

REPRODUCTIVE SEASONS AND LIFE HISTORIES OF THREE TEXAS PERCINA
(ACTINOPTERYGII)

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By

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ABSTRACT

REPRODUCTIVE SEASONS AND LIFE HISTORIES OF THREE TEXAS PERCINA (ACTINOPTERYGII)

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Reproductive seasons of fishes in temperate regions are influenced by water temperature and, to a lesser extent, photoperiod, corresponding in theory to adaptive benefits of producing young during periods of adults and juvenile food availability, times of minimal predation of eggs and young, and availability of breeding sites. Often, phylogenetic constraints or inertia of reproductive timing obscure contemporary environmental influences on reproductive seasonality. In this study, reproductive seasons of three closely-related percine fishes of central Texas were determined by

gonadosomatic indices (GSI), ovarian stages, and oocyte diameters to test the effects of water temperature, photoperiod, river discharge, and food availability on seasonal and aseasonal reproduction. The three percinid species inhabit different stream environments, ranging from highly stable spring systems to variable run-off dominated systems. Additional life history parameters, such as age of sexual maturity, population structure, and age-group growth rates, were quantified to provide basic information for conservation efforts. Reproductive seasons ranged from five months in the river darter *Percina shumardi*, which inhabits abiotically variable, run-off dominated reaches of the lower Guadalupe River, to nine months in the endemic Guadalupe darter *Percina apristis*, which generally inhabits the abiotically stable reaches of the San Marcos River. Regionally endemic Texas logperch *Percina carbonaria*, which inhabits moderately variable systems within Central Texas, had a reproductive season of six months. Pooled GSIs among all three species were inversely related to water temperature ($P = <0.001$) and photoperiod ($P = 0.013$). Relationships were not detected between GSIs and river discharge or adult food availability. Though reproductive seasons and habitats differed among the three percinids, reproduction, as measured by presences of mature ovaries, ceased at water temperatures near 23°C. The start of reproductive quiescence at or near 23°C is reported for *Percina* throughout their North American distribution, suggesting that ancestral condition influences contemporary reproductive seasons versus an alternative hypothesis that predicts aseasonal reproduction in abiotically stable systems is a derived trait (i.e., spring-adapted).

CHAPTER 1

REPRODUCTIVE SEASONS AND LIFE HISTORIES OF THREE TEXAS PERCINA (ACTINOPTERYGII)

INTRODUCTION

Reproductive seasons of fishes in temperate regions are influenced by water temperature and, to lesser extent, photoperiod. These proximate cues correspond in theory to adaptive benefits of producing young during periods of adults and juvenile food availability, times of minimal predation of eggs and young, and availability of breeding sites (de Vlaming 1971, Kramer 1978). Among 699 native (USA) freshwater fishes listed in the FISHTRAITS database, 82% of the fishes have limited reproductive seasons of 4 months or less, 14 % have protracted spawning seasons (5 to 8 months) and 4% have continuous or near continuous reproductive seasons (9 – 12 months) (Frimpong et al. 2009). Among freshwater fishes with reproductive seasons from 9 to 12 months ($n = 21$), 81% occur in thermally constant environments or at lower latitudes where the proximate cue of water temperature is lessened or eliminated. The general trend of extended breeding seasons among species at lower latitudes and short seasons among species at higher latitude has been documented for fishes, as well as other vertebrates (Berry 1964, MacArthur 1964, Hubbs 1985, Gotelli and Pyron 1991). However, fishes and other animal groups (Brown and Shine 2006) in tropical areas often have seasonal reproduction independent of water temperature (Lam 1983, Winemiller 1989). As with fishes in temperate areas, reproductive seasons correspond to times of food availability (wet

seasons), periods of thermally, hydrologically, and chemically stable environments for young (dry seasons), minimal interspecific competition for food among juveniles, competition for breeding sites (Kramer 1978), or solely or in part for the purpose of synchronizing reproduction to ensure sufficient numbers of reproductively active aggregates (Bye 1984). Exact abiotic influences sometimes are obscured because of phylogenetic constraints in species evolution (i.e., reproductive seasonality is constrained by ancestral condition; Kramer 1978). Regardless, seasonal timing of reproduction is common among fishes within both temperate and tropical regions. Selection of continuous or aseasonal reproduction is uncommon.

Among species of *Percina* (Percidae), three species occur near the southwestern most extent of *Percina* distributions (Page and Burr 1991). Texas logperch *Percina carbonaria* (subgenus *Percina*) is found throughout the Edwards Plateau region of central Texas and has a protracted reproductive season of six months (Hubbs 1985). River darter *Percina shumardi* (subgenus *Imostoma*) is widely distributed in eastern and central North America, but a disjunct population persists in the lower Guadalupe River drainage of south Texas (Page 1983, Hubbs et al. 2008). The reproductive season of *P. shumardi* ranges from one to two months among higher latitude drainages of North America (Cross 1967, Thomas 1970, Scott and Crossman 1973). In Texas, *P. shumardi* has a four month reproductive season in the lower Guadalupe River (Hubbs 1985). Guadalupe darter *Percina apristis* (subgenus *Hadropterus*) was recently elevated as a distinct species from the dusky darter *Percina sciera* (Robins and Page 2007), and is endemic to the Guadalupe River drainage. *Percina apristis* is distributed throughout the Guadalupe River drainage but is most common in thermally-stable spring systems of the Edwards

Aquifer (Perkin and Bonner, in review). Upper San Marcos River *P. apristis* spawn for five months based on collections of reproductive individuals (Hubbs 1985). Collectively, these three *Percina* allow a unique opportunity to assess abiotic factors affecting reproductive seasons among taxa sharing similar ancestry (basal condition of multiple spawning during the spring; Heins et al. 1992) ranging in distributions along similar latitudes (i.e, similar photoperiods and seasons), but inhabiting different abiotic environments. The lower Guadalupe River is a widely variable lowland river, with large fluctuations in discharge and annual water temperatures (Figure 1). The Pedernales River is moderately variable in discharge and has a temperature range similar to that in the lower Guadalupe River. The upper San Marcos River has relatively stable spring-fed discharges and water temperatures.

Purposes of this study were to determine reproductive seasons and to assess the role of local influences, such as variation in food habits and water temperature and other abiotic factors, and regional influences such as photoperiod among three taxa sharing similar ancestry (phylogenetically constrained). This study could provide insight into the mechanisms and adaptive consequences influencing reproductive timing, especially for the small number of Edwards Plateau fishes that inhabit spring outflows and exhibit aseasonal or continuous reproductive seasons (*Etheostoma fonticola*, Schenck and Whiteside 1977; *Notropis chalybaeus*, J. Perkin, unpublished data). In addition, life history information will be described to provide greater understanding of the ecology of our study species, which will benefit conservation efforts of these regionally unique fishes. Specific objectives of this study were to quantify reproductive effort in the three *Percina* with gonadosomatic indices (GSI), ovarian status, and oocyte diameters to infer

reproductive season, to determine age of sexual reproduction, and sex ratios. Additional objectives were to determine age groups and growth rates, to describe food habits of adult fishes, and to test relationships among GSI, water temperature, photoperiod, and discharge.

