ABUNDANCE AND SURVIVAL OF COMMON BENTHIC BIOTA IN A RIVER

AFFECTED BY WATER DIVERSION DURING AN HISTORIC DROUGHT

by

RACHEL ALLISON KATZ

(Under the Direction of Mary Freeman)

ABSTRACT

Hydrologic changes, such as drought or managed flow, can influence the abundance and survival of aquatic biota. The purpose of this research is to understand the effects of naturally low streamflows coupled with water withdrawals on an abundant net-spinning caddisfly (Hydropsychidae) and a common benthic darter (Percidae). Results show that caddisfly production was lower than in a previous study and that larvae preferred habitats vulnerable to periodic exposure from water withdrawals, likely leading to the observed decline in abundance and production. Using capture-recapture methods, fish were estimated to be abundant with considerable site fidelity; estimated survival rates were lower for young-of-year fish compared to adult fish. Results from this study allow for future comparisons of fish population responses to interannual changes in streamflow. The coupling of natural drought and human-induced flow alterations provided a unique opportunity to study flow-ecology linkages in a sixth-order flow-altered stream.

INDEX WORDS: Middle Oconee River, sixth-order stream, drought, water withdrawal, low streamflow, environmental flows, shoal, caddisfly, Hydropsychidae, secondary production, darter, *Etheostoma inscriptum*, survival, abundance, capture-recapture, tag loss

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RACHEL ALLISON KATZ

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Major Professor: Mary C. Freeman

Committee: Alan P. Covich
                    Todd C. Rasmussen

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TABLE OF CONTENTS

CHAPTER 1

INTRODUCTION

A major concern among aquatic ecologists is the lack of understanding of ecosystem

responses to changes in streamflow (Baron et al. 2002, Arthington et al. 2006), and quantifying

these effects is key to measuring and understanding the status and trends of riverine resources.

Low-streamflows are of interest particularly because they can be caused either by naturally

occurring drought periods or human water withdrawals, and both can have substantial effects on

stream biota. Inconsistencies in the definition of drought are common among various disciplines

(e.g., meteorology, hydrology, agriculture, and biology) and drought often has differing

meanings depending on climatic and ecological regions (Wilhite and Glantz 1987, Humphries

and Baldwin 2003). Aquatic ecologists tend to define drought as a disturbance in which

organization, structure, or function within stream ecosystems is affected by a reduced streamflow

period that is unusual in duration, extent, severity, and intensity (Resh et al. 1988, Pickett et al.

1989, Humphries and Baldwin 2003, Lake 2003).

In freshwater ecosystems, extremely low-flow events are considered a component of the

natural flow regime, which is a major driver of lotic ecosystems and plays a vital role in

structuring aquatic communities (Poff and Ward 1989, Poff et al. 1997). Many aquatic species

are adapted to the variability of streamflow features that occur at seasonal, annual, and decadal

scales (Poff et al. 1997, Ward 1998, Bunn and Arthington 2002, Lytle and Poff 2004). For this

reason, human demand for water resources, which can cause the decline and homogenization of

flows, is considered one of the largest threats to aquatic systems, contributing to the precipitous decline of many animals and plants (Wilcove et al. 1998, Malmqvist and Rundle 2002, Arthington et al. 2006, Poff et al. 2007). Meeting the water needs of both aquatic systems and human populations is a major challenge in flow regulation and management, and is of highest concern when water withdrawals during drought cause dewatering of entire river channels (Baron et al. 2002, Naiman et al. 2002, Richter et al. 2003, Arthington et al. 2006). Due to changing climate and growing needs of human populations, these extreme low-flows may increase in frequency, duration, and severity and are likely to affect aquatic ecosystems and the distribution of species (Rahel and Olden 2008, Palmer et al. 2008).

Linking biotic responses to changes in streamflow can provide information to improve flow management so that ecosystem services and integrity are maintained and protected (Baron et al. 2003, Arthington et al. 2006). The current understanding of flow-ecology linkages focuses on the importance of natural flow variability (Poff et al. 1997, Doyle et al. 2005). Ecologists specifically propose a variety of measures of flow including magnitude, frequency, duration, timing, and rate of change as potentially useful predictors of biological response to flow alteration (Poff et al. 1997, Richter et al. 1996, Olden and Poff 2003). Analyses typically are conducted over coarse time series (i.e., monthly or annually), which may fail to capture the nature of short-term flow variability. A particularly common example of this is hydropeaking, in which rapid changes in discharge (i.e., peak flow occurs within hours or minutes) are not recorded in daily discharge, yet often have adverse effects on macroinvertebrates and fishes (Cushman 1985, Bain et al. 1988, Freeman et al. 2001). Measuring daily, monthly and seasonal changes in flow can be useful in understanding biotic conditions, but water withdrawals occur

over shorter intervals and fine-scale hydrologic assessments (e.g., hourly data) are needed to understand effects of such water use on aquatic biota.

The effects of reduced streamflow on stream ecosystems have been measured at many spatiotemporal scales and response can vary depending on physiographic region and ecological community. Direct effects of reduced flow can include loss of wetted habitat and connectivity, and indirect effects may consist of changes in water quality and food availability (Stanley et al. 1997, Covich et al. 2003, McKay and King 2006, Miller et al. 2007). Reduced flows can affect population densities and community compositions of many aquatic organisms including mussels, shrimps, fishes and macroinvertebrates (Boulton 2003, Covich et al. 2003, Lake 2003, Gagnon et al. 2004). For example, reduced flows can concentrate aquatic biota into refugia where fishes and macroinvertebrates compete for resources, are limited in dispersal, and are exposed to extreme physiochemical conditions that may affect survival (Magoulick and Kobza 2003). Much of our understanding of these effects comes from studies conducted opportunistically during drought periods and have focused on macroinvertebrate and fish assemblages (Humphries and Baldwin 2003, Lake 2003). Response variables in these studies vary depending on their objective, but typically include estimates of species-specific abundance and density, and community-level measures such as species diversity and indices of ecosystem integrity (Freeman and Marcinek 2006, Miller et al. 2007, McKay and King 2006). Using species and community measures can provide useful snapshots of biological assemblages and aid in understanding biological responses to recent hydrologic events (i.e., floods or droughts). However, functional responses, such as production or survival, may be better measures to understand the effects of flow on ecological processes and to predict consequences of streamflow alteration (Brooks et al. 2002).

The studies described in this thesis focus on functional responses of two benthic taxa to low streamflow in bedrock shoals, a specific river habitat that may be particularly affected by water withdrawals. Shoals are distinct geomorphic features in larger streams and are relatively shallow, rocky areas with swift flowing water (Wharton 1978). Shoals typically create distinctive habitats for a diversity of shoal-dependant aquatic organisms, including submerged macrophytes, macroinvertebrates, and fishes (Marcinek et al. 2005). Lowered discharge can reduce fast-flowing, shallow habitats in shoals, exposing substrate to dry conditions, contracting channel widths, and reducing lateral connectivity (Stanley et al. 1997). Due to their high diversity and production, shoals are interesting for studying the effects of streamflow dynamics on aquatic communities.

The following studies were conducted in two middle-order river shoals in the Piedmont of northeastern Georgia during a naturally occurring low streamflow period (i.e., drought of 2007-2008). The Middle Oconee River, near Athens Georgia, has two municipal water withdrawal facilities that extracted a significant portion of the streamflow, drying portions of the streambed during the study period. My research focused on the effects of the extreme low-flows caused by drought and water withdrawals on two benthic organisms: net-spinning caddisflies and a common darter species. In the first study (Chapter 2), I examined the abundance and production of two abundant net-spinning caddisfly genera in relation to low-flow periods. I also evaluated the effect of streamflow-related variables on abundances of larvae using fine-scaled estimates of temporal flow conditions. Results show that hydropsychid abundances and production were an order of magnitude lower than found in a previous study at the same site. Streamflow-related variables were useful in predicting the abundances of hydropsychids. In particular, hourly depth variability had a relatively large, negative effect on larval abundances.

4

However, contrary to expectations, hydropsychids were most abundant in areas on the shoal that were vulnerable to exposure during low-flow periods. The result likely reflected larval requirements for high-velocity habitats, and showed continual larval displacement by frequent low-flow pulses as a probable mechanism underlying depressed hydropsychid productivity.

In the second study (Chapter 3), I evaluated the efficacy of using a robust design capture-recapture approach (Kendall et al. 1997) in a large-river setting to estimate the abundance and survival of Turquoise darters (*Etheostoma inscriptum*). The study was conducted during the late summer/early fall, when low streamflows caused by drought were exacerbated by two water withdrawal facilities upstream of the site. Results show that *E. inscriptum* was abundant in this shoal, with up to 2900 individuals and 2.1 fish per square-meter. Recapture rates were sufficient to permit estimation of survival rates, which was estimated higher for adults than young-of-year fish (individuals hatched from the current year's spawning class). The survival of the young-of-year age group, however, was biased low by growth of individuals into the adult size range, resulting in misclassification on recapture. In addition, survival rates of both age groups were potentially biased low by tag losses. Therefore, a multistate modeling approach was used to estimate these biases and to adjust accordingly. Resulting survival rate estimates provide a basis for comparing with higher flow years and for estimating the effects of low streamflow on this common and abundant shoal fish.

Together, these studies provide further insight into the effects of low streamflows on aquatic organisms, measured as production by a numerically dominant macroinvertebrate and the survival rate of a common darter species. In addition, the fine-scaled hydrologic assessment used to study hydropsychid responses to flow alterations offers a novel method for connecting specific streamflow characteristics and the benthic community. Also, applying the robust design

capture-recapture method allowed for more accurate estimates of fish survival given typical low capture probabilities of many riverine fish species. By understanding the effects of low-flows coupled with human water withdrawals on biological functions, such as production and survival, aquatic ecologists can better predict ecosystem responses to instream flow management decisions and work toward flow management that protects and sustains ecological functions and the persistence of aquatic species.

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CHAPTER 2

PREDICTING THE EFFECTS OF EXTREMELY LOW STREAMFLOW ON THE ABUNDANCE OF NET-SPINNING CADDISFLY LARVAE (HYDROPSYCHIDAE) IN A BEDROCK SHOAL

Introduction

Net-spinning caddisfly larvae (Trichoptera: Hydropsychidae) are a common group of caddisflies in North American waters that regularly occur throughout the eastern United States (Wallace and Merritt, 1980). These filter-feeding aquatic larvae strongly influence multiple aspects of stream ecosystems. In particular, hydropsychid larvae are important because they process nutrients, impact macroinvertebrate community structure, and contribute substantially to secondary production (Wallace et al. 1977, Wallace and Merritt 1980, Wallace and Webster 1996, Huryn and Wallace, 2000).

Often, macroinvertebrate assemblages are dominated by caddisfly larvae, and hydropsychids specifically can contribute more than half of total benthic secondary production (Nelson and Scott 1962, Grubaugh and Wallace 1995). Larvae can also affect community assemblage structure by competing for space with conspecifics and by facilitating the recruitment of other taxa (mayflies, case building caddisflies, and midge flies) through the construction of silk nets and retreats, which provide refuge from high water velocities (Diamond 1986, Cardinale et al. 2001, Cardinale et al. 2004, Nakano et al. 2005). In addition, species richness of hydropsychid larvae can have significant effects on the rate of organic matter

processing and gross primary production (Cardinale and Palmer 2002). Given the potential influence of net-spinning caddisfly larvae on stream production and community structure, evaluating effects of environmental change on hydropsychids will improve the ability to understand food web, trophic dynamics, and functional processes in stream ecosystems.

Changes in local environmental factors, such as water velocity, food availability and macrophyte abundance, can affect the distribution, abundance, and production of net-spinning caddisfly larvae (Mackay and Wiggins 1979, Cudney and Wallace 1980). In particular, water velocity is a major driver of hydropsychid distribution because larvae prefer areas where high filtering rates can be sustained (Edington 1968, Cudney and Wallace 1980, Georgian and Thorp 1992). In fact, larvae will frequently expend energy and risk morality to move to and to compete for areas with more favorable velocities (Hildrew and Edington 1979, Matczak and Mackay 1990, Englund 1993).

Aquatic ecologists consider streamflow as a master driver of lotic ecosystems, influencing processes from watershed to microhabitat scales (Townsend 1989, Poff and Ward 1990, Poff et al. 1997, Montgomery 1999). Changes in streamflow at various scales can impact local biota, as well as ecosystem structure and function (Townsend 1989, Poff and Ward 1989, Allan 1995, Hart and Finelli 1999, Doyle et al. 2005). For example, variation in discharge influences organic matter delivery and water chemistry (Doyle et al. 2005), which are both important for macroinvertebrate growth and survival (Nelson and Scott 1962). In contrast, local hydraulics can affect biotic interactions and behavior (e.g., drift) of macroinvertebrates, including hydropsychid larvae (Mackay 1992, James et al. 2008). In order to predict aquatic ecosystem responses to changes in streamflow, ecologists have suggested understanding flow-ecology linkages by relating features, such as flow magnitude, frequency, duration, timing, and

rate of change, to specific biotic responses (Hart and Finelli 1999, Olden and Poff 2003, Arthington et al. 2006).

Low-streamflow periods are of particular interest because they are caused by both naturally occurring droughts and human water withdrawals, with the coupling of these events having distinct effects on macroinvertebrate communities. Boulton (2003) suggests that critical ecological thresholds may exist during low-flow periods, when streamflows are reduced to levels that cause habitats to become dewatered or isolated, resulting in major changes in the benthic community. Although many macroinvertebrate species have evolved specific functional-traits to cope with reduced streamflow conditions, changes in local microhabitat hydraulics can influence community structure and function (Hynes 1970, Resh 1979, Merigoux and Doledec 2004, Brooks et al. 2005, Churchel and Batzer 2006, Poff et al. 2006).

Studies that have focused on the impact of water diversions have typically been in smaller-order streams and have documented changes in macroinvertebrates after months or years of reduced streamflow. Results typically include significant long-term reductions in taxonomic richness and densities, and short-term increases in densities (Miller and Golladay 1996, Rader and Belish 1999, McIntosh et al. 2002, McIntosh et al. 2003, Dewson et al. 2007). However, water withdrawals can occur in larger-order streams and also over short-intervals (e.g., hours or days), which can result in pulsed or extended low-flow periods that periodically dewater the streambed (Stanley et al. 1997, Extence et al. 1999, Gasith and Resh 1999, Lake 2003).

The objective of this study was to evaluate the influence of extremely low streamflows, caused by drought and water withdrawals, on hydropsychid caddisfly larvae. Two previous studies were conducted near the study site in the Middle Oconee River, GA, one in the late 1950s by Nelson and Scott (1962) and the other in the early 1990s by Grubaugh and Wallace (1995).

Since these two studies, a major water diversion was constructed upstream of the site (Fig 2.1), allowing the opportunity to study effects of low-flow events caused or exacerbated by water withdrawals. The goals of this study were to use a fine-scale temporal and spatial approach to quantify and compare hydropsychid abundances and production with estimates from the 1990s study, and to evaluate abundances in relation to the frequency and duration of near-dewatering (i.e., water depth less than 5 cm) periods caused by naturally low streamflow coupled with water withdrawals. I predicted that infrequent low-flow events would increase hydropsychid larvae abundances by removing macroinvertebrates that competed for space and algae; and that frequent low-flow events would decrease larvae abundances by sustaining unfavorable habitats with low velocities.

Methods

Study Site

The study has been conducted in a reach of the Middle Oconee River near Athens, GA, which drains approximately 1000 km^2 of the Piedmont physiographic province in the Upper Oconee watershed (Altamaha River Basin). The Middle Oconee River is a sixth-order stream at the site, which is adjacent to Athens-Clarke County's Ben Burton Park and upstream of the confluence of the Middle Oconee and North Oconee Rivers (Fig 2.1). The shoal is a granite bedrock outcrop dominated by bedrock and large boulders with patches of sand, gravel, and cobble. The total length of the shoal is approximately 500 m with an average width of 80 m, and contains irregular topography with higher elevations in the center and lower elevations along channel edges. The shoal supports a diverse macroinvertebrate assemblage that is associated with the presence of a submerged macrophyte, *Podostemum ceratophyllum,* which has been

historically documented as widespread at the site, forming dense lush mats during the summer and persisting throughout the winter in a dormant stage (Nelson and Scott 1962, Grubaugh and Wallace 1995). Recent land cover (derived from 2005 National Land Cover Database) in the Upper Oconee watershed is mostly forest (55%), with some pasture and row crop (21%), low and high impact urban development (10%), and clear cut land (7%) (NARSAL 2009).

Extremely low streamflows occurred in the study region from 2007-2008. Two U. S. Geological Survey (USGS) stream gages were located near the study site, one approximately 30 km upstream (#02217475) and the other approximately 2 km downstream (#02217500; Fig 2.1). Streamflow data from the downstream gage were used to assess the extent of streamflow decline during the study period, compared to flows recorded over the past 70-years (Fig 2.2). As a result of reduced rainfall, which began in late 2006 and continued through 2008, the annual discharge in the Middle Oconee River near Athens, GA (2007-2008) was 200 cfs, 60 percent below the period of record average annual discharge (USGS 2009). Although both study years experienced drought conditions, streamflow in 2008 was lower than 2007 by 30 percent. In addition, streamflow was differentially reduced across months with an 85% reduction of summer-fall flows compared to a 60% reduction in winter-spring flows when compared to period of record flows.

Water was extracted frequently from the river during 2007 and 2008 by an off-channel pump-storage reservoir, located 13.5 km upstream of the study site and between the USGS gages. The facility extracted water from the main river channel and transported it to Bear Creek reservoir, a 204-ha reservoir that supplied water to four surrounding counties and was constructed by impounding a tributary stream. Although the seven-day low, ten-year recurrence streamflow level (7Q10) is 45 cfs for this locality, streamflow often reached lower levels during

the study period due to water withdrawals. The Upper Oconee Basin Authority is permitted to withdrawal 60 million gallons per day (MGD) (90 cfs) from the river under normal flow conditions, with the stipulation that under drought conditions the withdrawal limit would be reduced to 15 MGD (GAEPD Permit #078-0304-05). However, with water in short supply during the prolonged drought, the withdrawal limit was replaced with the higher, normal limit of 60 MGD (*pers. com.*, Jeff Williams: Bear Creek Reservoir 2007). On average, about 60 cfs (40 MGD) were extracted when the pumps were in operation. The coupling of drought and withdrawals resulted in frequent extremely low streamflows (less than 45 cfs) in late summer and fall seasons (Fig 2.3). Streamflows during the study were not influenced by a low-head hydropower dam located 12.8 km upstream of the site because the hydropower facility was non-operational during 2007 and 2008 (*pers. com.*, Robert Davis: Fall Line Hydro 2008).

