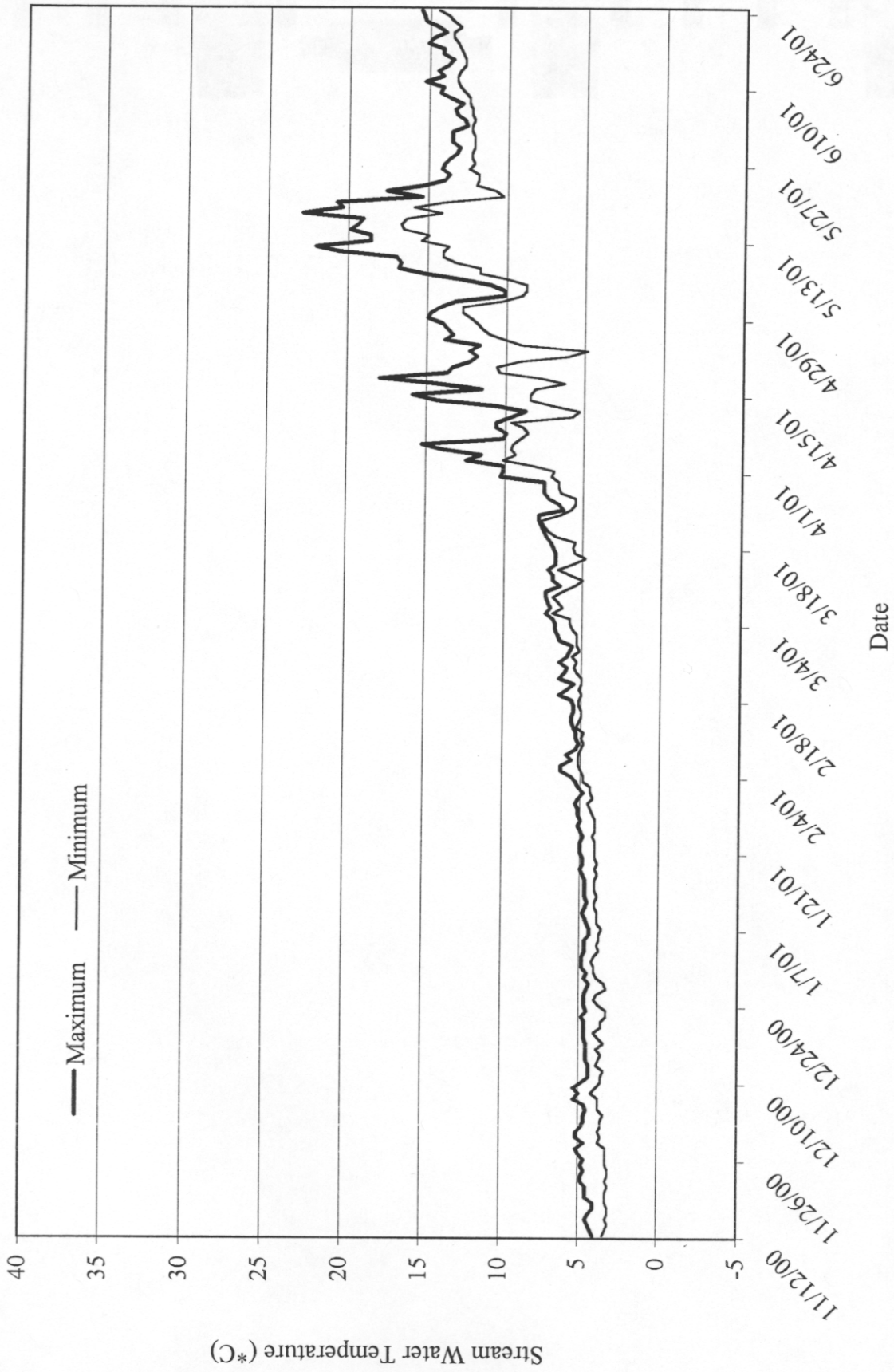


Figure A4-8. Maximum and minimum daily water temperatures in a deep backwater of the Upstream Segment, Reach 5, Backwater 1, in the Arikaree River, 11/12/00 - 6/24/01, measured with an Onset StowAway(R) Tidbit(R) thermograph placed in the deepest part of the pool.