METHODS

Fishes were collected from three rivers that originate on the Edwards Plateau of central Texas. *Percina shumardi* was taken from the lower Guadalupe River, upstream from Hwy 766 crossing (29°08'58" N, 97°19'01" W; October 2007 – September 2008) northwest of Cuero, Texas and upstream from Hwy 183 crossing (29°29'04" N, 97°26'52" W; February – September 2008) in Gonzales, Texas. Fish were collected from riffle and run habitats that were <1 m in depth, current velocities ranging from 10 to 50 cm/s, and with cobble and packed gravel substrates. *Percina apristis* was taken from the San Marcos River, downstream from County Road 299 crossing (29°52'08" N, 97°55'51" W; October 2007 – June 2007, September 2008) and from County Road 265 crossing (29°51'26" N, 97°53'49" W; July – September 2008) in San Marcos, Texas. Fish were taken from riffle and run habitats that were <0.5 m in depth, current velocities ranging from 10 to 40 cm/s, and with gravel and cobble substrates and submergent vegetation. *Percina carbonaria* was taken from the upper Pedernales River, downstream from Boos Lane crossing (30°13'17" N, 98°54'02" W; May 2007 – April 2008) and downstream from Alfred Petsch Road (30°12'34" N, 99°00'20" W; May 2007 – April 2008) southwest of Fredericksburg, Texas. Fish were taken from riffle and run habitats that were <0.5 m in depth, current velocities ranging from 10 to 40 cm/s, and with gravel and cobble substrates.

At each location, fish were collected by seine hauls or backpack electrofisher. Up to 10 individuals per month were targeted for each species among sites. Only one species was collected at each site and seven to twelve individuals were collected in most months. Individuals were anesthetized with a lethal concentration of tricaine methanesulfonate and fixed in 10% buffered formalin. In the laboratory, all individuals were weighed to the nearest 0.001 g and measured to the nearest millimeter total length. Gonads and digestive tracts were removed, and gonads weighed to the nearest 0.001 g. Gonads were used to sex individuals and ovaries were classified into one of three categories, following Williams and Bonner (2006). Latent describes ovaries that are small and clear, lacking vitellogenic oocytes. Developing ovaries are somewhat enlarged and opaque, usually cream or yellow in color, but lack a group of large, yellow or orange mature oocytes. Mature ovaries are found in reproductive females and are greatly enlarged, with the largest class of oocytes yellow to orange in most cases. The most developed mature ovaries contained a group of clear, orange eggs. Gonad and body weights were used to calculate gonadosomatic index (GSI; $[(\text{gonad weight}/\text{body weight}) \times 100]$). Size at maturity was estimated using the smallest individual of each species to contain mature ovaries. Gonadosomatic indices of sexually mature individuals were then pooled across sites within species to get mean monthly GSI. For each month in which females containing mature ovaries were collected, three individuals were chosen for measuring oocyte diameters to assess batch spawning. For *P. carbonaria*, one female for each month was used. The left ovary was separated, placed in a plastic dish, and teased apart with dissecting probes and forceps. The loose oocytes were gently swirled to distribute them as evenly as possible across the dish and placed under a dissecting microscope. A

calibrated camera attachment was used to take two diameters on each oocyte in the field of view, as close as possible to the largest and smallest diameters of the oocyte and 90 degrees apart. The average of the two measurements was recorded to the nearest 0.01 mm. After all oocytes in the field of view were measured, the dish was moved to show a new field of view. This procedure was repeated until 100 oocytes from each female had been measured. Oocyte measurements for *P. carbonaria* were conducted using an ocular micrometer. The procedure was otherwise identical to those for *P. apristis* and *P. shumardi*. For each individual, oocyte diameters were grouped into 0.05 mm bins and frequency histograms were created. Total fecundity was not measured because multiple batch spawners produce and spawn a series of clutches throughout the season and counting the oocytes in a given female does not provide an accurate picture of total eggs produced in one season.

Stomach contents were analyzed for all collected individuals. Each stomach was dissected from the esophagus to the first loop of intestine. Stomach contents were removed and placed in a plastic dish under a dissecting microscope. Food items were identified to the lowest practical taxon, usually family-level for aquatic insect taxa. The wet weight of each food type was taken to the nearest 0.001g. Weights were pooled across sites to determine the percent composition of each food item, both overall and seasonally. Seasonal differences in diet composition were tested with Analysis of similarity (ANOSIM) in Primer 5 (version 5.2.9). Seasons were defined as Winter being December-February, Spring being March-May, Summer being June-August, and Fall being September-November.

To quantify population structure, length frequency histograms were constructed from total length data. Chi-square analysis was used to determine if sex ratio differed significantly from 1:1. Pearson product-moment correlation was used to assess similarity between trends in male and female GSI. Age groups were determined using the Fisheries Stock Assessment Tools II software (FiSAT II, version 1.2.2). *Percina shumardi* and *Percina carbonaria* were conducive to assessment because of total length distinctions within each population. However, *P. apristis* lacked distinct total length distributions and therefore I was unable to confidently identify modal size distributions within the population. Aging by otoliths was attempted but failed due to lack of distinct bands that denote age. Instead, I report a scatter plot of total lengths by month for *Percina apristis*.

RESULTS

Population Structure

A total of 117 *Percina shumardi* and 132 *Percina apristis* were taken between October 2007 and September 2008, and a total of 187 *Percina carbonaria* were taken between May 2007 and April 2008. Number of age groups among species ranged from three to four. *Percina shumardi* population consisted of three age groups (Figure 2). Age-0 *P. shumardi* were first detected in May 2008 and reached a maximum length of 48 mm TL. Age-1 *P. shumardi* were collected year round and ranged in length between 50 and 64 mm TL. Age-2 *P. shumardi* were collected through June and reached a maximum length of 72 mm TL. Total lengths of *Percina apristis* were not modally distributed (Figure 2). The smallest fish, likely age 0, was 37 mm TL and captured in September. The largest fish, likely age 2 or age 3, was 100 mm TL and captured in January. *Percina*

carbonaria population consisted of four age groups (Figure 2). Age-0 *P. carbonaria* were first detected in June 2007 and reached a maximum length of 71 mm TL. Age-1 *P. carbonaria* were collected year round and ranged in length from 74 to 98 mm TL. Age-2 *P. carbonaria* were collected year round and ranged in length from 99 to 121 mm TL. Age-3 *P. carbonaria* were collected from September 2007 to March 2008 and reached a maximum length of 138 mm TL.