Sampling and processing methods

Benthic samples were collected monthly from November 15, 2007 to October 15, 2008 from a 104 meter long bank-to-bank transect. Due to the naturally variable topography of the shoal, I divided the transect into five sections based on differences in bed elevation in order to represent areas that may have been differentially affected by reduced flows (Fig 2.4). For example, the middle section appeared more susceptible to dewatering at low flow compared to other sections because it was higher in elevation and diverted water to the channel edges (Fig 2.5). As a result of topographical variation, I sampled areas that experienced a wide range of flows over the study period, from areas that periodically had no flow (i.e., drying) to areas that were continuously covered by high water levels.

Each month, I used stratified random sampling to select two locations within each of the five sections (n=10 samples). I sampled the benthos with a 103.87 cm^2 t-sampler fitted with a 243 μm mesh sleeve, which was comparable to the sampler used in the previous study by Grubaugh and Wallace (1995). The t-sampler was pressed firmly to the substrate and a metal putty knife was used to dislodge any matter attached to the substrate into the mesh sleeve. The sleeve was then inverted and scraped to transfer materials into individual plastic bags, which were stored on ice and transported to the laboratory. For each sampled location, I measured depth and velocity (0.6 water depth) with a wading rod and Marsh-McBirney Flo-Mate^{TM} Model # 2000, and visually assessed substrate as either fine (sand, cobble, gravel) or coarse (boulder and bedrock). Then, I surveyed the elevation (relative to a benchmark) and distance along the transect of the sampled location with a Leica TC600 Total Station^{TM}. Distance along the transect was surveyed because the meter intervals marked along the transect line were slightly longer than actual meters due to the transect line stretching across the channel. If a randomly selected location was completely dry or in a sandy pool (e.g., between sections 1 and 2), I chose a replacement random location. The shoal was unwadeable during most of January because of high flows, which also precluded sampling section 1 in February, March, and April so that eight samples were collected during these months.

Samples were refrigerated for no more than 72 hours before I sorted the organic matter using dissecting microscopes (8-50 x magnification). First, detritus, algae, and macroinvertebrates were separated from *P. ceratophyllum*. Then, *P.ceratophyllum* was pre-weighed and dried at 60°C for 5-7 days, weighed, ashed in a muffle furnace at 500°C for 5 hours, and allowed to cool for 24 hours in a desiccator (see Pahl 2009). Ash free dry mass (g AFDM) was then calculated by subtracting the ashed mass from the dried mass. Remaining organic

matter was stained with Rose Bengal to facilitate faster removal of macroinvertebrates, which were examined under a microscope (50 x) and placed in 10% formalin. Hydropsychidae caddisfly larvae were identified as either *Hydropsyche spp.* or *Cheumatopsyche spp.* (Merritt and Cummings 1980, Mackay 1978). A third genus, *Ceratopsyche spp.*, was also identified, but was grouped with *Hydropsyche spp.* for analysis to facilitate comparison with previous studies. Larval head capsule widths were measured with an ocular micrometer and individuals were categorized into instars (i.e., one of the five larval stages between molts) by plotting the size frequency distribution for all head capsule widths and identifying the size range of each instar (Mackay, 1978). The abundances per square-meter of each instar were used as independent response variables for analysis.

I was also interested in comparing hydropsychid abundance and secondary production to a previous study at the study site. To estimate average abundances on each date, I weighted abundances collected from each section by the proportional section length. I used average larval weights (mg AFDM) for instars of *Hydropsyche spp.* and *Cheumatopsyche spp.* sampled in a nearby GA Piedmont stream (Freeman and Wallace 1984). Cohort production intervals (CPI's) were also taken from Freeman and Wallace (1984) for the genus *Hydropsyche* (124 days). However, the CPI reported by Freeman and Wallace for *Cheumatopsyche spp.* was based on the presence of instars only from June to September, whereas during the present study instars were present year-round with similar cohort development compared to *Hydropsyche spp*. Therefore, a CPI of 124 days was also used for this genus. CPI's were used with the size-frequency method to estimate production (Hamilton and Hynes 1969, Benke 1979). Grubaugh and Wallace (1995) also estimated production using this method, which is commonly applied when individual

cohorts are difficult to distinguish and populations develop asynchronously (Wohl et al. 1995,

Huryn and Wallace 2000, Alexander and Smock 2005).

Streamflow survey methods

I evaluated the effects of five streamflow-related parameters on the abundance of

hydropsychid caddisflies by using a fine-scaled spatiotemporal approach. Each streamflow

variable was sample-specific, which enabled estimation of streamflow characteristics at the

microhabitat level. Also, streamflow was recorded at an hourly time-step to ensure detection of

short-term water withdrawal events. The streamflow-related variables were: mean depth,

variability of streamflow depths, an interaction between depth and variability, frequency of low-

flow events, and duration of low-flow events. All variables were based on estimated water

depths for the 30 days prior to sampling at each sample location and were quantified using: water

depth recorded at the study shoal, surveyed water levels within sections along the transect, and

USGS gage discharge data.

Water depths at the study shoal were recorded by pressure transducers in two locations

along the transect. In December 2007, a pressure transducer (Onset HOBO model # U20-001-04,

Sensor 1) was secured to a large stable boulder in a deep area near section 1. A second

transducer (Sensor 2) was secured to a boulder in April 2008 and placed in the middle of the

shoal to assess possible effects of topography on streamflow. Both transducers measured total

pressure (water + air) every hour; data were adjusted using a third transducer that recorded air

pressure near the edge of the channel. Water pressure was then converted to water depth through

the use of prior lab calibration and Onset HOBOware Pro^{TM} software. Sensor 1 proved adequate

and more sensitive to changes in depth along the entire transect than Sensor 2, and was used to track hourly changes in water depths from December 2007 through October 2008.

Next, water levels were measured at two-meter interval segments across the sampling transect during a range of discharges (approximately 4.2 to 202 cfs) to account for fine-scale differences in water-surface elevations due to transect topography. Water-surface and bed elevations were surveyed with the Total Station relative to a fixed point on the bank. Instantaneous water depths were calculated by subtracting the bed elevation from the water elevation. Linear regressions were used to correlate water depth at each two-meter segment to Sensor 1 water depth at the time of survey, and this linear relationship was then used to estimate water depth at hourly intervals for each two-meter segment using only depths recorded by the sensor. To estimate depth histories prior to sensor installation, I correlated hourly gage data from the USGS gage at Athens, GA (#02217500; downloaded monthly from http://www.waterdata.usgs. gov) with recorded sensor depths to determine a relationship between discharge and sensor depth at the shoal.

Sampled locations were assigned to the nearest two-meter segment and samples collected within a particular segment were assumed to experience a similar pattern of depths. The elevation of sampled locations was either lower or higher than the bed elevation used to estimate depth histories; therefore, depths were adjusted accordingly by adding or subtracting the difference between the elevation used to estimate depth history of the segment and the elevation of the sampled location.

The five streamflow-related parameters were then calculated from the 30-day depth histories at each sample location. Three parameters represented overall streamflow conditions and two parameters represented specific low-flow events, which were defined as occurrence of

19

water depths less than five centimeters. Mean depth was calculated as the average of hourly depths, and variability of streamflow was calculated as the standard deviation of hourly depths, for each sampled location 30 days prior to sampling. The interaction term between variability and depth was included to represent the hypothesis that variability has a greater effect on benthic biota when average depths are lower; to test this hypothesis the interaction term was included with streamflow variability in regression models. Specific effects of low streamflows were represented by the frequency and duration of low-flow events. Frequency was defined as the total number of hours a sampled location experienced flow less than five centimeters in depth. Duration was defined as the number of hours of the longest single continuous low-flow event. Frequency and duration occurrences both displayed skewed distributions, with few occurrences between low and high numbers of hours. Therefore, both parameters were divided into three categories: none (0), few (< 200), or many (> 200) hours.

Data Analysis

I used an information theoretic approach with model selection (Burnham and Anderson, 2002) to explore the relative importance of streamflow-related parameters, and model averaging to estimate effect-size of each streamflow variable on the abundances of net-spinning caddisfly larvae. Abundances per sample (n=92 for each instar) were not normally distributed and were ln(x+1) transformed to better meet the assumptions of normality. Generalized linear models were used for analysis because explanatory variables, abiotic and biotic, were hypothesized to have additive effects on the dependent variable, the abundance of caddisflies. I modeled abundance of each instar (I-V) separately for *Hydropsyche spp.* and *Cheumatopsyche spp.* to detect differences in larval responses.

20

In order to promote model parsimony by avoiding over-parameterization, I first evaluated

the support for habitat covariates before assessing streamflow variables. I included four abiotic

factors and one biotic factor, each hypothesized *a priori* to be biologically important in caddisfly

larval abundances: day of the year (and its squared value), substrate (i.e., fine or coarse), water

velocity measured at the sample location when the sample was taken, biomass of

P.ceratophyllum, and an interaction between substrate and *P.ceratophyllum* (Table 2.1). With

these five covariates, I created a set of 32 competing models for analysis (Appendix A: Table 1)

where all explanatory variables were continuous except for substrate, which was coded as a

binary term (0 = sand, cobble, gravel; 1 = bedrock, boulder). Each model also included an

intercept and variance term, resulting in a range of three to eight parameters (K) within any given

model. I used program SAS v 9.1 (SAS Institute, Inc., Cary, NC, USA) and generalized linear

regression modeling to estimate the model variance (e.g., residual sums of squares) for each

candidate model. Then, I used Akaike's Information Criterion corrected for small sample size

(AICc), delta AICc, ΔAICc (i.e., model AICc compared to the best-supported model in set), and

AICc weights (w_i) to evaluate the support of each model (Burnham and Anderson 2002). I chose

the best-supported models (ΔAICc <2) as a confidence model set (Burnham and Anderson 2002)

for each instar before assessing and adding the effect of streamflow-related variables (Appendix

A: Table 2).

Using confidence sets of covariate models, support for the five streamflow-related

parameters was then evaluated. Each variable represented an *a priori* biologically reasonable

hypothesis about hydropsychid abundance responses to different streamflow conditions (Table

2.2). I was specifically interested in comparing the support for and effects of each parameter

compared with other parameters and thus did not combine any of the streamflow parameters in

any single model, with the exception of the interaction between depth-variability and variability (Table 2.2). I created a set of competing streamflow models, which included every covariate model in the confidence set with each of the five streamflow-related variables added one at a time, along with the covariate only models. The total number of competing models (which depended on the number of well-supported habitat covariate models) ranged from six to thirty-six for *Hydropsyche spp.* and twenty-four to fifty-four for *Cheumatopsyche spp.* (Appendix A: Table 3-4).

Linear regression modeling for a given data set can result in a large number of similarly-supported models and designating the *single* best model is often an inadequate measure of the likely importance of a particular variable. Therefore, the relative importance of each streamflow parameter was estimated by using the summed model weights (Σwi) across all candidate models with a particular streamflow variable (Burnham and Anderson 2002). Model-averaging was then used to estimate the effect size of streamflow variables on log-transformed values of hydropsychid abundances and an unconditional variance estimator was used to calculate and determine the error of the estimated effect (Burnham and Anderson 2002).

Results

I collected 104-samples within the study shoal in the Middle Oconee River; 92 of these samples were used in streamflow analysis and 12 samples were discarded from linear-regression analysis because velocity was not recorded for ten November samples and two August samples. Despite lack of velocities, all samples were used in abundance, biomass, and production estimations. Samples were primarily collected on boulders and bedrock (80%), and even though sand was often observed as a fine layer on most substrate types, no samples were collected from

sandy substrates. Water velocities measured at sampled locations on the sampling day were relatively low (i.e., for a swift water habitat) with 77% of measured velocities less than 50 cm sec^{-1} (range -6 to 117 cm sec^{-1}; average 30 cm sec^{-1}). Only five samples were collected in "high" velocity habitats (> 75 cm sec^{-1}; Table 2.3).

Streamflow Observations

Annual average discharge during the study period was 150 cfs, 70% below the long-term annual average of 500 cfs (USGS 2009). Average daily flows ranged from 17 cfs to 1040 cfs, and 15 min-interval data documented minimum discharge as 8 cfs and maximum discharge as 1380 cfs (Fig 2.3). Streamflow (between storm events) was generally higher (>100 cfs) in late winter and spring, and decreased in the summer and fall. The lowest average monthly discharges occurred in July (44 cfs) and September (61 cfs). Over the study period, low streamflow occurred frequently, with 1151 hours (totaling to 63 days) of discharge less than the seven-day minimum low-flow standard (7Q10) of 45 cfs. However, low-flow periods were not necessarily continuous or consecutive in occurrence. For example, withdrawals reduced streamflow to levels less 45 cfs on at least 29 different days, mostly occurring in the late summer/fall of 2008 (Fig 2.3).

Random sample collection resulted in samples representing a broad range of flow histories over the 30 days prior to sampling. Mean depths over the prior 30-day periods ranged from -6.7 to 53.7 cm (average 19.7 cm), with the lowest individual values occurring in the late fall. Negative depths were recorded when the estimated water level at a sample location was lower than the bed elevation (dry), and were retained as representing the vertical distance an organism would need to travel to remain below the water level. The standard deviation of depths

ranged from 1.0 to 12.1 cm (average 4.1 cm) and was highest in September. Extremely low

streamflows that likely exposed the streambed occurred in 28% of the samples collected (n=26),

mostly occurring in samples collected in the fall. The greatest frequency (total number of hours)

that one sample experienced streamflow depths less than 5 cm was 687, and the longest

continuous low-flow event lasted a maximum of 553 hrs (within a 30 day period; Table 2.3).

Trends in hydropsychid abundance

Hydropsychids dominated the Trichopteran assemblage, composing 80% of the total

abundance of caddisflies collected during the study period. All instars were collected within

both genera, with a total of 1363 *Hydropsyche spp.* and 2595 *Cheumatopsyche spp.* individuals.

Overall, a greater abundance of smaller larvae (first, second, and third instars) compared to

larger instars were collected of both genera; however, larger larvae (fourth and fifth instars)

contributed the most biomass to production estimates because they composed 87% of the

biomass with only 34% of the abundance.

Hydropsyche spp. and *Cheumatopsyche spp.* standing stock densities and biomasses were

reduced compared to values reported by Grubaugh and Wallace (1995). Standing stock averaged

1455 ± 526 m^{-2} (mean $\pm$ SE) and 3094 ± 823 m^{-2} for *Hydropsyche spp.* and *Cheumatopsyche spp.*

respectively, an 85% and 23% decline compared with 1991-1992; similar declines occurred in

the average biomasses of both genera (Table 2.4). Annual secondary production of *Hydropsyche*

spp. was almost double that of *Cheumatopsyche spp.* (10.7 g AFMD m^{-2} yr^{-1} and 6.3 g AFDM

m^{-2} yr^{-1}, respectively), and compared with the 1991-1992 study was reduced by 88% for

Hydropsyche spp. and 40% for *Cheumatopsyche spp.* (Table 2.4).

Relative abundances of each instar during each month showed that both genera were multivoltine, but distinct summer cohorts were difficult to discern. One winter generation was observed with one or two summer generations (Fig 2.6). Despite differences among larval instar abundances throughout the year, the total abundance of *Hydropsyche spp.* and *Cheumatopsyche spp.* per sample were positively correlated (r = 0.49 and 0.55, respectively) with the sample-specific biomass of *P.ceratophyllum*, which was highest in April and June and also was an order of magnitude lower than the previous study (annual average of 61 g AFDM m^{-2} compared to 523 g AFDM m^{-2}; Fig 2.7).

Estimated effects of streamflow on hydropsychid abundance

The confidence sets of covariate models for all instars (Table 2.5) included many alternative combinations of covariate variables, which indicated that most habitat covariates had some support as predictors for the abundances of *Hydropsyche spp.* and *Cheumatopsyche spp.* Time of year, velocity, and biomass of *P.ceratophyllum* were the most common predictors for both genera, while the interaction of substrate and *P.ceratophyllum* was more predictive for *Cheumatopsyche spp*. Substrate was the least predictive covariate for both genera (Table 2.6). Specifically, velocity and the biomass of *P.ceratophyllum* were consistently positively related to the abundance of all instars for both genera, with velocity (cm/sec) having a larger effect compared to 1 g AFDM of *P.ceratophyllum* (Table 2.6). As expected (Table 2.1), larval abundances generally increased with calendar day and decreased slightly later in the year; however, overall effect of time of year on abundance was small (Table 2.6). Substrate type was included in most of the confidence model sets, however showed opposite effects between the two genera, with *Hydropsyche spp.* instars generally positively related to boulder or bedrock, and

larger instars of *Cheumatopsyche spp.* positively related to gravel or cobble substrate (Table 2.6). Contrary to my hypothesis (Table 2.1), the interactive effect of *P.ceratophyllum* and substrate showed that the effect of the submerged macrophyte on larval abundance increased on boulder or bedrock, as opposed to cobble or gravel dominated habitats (Table 2.6).