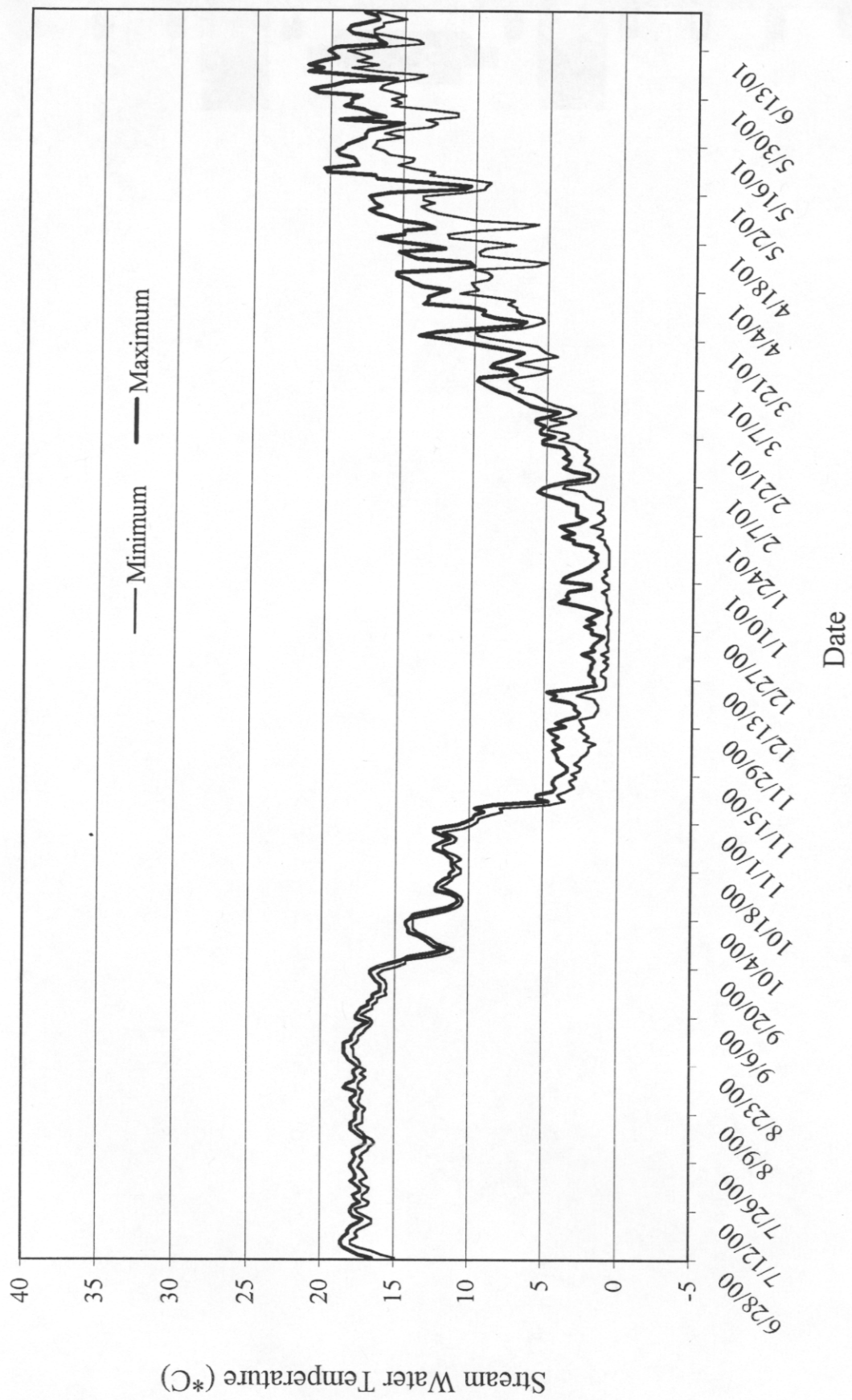


Figure A4-9. Maximum and minimum daily water temperatures in a deep pool in the Upstream Segment, pool at boundary between Reaches 5 and 6, of the Arikaree River, 6/28/00 - 6/23/01, measured with and Onset StowAway^(R) Tidbit^(R) thermograph placed in the center of the pool.