Food habits

Stomach contents consisted primarily of aquatic insects among the three species. *Percina shumardi* consumed aquatic insects from 14 families and 5 orders. The most common food item of *P. shumardi* was ephemeropterans (mean percent biomass across seasons = 52%), followed by dipterans (27%), and trichopterans (18%) (Figure 5; Appendix 1). Non-insect contents were fish eggs, plant material, and sand, representing <0.4% of stomach content weight. Food items consumed differed seasonally ($R = 0.179$; $P < 0.001$), due to greater consumption of dipterans during the winter (69%) compared to spring (20%), summer (8%), and fall (11%).

Percina apristis consumed aquatic insects from 20 families and 6 orders. The most common food item of *P. apristis* was ephemeropterans (63%), followed by trichopterans (15%) and odonates (9%) (Appendix 2). Non-insect contents were fish eggs, plant material, and sand, representing <0.3% of stomach content weight. Food items consumed differed seasonally ($R = 0.07$; $P < 0.01$), due to greater consumption of ephemeropterans during the winter (76%) and fall (79%) compared to spring (47%) and

summer (51%) and to greater consumption of trichopterans during the spring (23%) and summer (19%) compared to winter (7%) and fall (10%).

Percina carbonaria consumed aquatic insects from 20 families and 9 orders. The most common food item of *P. carbonaria* was ephemeropterans (46%), followed by dipterans (35%) and trichopterans (11%) (Appendix 3). Non-insect contents were fish eggs, detritus, nematodes, and leeches, representing <0.5% of stomach content weight. Food items consumed differed seasonally ($R = 0.16$; $P < 0.01$), due to greater consumption of dipterans during the Winter (69%) compared to Fall (30%) and Spring (4%) and lesser consumption of trichopterans during the Winter (1%) compared to Fall (11%) and Spring (26%).

Reproductive Characters

Male to female ratios varied among species. The ratio of male to female *Percina shumardi* was not different from 1:1 ($X^2 = 0.692$, $P = 0.406$). The ratio of male to female *P. apristis* was 1.4:1 and differed from 1:1 ($X^2 = 4.36$, $P = 0.037$). The ratio of male to female *P. carbonaria* was 0.7:1 and differed from 1:1 ($X^2 = 8.2$, $P = 0.004$).

Spawning seasons ranged from five to nine months among the three species. Mean monthly GSIs for female *P. shumardi* were elevated (>4.7%) and mature ovaries were present for five months (December 2007 through April 2008) (Figure 3). Male *P. shumardi* GSIs followed similar trend and were positively correlated with female GSIs ($r = 0.79$; $P < 0.01$). Sexual maturity was reached by age-1 in *P. shumardi*, with the smallest sexually mature male at 56 mm TL and smallest sexually mature female at 49 mm TL. Mean monthly GSIs for female *P. apristis* were elevated (>3.0%) and mature

ovaries were present for nine months (October 2007 through June 2008), with the exception of May 2008 when only one female was collected and had developing ovaries (Figure 3). Male *P. apristis* GSIs followed similar trend and were not correlated with female GSIs ($r = 0.42$; $P = 0.17$). Sexual maturity was reached by age-1 in *P. apristis*, with the smallest sexually mature male at 46 mm TL and smallest sexually mature female at 53 mm TL. Mean monthly GSIs for female *P. carbonaria* were elevated ($>4.0\%$) and mature ovaries were present for six months (May 2007 and from December 2007 through April 2008) (Figure 3). Male *P. carbonaria* GSIs followed similar trend and were positively correlated with female GSIs ($r = 0.81$; $P < 0.01$). Sexual maturity was reached by age-1 in *P. carbonaria*, with the smallest sexually mature male at 74 mm TL and smallest sexually mature female at 76 mm TL.

Oocyte diameters were distributed among multiple cohorts concurrently throughout the reproductive season for each female and species. Distribution of oocyte diameters in *P. shumardi* consisted of at least three size cohorts, including the largest diameter cohort (1.2 to 2.1 mm), during the five month reproductive season (December 2007 through April 2008) (Figure 4; distribution is shown for only one female per month). Distribution of oocyte diameters in *P. apristis* consisted of at least three size cohorts, including the largest diameter cohort (1.3 to 1.6 mm), during the nine month reproductive season (October 2007 to April 2008 and June 2008). Distribution of oocyte diameters in *P. carbonaria* consisted of at least three size cohorts, including the largest diameter cohort (1.3 to 1.6 mm), during the six month reproductive season (May 2007 and December 2007 to April 2008).

Environmental factors related to reproductive season

Gonadosomatic indices of *Percina* were related to water temperature and number of daylight hours but not discharge (Figure 6). Collective GSIs were negatively related to water temperature ($P < 0.001$) and to number of daylight hours ($P = 0.013$). Collective GSIs were not related to discharge ($P = 0.99$). Consequently, I rejected the null hypotheses that water temperature and number of daylight hours have no effect on GSIs. Among females containing mature ovaries (Figure 6, shaded area), mean monthly water temperatures ranged from 11.4 to 23.1°C, number of daylight hours ranged from 10.2 to 14.1 hours, and discharge ranged from 1 to 62 m³/s.

DISCUSSION

Length of the reproductive season was notably divergent among the three *Percina*, compared to length of reproductive season of conspecifics and congeners in cooler and more humid climates. As predicted, the disjunct population of *P. shumardi* in the Guadalupe River had a one to two month longer reproductive season than its northern conspecifics (Cross 1967, Thomas 1970, Scott and Crossman 1973, Robison and Buchanan 1988). Likewise, *P. carbonaria* had a spawning season of three to five months longer than sister taxon *P. caprodes*, which spawns from one to three months during the Spring and Summer seasons at higher latitudes (mid March through July; Winn 1958, Hubbs 1985). The most divergent, however, was *P. apristis*, which spawned for at least nine months in the San Marcos River. Previous studies report spawning from January to June in the upper San Marcos (Brown 1955, Hubbs 1985) and sister taxon *P. sciera* spawns for three to five months (Hubbs 1961, Page and Smith 1970).

Collective reproductive season across all species examined by this study, as measured by gonadosomatic indices, was inversely related to water temperature. Mature ovaries, perhaps a more sensitive measure of reproductive season, were not found at water temperatures $>23.5^{\circ}\text{C}$ (range of water temperatures observed: $12 - 30^{\circ}\text{C}$). Gonadal quiescence at temperatures $>23.5^{\circ}\text{C}$ supports Hubbs (1985) theory that water temperatures are terminating cues for percinids. In fact, among available maximum spawning temperatures reported, all *Percina* cease spawning near 23°C : 20°C for *P. pantherina* (James et al. 1991), $<25^{\circ}\text{C}$ for *P. phoxocephala* (Brewer et al. 2006), 23°C for *P. nigrofasciata* (Mathur 1973), 22°C for *P. vigil*. Because of the support of water temperature as a terminating cue (this study) and ubiquity of 20 to 24°C as a maximum spawning temperature across small scale (this study) and large-scale geography within a phylogenetic lineage, I hypothesize that termination of spawning around $20 - 24^{\circ}\text{C}$ is an ancestral condition within the *Percina* lineage. An alternative explanation is that in at least some spring fishes, continuous or near continuous spawning is a derived condition and one of many traits associated with a spring systems (Hubbs 1995). However, retention of ancestral traits in spring-associated fishes has been reported for the desert pupfish (*Cyprinodon*) populations (thermal tolerances; Brown and Feldmeth 1971), fountain darter *Etheostoma fonticola* (thermal tolerance; Bonner et al. 1998), and *Percina* (batch spawning; Heins et al. 1992). Consequently, retention of the ancestral condition is the more parsimonious explanation that links phylogenetically similar taxa across diverse habitats and would provide a mechanism (i.e., lack of adequate terminating cue) for continuous or near continuous spawning of *P. apristis* in the thermally constant, but $<23^{\circ}\text{C}$, San Marcos River.