By including a variable related to streamflow conditions over the 30 days prior to sample collection, models were generally more supported for most instars of both genera (Fig 2.8). Late instars in particular were better predicted with streamflow variables, and third-instar *Hydropsyche spp.* models were least supported by the addition of any streamflow-related parameter compared to habitat covariate only models (Fig 2.8). Effects of streamflow parameters varied in size and direction, however overall streamflow conditions (i.e., mean depth, variability of depths, and interaction between depth and variability) were generally predicted to have larger effects on the abundance of hydropsychids compared with specific low-flow event parameters (frequency and duration of low-flow; Table 2.7, Fig 2.9). Specifically, increasing variability of depths was consistently estimated to decrease larval abundances (Table 2.7) and was a relatively important variable for most *Cheumatopsyche spp.* instars and *Hydropsyche spp.* IV instars (Fig 2.8). Mean depth also had a consistent effect on all instars of both genera (less than variability) but was opposite of expected. Increasing the mean depth was estimated to decrease larval abundance (Table 2.7), which was contrary to expected because shallow areas vulnerable to drying were expected to be unfavorable habitat (Table 2.1). Also, there was little evidence that the effect of variability was reduced at greater depths. Only the *Cheumatopsyche spp*. fifth-instar had a positive effect of the depth*variability interaction term (Table 2.7).

The estimated effects of specific low streamflow events were relatively small and positive compared to effects of overall streamflow conditions, which was contrary to hypotheses

(Table 2.1). Frequency or duration of low-flow events was well-supported as a predictor of abundance for three instars: second and fifth-instar *Hydropsyche spp.* and fourth-instar *Cheumatopsyche spp.* when compared to other streamflow variables (Fig 2.8). For almost all instars, larval abundances were estimated to *increase* with the occurrence of few (< 200 hrs) low-flow events compared to none, and were also estimated to increase with a low duration (< 200 hrs of continuous low-flow; Fig 2.9). Moreover, with the exception of fifth-instar *Cheumatopsyche spp.* and smaller instars of *Hydropsyche spp.*, larvae were also estimated to increase with *high* frequency and duration of low streamflow events (Fig 2.9).

Discussion

Overall, the results of this study showed that hydropsychid larvae were influenced by streamflow at small spatiotemporal scales, and that abundances and production of two dominant taxa during extreme low streamflows were up to an order of magnitude lower compared 1991-1992. Data generally supported a hypothesis that larvae occur most abundantly in shallow areas with swift flow as well as in areas with the aquatic macrophyte, *P.ceratophyllum*. In contrast to *a priori* hypotheses, results generally did not support a direct negative effect of frequent or prolonged low-flow events on larval abundance. However, results showed the strongest streamflow-related variable was temporal flow variability (measured as standard deviation of hourly depths), which was expected to reduce habitat suitability for hydropsychids.

Hydropsychid larval decline

Secondary production estimates of both genera of hydropsychids were lower than previously reported values at the study site. Nelson and Scott (1962) did not report production or

27

abundances separately for hydropsychids, but found that filter-feeding taxa contributed the bulk of total production, with hydropsychids composing a majority of macroinvertebrates. Grubaugh and Wallace (1995) found hydropsychid larvae in particular composed 93% of caddisfly larvae biomass and contributed 57% to total secondary production. Decline of sensitive macroinvertebrate taxa has commonly been attributed to changes in watershed land use. Land use, however, did not change substantially in the Upper Oconee Watershed between the 1990s and early 2000s (NARSAL 2009) and Grubaugh and Wallace found no detectable effect on macroinvertebrate assemblage despite changes in land use over the prior 30 years (Grubaugh and Wallace 1995); therefore, land use change was likely not a major cause of the observed decline between the 1992 study and the present study.

The observed decline could be attributed to a variety of factors, including changes in water chemistry or overall lowered streamflow from drought (Wohl et al. 1995, Feminella 1996, Allan 2004). Alternatively, small scale changes in available habitat could also cause declines. Numerous studies have documented the decline of macroinvertebrate taxa when streambeds are dewatered, possibly because certain taxa increase drifting behavior in response to changing streamflows (Brittain and Eikeland 1988, Poff and Ward 1991, Mackay 1992, James et al. 2008). Drift was not specifically measured in this study, but could be the mechanism for decline, given that habitats that had highest densities of hydropsychids were the most vulnerable to disturbance from flow fluctuations.

Reduced quality of preferred habitat

Hydropsychid larvae differentially occupied shallow water habitats throughout the year as well as areas that contained the submerged macrophyte, *Podostemum ceratophyllum.* These

observations were consistent with other studies that demonstrate hydropsychid occurrence in shallow habitats, which are associated with high velocities and often occur at the tops of boulders and at outflows of pools into riffles (Edington 1968, Georgian and Thorp 1992). Small differences in water velocities can have large effects on the production of hydropsychids. In the Savannah River, another larger-order river in GA, production of *Hydropsyche spp.* and *Cheumatopsyche spp.* were reported to be lower in slow velocity (25-50cm/sec) habitats compared to medium and high velocity habitats (50-75cm/sec; Cudney and Wallace 1980). Considering that drought and water withdrawals reduced streamflow more than 60%, it is not surprising that slow velocities were commonly observed in the present study, with 50% of the samples collected having velocities less than 25 cm/sec and only 5 samples having velocities greater than 75 cm/sec. The impact of overall slower velocities from reduced streamflow could influence growth and production of filter-feeding macroinvertebrates by reducing the delivery of particulate organic matter and drifting prey.

Another reason for larval decline could be associated with the reduction in *P.ceratophyllum*. Consistent with observations in 2007-2008, macroinvertebrate abundances are generally correlated with the standing crop of *P.ceratophyllum*, with collector-filterers having the highest correlative relation (Grubaugh and Wallace 1995, Hutchens et al. 2004). During low streamflows, *P.ceratophyllum* has been observed to dry out and break off the substrate (Nelson and Scott 1962) and empirical evidence showed that substrate exposure decreases *P.ceratophyllum* biomass (Pahl 2009). The overall effect of *P.ceratophyllum* on hydropsychid abundances in the current study may be smaller compared to the 1991-1992 study because of the per gram of biomass effect and large reduction of the submerged macrophyte. The effect of *P.ceratophyllum* on larval abundance may have been greater if the flow regime allowed the

development of lush mats during summer months, as previously documented (Grubaugh and Wallace 1995).

Effects of extremely low streamflows caused by water withdrawals

Contrary to hypotheses, hydropsychids were more abundant in areas that were more vulnerable to low streamflow and dewatering from withdrawals. Results supported the notion that some dewatering may benefit hydropsychid larvae because these locations were periodically cleaned of potential competitors and also had consistently swifter velocities than deeper areas when discharge was low. Increased abundances in frequently shallow or exposed habitats can be explained by rapid larval movements into these higher velocity areas to filter-feed (Edington 1968, Lancaster and Hildrew 1993, Lancaster 1999) after areas have become re-wetted. Within hours or minutes, individuals can establish new net-spinning sites in previously occupied or newly accessible habitats (Mackay 1992, Englund 1993, Winterbottom et al. 1997).

In addition, increases in macroinvertebrate drift has been commonly observed as a result of reduced streamflow in lower-order streams (Brittain and Eikeland 1988, Poff and Ward 1991, Mackay 1992, James et al. 2009), which supports the possibility that the observed decline in larval abundance may be a consequence of increases in drifting larvae during naturally reduced flows as well as withdrawal events. Thus, retreat into preferred habitat patches during frequent low-flow events may have resulted in lower larval survival or persistence in the study shoal compared to previous studies.

The spatial arrangement of suitable habitat patches and their connectivity within river reaches at the scale of macroinvertebrate movements may also affect the ability for hydropsychids to recolonize repeatedly disturbed habitats (Palmer et al. 2000). Typically,

studies have documented a decrease in macroinvertebrate abundance in response to reduced streamflow of over the long-term and an increase in macroinvertebrates within refugia over the short–term (Cooling and Boulton 1993, Lancaster and Hildrew 1993, Lancaster 2000). Rader and Belish (1999) also reported that abundances and densities of macroinvertebrates declined when streamflow was frequently diverted over several months, but in contrast, that macroinvertebrates were resilient to infrequent diversions that generally maintained natural flow regime features downstream.

Conclusions

Assessing short-term changes in streamflow was useful in describing the factors influencing the abundance of caddisfly larvae in a sixth-order stream shoal. The coupling of drought and water withdrawals provided a unique opportunity to study the effects of patchy streambed dewatering within a previously productive shoal environment. Efforts to understand impacts of drought and altered streamflow have primarily focused on long-term changes in streamflow variability at seasonal, annual, and interannual time-scales (Richter et al. 1996, Lake 2003) and this study contributed evidence of the effects of low-flows over shorter-time periods (e.g., daily and monthly).

Net-spinning caddisflies are known to respond to changes in streamflow and velocities, but studies have not typically addressed the effects of dewatering in a larger-river setting. This study showed the importance and effects of flow fluctuations and extremely low-streamflows on observed caddisfly abundances. Hydropsychids did not persist during low-flow periods by remaining in deeper water sites in the shoal, but rather occurred in areas most vulnerable to disturbance from fluctuating flows. Measuring hourly depths and the degree (frequency or

duration) to which habitats were vulnerable to dewatering was essential to best-predict larval

abundances. This analysis has shown the influence of flow variability at the particular sites

where currents are most swift on reducing hydropsychid densities and production.

Small scale spatial differences in hydraulics (depth and velocity) within shoals over

short-time periods could drive the secondary production of dominant taxa. Rivers with regulated

streamflow provide opportunities to evaluate community responses to various flow regimes, or

the maintenance of particular flow features. As shown here, elucidating the mechanisms driving

biotic responses to flow conditions, such as drought exacerbated by water withdrawals, may

require investigation at small spatial and temporal scales.

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Table 2.1. Covariate model parameters and associated hypothesis for the effect of each on the abundance of hydropsychid larvae.

Covariates			
Parameter	**Code**	**Description**	**Biological Hypothesis**
Time of Year	Day	Calendar day	Abundance increases with day of year into the summer, when multiple cohorts overlap
	Day^2	Calendar day-squared	Abundance decreases in the late summer and into the autumn
Substrate	Sub	0 (unstable) = Gravel, Cobble, Sand 1 (stable) = Bedrock and Boulder	Abundance is higher when substrate is large and stable
Velocity	Vel	Velocity at sample point (m sec^{-1})	Abundance increases with increasing velocity
P. ceratophyllum	Pod	Biomass of *P.ceratophyllum* (g AFDM m^{-2})	Abundance increases with increasing *P.ceratophyllum* biomass
Interaction between substrate and *P.ceratopyllum*	Sub* Pod	Interaction term between substrate and *P.ceratophyllum* biomass	The effect of substrate (unstable) is less if biomass of *P.ceratophyllum* is high

Table 2.2. Streamflow-related model parameters and associated hypothesis for the effect of each on the abundance of hydropsychid larvae. Low-flow event refers to the occurrence of water depths less than 5 cm at the sample location 30 days prior to sampling and hypotheses refer to expected changes in larval abundances compared to the absence of low-flow events.

Streamflow			
Parameter		**Description**	**Biological Hypothesis**
Low-Flow Event			
Frequency	Low	Low frequency of low-flow events (< 200 hrs of depth < 5 cm)	Infrequent low-flow pulses have small effects on abundance and may increase abundance by removing competitors, filamentous algae accumulation
	High	High Frequency of low-flow events (> 200 hrs of depth < 5 cm)	Frequent low-flows decrease abundance due to unsuitable habitat from desiccation and low velocities (food availability)
Duration	Low	Longest continuous low-flow event is less than 200 hrs	Short duration of low-flows increases abundance by removing competitors, etc.
	High	Longest continuous low-flow event is greater than 200 hrs	Long duration of low-flows decreases abundance due to unsuitable habitat from drying and low food availability
Overall Flow			
Mean Depth	Depth	Mean depth, as the average of hourly depths	Abundances increase with mean depth because habitat is less disturbed by flow fluctuations
Variability	Var	Variability of depth, as the standard deviation of hourly depths	Abundances decrease with flow variability because changes in flow induce drifting and movement into other habitats
Mean Depth* Variability	Depth* Var	Interaction between depth and variability	Abundances decrease with variability, but effect is greater at shallower depths

42

Table 2.3. Summarized streamflow-related parameter values for samples collected each month. Average values across all samples (N) per date include: velocity at the sample location on the sampling day (cm/sec), mean depth (cm) and variability of depths (standard deviation of depths, cm) at sample locations over 30 days prior to sampling. The occurrence of low-flow events are represented by the number of samples that experienced low (<200 hrs) and high (>200 hrs) frequency and duration events per month, followed by the range of actual hours within month and group. A dash (-) represents no samples in that category.

						Streamflow-related Parameter Values		
Date	N	Velocity (cm/sec)	Mean Depth (cm)	Variability (SD of depths, cm)	Low Frequency	High Frequency	Low Duration	High Duration
12/13/07	10	57.5 (41.5-85.3)	19.8 (8.0-51.8)	2.2 (1.0-3.3)	1 (78)	-	1 (15)	-
2/11/08	8	43.1 (23.0-75.0)	21.8 (13.0-35.8)	4.1 (2.1-7.4)	-	-	-	-
3/25/08	8	52.0 (-0.6-82.0)	19.7 (6.3-33.0)	3.2 (2.1-5.1)	-	1 (248)	1 (100)	-
4/21/08	8	45.6 (-1.5-117.0)	28.6 (10.4-53.7)	4.7 (2.3-8.1)	-	-	-	-
5/27/08	10	36.4 (3.0-65.0)	24.3 (9.3-48.0)	3.6 (1.8-5.0)	2 (3-6)	-	2 (3)	-
6/19/08	10	9.6 (1.5-18.6)	20.0 (3.0-36.0)	3.4 (1.7-5.5)	6 (3-27)	2 (343-452)	6 (3-8)	2 (205-336)
7/14/08	10	11.5 (-4.0-34.4)	17.2 (0.0-36.0)	2.3 (1.1-3.5)	1 (2)	2 (542-661)	1 (2)	2 (235-305)
8/18/08	8	15.0 (0.3-33.8)	15.4 (5.2-28.2)	3.9 (2.2-5.8)	2 (1-129)	1 (443)	2 (1-51)	1 (325)
9/19/08	10	21.6 (3.7-40.8)	16.2 (2.9-26.2)	8.9 (5.1-12.1)	2 (119-138)	3 (440-626)	4 (95-149)	1 (437)
10/15/08	10	20.0 (-6.4-74.7)	13.9 (-6.7-33.7)	4.3 (2.0-6.5)	-	3 (565-687)	-	3 (550-553)
Average		30.4	19.7	4.1	37	512	42	389

Table 2.4. Standing-stock abundance (individuals per m^2, x 10^3), biomass (g AFDM per m^2), and production (g AFDM per m^2 per yr) of *Hydropsyche spp.* and *Cheumatopsyche spp.* on the bedrock outcrop in 2007-2008 and 1991-1992, from Grubaugh and Wallace (1995), with the percent decline.

	2007-2008	1991-1992	% Decline
Hydropsyche spp.			
Standing-stock no. m^{-2}, x 10^3	1.5	10.0	85
Biomass g AFDM m^{-2}	0.7	5.5	87
Production g AFDM m^{-2} yr^{-1}	10.7	92.8	88
Cheumatopsyche spp.			
Standing-stock no. m^{-2}, x 10^3	3.1	4.0	23
Biomass g AFDM m^{-2}	0.5	0.8	35
Production g AFDM m^{-2} yr^{-1}	6.3	10.5	40

Table 2.5. Linear regression models within two delta AICc values of the best-supported model for ln-transformed abundances of *Hydropsyche spp*. and *Cheumatopsyche spp*. instars (I-V). The best-supported model is in bold for each instar. Models included up to six parameters (indicated by X) in addition to the intercept and variance terms: day the sample was collected; day^2, the squared value of day; substrate (sub), a binary parameter with 1 designating boulder or bedrock (as opposed to gravel or cobble); velocity (vel), measured at 60% depth; *P. ceratophyllum* (Pod), the ash-free dry mass of riverweed; and substrate**P. ceratophyllum* (Sub*Pod), designating an interaction between substrate and *P. ceratophyllum*. Day and day^2 always co-occurred as a time of the year factor and all other measures were at the sampled location on the day of sampling. The number of total parameters, K, delta AICc, relative likelihood (ratio of model weight to weight of best-supported model), and model weight, w_i, are shown for each model.

	Covariate Models								
Instar	**Parameter**					**K**	**ΔAICc**	**relative**	**wᵢ**
	Day, Day²	**Vel**	**Sub**	**Pod**	**Sub*Pod**			**likelihood**	
Hydropsyche spp.									
I	**X**	**X**		**X**		**6**	**0.0**	**1.000**	**0.165**
	X	X	X	X		7	0.8	0.682	0.113
				X		3	1.0	0.598	0.099
	X	X		X	X	7	1.5	0.461	0.076
			X	X		4	1.8	0.407	0.067
II	**X**	**X**			**X**	**6**	**0.0**	**1.000**	**0.389**
	X	X		X		6	1.6	0.448	0.174
	X	X		X	X	7	1.9	0.378	0.147
III	**X**	**X**		**X**		**6**	**0.0**	**1.000**	**0.306**
	X	X			X	6	1.8	0.410	0.125
	X	X	X	X		7	1.9	0.384	0.118
IV	**X**				**X**	**5**	**0.0**	**1.000**	**0.177**
	X			X	X	6	0.8	0.660	0.117
	X		X	X		6	1.1	0.589	0.104
	X	X			X	6	1.1	0.575	0.102
	X	X	X	X		7	1.9	0.384	0.068
	X	X		X	X	7	2.0	0.372	0.066
V		**X**		**X**		**4**	**0.0**	**1.000**	**0.458**
Cheumatopscyhe spp.									
I	**X**	**X**			**X**	**6**	**0.0**	**1.000**	**0.122**
	X	X		X	X	7	0.3	0.878	0.108
	X				X	5	0.3	0.842	0.103
	X			X	X	6	0.6	0.739	0.091
	X	X		X		6	1.3	0.533	0.065
					X	3	1.5	0.465	0.057
				X	X	4	1.8	0.400	0.049
	X			X		5	2.0	0.369	0.045
II	**X**	**X**	**X**	**X**		**7**	**0.0**	**1.000**	**0.132**
	X	X			X	6	0.3	0.844	0.111
	X				X	5	0.4	0.807	0.107
	X		X	X		6	0.4	0.805	0.106
	X	X		X	X	7	1.0	0.594	0.078
	X			X	X	6	1.1	0.573	0.076
	X	X		X		6	1.3	0.522	0.069
	X			X		5	1.7	0.422	0.056
	X	X	X	X	X	8	1.9	0.389	0.051
III	**X**	**X**			**X**	**6**	**0.0**	**1.000**	**0.163**
	X	X	X		X	7	1.0	0.613	0.100
					X	3	1.2	0.553	0.090
			X		X	4	1.5	0.483	0.079
	X	X		X	X	7	1.5	0.464	0.076
IV				**X**		**3**	**0.0**	**1.000**	**0.178**
		X		X		4	0.8	0.663	0.118
	X			X		4	1.3	0.513	0.091
			X		X	4	1.5	0.481	0.086
			X	X	X	5	1.5	0.463	0.082
V		**X**	**X**	**X**	**X**	**6**	**0.0**	**1.000**	**0.235**
	X	X	X	X	X	8	0.7	0.718	0.169
		X	X	X		5	1.4	0.488	0.115
	X	X	X	X		7	1.8	0.411	0.097

Table 2.6. Model averaged effect-size estimate (with standard error) of covariate parameters for each instar of *Hydropsyche spp.* and *Cheumatopsyche spp.*, based on the confidence set of streamflow models (Appendix A). Dependent variables are ln-transformed abundances per square-meter for each larval instar. Day and Day2 are calendar day, and represent a time of the year effect. Substrate (Sub) represents the effect of sampling boulder or bedrock (as opposed to gravel or cobble). Dashes (-) are shown for variables not included in any model in the confidence set for an instar.