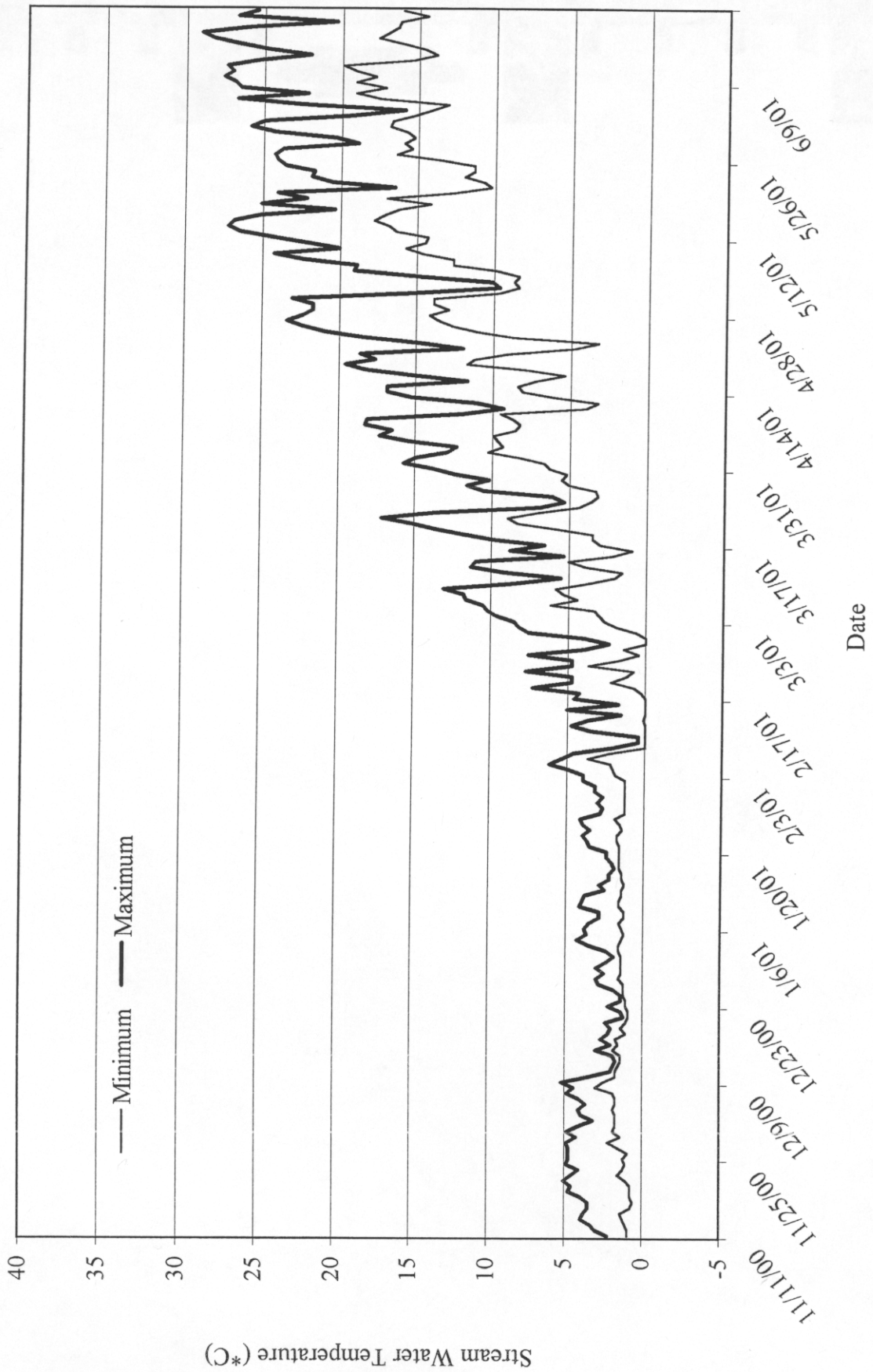


Figure A4-10. Maximum and minimum daily water temperatures in the Upstream Segment, Reach 6, Shallow Pool 2, of the Arikaree River, 11/11/00 - 6/22/01, measured with an Onset StowAway(R) Tidbit(R) thermograph placed in the deepest part of the pool.

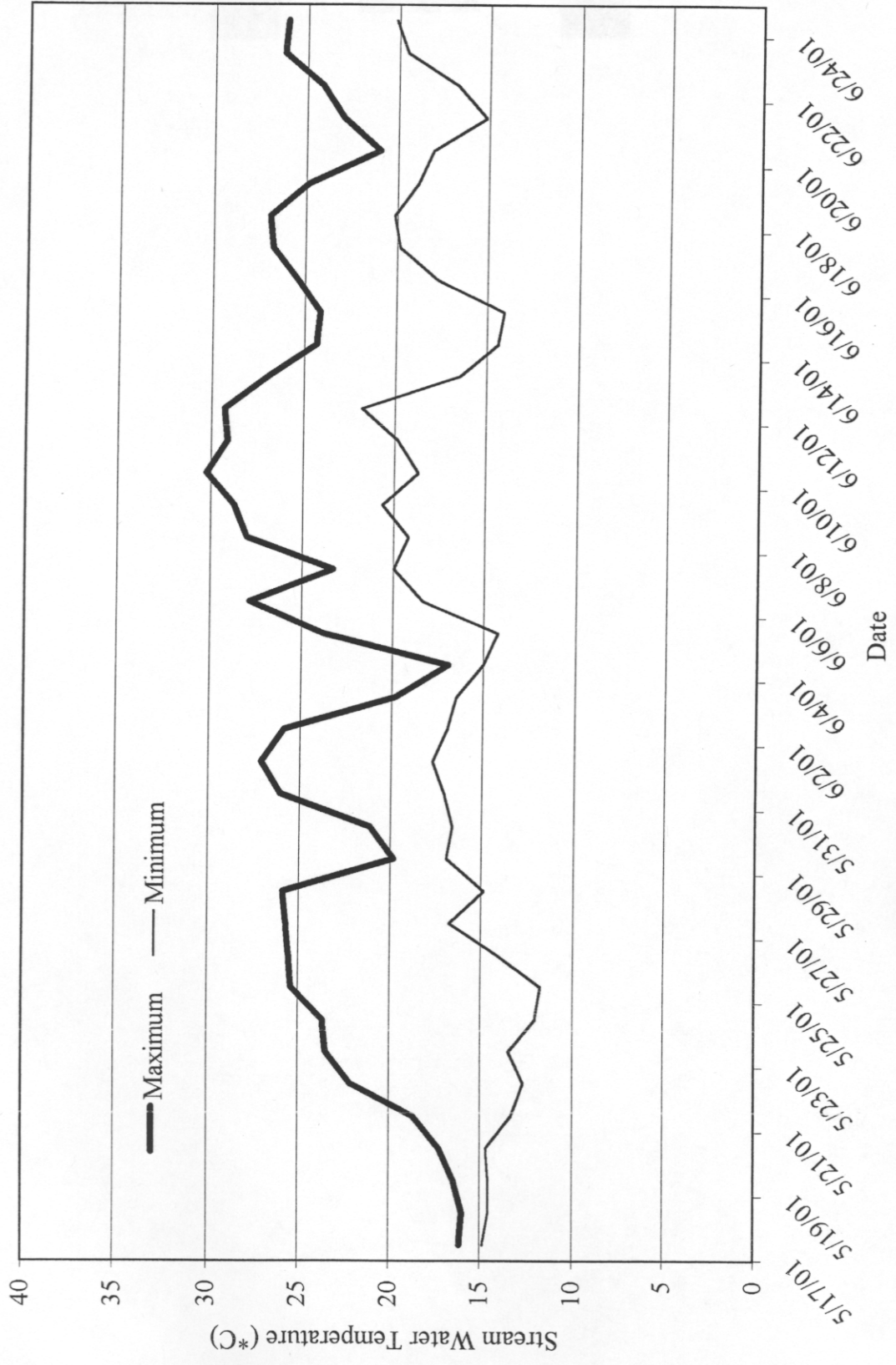


Figure A4-11. Maximum and minimum daily water temperatures in adult spawning and larval rearing habitat in Black Wolf Creek, Downstream Segment, of the Arikaree River, 5/17/01-6/25/01, measured with an Onset StowAway® Tidbit®