Photoperiod was inversely related to collective *Percina* GSIs, but mature ovaries persisted throughout the range of photoperiod (10.3 to 14.1 hours of daylight). Hubbs (1985) suggested that photoperiod is a predictive cue for gonadal recrudescence. Additional support for photoperiod as a predictive cue is found in *P. pantherina* populations in Oklahoma, where spawning began in two successive years at 12 and 17°C, but at the same time of year (James and Maughan 1989). Our results were similar for *P. shumardi* and *P. carbonaria*, which had gonadal recrudescence in November and December at water temperatures ranging from 11 to 18°C.

Effects of adult food availability and river discharge on reproductive season were not detected in this study. *Percina shumardi*, *P. apristis*, and *P. carbonaria* are benthic invertivores, consuming a variety of aquatic insects throughout the year and typical among *Percina* (Goldstein and Simon 1999). Intra-annual variation in food items consumed was observed in all three species, but these differences likely were attributed to local availability of food items and not changes nutritive quality. Consequently, availability of adult food items is unlikely a contemporary influence on reproductive season. Likewise, elevated GSIs and mature ovaries were found over a wide range (1-62 m³/s) of river discharges and therefore unlikely to be influence by discharge regimes. Nevertheless, river discharge influences reproductive success (i.e., post hatch larval survival) in many riverine fishes (Arumugam and Geddes 1987, Lehtinen and Layzer 1988, Durham and Wilde 2006) and should not be discounted as an important variable in overall reproductive success of percinids.

Life history parameters assessed in this study for percinids in the most southwest extent of *Percina* distribution were similar to those of percinids elsewhere. *Percina*

shumardi, *P. apristis*, and *P. carbonaria* reached sexual maturity by age 1, produced multiple batches of oocytes throughout their respective reproductive seasons, and had a maximum life span of 2 to 3 years. Sexual maturity by age 1 and maximum life span of 2 to 3 years are common among congeners, though some species live up to six years and sizes up to 200 mm TL (Winn 1958, Page and Smith 1970, Mathur 1973, Page 1974, Starnes 1977, Lutterbie 1979, Burkhead 1983, Page 1983, Heins and Baker 1989, Page and Burr 1991, Etnier and Starnes 1993, Hugg 1996, Rosenberger and Angermeier 2002, Roberts and Rosenberger 2008). Producing multiple batches throughout the spawning season is likely a basal character of *Percina* and of percinids in general (Heins et al. 1992). Typical oocyte diameter distributions or spawning of multiple clutches has been observed in several *Percina* to date, including *P. pantherina*, *P. vigil*, and all three species in this study (James and Maughan 1989, Heins and Baker 1989). Production of multiple batches of eggs is documented in numerous freshwater fishes (Heins and Rabito 1988, Fox and Crivelli 1998, Fuller 1998, Platania and Altenbach 1998, Barron and Albin 2004), and is most commonly seen in small-bodied fish with extended spawning seasons (Burt et al. 1988). Multiple batch spawning confers benefits including increasing potential fecundity in small-bodied fishes, which are limited by body size in how many eggs can be produced at once (Hubbs et al. 1968, Blueweiss et al. 1978, Kramer 1978, Roff 1986, Trippel 1993). The mass and/or volume of eggs produced in one season by a multiple spawning fish can exceed that of the female herself (Wootton 1973, Gale and Deutsch 1985, Gale 1986, Burt et al. 1988). In addition, in unstable environments, spawning multiple clutches increases the odds that at least one clutch will find favorable conditions for larval survival (Nikolsky 1963, Giesel 1976, Lambert and Ware 1984).

While this does not necessarily apply for *P. apristis* in the environmentally stable upper San Marcos River, it may for *P. shumardi* and *P. carbonaria*, which inhabit reaches with more variation in water temperature and discharge.

Among the three perciniids in this study, only *P. apristis* is considered a species of concern (Hubbs et al. 2008). Population of *P. apristis* in the San Marcos River is not considered to be increasing or decreasing overall, comprising about 2% of the current fish assemblage (Perkin 2009). However, relative abundance of *P. apristis* has declined in the lower Guadalupe River, and *P. apristis* has not been reported in the upper Guadalupe River since 1960s (Perkin 2009). Recent efforts to document *P. apristis* in the upper Guadalupe River have not yielded any specimens (C. Folb, unpublished data). Status of the disjunct population of *P. shumardi* in the Guadalupe River drainage cannot be confidently determined (Perkin 2009), but considered stable in the lower Guadalupe River by Edwards (1997). Consistent collections of *P. shumardi* for this study support Edwards (1997) concept of a stable population persisting in the lower Guadalupe River. Populations of *P. carbonaria* are stable in the upper Guadalupe River (Perkin 2009), likely stable in the Pedernales River (Z. Shattuck, unpublished data), persisting in the Brazos River drainages (B. Labay, unpublished data), unknown in the San Antonio River (Runyan 2007), and declining in the lower Guadalupe River and San Marcos River (Perkin 2009). Reasons for decline of *P. apristis* in the upper Guadalupe River and of *P. carbonaria* in the lower Guadalupe River and San Marcos River are not immediately apparent, though Perkin (2009) detected corresponding declines in small flood events in the San Marcos River and population declines in other riverine fishes. As with other perciniids, life-history characters, including fluvial-type habitat specialization, lithophilic

spawning (Simon 1998), and large-scale instream movements, make them susceptible to changes in water quality, water quantity, and instream impediments.