Covariate Effect Estimates							
Instar	Intercept	Day	Day^2	Substrate	Velocity (m/sec)	*Podostemum ceratophyllum* (g AFDM m^{-2})	Substrate* *Podostemum ceratophyllum*
Hydropsyche spp.							
I	-1.17 (0.97)	0.02 (0.01)	-4.96E-05 (1.79E-05)	0.68 (0.19)	2.21 (0.67)	1.28E-02 (3.17E-03)	4.81E-03 (7.52E-04)
II	-3.27 (1.14)	0.04 (0.01)	-4.00E-05 (2.60E-05)	0.00 (0.00)	2.50 (0.95)	4.99E-03 (1.94E-03)	5.70E-03 (2.12E-03)
III	-2.06 (1.21)	0.03 (0.01)	-1.34E-05 (2.71E-05)	0.33 (0.11)	2.30 (1.00)	7.46E-03 (2.20E-03)	7.03E-03 (7.63E-04)
IV	-1.21 (0.91)	0.03 (0.01)	-6.84E-05 (2.25E-05)	1.02 (0.12)	1.21 (0.40)	7.62E-03 (1.63E-03)	1.22E-02 (2.43E-03)
V	-0.05 (0.32)	-	-	-	2.13 (0.65)	1.07E-02 (2.16E-03)	-
Cheumatopsyche spp.							
I	-0.73 (0.89)	0.01 (0.01)	-1.56E-05 (1.98E-05)	-	1.65 (0.46)	8.31E-03 (2.15E-03)	1.24E-02 (3.22E-03)
II	-2.56 (1.18)	0.03 (0.01)	-6.34E-05 (2.77E-05)	1.08 (0.24)	1.86 (0.67)	1.12E-02 (2.80E-03)	1.13E-02 (2.34E-03)
III	-0.69 (1.20)	0.03 (0.01)	-4.42E-05 (2.45E-05)	-0.55 (0.17)	2.83 (0.92)	2.92E-03 (9.41E-04)	1.44E-02 (3.95E-03)
IV	1.99 (0.51)	-	-	-0.93 (0.25)	1.36 (0.28)	1.50E-02 (3.19E-03)	1.28E-02 (1.15E-03)
V	2.45 (0.73)	-0.01 (0.00)	3.71E-05 (6.02E-06)	-1.21 (0.55)	2.42 (0.81)	1.23E-02 (4.57E-03)	1.25E-02 (4.51E-03)

Table 2.7. Model-averaged effect-size estimate (with standard error) of streamflow-related parameters for each instar of *Hydropsyche spp.* and *Cheumatopsyche spp.* based on the confidence set of streamflow models (Appendix A). Dependent variables are ln-transformed abundances per square-meter for each instar and bold values represent parameters having the greatest importance based on summed model weights. Asterisks denote the model with the interaction between mean depth and variability, which includes estimates of both effects.

	Streamflow Effect Estimates			
Instar	**Mean Depth**	**Variability**	**Variability***	**Mean Depth*Variability***
Hydropsyche spp.				
I	**-2.90 (0.63)**	-0.87 (0.80)	18.66 (2.29)	-69.26 (6.31)
II[1]	-2.31(0.003)	-23.77 (0.46)	-21.21 (0.23)	-9.12 (0.63)
III[2]	-0.62 (0.19)	-10.14 (1.77)	-7.24 (0.88)	-10.29 (2.44)
IV	-1.93 (0.11)	**-17.23 (4.13)**	-10.71 (2.60)	-22.46 (7.18)
V[1]	-2.69 (0.34)	-8.54 (0.53)	-3.12 (0.34)	-19.69 (0.96)
Cheumatopsyche spp.				
I	**-2.47 (0.43)**	-11.53 (1.74)	-0.59 (1.54)	-37.16 (4.27)
II	-3.39 (0.41)	**-17.24 (2.28)**	-5.21 (2.10)	-43.20 (5.79)
III	-4.28 (0.30)	**-24.79 (3.56)**	-7.76 (5.15)	-60.67(14.33)
IV[1]	-4.78 (0.45)	-21.03 (1.34)	-3.54 (2.13)	-63.41 (5.92)
V	-1.08 (0.01)	**-24.84 (5.58)**	-31.17 (3.32)	22.78 (9.25)