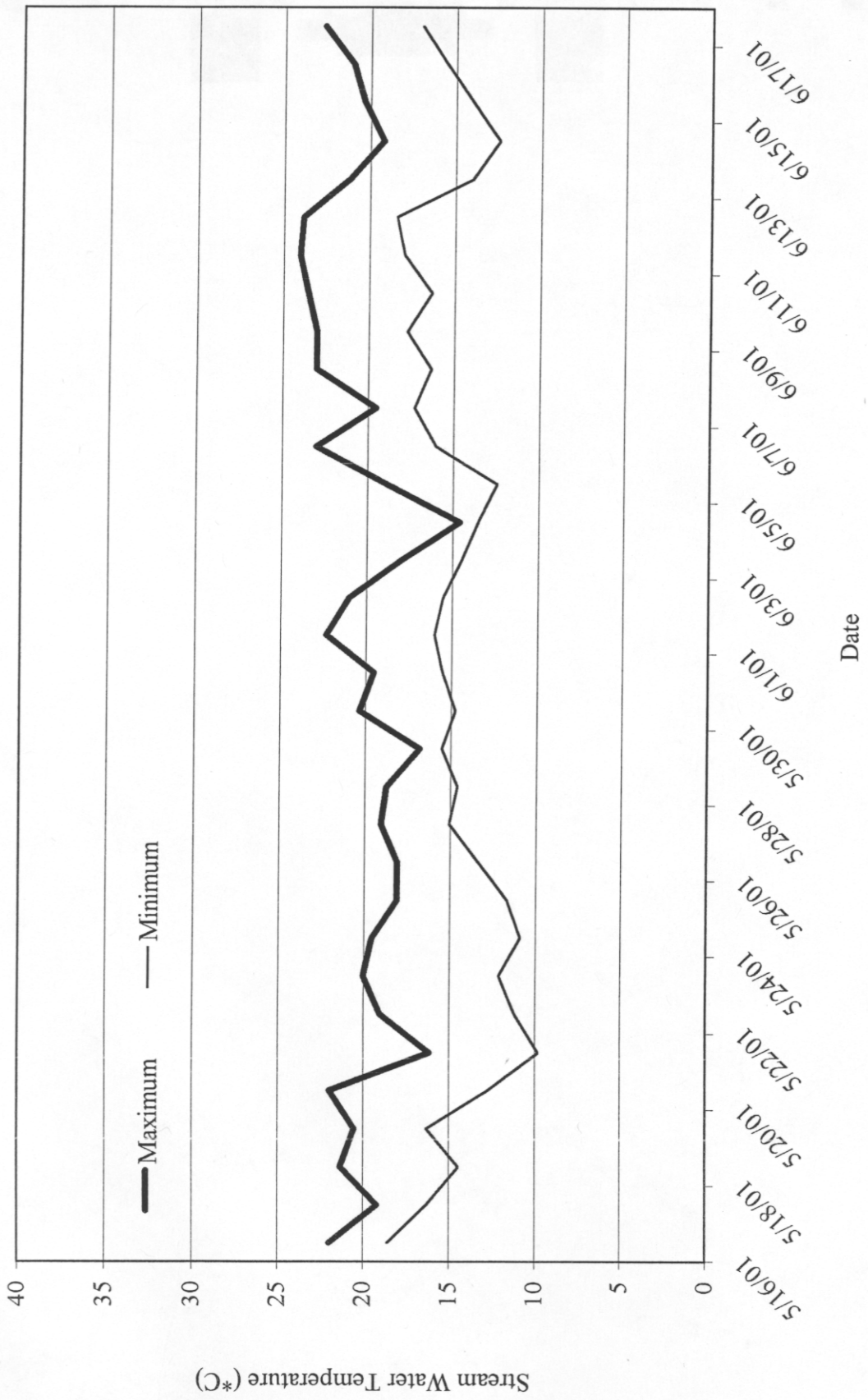


Figure A4-12. Maximum and minimum daily water temperatures in larval rearing habitat in the Middle Segment, Reach 4, Backwater 4, of the Arikaree River, 5/16/01-6/20/01, measured with an Onset StowAway® Tidbit® thermograph.