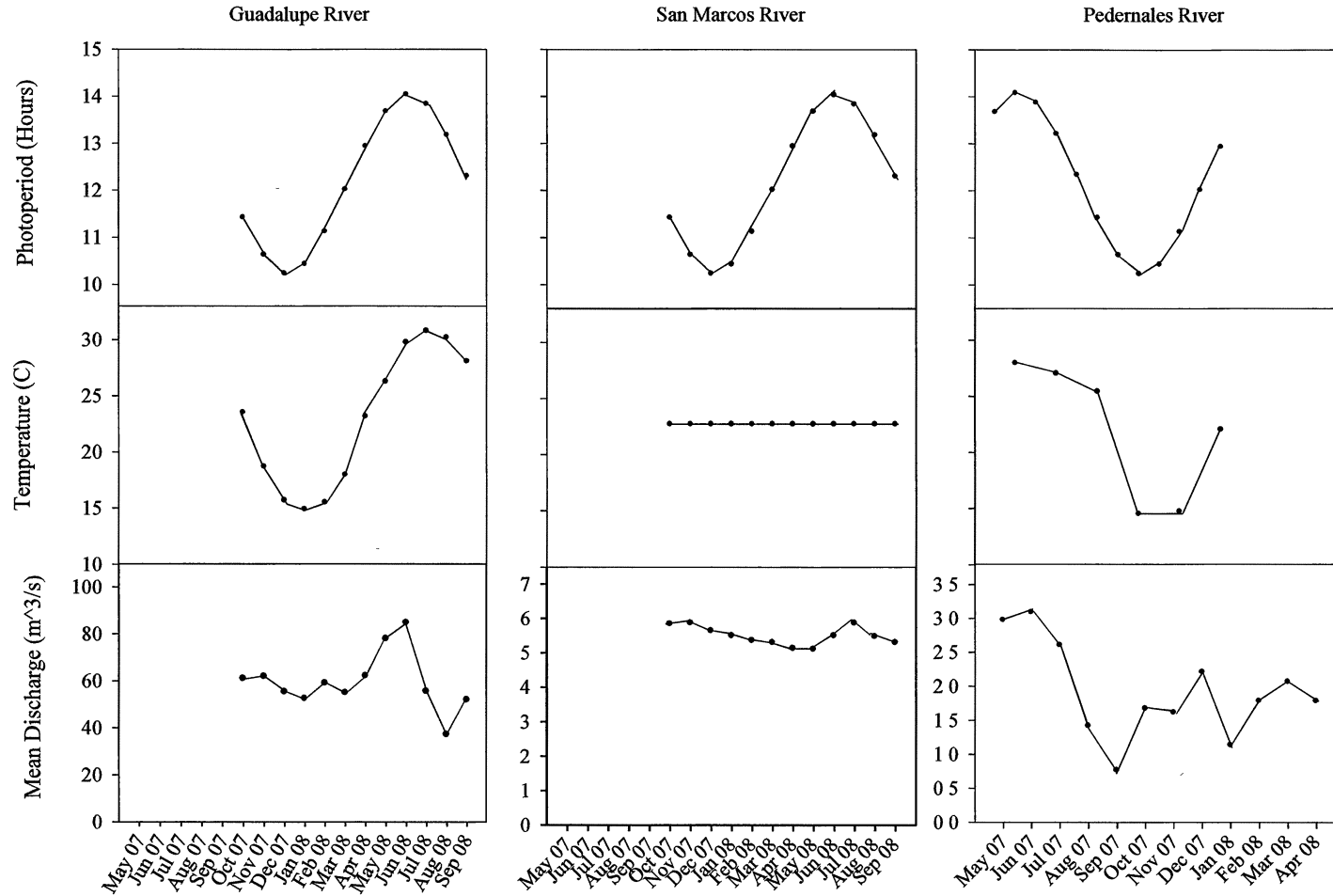


FIGURE1.- Photoperiod and water temperatures for all three rivers during the study period and mean discharge for each month. Discharges are mean monthly values for 45, 15, and 30 years of records, respectively, from the USGS.

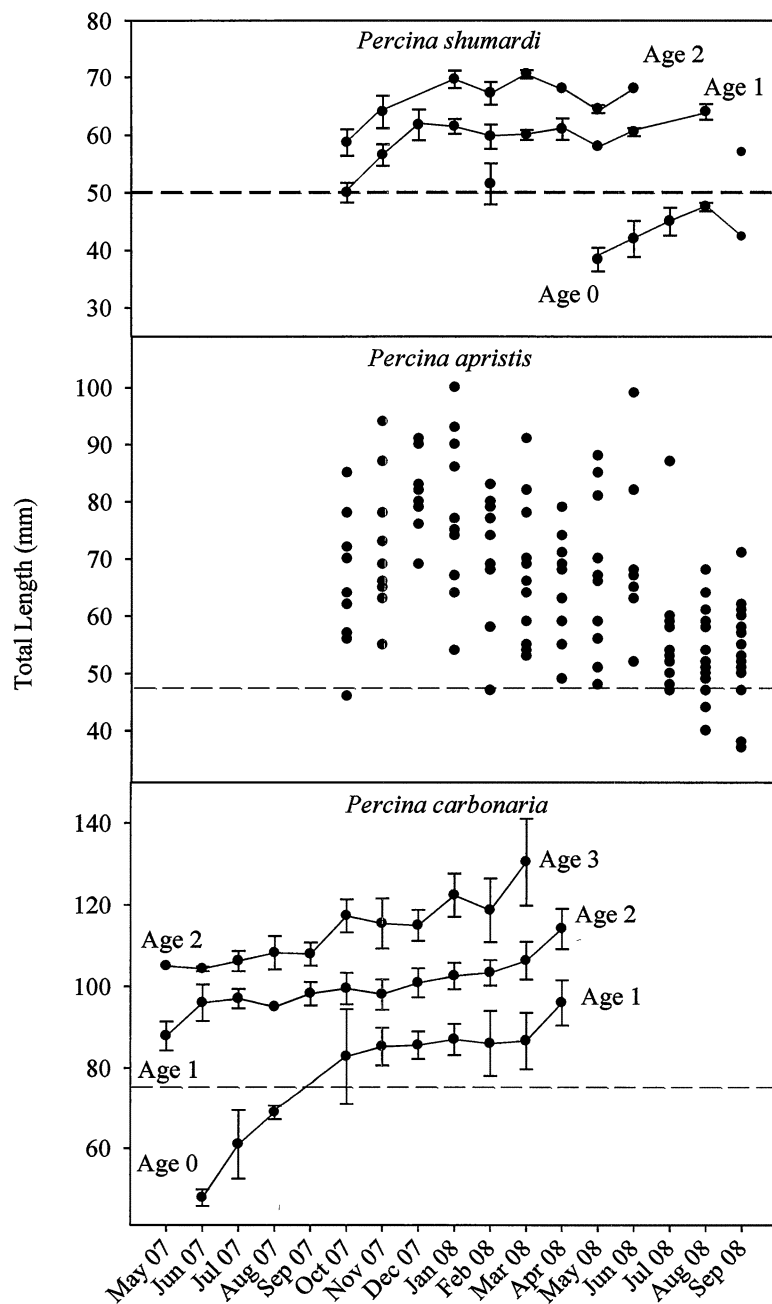


FIGURE 2.-*Percina shumardi* (top) displayed three age groups, *P. apristis* (center) lacked defined age groups, and *P. carbonaria* (bottom) displayed four age groups. Horizontal dotted lines represent size at sexual maturity.