[1]Instars for which a low-flow event parameter had highest importance values based on summed model weights.
[2]Instars for which importance values for all streamflow-related parameters were less than summed model weights across habitat covariate-only models.
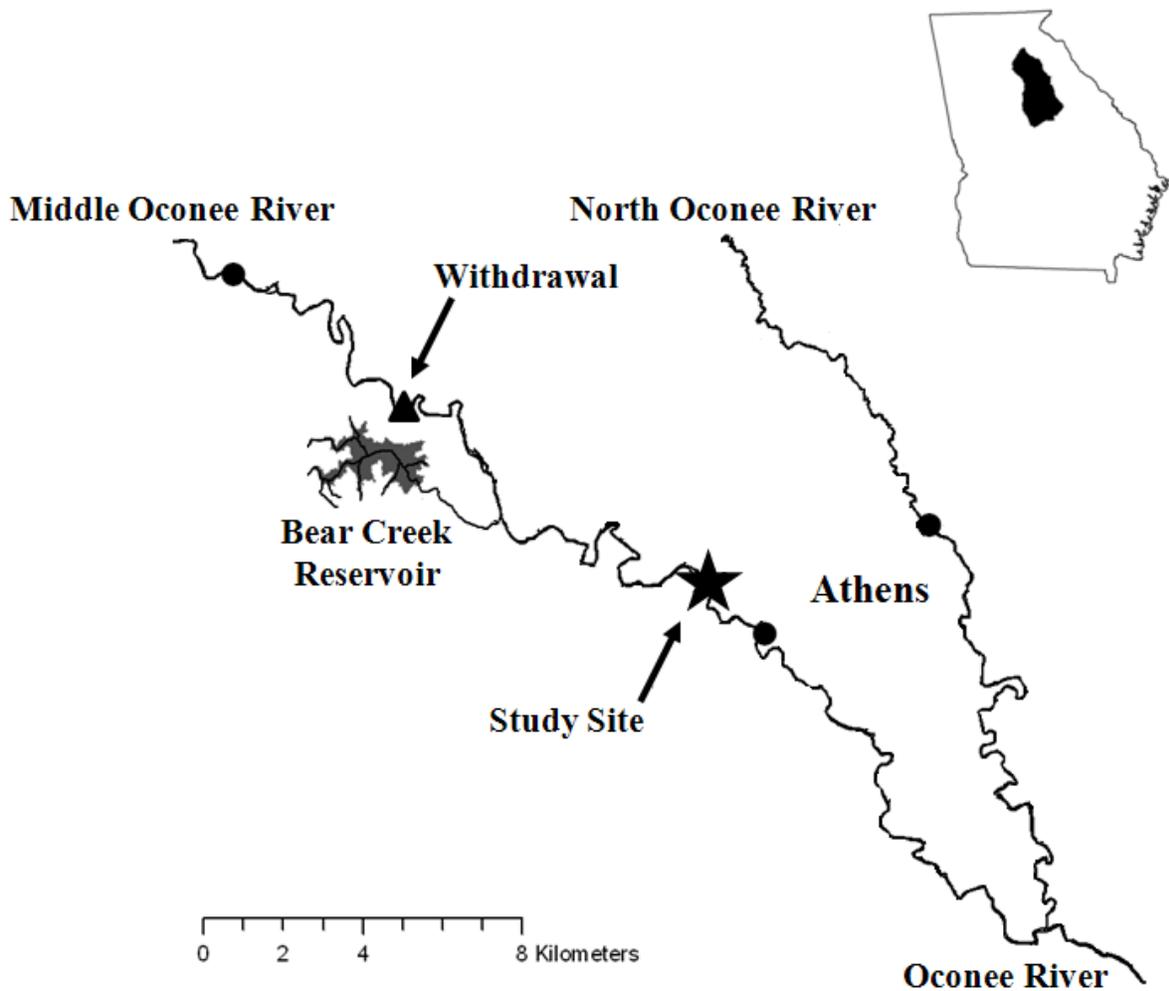
Figure 2.1. The study site (star) is located within the Upper Oconee Watershed, GA (inset) in the Middle Oconee River, upstream of the confluence of the North and Middle Oconee Rivers that converge to create the Oconee River near Athens, GA. Two stream gages (circles) are located near the site, one upstream in Arcade, GA (USGS gage #02217475) and the other downstream in Athens, GA (USGS gage #02217500). The withdrawal location (triangle) for the off-channel reservoir (Bear Creek reservoir, gray) is located 13.5 river km upstream of the site.
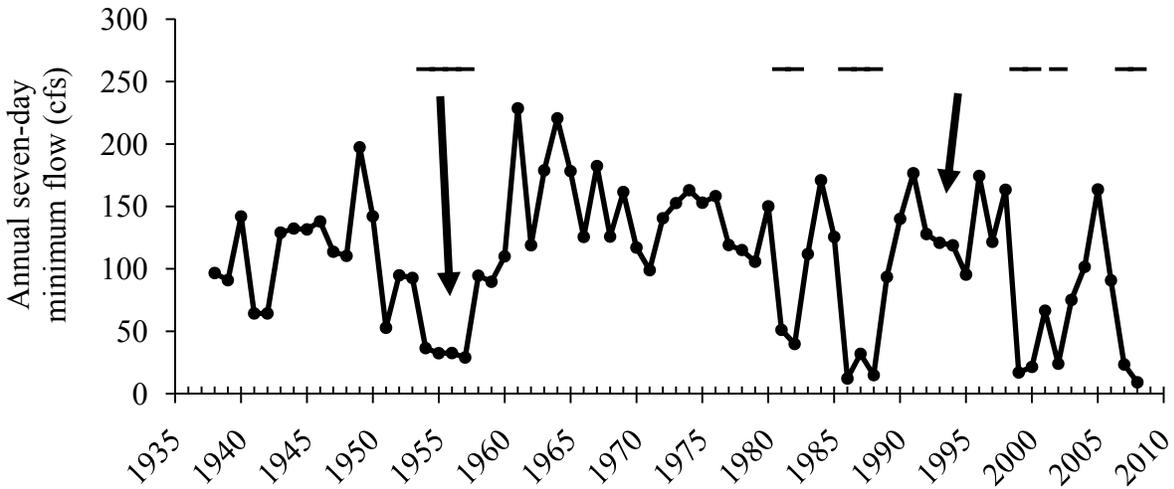
Figure 2.2. Annual seven-day minimum streamflow (cfs) in the Middle Oconee River at Athens, GA for the period of record (USGS gage #02217500). Previous low-streamflow years are represented (dashes above streamflow), when the minimum seven-day consecutive flow was below 45 cfs (7Q10). Two previous studies were conducted at the site (arrows), from 1956-157 and from 1991-1992 (Nelson and Scott 1962, Grubaugh and Wallace 1995).
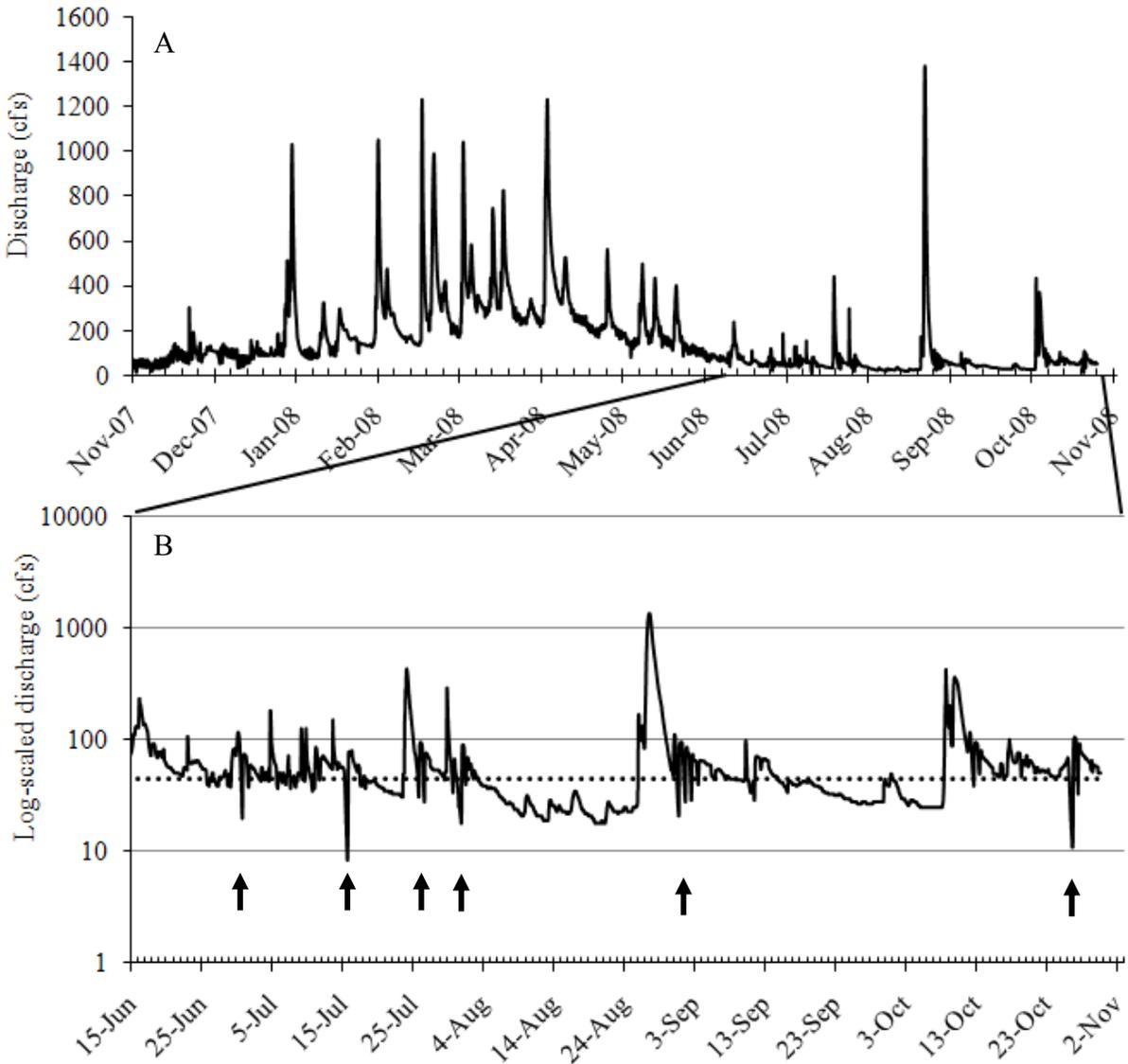
Figure 2.3. A. Streamflow (cfs) from November 2007 through October 2008 (recorded at15 min-intervals). B. Log-scaled streamflow (cfs) during the late summer and fall, and the occurance of water withdraw events (arrows) that frequently lowered streamflow below 45 cfs (7Q10, dashed horizontal line).
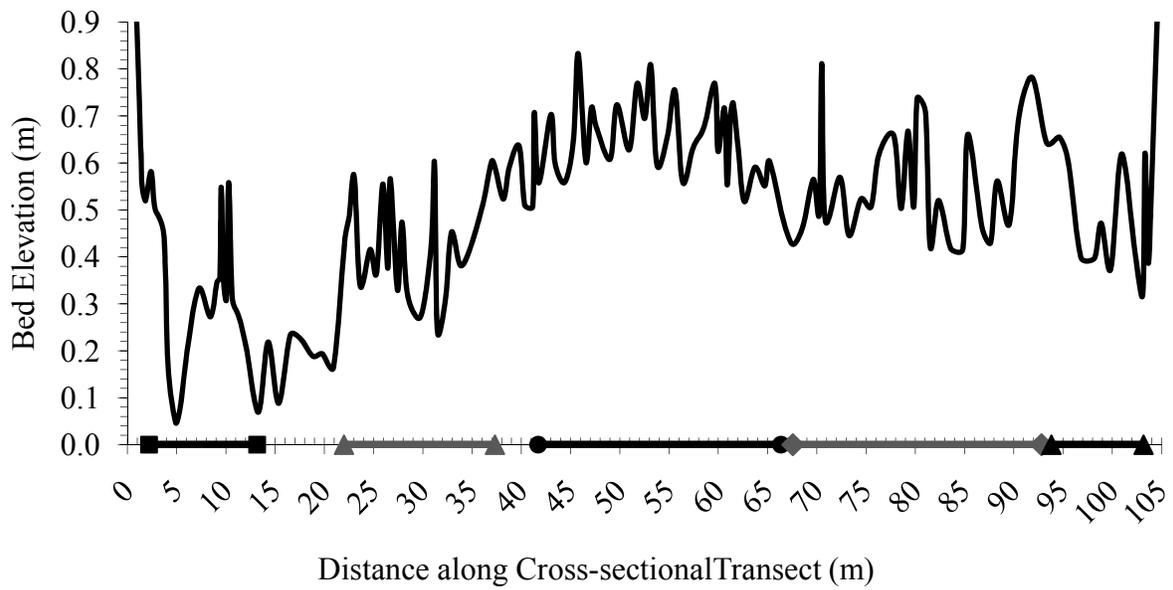
Figure 2.4. Topographic variation of cross-sectional transect from bank to bank (river left to river right) measured as bed elevations (m) relative to a fixed point. Samples were collected from five sections shown as lines along x-axis and had apparent differences in patterns of streamflow variation due to upstream and downstream topography.
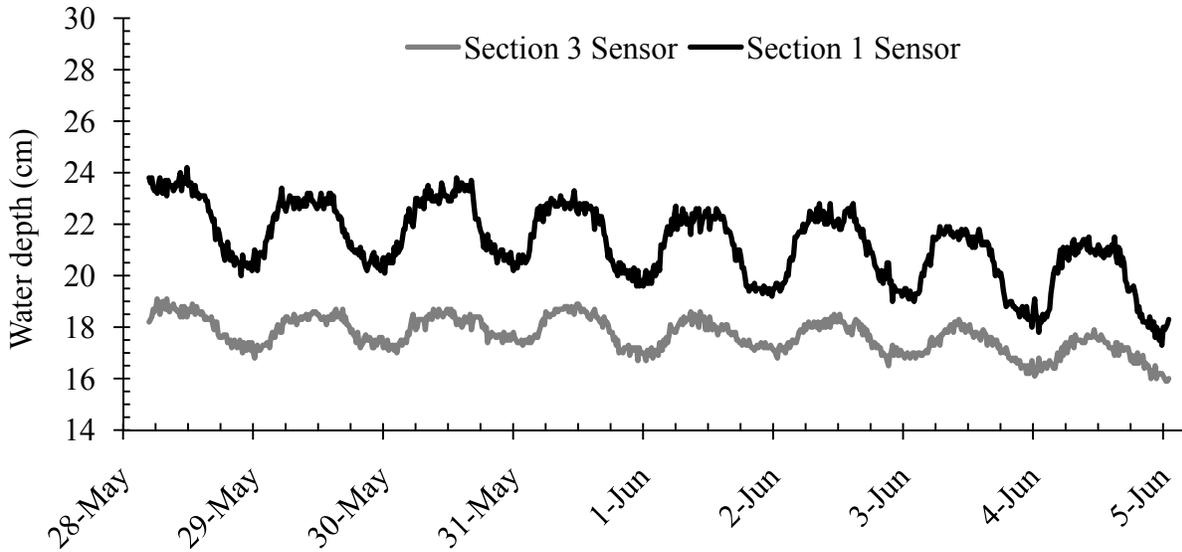
Figure 2.5. Differences in streamflow variation, recorded as water depth at 15-minute intervals in two transect sections from May to June 2008. Section 1 sensor (black line) was located in a low elevation section (river left) and section 3 sensor (gray line) was located in high elevation section (mid-channel). Sections varied in magnitude and rate of change of depth during flow-fluctuations induced by periodic water withdrawals.
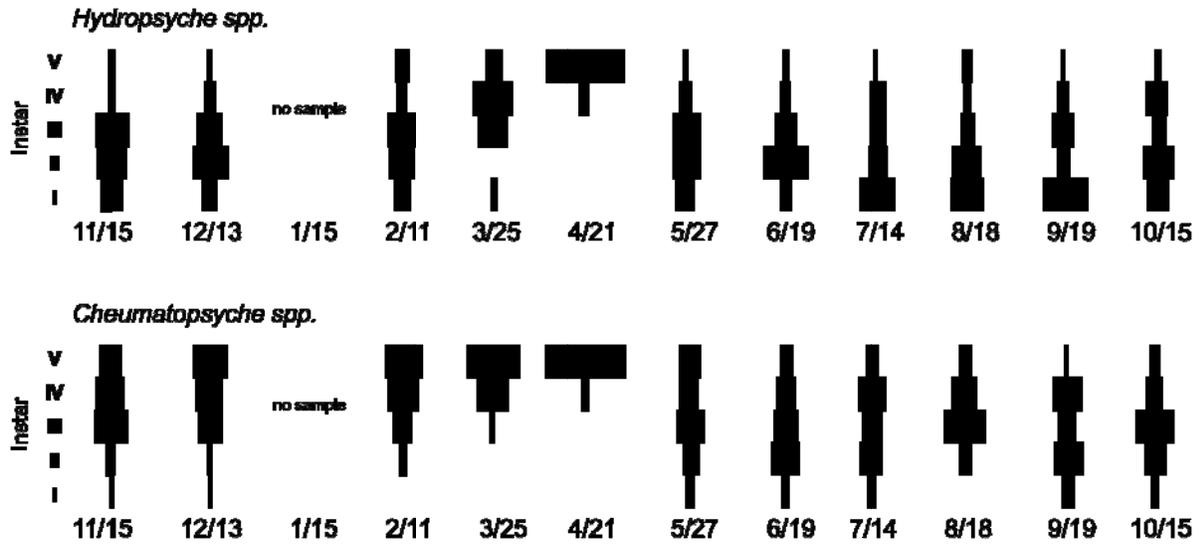
Figure 2.6. Relative abundances of larval instars (I-V) for *Hydropsyche spp.* and *Cheumatopsyche spp.* from November 2007 to October 2008. Both genera were multivoltine with asynchronous development, and abundances were dominated by smaller instars May through October.
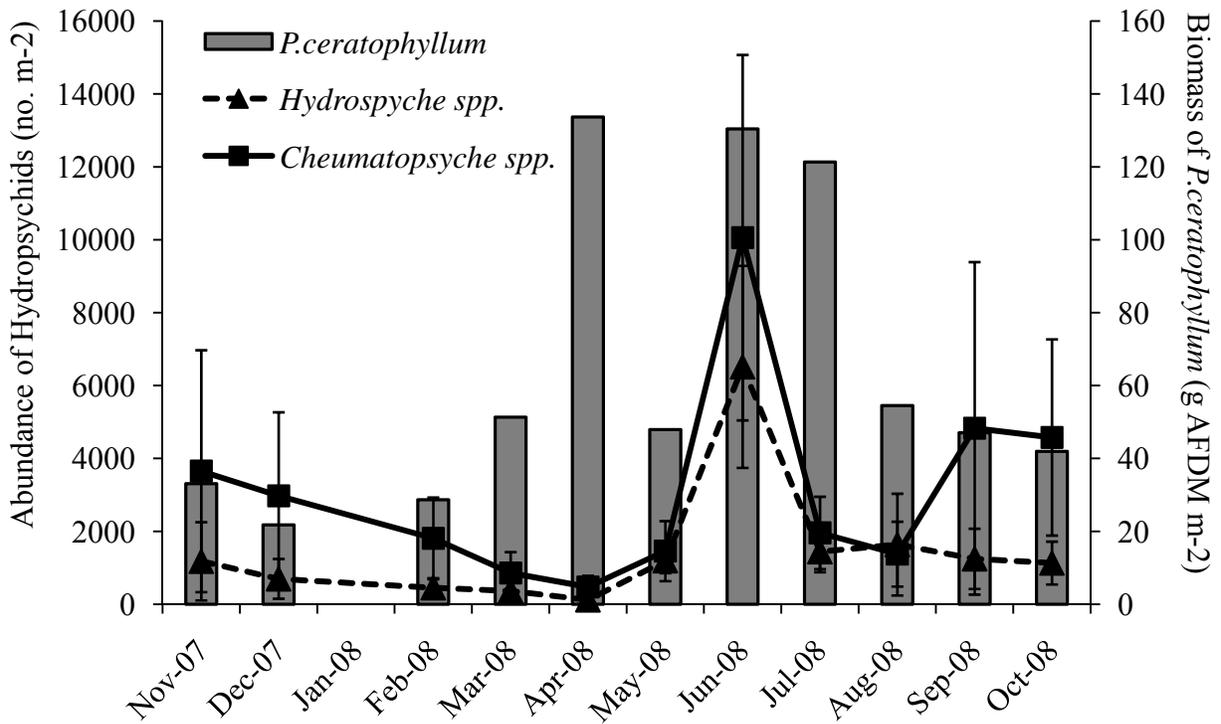
Figure 2.7. Average larval abundance (weighted) of *Cheumatopsyche spp.* and *Hydropsyche spp.* (no. m^{-2}) and biomass of *P.ceratophyllum* (g AFDM m^{-2}) per month. Both genera had similar patterns of abundance with lowest values occurring in April and highest values occurring in June. Samples were not collected in January and $\pm$ 1standard errors of larval abundances are represented by error bars for each genera.
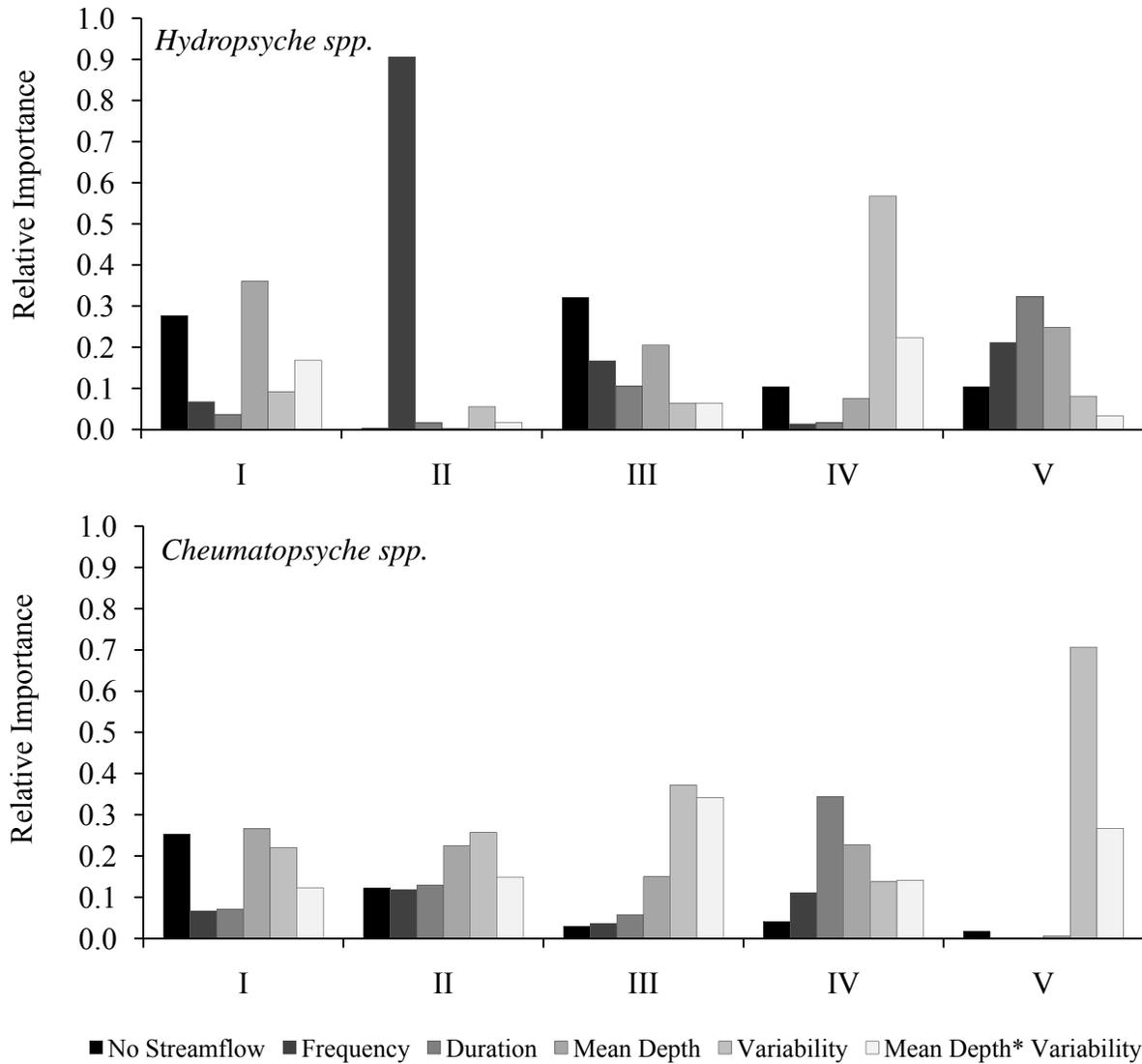
Figure 2.8. Relative importance of alternative streamflow parameters for predicting instar (I-V) abundances for *Hydropsyche spp.* and *Cheumatopsyche spp.* Relative importance is measured as the sum of AIC weights w_i of all models that include the streamflow parameter of interest, or of all habitat covariate only models (no streamflow).
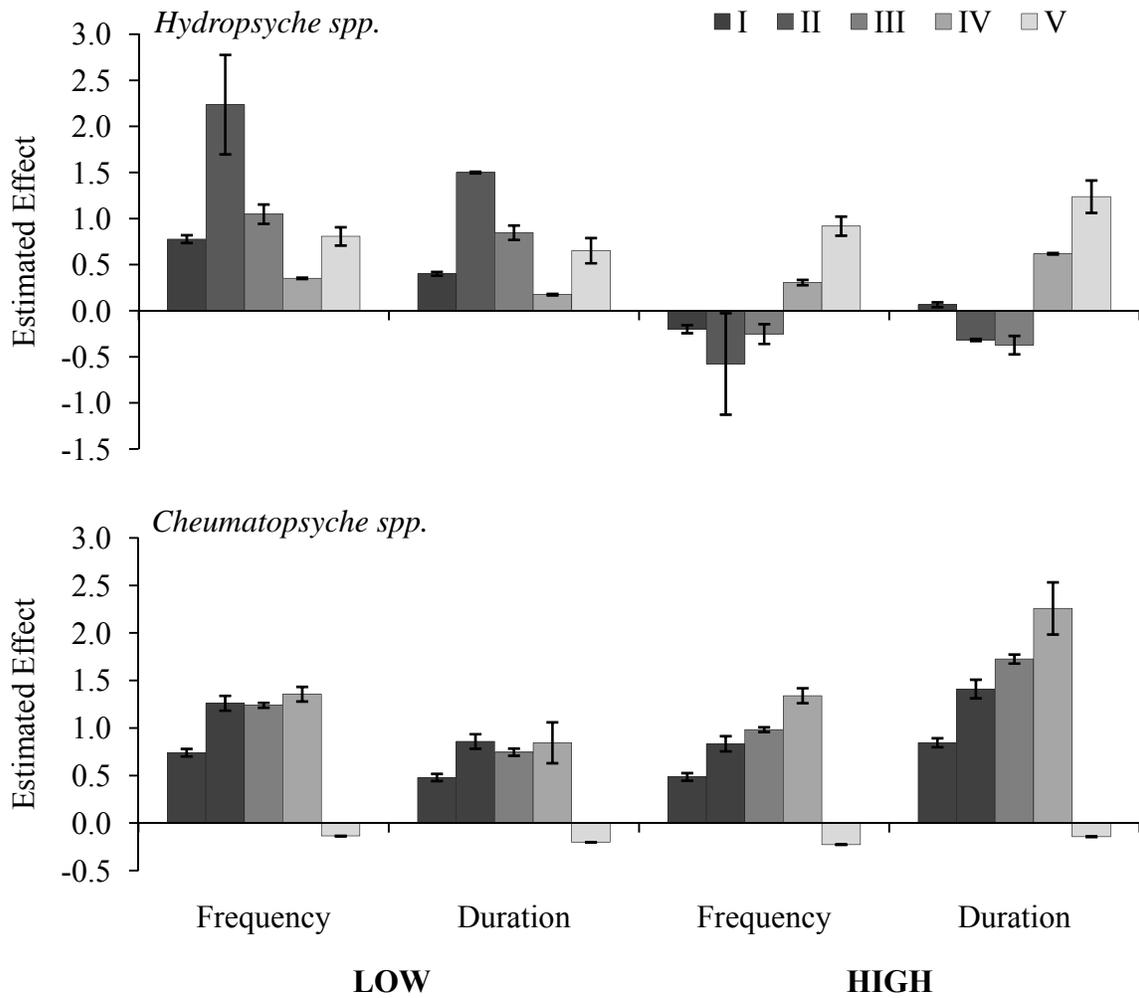
Figure 2.9. Effect-size estimate (with standard error) of each low-flow event parameter, low and high frequency and duration of depth less than five centimeters, on ln-transformed abundances per square-meter of *Hydropsyche spp.* and *Cheumatopsyche spp.* instars (I-V).

ESTIMATING DARTER (*ETHEOSTOMA INSCRIPTUM*) ABUNDANCE AND SURVIVAL USING CAPTURE-RECAPTURE IN A MIDDLE OCONEE RIVER SHOAL DURING EXTREMELY LOW STREAMFLOWS

Introduction

Stream fishes have a large influence on aquatic food webs and stream ecosystems (Power 1990, McIntyre et al. 2007). Small-bodied fishes belonging to a group known as "darters" (family Percidae) are endemic to North America and constitute a species-rich group with over 200 species, many of which are imperiled (Jelks et al. 2008). Darters commonly occur in the eastern United States in small to large-order streams (Boschung and Mayden 2004) and may compose a prominent portion of the benthic faunal community (Lotrich 1973, Grossman et al. 1982, Small 1975). Small-bodied fishes, such as darters, that attain high densities and grow rapidly can contribute substantially to community productivity (Schlosser 1982, Freeman and Freeman 1985, Randall et al. 1995). Darters can also play important roles in stream food webs by foraging on aquatic insects (Lotrich 1973, Layman 1993, Gray et al. 1997), and by serving as prey for aquatic higher order predators (Angermeier 1992, Roberts and Kilpatrick 2004). Given the range of influences of darters on stream ecosystems, and the imperiled status of many members of the group, it is important to understand the effects of environmental fluctuations on darter populations.