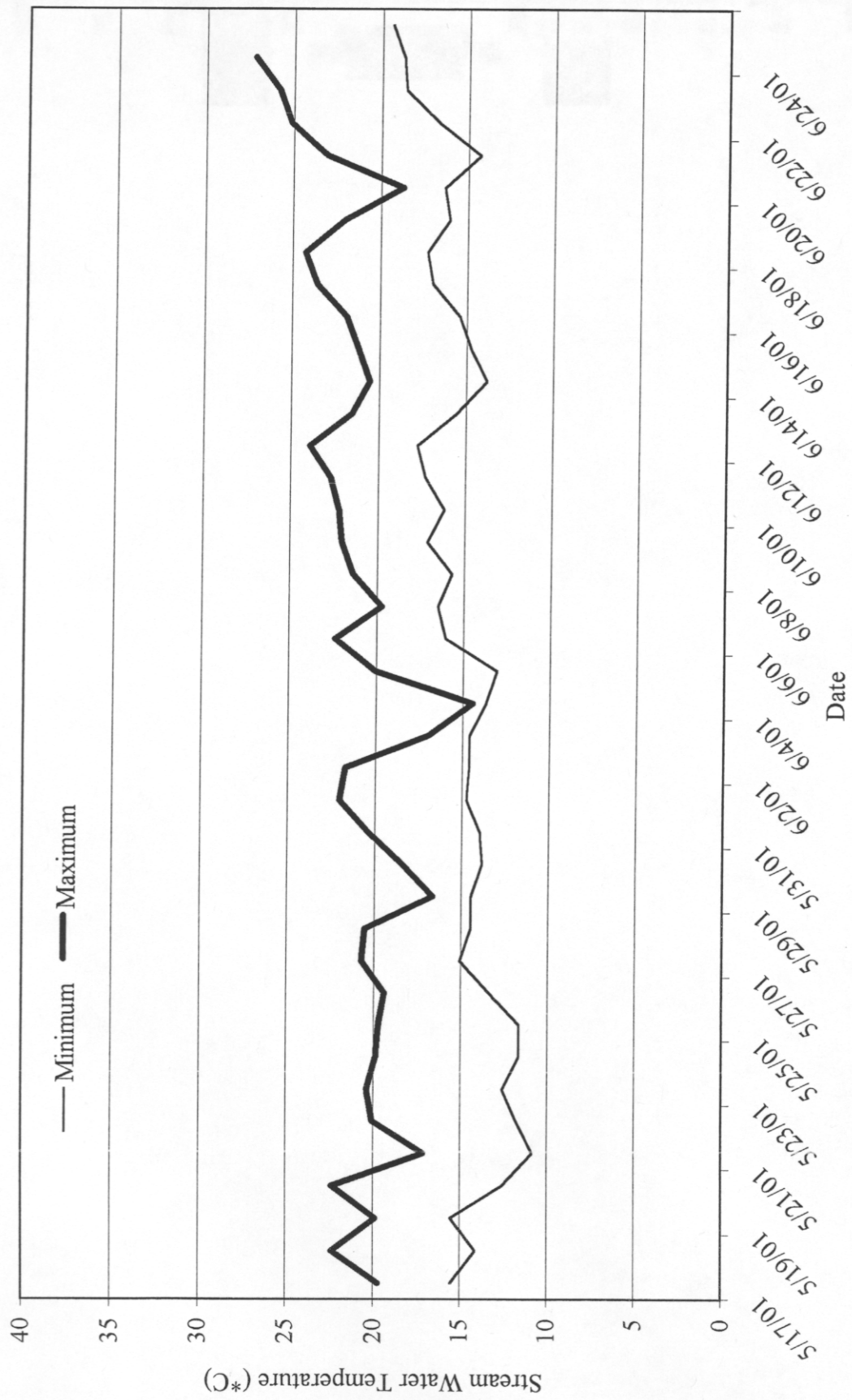


Figure A4-13. Maximum and minimum daily water temperatures in brassy minnow spawning and larval rearing habitat in the Middle Segment, Reach 5, Backwater 2, in the Arikaree River, 5/17/2001-6/25/2001, measured with an Onset StowAway® Tidbit ® thermograph.

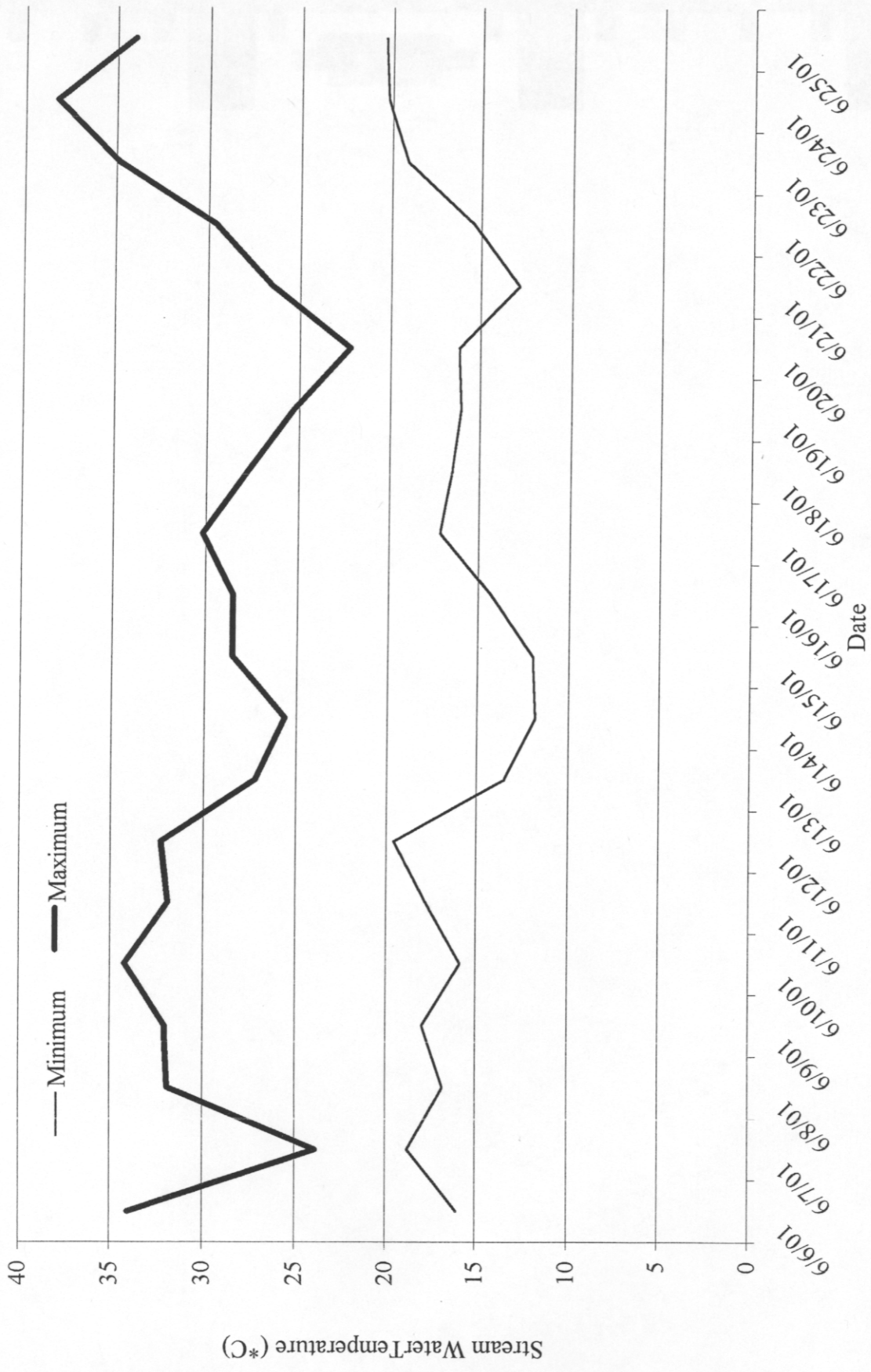


Figure A4-14. Maximum and minimum daily water temperatures in larval rearing habitat in the Middle Segment, Reach 8, Pool 5, of the Arikaree River, 6/6/01-6/25/01, measured with an Onset StowAway® Tidbit® thermograph.