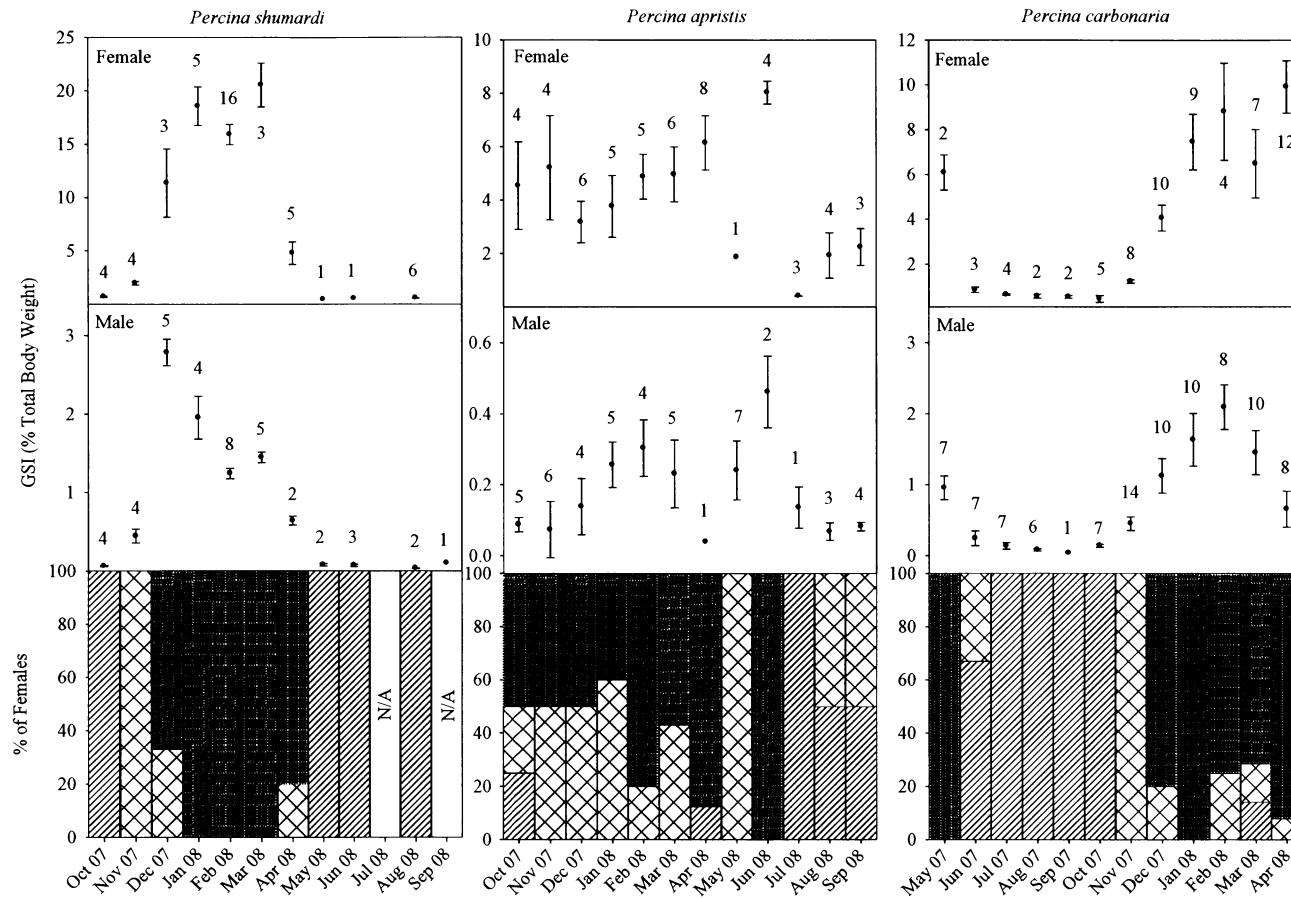


FIGURE 3. —Ovary condition and GSI trends found spawning seasons of five and six months in *P. shumardi* and *P. carbonaria*, and at least nine months in *P. apristis*. Numbers above GSI points represent number of individuals. Diagonal lines represent latent, crosshatching developing, and dark grey mature ovaries. No sexually mature female *P. shumardi* were collected in July or September 2008.

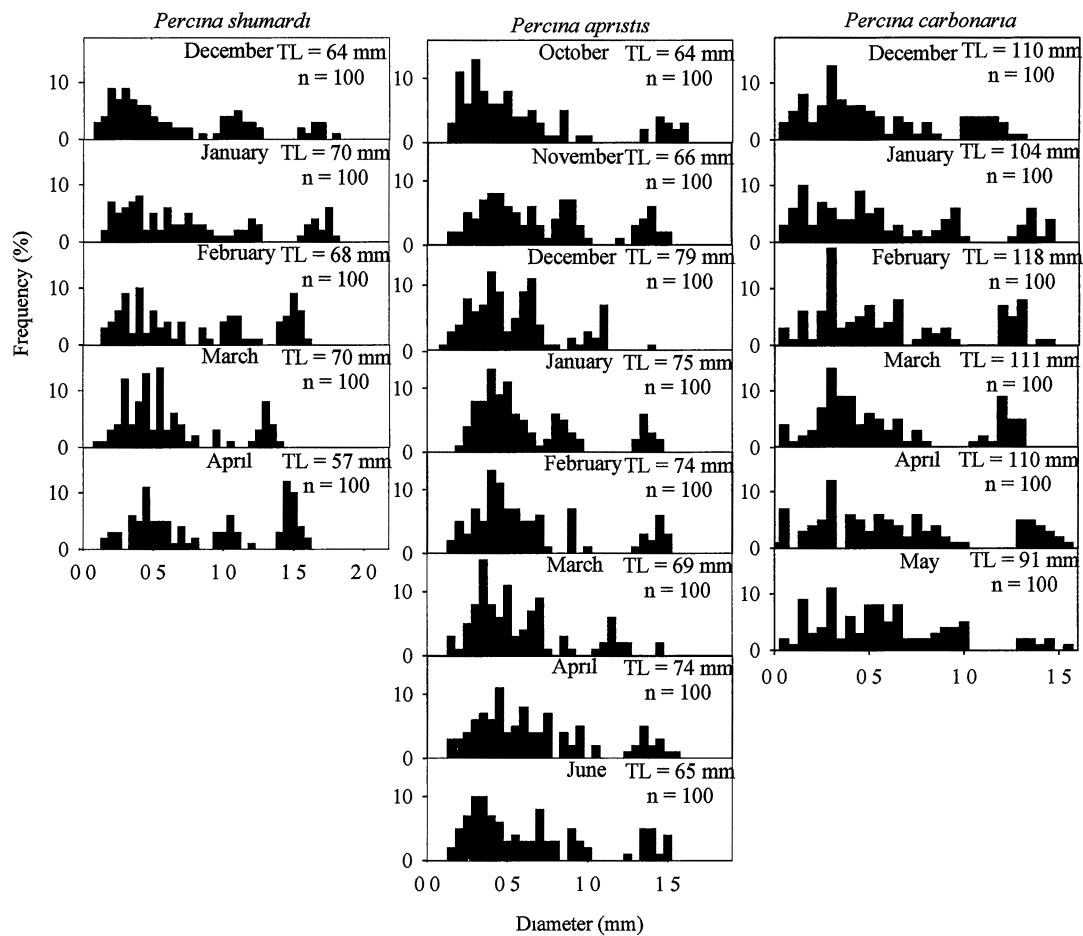


FIGURE 4.-Oocyte diameter distributions in reproductive female *P. shumardi* (left), *P. apristis* (center), and *P. carbonaria* (right) consisted of three cohorts, consistent with multiple batch spawning. One representative female is shown for each month.