Darters provide a useful model for evaluating the effects of environmental fluctuations on aquatic communities because species typically display habitat specificity and relatively small home ranges. Many species are consistently found in fast-flowing riffle habitats (Freeman et al. 1997), and studies of darter movements have shown that individuals are frequently recaptured within riffle areas, with periodic movements of 100-200 m and less frequent long-distance movements up to 3 km (Freeman 1995, Albanese et al. 2003, Roberts and Angermeier 2007, Roberts et al. 2008). Estimating the effects of local habitat fluctuations, such as year-to-year changes in flow, on populations that typically display site fidelity can be useful in understanding aquatic community responses to natural or human induced perturbations.

Streamflow is widely recognized as a major driver of stream ecosystems, sustaining freshwater biota by providing annual and seasonal flow variability that structures channels and instream habitats (Poff et al. 1997, Hart and Finelli 1999, Montgomery 1999, Richter et al. 2003). In particular, changes in flow patterns and variability, which may be caused by changes in climate, land cover alteration (e.g. urbanization) and water diversions, have been shown to substantially affect fish communities (Grossman et al. 1998, Roy et al. 2005, Rahel and Olden 2008, Freeman and Marcinek 2006). In addition, low streamflows during drought can significantly dewater habitats and result in shifts in habitat use by fishes seeking refuge, as well as isolating and fragmenting habitats which can leading to local extirpations (Labbe and Fausch 2000, Magoulick and Kobza 2003, Matthews and Marsh-Matthews 2003, Davey et al. 2006).

Linking environmental condition to biological response requires methods that measure biological function (such as rates of growth, survival or production) that also account for sampling biases (Williams et al. 2002, Peterson et al. 2004). Methods for estimating population parameters for stream fishes typically include block-netting stream reaches and applying multi-

pass depletion models (Freeman et al. 1988, Peterson et al. 2004, Wine et al. 2008). However, block-netting in larger streams frequently is not feasible because of high discharge and larger sampling areas, and depletion -sampling without block nets may result in biased population estimates (Peterson et al. 2005). In addition, depletion models assume that individual capture probabilities are constant, which may not hold true for fishes that move or hide in response to sampling efforts (Peterson et al. 2005). Using a capture-recapture approach may allow for better estimation of abundance and survival rates of stream fishes (Olsen and Vollestad 2001, Skyfield and Grossman 2008, Peterson et al. 2004).

The objective of this study was to measure population parameters of a common darter species during an extreme low streamflow period caused by drought and water withdrawals using a capture-recapture approach. A closed-population robust design model was implemented to estimate survival and abundance within a Piedmont river shoal over a four-month period, late summer into late autumn. Double-marking one group of darters permitted use of a multistate model to estimate tag-loss rates. Survival rates were corrected for tag loss and used to estimate the median survival time of the summer population. Data from this study have provided a basis for estimating population responses to interannual flow variability.

Methods

Study Site

The study has been conducted in a reach of the Middle Oconee River near Athens, GA, which drains approximately 1000 km^2 of the Piedmont physiographic province in the Upper Oconee watershed (Altamaha River Basin). The Middle Oconee River is a sixth-order stream at the study site, which is adjacent to Athens-Clarke County's Ben Burton Park and upstream of

60

Mitchell Bridge Road (Fig 3.1). The site is a river shoal that is dominated by small to large boulders with patches of sand, gravel, and cobble. The total area of the shoal is approximately 1500 m², 50 m in length and 30 m wide. Bed topography is variable, with a fast-flowing main channel on river-right (i.e., right side when facing downstream) and slow, shallow areas dominating river-left (Fig 3.2). Above the shoal, a deeper pool with low current and sandy substrate extends at least 300 m upstream, and the study shoal terminates downstream in a combination of runs and flowing pools. Recent land cover (derived from the 2005 National Land Cover Data) in the Upper Oconee watershed is mostly forest (55%), with some pasture and row crop (21%), low and high impact urban development (10%), and clear cut land (7%) (NARSAL 2009).

Extremely low streamflows occurred in the study region from 2007-2008. Two U. S. Geological Survey (USGS) stream gages were located near the study site, the first approximately 30 km upstream in Arcade, GA (#02217475) and the second approximately 1.5 km downstream of the site in Athens, GA (#02217500; Fig 3.1). The gages were used to assess the extent of streamflow decline in 2008 compared to the 70-yr period of record. As a result of reduced rainfall, the annual discharge in the Middle Oconee River in Athens GA during 2008 was 168 cfs, 33% of the 70-yr average (USGS 2009). Specifically, during the study period of July to November 2008, discharge averaged 62 cfs across all months, which was 22% of the long-term average for this same time period (USGS 2009).

Drought-induced low streamflow conditions were exacerbated by water withdrawals from two upstream facilities. The largest withdrawals were made by the Upper Oconee Basin Authority, which has been permitted to pump 60 million gallons per day (MGD) (90 cfs) from the river to an off-channel reservoir (Bear Creek reservoir), 14 km upstream of the study site

(GAEPD Permit #078-0304-05). Under drought conditions the permitted withdrawal was suppose to have been reduced to 15 MGD; however, with water in short supply during the prolonged drought, the withdrawal limit was replaced with the higher, normal limit of 60 MGD (*pers. com.*, Jeff Williams: Bear Creek Reservoir 2007). The second facility that extracted water from the river was the Athens-Clarke County municipality, which was permitted to withdraw 16 MGD (25 cfs) from a pump station located immediately upstream of the site (GAEPD Permit #029-0304-02) (*pers. com.*, J. Knight, ACC). The coupling of drought and withdrawals resulted in frequent extremely low streamflow levels (less than 45 cfs, Fig 3.3) during the study period. Streamflows during the study were not appreciably influenced by a low-head hydropower dam located 3.2 km upstream of the site because the hydropower facility was non-operational during the summer of 2008 (*pers. com.*, Robert Davis: Fall Line Hydro 2008).

Study Species

The Turquoise darter, *Etheostoma inscriptum*, belongs to the family Percidae and subgenus *Etheostoma*. *E. inscriptum* is distributed along the Atlantic slope of the southeast U. S. in SC, NC, and GA, including the Altamaha, Ocmulgee, and Savannah drainages of GA (Richards, 1966). Species of the subgenus *Etheostoma* typically inhabit shallow water habitats and are found close to the benthos, near or under cover (Greenberg 1991). Dietary preference and life history of *E. inscriptum* has not been extensively studied; however, species within the genus *Etheostoma* share similar characteristics, with most species feeding opportunistically on benthic aquatic insect larvae. *E. inscriptum* adults have been documented feeding on black fly, mayfly, and caddisfly larvae (Baker 2002), while juvenile *Etheostoma* typically ingest smaller prey, in particular chironomids (Gray et al. 1997, Baker 2002). Life history of *E. inscriptum* appears similar to other *Etheostoma* species, with spawning season likely occurring from late

March to early June and life span typically extending three to four years, with sexual maturity reached at the age of one-year (Richards 1966, Layman 1991, Rohde et al. 2009).

Mark-Recapture Study

Preliminary sampling was conducted in June, after the spawning period, to ensure minimal effects on reproductive success and to assess whether an adequate number of individuals could be captured for analysis. Sampling under the robust design then began on July 29, 2008 and ended on November 5, 2008 (Table 3.1). Sampling consisted of three consecutive sampling days once a month across a four-month period. Kendall et al. (1995, 1997) termed the sampling occasions separated by long intervals as *primary* periods, and consecutive sampling days as *secondary* periods. Intervals between primary periods are assumed to be open to immigration, emigration, births, and deaths and during secondary period intervals the population is assumed to be closed to gains and losses (Kendall et al. 1997; Fig 3.4). Therefore, each consecutive three-day sampling occasion was viewed as a closed-capture survey. Advantages of the robust design include: higher net probability that an individual will be captured during a primary period, leading better precision on estimates of survival (White and Burnham, 1999); ability to estimate population size during each primary period using capture-recapture models for closed populations (Otis et al., 1978); and the possibility of estimating rates of temporary emigration by individuals from the study site (Kendall et al., 1997).

On each occasion, sampling started at the downstream edge of the shoal and proceeded upstream for one-hour, using a seine (2.4 x 2 m with 3.2 mm mesh) in conjunction with a backpack electrofisher (Smith Root model 12-B POW^{TM}). Two individuals set the seine, and two others shocked and disturbed the bed sediment in an area of about four square-meters

upstream, corralling fishes downstream into the seine. The electofisher was used to displace

fishes and improve capture efficiency, but shock-time was minimized to prevent moralities.

Sampling proceeded in a zigzag pattern from downstream to upstream, sampling available

wetted habitats. Sampling was conducted during the morning or early afternoon, and

temperature and turbidity (2100P HACH Turbidmeter[TM]) were recorded on each sampling day.

Fishes were identified in the field and *Etheostoma inscriptum* were retained for marking

after sampling. Upon capture, *E. inscriptum* were placed in a bucket with an aerator and

frequently moved to a cooler that was located on the bank. The cooler contained fresh river water

and a bilge-pump aerator to maintain dissolved oxygen. Young-of-the-year fish less than 35 mm

in standard length (SL), were considered to have a high risk of mortality from handling and

marking, and were released unmarked in the field. Individuals injured during capture or marking

were preserved in 10% formalin.

Individuals were measured, tagged, and released on-site within five hours of capture.

Latex gloves were worn while handling fish to minimize stress. All fish were measured for SL

to the nearest millimeter and examined for marks (after the first sampling occasion). Marks were

administered using Visual Implant Elastomer (VIE) tags (Northwest Marine Technology[TM]),

injected as a liquid from a 0.5 ml syringe with a 29-gauge needle inserted just below the skin, in

the top layer of the muscle tissue. Tags were approximately five mm in length and varied with

the size of the individual. Ten body positions and four VIE tag colors were used in combination

to make unique marks that represented capture on specific sampling occasions. The ten body

positions consisted of five locations on both sides of the body: below the first dorsal fin, below

the second dorsal fin, the dorsal edge of the caudal peduncle, the ventral edge of the caudal

peduncle, and above the anal fin; and the four colors used were yellow, pink, orange and blue (Table 3.1).

The first cohort of fish, captured during the first primary period (July 28-30), was given a unique combination of marks with two tags (using of all body positions and three colors; Table 3.1) upon first capture, so that individuals could be identified at recapture on any sampling occasion thereafter. The initial intent was that fish would receive two tags on their first capture throughout the study, so that individuals would be identifiable and not require subsequent marks. However, the large number of fish (486) captured and marked during the first primary period exhausted many of the unique mark combinations intended to be used in later periods. Therefore, each new fish captured in primary periods two, three, and four was given one or two marks using a color and body location unique to the sampling occasion on which it was captured (Table 3.1). The disadvantage of this marking scheme was that individuals (except those marked in the first primary period) were required to be marked each time that they were recaptured to allow identifiable capture histories. An additional advantage of double-tagging the first cohort of fish was that observations of recaptures could be used to estimate rate of tag-loss (Arnason and Mills 1981, Reinert et al. 1998). When double-marked fish from the first primary period were recaptured with only one tag in a later sampling occasion, standard lengths were used to identify a pool of possible individuals with the same tag. The individual was recorded as a recapture from the first primary period and then given a new tag that represented the day it was captured, allowing it to retain a unique (or nearly so) combination of marks throughout the remainder of the study.

After marking, fish were placed into a bucket with an aerator to aid recovery from handling and marking. Fish were released back into the stream at locations throughout the shoal

by facing the bucket upstream and requiring active swimming out to ensure that fish had completely recovered. Individuals that did not recover at this point were preserved in 10% formalin solution and removed from the population.

Estimating abundance and survival under no tag loss

Pollock's robust design capture model was used to estimate abundance and survival during monthly intervals from July to November 2009 (Pollock 1982, Kendall et al. 1995). The robust design is a combination of the Cormack-Jolly-Seber (CJS) live recapture model used to estimate the probability of survival, φ_i, between primary sampling intervals, and closed-capture models used to estimate capture and recapture probabilities, p_{ij} and c_{ij}, respectively, as well as the number of individuals in the survey area, N_i during secondary periods (Cormack 1964, Jolly 1965, Seber 1965, Otis et al. 1978, Kendall et al. 1995, Kendall et al. 1997; Figure 3.4). With sufficient data, the robust design can be useful for estimating temporary emigration from the study site (Kendall et al. 1997).

Modeling survival, capture and recapture probabilities, and abundance was achieved by using Program MARK (White and Burnham, 1999) to implement a closed-capture robust design model with live captures released over the four month period. Young-of-year (yoy; ≤ 42 mm SL) and adult (> 42 mm SL) age classes were categorized by using the size-frequency distribution of individuals captured in July. I initially assumed that all tags were retained, and used the recapture data to evaluate support for three hypotheses of interest: 1) that survival differed between young-of-year (yoy) fish; 2) that survival rates differed among months; and 3) that capture probabilities differed among months.

The probability of survival, φ_i, represents apparent survival, or the probability that an animal at time i+1 is alive and available for capture (i.e., in the site) at time i. Survival rates could vary in four ways that are of biological interest. First, survival rate of yoy and adult age groups could differ, yet each rate remain constant over each month, i.e., φ (age). Second, survival of yoy and adult age groups could be similar to each other but vary among months, φ (t). Third, survival of yoy and adult age groups could differ and vary among months, with each time interval having an additive effect on survival, φ (age + t). Last, survival of both age groups could be similar as well as constant over all months, φ (.).

The parameter p_{ij} is the probability that an animal is captured or observed at sample j of period i and the parameter c_{ij} is the probability that an animal is recaptured in sample j of period i, given that the animal has been previously captured in period i (Kendall et al. 1995). Under the assumption that VIE tags do not affect an individual's ability to be recaptured, p_{ij} was set equal to c_{ij} for all models. This assumes that the probability an individual was captured would be similar on each sampling occasion, however, p_{ij} could vary among sampling months. Therefore, capture probabilities were modeled as either constant, p=c (.), or variable, p=c(t). Lastly, abundance, N_i, is defined as the number of individuals (estimated separately for yoy and adult) in the population available for capture in the shoal sampling area in primary sampling period, i.

Program MARK was used to evaluate support for eight candidate models representing the above hypotheses. The best supported model was selected using Akaike Information Criterion corrected for small sample size (AICc) (Akaike 1974, Burnham and Anderson, 2002). The model with the smallest AICc value was considered the best-supported model given the data set, with models having AICc values within two of the lowest AICc model (i.e., < 2 delta AICc) considered relatively well-supported models (Burnham and Anderson 2002). Model likelihood

67

(estimated as model AIC weight divided by AIC weight for the best-supported model) also was used to evaluate relative support for other models in the candidate set. Ninety-five percent confidence intervals of the parameter estimates were estimated with Program MARK based on estimated standard errors.

Estimating tag loss and growth

Multistate models are an extension of CJS models to multiple-strata or states, and are commonly used to estimate tag loss (Kremers 1988, Hestbeck et al. 1991, Nichols et al. 1992, Brownie et al. 1993, Reinert et al. 1998, Conn et al. 2004). A multistate model was used to estimate the probability of tag loss from double-marked fish tagged in the first primary period. Recaptured individuals were categorized into four states: yoy with two tags (Y2), yoy with one tag (Y1), adults with two tags (A2), and adults with one tag (A1). Thus, individuals could transition from a 2-tag state to a 1-tag state (i.e., by losing a VIE tag), however yoy could also "transition" (i.e., grow) into the adult size class. Note that for double-marked fish from the first primary period, a yoy that grew into the adult size class would remain individually identifiable as having been a yoy. However single-marked yoy (from later primary periods) that transitioned to the adult class and were recaptured would have been incorrectly recorded as a recapture for an adult, which would cause yoy survival to be under-estimated. Thus, both tag-loss and yoy growth into the adult size class could bias survival estimates.

A robust design closed-capture multistate model was used to estimate the probability, Ψ_i^{ab}, that an animal moves from the first state, *a*, to the second state, *b*, during interval *i* (between primary periods) and four transition probabilities were modeled:

1) $\Psi_i^{Y2A2} = \text{Pr}$ (a yoy with two tags grows into an adult and retains both tags)

68

2) Ψ_i^{Y2A1} = Pr (a yoy with two tags grows into an adult and loses one tag)

3) Ψ_i^{Y2Y1} = Pr (a yoy with two tags remains a yoy and loses one tag)

4) Ψ_i^{A2A1} = Pr (an adult with two tags loses one tag).

Estimating the first two probabilities assessed whether there was significant growth of yoy animals into the adult class. The last two probabilities represented tag loss within each age class.

The probability of transitioning from two tags to one tag, Ψ^{21}, could be viewed as the probability that either tag is lost (but not both), which is expressed as $[(\theta^1)(1-\theta^2) + (1-\theta^1)(\theta^2)]$ where θ^1 is the probability that the first tag is lost and θ^2 is the loss of the second tag. I assumed that the probability of losing one tag was independent from losing the other tag, so that $\theta^1 = \theta^2$ and θ was the probability of losing any tag. The probability θ was thus derived from Ψ^{21}, which was estimated for double-marked yoy and adults from the first primary period that were recaptured in later periods with only one mark. The probability that a single-marked fish would retain a tag between primary periods was estimated as $(1-\theta)$.

Four candidate models were constructed to evaluate support for the hypotheses that tag loss differed between yoy and adult fish, and that tag loss varied among months. First, the rate of tag loss was allowed to differ between yoy and adult age groups, yet each rate remained constant over each month, Ψ^{21} (age). Second, rate of tag loss for yoy and adult age groups were constrained to be the same, but allowed to vary over each month, Ψ^{21} (t). Third, rate of tag loss of yoy and adult age was allowed to differ, and allowed to vary over each month with each time interval having an additive effect on rate of tag loss, Ψ^{21} (age + t). Last, rate of tag loss was estimated as equal for yoy and adults and constant over all months, Ψ^{21} (.). In all models, yoy-to-adult transition probability was allowed to vary among months, because the individual yoy marked in the first primary period were expected to grow through time, Ψ^{YA} (t).

The probability of survival and capture were constrained in the multistate models using the results of the best-supported robust design model for all captures, across all months. Accordingly, survival was modeled as function of age class, φ (age), and probability of capture was modeled as a function of month, p=c(t). Abundance in the multistate models was allowed to vary over time and age group, N(age+t). Model support for alternative models of rate of tag loss and yoy transition rates were evaluated using AICc values, as previously outlined.