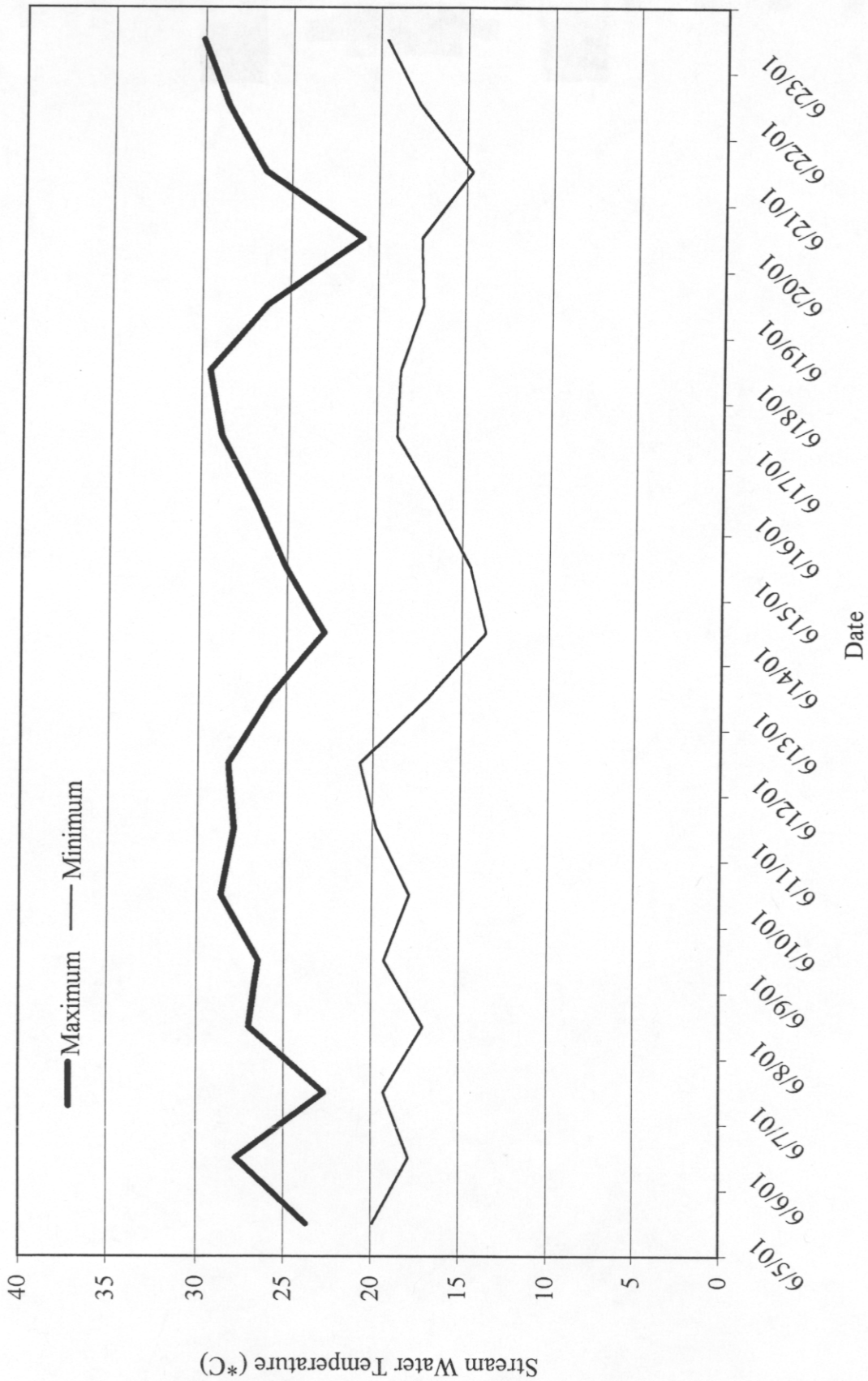


Figure A4-15. Maximum and minimum daily water temperatures in brassy minnow larval rearing habitat in the Upstream Segment, Reach 3, Backwater 1, in the Arikaree River, 6/5/2001-6/23/2001, measured with an Onset StowAway® Tidbit ® thermograph.