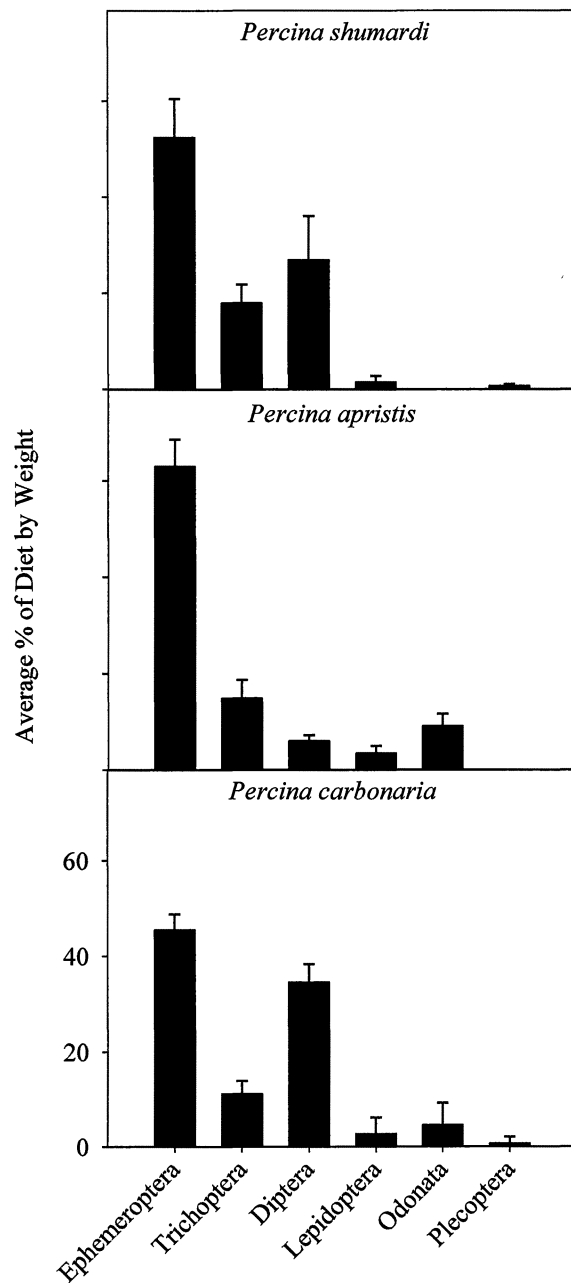


FIGURE 5.- Six most common food items by weight found in the stomachs of three percine fish taken from the lower Guadalupe River (*P. shumardi*), San Marcos River (*P. apristis*), and the Pedernales River (*P. carbonaria*). Standard error bars are included.

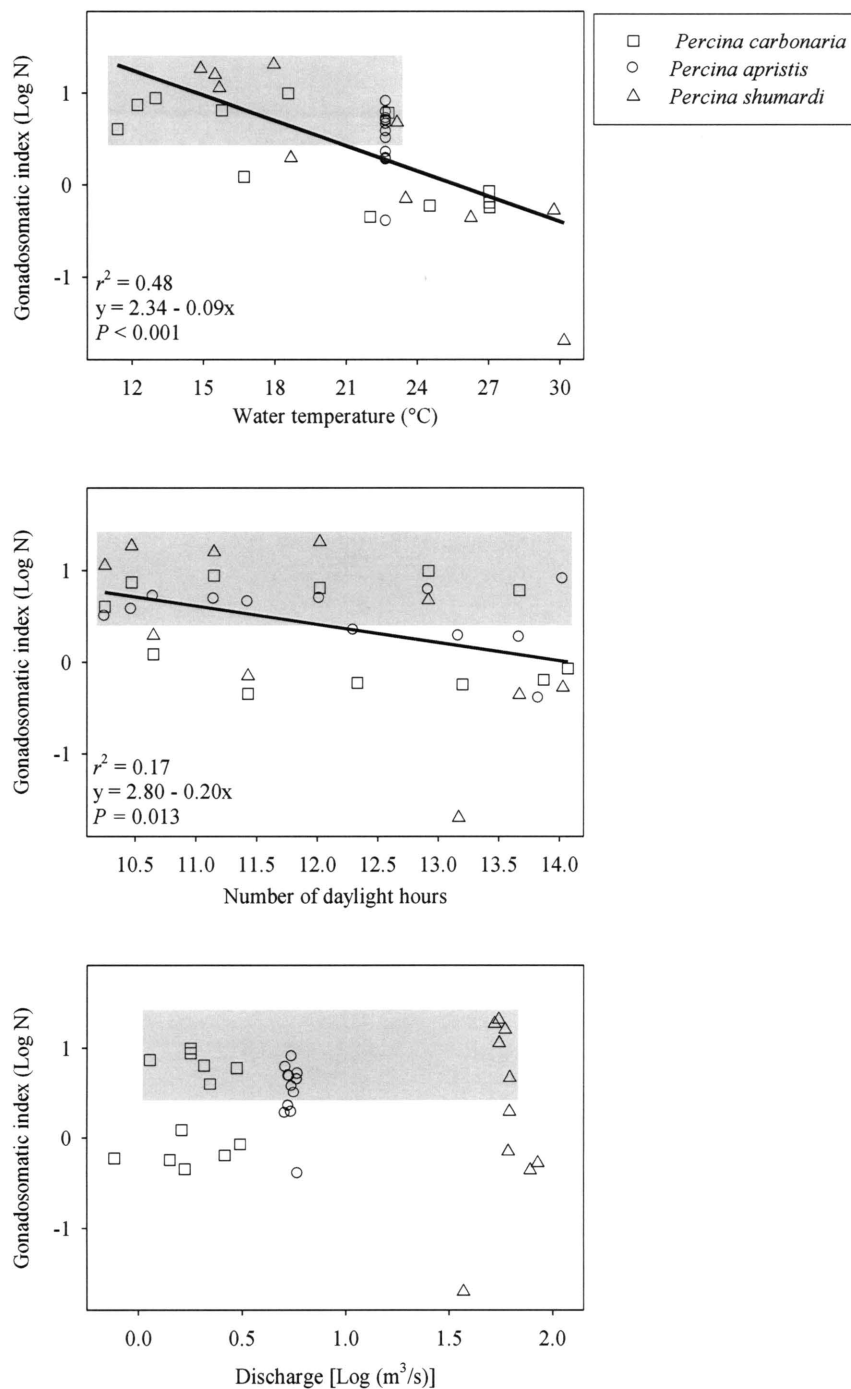


FIGURE 6.- Relationships between collective percine gonadosomatic indices (dependent variable) and water temperature, number of daylight hours (i.e. photoperiod), and discharge.