A corrected survival rate, φ*, was estimated to account for bias caused by tag loss and yoy transition to the adult size class. Corrected survival probability for each age group was estimated by dividing the uncorrected survival by the probability of retaining one tag and the probability of remaining a yoy (for yoy only; Pollock, 1981). This corrected survival rate actually applied to fish that were marked with only one tag during a given primary period, which represented the majority of tagged individuals. A variance estimate of tag retention was derived using upper and lower confidence bounds on transition probabilities computed in MARK, and used to estimate the variance of corrected survival rates, as described by Pollock (1981). Corrected survival estimates were then used to predict the proportion of the summer population, N_t/N_o, that survived to the beginning of the next spawning season using an exponential mortality function, $N_t/N_o = e^{-rt}$, where r (mortality per month) was estimated as 1-survival. I also estimated the median number of months adults and yoy were expected to survive, given estimated survival rates and by setting $N_t/N_o = 0.5$ to solve for t.

Growth rate of *E. inscriptum* was estimated over the study period by assessing the change in SL from animals double-marked in the first primary period and recaptured in a later period. Three different rates were used, 1-36 day, 1-64 day, and 1-99 day, to estimate daily and monthly (30 day) growth rates, and then converted to a growth rate from July to November.

Results

Environmental Parameters

Discharge at the study site averaged 66 cfs for the months spanning the sampling period. Three substantial rainfall events occurred during the study period, the first in late August, the second in late September, and the third in early October. The first two occurred approximately one week prior to sampling occasions and smaller rainfall events occurred throughout the sample period (Fig 3.3). During sampling occasions, discharge ranged from 35 to 66 cfs (average 52 cfs). The lowest discharges were 8 cfs on July 15 (just prior to sampling) and 11 cfs on Oct 26. Water withdrawals from both upstream facilities occurred frequently during the sampling period, with detectable changes in water level on some sampling days. For example, on September 2, discharge was 55 cfs at 0900 h, declined to 47 cfs by 1300 h and increased to 58 cfs by 1600 h. Water withdrawals lowered water levels within shallow areas of the shoal, reducing depths and velocities across the river-left portion of the channel (Fig 3.2).

Turbidity and temperature decreased over the study period with turbidity ranging from 6.7 to 45.9 NTU (average 18 NTU), and stream temperature ranging from 13.5^{o} to 28° C (average 22° C) (Table 3.2). There were no relationships among daily turbidity, temperature and discharge, however temperature and turbidity were correlated when averaged over primary sampling periods (r = 0.62).

Capture Data

Over the course of the study period, a total of 2300 *E. inscriptum* were marked and released. An additional 24 fish died at first capture, and 6 fish died during marking or recapture. The total number of new captures and captures of tagged fish increased over each successive sampling occasion, with twice as many captures in November compared to July (Table 3.3). The

71

number of animals marked in the first primary period (n=487) with double-marks used to estimate tag loss composed 21% of all individuals marked over the study period. Of the 2300 individuals marked over four months, 63% (1448) were never recaptured and 37 % (852) were recaptured at least once. Recapture rates were substantial, with 21% to 41% of fish marked in a particular primary period being recaptured in a subsequent month (Fig 3.5). For example, of the fish newly marked during the second primary period (early September; n=485), 184 (38%) and 159 (33%) of these fish were recaptured in next two months, respectively. By the last month (early November), 50% of all the animals captured had at least one mark from a prior sampling occasion (Fig 3.5).

Estimates of survival, capture probability, and abundance

The best-supported model held the probability of survival constant over time (Table 3.4) with young-of-year having substantially lower survival (0.58) compared to adults (0.88) per month (Table 3.5). However, there was also considerable support for the model that allowed survival of both age groups to vary among months, although variation was moderate compared to the confidence intervals for individual estimates (Table 3.5). Both of the two best-supported models were based on the probability of capture varying among sampling occasions (Table 3.4), with the probability an animal was captured ranging from 0.08 to 0.16 (Table 3.6). Support for all other models was substantially lower relative to the top two models (Table 3.4).

Estimated abundance of adult *E. inscriptum* within the shoal was relatively constant from July to November with an average of 1430 fish. However, young-of-year abundances increased from month to month (Table 3.6), most likely a result of small individuals growing into a size

that were more easily caught by seining. Total abundances of adults and yoy together ranged from 1756 to 2929 (Table 3.6) or between about 1.2 and 2 individuals per square-meter.

Estimates of tag loss and yoy-to-adult transition rates

Time-dependent and age-with-time-dependent tag loss models (based on double-marked fish from the first primary period) were both supported by the multistate closed robust design models (Table 3.7). There was relatively weak support for age-dependent probability of tag loss that was constant through time (10.26 ΔAICc compared to most-supported model); however, rate of tag loss estimated for this model fell in the middle of the range of those for time-dependent rates (Table 3.8). A constant rate of tag loss was therefore used for each age group to evaluate the effects of tag loss on estimates of survival.

The estimated probability of an individual losing one tag, θ, was slightly higher for adults than yoy, 0.044 (SE=0.0003) and 0.034 (SE=0.011), respectively. Tag retention (1- θ) was consequently similar between for yoy and to adults (0.966 compared to 0.956). The probability of yoy-to-adult transitioning between the first and second primary period, and ignoring tag-loss, was estimated from the best-supported multistate model as 0.2507 (Table 3.8). The probability of yoy growing into the adult group as well as losing one tag (Ψ^{Y2A1}) was relatively small (Table 3.8). Conversely, the probability of a single-marked yoy remaining in the yoy size class, and remaining tagged was estimated as (1-0.2507)*0.956, or 0.716. Note that transition rates in these multistate models are assumed to be constant across individuals, and this assumption clearly was violated because individuals near the larger end of the yoy size-range were more likely to grow to the adult size-range in a one-month period compared to smaller fish. Yoy were continuously recruited into the sampled population throughout the sampling period (Table 3.6), and had

73

similar size-frequency distributions across periods (not shown); therefore, the transition probability of yoy-to-adult from the first primary period was representative of the probability that a tagged yoy transitioned to an adult between any two primary periods.

The growth rate for all fish (regardless of age) was estimated as 1.41(SE=0.25) mm per month, and 3.72 (SE=0.54) mm over the study period. Growth rates for yoy individuals marked in the first period were estimated as 3.08 (SE=0.40) mm per month, showing the potential for yoy to grow into adults by the last sampling period.

Corrected survival estimates

Survival estimates increased after accounting for the probability of both tag loss and transition from yoy to adult age groups, although the effect of tag loss was relatively low. Adult survival (corrected for tag loss) increased to 0.92, a 7% increase over the uncorrected estimate (Fig 3.6). However, the effect of growth of yoy out of the yoy age class substantially affected survival for this age group; correcting for tag-loss and yoy-to-adult transition increased estimated survival to 0.82, 42% higher than the original estimate. Both corrections were approximate, based on all fish having a single tag and homogeneous transition rates for yoy, but show the scale of transition-effects on estimated survival.

A greater proportion of adults were estimated to survive to the next spawning season (late March) compared to yoy fish. Approximately 67% of the early fall adult population was expected to survive until March. Using an averaged survival estimate of both age groups, about 52% of the population was expected to survive to late March of the next year. By reducing bias in estimates of survival, adult median survival time was estimated to be 9.0 months, 3.1 months

longer than the estimate from uncorrected survival. Median yoy survival time was much lower, with an estimate of 3.8 months compared to 1.6 months for the uncorrected survival rate.

Discussion

Capture-recapture methods proved sufficient for estimating survival and abundance of *Etheostoma inscriptum* in this sixth-order stream during a prolonged low-flow period. Estimated survival of *E. inscriptum* was relatively high and data generally supported the hypothesis that darter survival differed between young-of-year (yoy) and adult age classes. However, VIE tag-loss and the growth of yoy fish into the adult size class both influenced estimates of survival. After reducing the biases in survival estimates, only about half of the late summer/fall population was expected to survive to the next spawning season.

Abundance and survival during drought

E. inscriptum reached densities as high as two per square-meter in the study shoal. Although there is a paucity of information on densities of darters in larger streams, these estimates are higher than reported in a southeastern Appalachian stream (0.31 fish per m^2; Skyfield and Grossman 2008). The Middle Oconee River is likely more productive than smaller streams where many studies of fish communities have focused. Fish production has previously been reported as dominated by only a few species, with production estimates ranging from 3 to 15 kcal m^{-2} in third and second-order streams, and benthic fish contributing considerably to total production (Lotrich 1973, Small 1975). Even a single species, with densities ranging from 0.09 to 1.0 m^{-2}, can contribute almost half of total fish production (Freeman and Freeman 1985).

Considering that *E. inscriptum* dominated the fish assemblage at the site, this species could contribute appreciably to stream production in a highly productive middle-order river.

The coupling of high abundance with high darter survival supports the hypothesis that fish preferred the site during drought likely due to the shoal maintaining good habitat for flow-dependent species. Upstream and downstream of the site, pools and riffle-run sequences may have become uninhabitable (or barriers to movement) because of low-flow effects on velocities, water chemistry and food availability, in which case the shoal became a preferred habitat or refuge for flow-dependant species (Magoulick and Kobza 2003). *E. inscriptum* have been reported to prefer shallower habitats (5 cm to 20 cm), and habitat for this species in particular may have been relatively unaffected by drought, as reduced water depths were common throughout the shoal (Rhode et al. 2009). In addition, high densities could have resulted from the reduction of available wetted habitat, which often concentrates animals into smaller areas (Stanley et al. 1997, Covich et al. 2003). Differences in microhabitat-use by *E. inscriptum* juveniles and adults are reduced when habitats are homogenized by low-flow (Henry and Grossman 2008), which supports the idea that crowding of age classes increased total density. Overall, the combination of good habitat in the shoal compared to upstream and downstream areas and reduced flows concentrating animals into a smaller area may have lead to high abundances and densities during the study period.

The number of fish that may have moved into the shoal during and prior to the study period is influenced by the distance between riffle habitats and quality of those habitats during environmental fluctuations (Roberts and Angermeier 2007). *E. inscriptum* movements would have to be extensive (100-600 m) if individuals immigrated from adjacent shoal habitats. Most studies have reported darter movements of less than 20 m, but with some individuals dispersing

up to 2 km (Freeman 1995, Rosenberger et al. 2007, Roberts et al. 2008, Skyfield and Grossman 2008). High survival estimates also support the idea that fish did not frequently leave the shoal to seek habitat in adjacent areas, and exhibited high site fidelity during the study period. Nonetheless, lower survival rates for young-of-year *E. inscriptum* may have reflected dispersal from the study site as marked fish have been observed nine months after the study period in a bedrock shoal approximately 600 m upstream from the study site, indicating that fish could disperse across a large pool.

Overall, extremely low streamflows may have increased densities and apparent survival of *E. inscriptum* in a 1500 m^2 shoal. Other studies have reported that reductions in flow variability and magnitude, often caused by drought, can stabilize habitats, benefitting stream fish populations by decreasing yoy mortality and increasing subsequent recruitment (Grossman et al. 1998, Freeman et al. 2001). A few large rainfall events did occur during the study period; however, the magnitude and frequency of elevated flows were likely reduced during the drought period. In addition, the magnitude of water withdrawal fluctuations may not have influenced yoy survival as reported in dam hydropeaking (Freeman et al. 2001). Comparing drought and non-drought year survival rates in a flow-altered river will allow estimates for the effects of streamflow on specific year-class survival.

Importance of estimating tag loss

Studies have reported rates of VIE tag retention as high as 90% in the laboratory and as low as 84% in the field (Catalano et al. 2001, Weston and Johnson 2008, Olsen and Vollestad 2001b). However, studies often fail to account for small biases in estimates of stream fish population parameters (Pollock et al. 2007). *E. inscriptum* retained tags in the field at a higher

rate of up to 97% per month and 91% over a 100-day period. Ignoring small tag losses can underestimate survival rates and have substantial effects on expected survival time, as shown in this study. Longer studies on marked fishes have reported that tags can remain visible over several months or years, yet rates of tag-loss are rarely quantified (Weston and Johnson 2008, Fabrizio et al. 1999). As future research continues on *E. inscriptum* in this study site, estimates of long-term tag-retention could be quantified and integrated to reduce bias in estimates of interannual survival.

Interannual flow effects on survival rates

Most studies have focused on the persistence of species in terms of presence and absence; however, quantifying the probability that a population will do well during specific years can increase the understanding of natural population dynamics in relation to abiotic factors. Rates estimated in this study can be used to understand the effects of interannual flow variability on the survival of year-to-year cohorts of fish. Comparing survival rates of fish during drought and higher flow years is not possible due to the paucity of information on fish survival rates. However, local abiotic and biological factors such as higher temperatures and predation are reported to influence fish populations and may also contribute to local rates of change (Angermeier 1992, Rosenberger and Angermeier 2003, Steinmetz et al. 2003). Comparing the results in this study to subsequent years will allow the evaluation of the importance of flow on the abundance, survival, and persistence of *E. inscriptum*.

Conclusion

Using capture-recapture methods with *E. inscriptum* in a larger-order stream allowed estimations of population parameters such as survival and abundance. Efforts to understand the impacts of drought on fish communities have primarily focused on changes in biological communities and this study contributed a rate-of-change estimate for an abundant species. Extremely low streamflows (caused by drought and exacerbated by water withdrawals) provided a unique opportunity to study apparent survival rate of an abundant darter species, as sampling in higher flows is often difficult due to faster and deeper water, which leads to reduced capture efficiencies.

Research on *E. inscriptum* will continue in future years and focus on relating interannual flow variability to survival probabilities. Estimating over-wintering survival rates and the effects of flow on specific cohorts of fish may prove useful in understanding flow-ecology linkages at a multi-year scale. As shown here, estimating survival can have challenges, and accounting for sources of possible bias, such as tag-loss and growth, may require more extensive modeling approaches.

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Table 3.1. Tag colors and locations used each day of marking. Sampling occasions (i.e., secondary periods within primary periods) received unique combinations of marks. In the first primary period all body positions were used (n=10). A single blue mark was used in the second and third primary periods in six different body positions, avoiding dorsal marks that were difficult to detect (i.e., along dorsal fin). In the fourth primary period, double-marks were used on fishes greater than 40 mm SL and single marks were used on smaller individuals.

Date	Event Primary	Secondary	First Mark	Second Mark	Notes
7/28/08	1	1	YELLOW	YELLOW	all positions
			PINK	PINK	all positions
			ORANGE	ORANGE	all positions
			YELLOW	PINK	all positions
7/29/08	1	2	YELLOW	PINK (cont.)	all positions
			YELLOW	ORANGE	all positions
			PINK	ORANGE	all positions
			PINK	YELLOW	all positions
7/30/08	1	3	PINK	YELLOW (cont.)	all positions
			ORANGE	YELLOW	all positions
			ORANGE	PINK	all positions
9/01/08	2	1	BLUE LEFT ANAL	NONE	
9/02/08	2	2	BLUE RIGHT ANAL	NONE	
9/03/08	2	3	BLUE LEFT VENTRAL CAUDAL PEDUNCLE	NONE	
9/29/08	3	1	BLUE LEFT DORSAL CAUDAL PEDUNCLE	NONE	
9/30/08	3	2	BLUE RIGHT VENTRAL CAUDAL PEDUNCLE	NONE	
10/01/08	3	3	BLUE RIGHT DORSAL CAUDAL PEDUNCLE	NONE	
11/03/08	4	1	YELLOW LEFT FIRST DORSAL	YELLOW LEFT FIRST DORSAL	Second mark only given if >40mm SL
11/04/08	4	2	ORANGE LEFT FIRST DORSAL	ORANGE LEFT FIRST DORSAL	Second mark only given if >40mm SL
11/05/08	4	3	NONE	NONE	

Table 3.2. Environmental conditions on each sampling occasion: time of sampling, water temperature (C) and turbidity (NTU) at the study site, and discharge (cfs) which was recorded at the downstream USGS gage (#02217500).

			Environmental Parameters		
Date	**Occasion**	**Time**	**Water Temperature (C)**	**Turbidity (NTU)**	**Discharge (cfs)**
7/28/08	1/1	10:30	26.0	25.4	54
7/29/08	1/2	09:50	25.5	23.7	45
7/30/08	1/3	10:00	24.0	45.9	65
9/01/08	2/1	10:10	25.0	30.5	58
9/02/08	2/2	10:10	24.0	30.5	47
9/03/08	2/3	14:00	28.0	14.8	43
9/02/08	3/1	13:20	25.0	7.9	35
9/30/08	3/2	10:30	21.0	10.9	50
10/01/08	3/3	10:30	20.0	7.9	43
11/03/08	4/1	13:40	14.0	6.7	62
11/04/08	4/2	11:30	13.5	7.9	57
11/05/08	4/3	11:50	14.0	8.5	66

Table 3.3. Number of individuals captured and released on each sampling occasion. The total number of individuals released with marks on each sampling date are shown with the number of those individuals that were unmarked and marked when captured. Event denotes the primary period and secondary period sampled.

Capture Data					
Date	**Event**	**No. Released**	**No. Unmarked**	**No. Marked**	**% Marked**
7/28/08	1/1	173	173	0	0
7/29/08	1/2	182	170	12	7
7/30/08	1/3	184	143	41	22
9/01/08	2/1	202	149	53	26
9/02/08	2/2	257	195	62	24
9/03/08	2/3	216	141	75	35
9/02/08	3/1	312	201	111	36
9/30/08	3/2	328	220	108	33
10/01/08	3/3	364	205	159	44
11/03/08	4/1	428	263	165	39
11/04/08	4/2	413	224	189	46
11/05/08	4/3	428	216	212	50
Total		**3487**	**2300**	**1187**	

Table 3.4. Support for probability of survival (S) and capture (p=c) models from the robust design capture-recapture model set. Survival rates were either held constant for age groups and months (.), allowed to vary by age group only (age), by age and month (age + t), or by month only (t). Probabilities of capture were either held constant (.) or allowed to vary by month (t). Abundance, N, varied over month and by age group (age + t). AICc values, delta AICc values, model weights (w_i), relative likelihood, and number of estimated parameters are shown for each model.