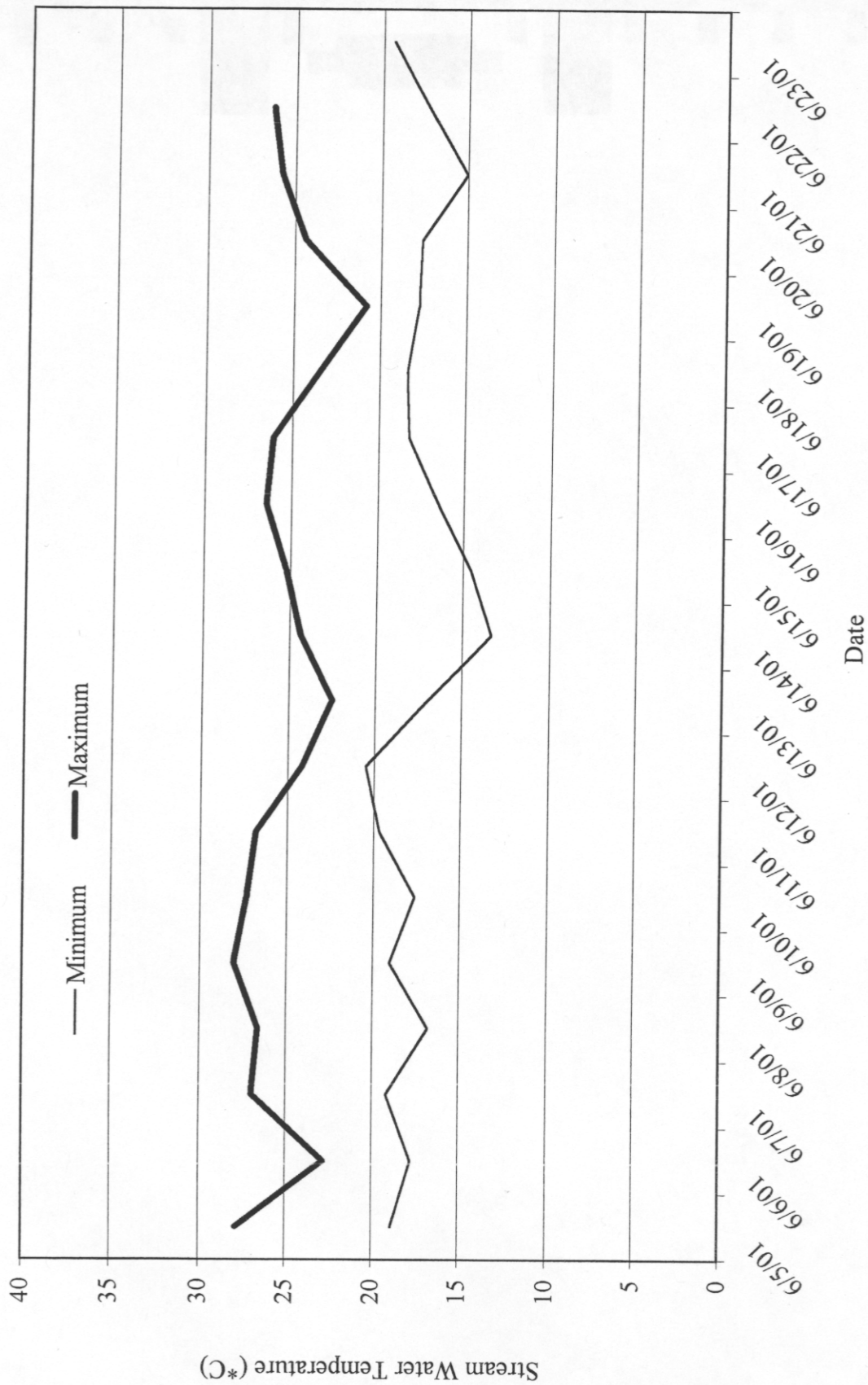


Figure A4-16. Maximum and minimum daily water temperatures in larval rearing habitat in the Upstream Segment, Reach 3, Deep Pool 2, of the Arikaree River, 6/6/01-6/23/01, measured with an Onset StowAway® Tidbit® thermograph.