APPENDIX 1

Seasonal percentage by wet weight of food items in
the diet of *Percina shumardi*

APPENDIX 1.-Seasonal percentage of the diet by wet weight made up by each food item found in *Percina shumardi*. Bolded values are the overall percentage each order or category made up in each season.

	Season			
	Winter	Spring	Summer	Fall
Ephemeroptera	18.33	54.13	65.30	71.71
Baetidae	1.62	1.53	9.98	10.13
Leptohyphidae	4.55	16.64	16.43	21.42
Leptophlebiidae	3.73	25.15	32.35	29.98
Heptageniidae	1.19	4.00	0.25	-
Isonychiidae	6.52	-	-	-
Unidentifiable	0.72	6.81	6.29	10.19
Plecoptera				
Perlidae	1.26	1.39	-	-
Trichoptera	11.48	24.02	20.15	16.02
Hydropsychidae	3.77	21.47	12.62	-
Leptoceridae	1.85	2.24	4.31	0.76
Hydroptilidae	0.02	0.09	2.15	-
Glossosomatidae	-	-	1.08	0.28
Unidentifiable	5.84	0.23	-	14.98
Diptera	68.83	19.77	7.88	11.03
Chironomidae	0.10	8.77	6.14	1.96
Simuliidae	68.68	10.41	-	8.78
Empididae	0.04	0.37	1.74	0.28
Unidentifiable	-	0.23	-	-
Lepidoptera				
Pyralidae	-	-	5.09	0.84
Unidentified				
Insects	-	0.68	0.50	-
Fish Eggs	-	-	-	0.40
Plant	0.10	-	-	-
Rock/Sand	-	-	1.08	-

APPENDIX 2

Seasonal percentage by wet weight of food items in
the diet of *Percina apristis*

APPENDIX 2.-Seasonal percentage of the diet by wet weight made up by each food item found in *Percina apristis*. Bolded values are the overall percentage each order or category made up in each season.

	Season			
	Winter	Spring	Summer	Fall
Ephemeroptera	75.84	46.46	51.11	78.60
Baetidae	41.78	19.43	14.88	55.44
Leptohyphidae	16.11	21.06	22.67	11.24
Leptophlebiidae	6.25	1.15	0.70	0.64
Heptageniidae	3.24	0.54	-	-
Isonychiidae	2.59	2.50	5.76	8.75
Caenidae	2.45	-	-	0.28
Unidentifiable	3.42	1.78	7.09	2.25
Trichoptera	7.45	22.91	19.24	10.04
Hydropsychidae	-	0.54	5.71	2.35
Leptoceridae	2.17	15.39	12.79	1.02
Hydroptilidae	-	1.24	0.42	0.83
Glossosomatidae	0.68	1.50	0.16	-
Polycentropodidae	0.79	-	0.16	3.70
Hydrobiosidae	3.71	3.70	-	-
Unidentifiable	0.10	0.54	-	2.15
Diptera	2.51	8.47	8.10	4.92
Chironomidae	1.85	5.70	6.84	2.14
Simuliidae	0.06	1.70	0.42	0.60
Empididae	-	0.54	0.83	-
Unidentifiable	0.60	0.54	-	2.17
Odonata	12.24	13.82	6.70	3.68
Calopterygidae	5.76	9.16	4.74	0.59
Coenagrionidae	2.08	2.70	1.14	1.54
Libellulidae	2.20	0.82	-	-
Zygoptera	0.46	-	-	-
Anisoptera	-	-	0.82	-
Unidentifiable	1.75	1.14	-	1.56

APPENDIX 2.-Continued.

	Season			
	Winter	Spring	Summer	Fall
Lepidoptera				
Pyralidae	0.75	4.44	8.45	0.24
Coleoptera				
Elmidae	0.10	0.13	-	-
Unidentified				
Insects	-	3.76	6.40	2.52
Fish Eggs	0.57	-	-	-
Plant material	0.42	-	-	-
Rock/Sand	0.11	-	-	-

APPENDIX 3

Seasonal percentage by wet weight of food items in
the diet of *Percina carbonaria*

APPENDIX 3.-Seasonal percentage of the diet by wet weight made up by each food item found in *Percina carbonaria*. Bolded values are the overall percentage each order or category made up in each season.

	Season			
	Summer	Fall	Winter	Spring
Ephemeroptera	44.37	48.97	27.25	61.48
Baetidae	26.18	27.37	25.91	17.77
Leptohyphidae	1.74	2.49	0.52	11.57
Leptophlebiidae	2.89	5.11	0.77	16.73
Heptageniidae	-	0.14	-	-
Isonychiidae	7.62	10.09	-	15.42
Siphonuridae	5.96	2.59	-	-
Unidentifiable	-	1.18	0.04	-
Plecoptera	-	-	-	2.55
Perlidae	-	-	-	2.55
Trichoptera	7.10	10.59	1.43	25.83
Hydropsychidae	4.47	7.77	0.02	18.48
Hydroptilidae	2.59	2.33	0.05	0.14
Philopotamidae	0.04	0.48	1.36	7.21
Diptera	35.40	29.95	68.77	4.03
Chironomidae	0.09	9.26	2.09	2.23
Simuliidae	35.25	20.68	66.68	1.80
Sciomyzidae	-	0.01	-	-
Ceratopogonidae	0.05	-	-	-
Odonata	7.34	9.47	1.34	0.09
Gomphidae	-	0.05	-	-
Libellulidae	7.34	9.42	1.34	0.09
Lepidoptera	4.81	0.57	0.30	5.07
Pyrilidae	4.81	0.57	0.30	5.07
Coleoptera	0.13	-	0.22	-
Halipilidae (adult)	0.13	-	0.22	-

APPENDIX 3.-Continued

	Season			
	Summer	Fall	Winter	Spring
Hemiptera	0.83	-	-	-
Unidentified	0.83	-	-	-
Neuroptera	-	0.24	-	-
Sisyridae	-	0.24	-	-
Phylum				
Nematoda	0.03	0.04	0.24	0.01
Subclass				
Hirudinea	-	0.18	-	-
Detritus	-	-	0.03	-
Fish eggs	-	-	0.43	0.93

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