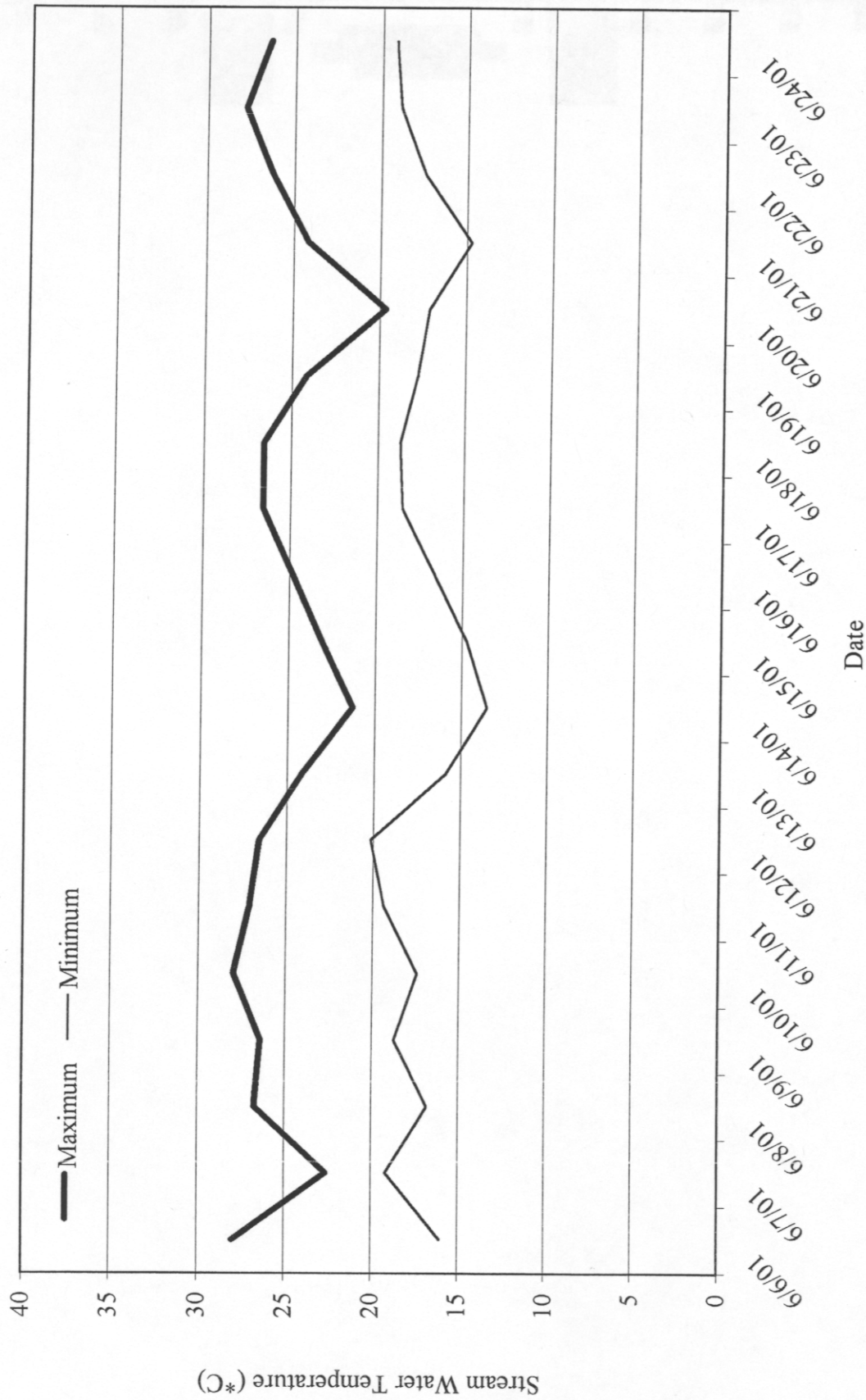


Figure A4-17. Maximum and minimum daily water temperatures in larval rearing habitat in the Upstream Segment, Reach 5, Shallow Pool 2, of the Arikaree River, 6/6/01-6/24/01, measured with an Onset StowAway® Tidbit® thermograph.

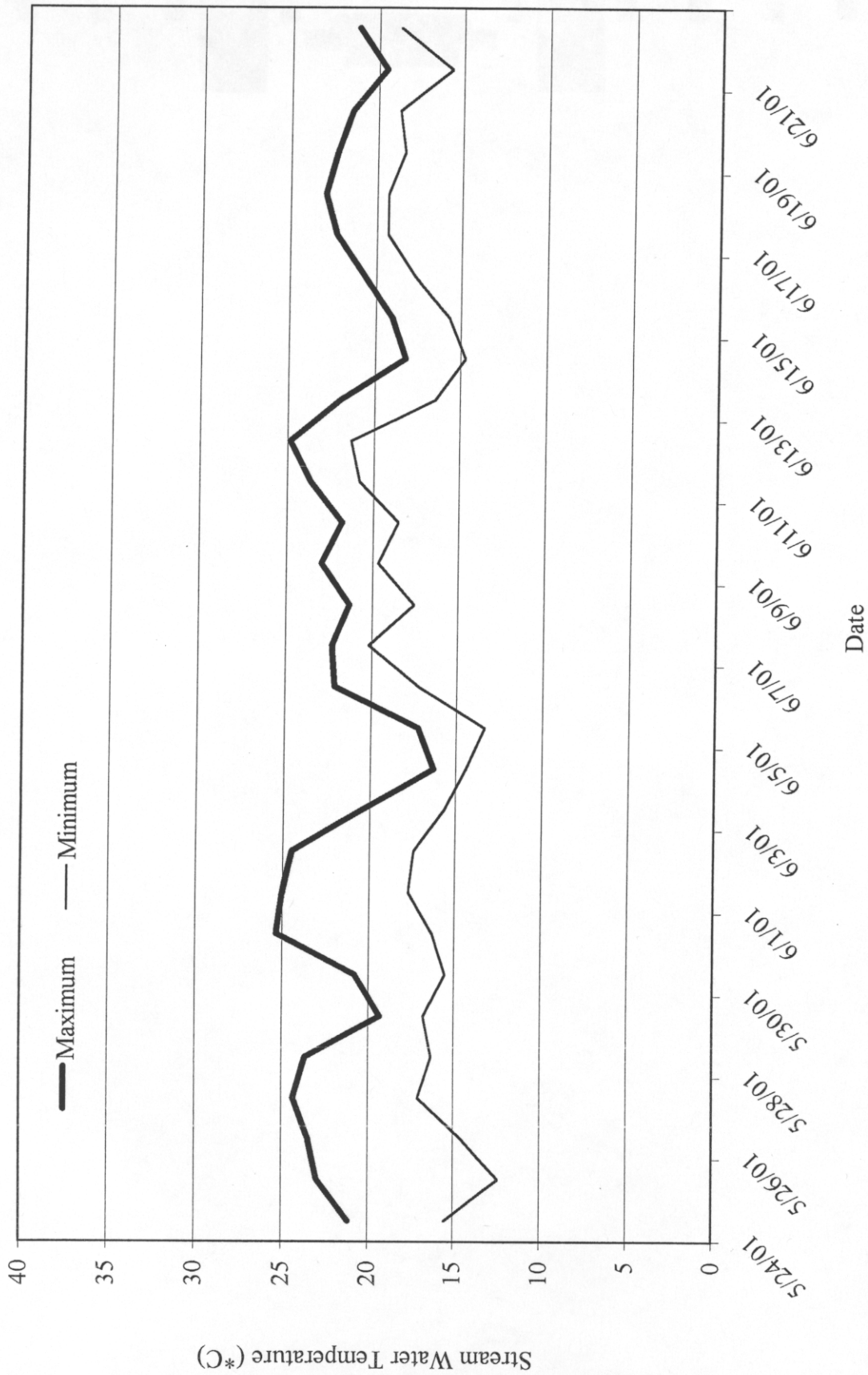


Figure A4-18. Maximum and minimum daily water temperatures in brassy minnow spawning and larval rearing habitat in the Upstream Segment, Reach 7, Backwater 1, in the Arikaree River, 5/24/2001-6/22/2001, measured with an Onset StowAway® Tidbit @ thermograph.