Robust Design Model Set				

Model	AICc	Δ AICc	w_i	relative likelihood	no. estimated parameters
S(age) p=c(t) N(age+t)	-18585.6	0.0000	0.6837	1.0000	14
S(age+t) p=c(t) N(age+t)	-18583.9	1.6618	0.2978	0.4357	16
S(age+t) p=c(.) N(age+t)	-18578.2	7.4438	0.0165	0.0242	13
S(age) p=c(.) N(age+t)	-18573.9	11.6920	0.0020	0.0029	11
S(.) p=c(t) N(age+t)	-18516.1	69.5198	0.0000	0.0000	13
S(t) p=c(.) N(age+t)	-18514.5	71.1148	0.0000	0.0000	12
S(t) p=c(t) N(age+t)	-18514.3	71.2843	0.0000	0.0000	15
S(.) p=c(.) N(age+t)	-18512.6	73.0243	0.0000	0.0000	10

Table 3.5. Parameter estimates for the probability of survival for young-of-year and adult fish over each monthly interval from the best, S(age),and second best-supported, S(age+t), models. Standard errors are shown in parentheses.

Model	Month	Young-of-year	Adult
S(age)	Each	0.58 (0.03)	0.88 (0.02)
S(age+t)	August	0.46 (0.08)	0.83 (0.04)
	September	0.62 (0.06)	0.91 (0.03)
	October	0.58 (0.06)	0.89 (0.03)

Table 3.6. Parameter estimates for the probability of capture during each sampling occasion (per day) and abundances for young-of-year and adult fish during each closed-survey period from the model that allowed survival to vary between age groups and among periods, S(age+t; < 2 delta AICc compared to top model). Upper and lower 95% confidence limits are shown in parentheses.

| Month | Probability of Capture | Abundance | |
		Young-of-year	Adult
July	0.10 (0.08-0.13)	260 (197-353)	1496 (1191-1908)
September	0.12 (0.10-0.13)	673 (571-803)	1313 (1134-1536)
October	0.13 (0.12-0.15)	1227 (1093-1389)	1310 (1168-1481)
November	0.15 (0.13-0.16)	1330 (1190-1499)	1599 (1435-1795)

Table 3.7. Support for each candidate model for the probability of transitioning from two tags to one tag (Ψ^{21}) and from young-of-year to adults. The transition probability of yoy-to-adult (Ψ^{YA}) and abundance of individuals (N) by age class were allowed to vary over time. AICc values, ΔAICc values, model weights, model likelihood, and number of estimated parameters are shown.

Model	AICc	ΔAICc	w_i	relative likelihood	no. estimated parameters
S(age) Ψ^{21} (t) Ψ^{YA}(t) p=c(t) N(age+t)	-2462.3	0.0000	0.7404	1.0000	21
S(age) Ψ^{21} (age+t) Ψ^{YA}(t) p=c(t) N(age+t)	-2460.2	2.1302	0.2552	0.3447	22
S(age) Ψ^{21} (age) Ψ^{YA}(t) p=c(t) N(age+t)	-2452.1	10.2556	0.0044	0.0059	20
S(age) Ψ^{21} (.) Ψ^{YA}(t) p=c(t) N(age+t)			Could not converge		

Table 3.8. Parameter estimates for the probability of tag loss (transitioning from two tags to one tag, Ψ^{21}) for models allowing rates to vary by age group and among months (age+t), between age groups (age) or among months (t). The probabilities of transition for two tagged yoy to two tagged adult, Ψ^{Y2A2}, and one tagged adult, Ψ^{Y2A1}, are shown for the first primary period. Standard errors are shown in parentheses.

Model	Parameter	Month	Young-of-year	Adult
(age +t)	Tag Loss, Ψ^{21}	August	0.039 (0.0004)	0.056 (0.0174)
	Tag Loss, Ψ^{21}	September	0.088 (0.0376)	0.122 (0.0288)
	Tag Loss, Ψ^{21}	October	0.011 (0.0001)	0.016 (0.0051)
(age)	Tag Loss, Ψ^{21}	Each	0.069 (0.0119)	0.090 (0.0003)
(t)	Growth, Ψ^{Y2A2}	Each	0.251 (0.0005)	
	Growth, Ψ^{Y2A1}	Each	0.002 (0.00001)	
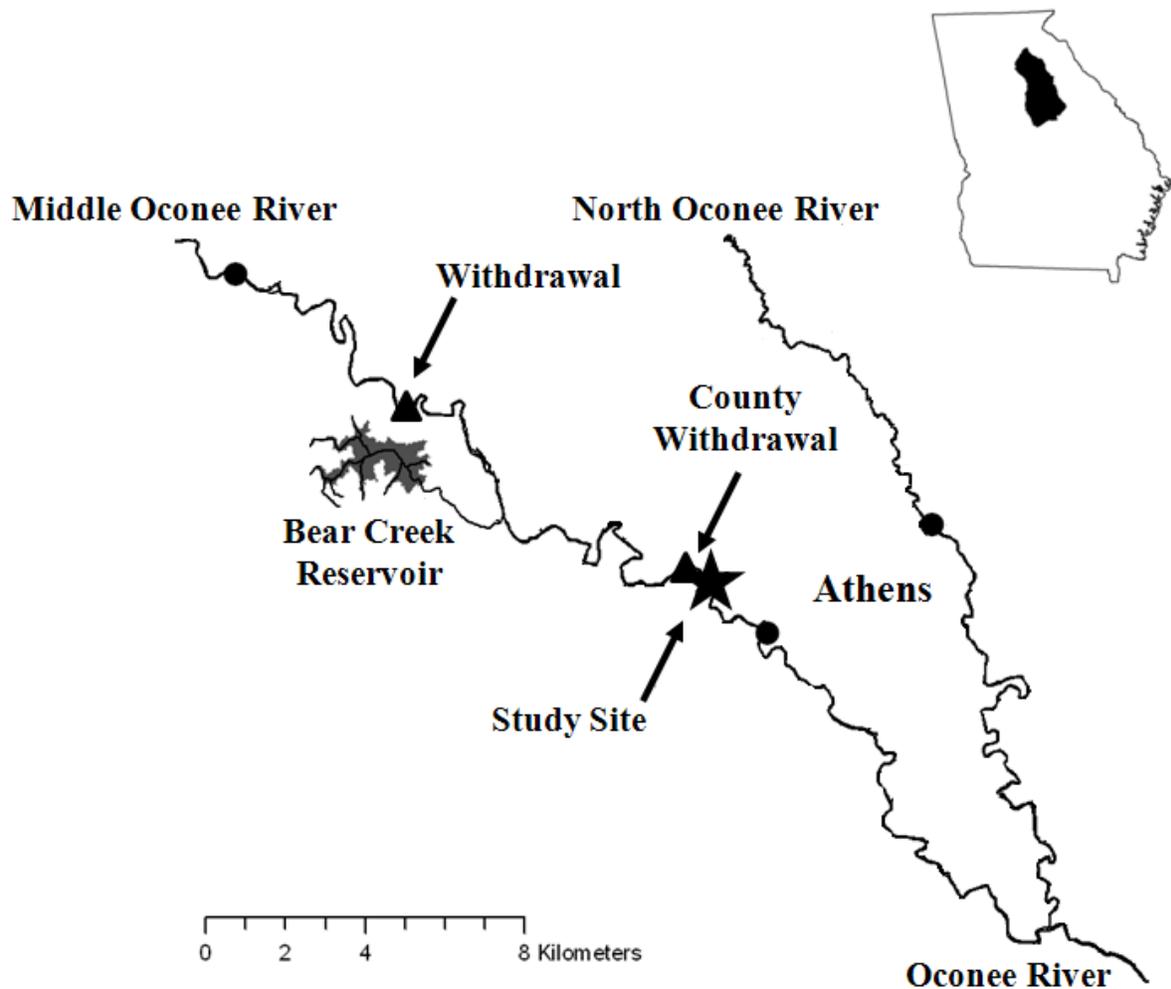
Figure 3.1. The study site (star) is located within the Upper Oconee Watershed, GA (inset) in the Middle Oconee River, upstream of the confluence of the North and Middle Oconee Rivers that converge to form the Oconee River near Athens, GA. Two stream gages (circles) are located near the site, one upstream in Arcade, GA (USGS gage #02217475) and the other downstream in Athens, GA (USGS gage #02217500). The withdrawal locations (triangles) for an off-channel reservoir (Bear Creek reservoir, gray) and county municipal withdrawal are located 13.5 river km and 0.01 km upstream of the study site, respectively.
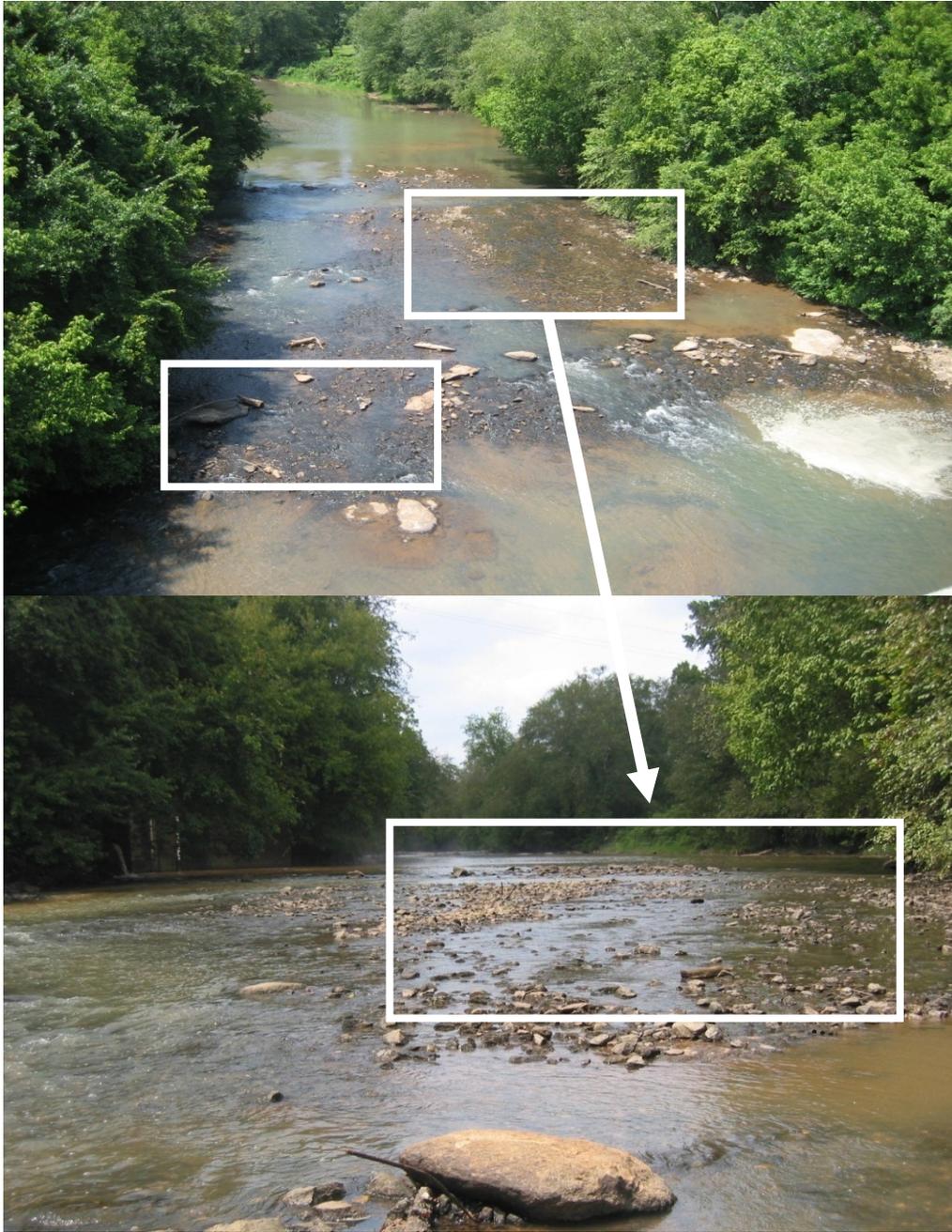
Figure 3.2. Photos of study site at a discharge of 33 cfs on July 22 at 1400 h (top) and 47 cfs on September 2 at 1330 h (bottom). Water withdrawals frequently dewatered the areas on the right and lower left (in boxes), with exposed habitat in the upstream middle portion of the channel. The discharge for September 2008 was 41 cfs, compared to a period-of-record average for September of 236 cfs.
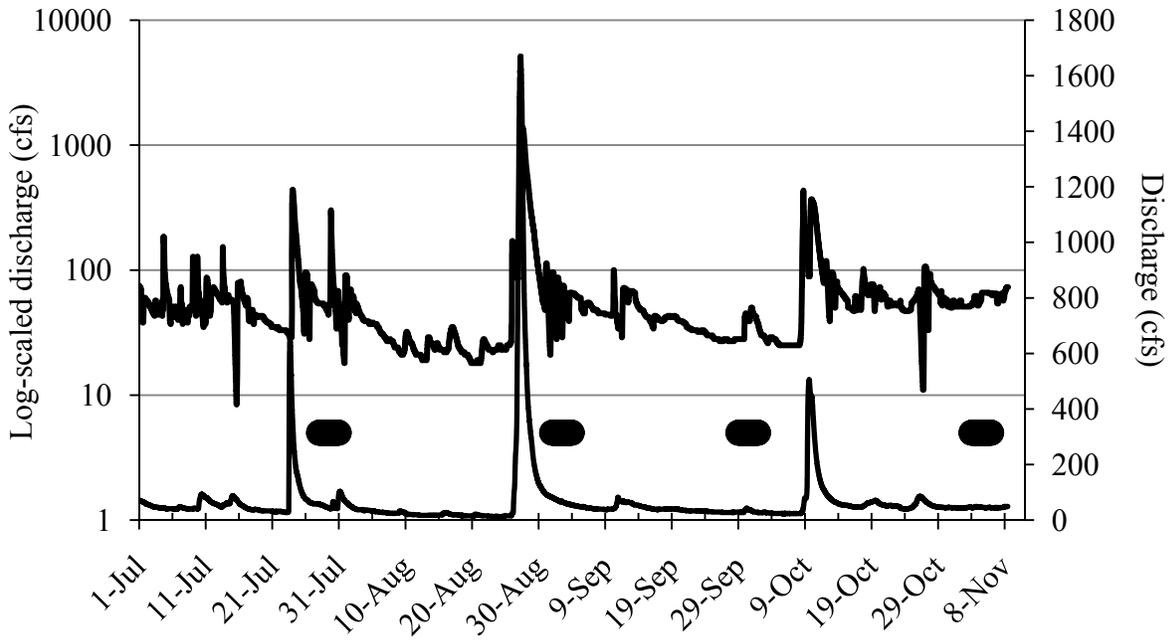
Figure 3.3. Discharge (log-scaled and non-log-scaled, cfs) during the study period, July to November 2008. Log-scaled discharge shows lowered streamflow from withdrawals, upper line, while non-log-scaled discharge shows magnitude of spates, lower line. Reduced flow from withdrawals and storm events both occurred around sampling occasions (black ovals).
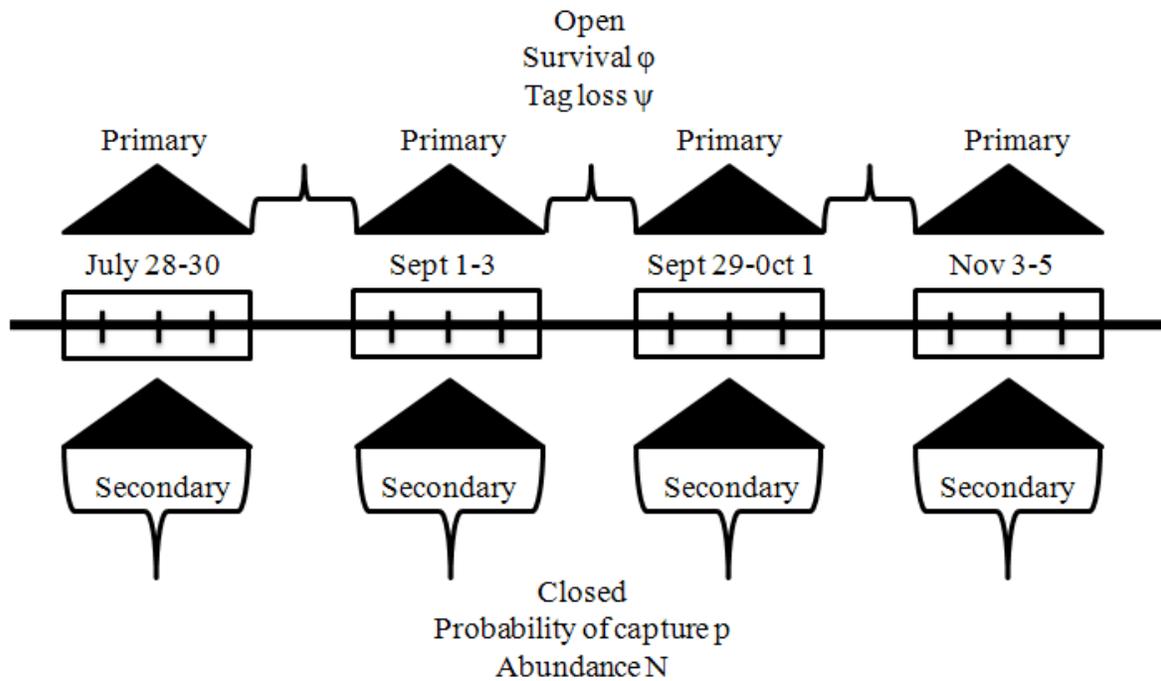
Figure 3.4. Closed capture robust design. Sampling occasions occurred every month from late July to early November of 2008; within each month, sampling occurred for three consecutive days. Between sampling occasions on consecutive days (secondary periods), the population was assumed to be closed to gains and losses, while between monthly sampling occasions (primary periods), the population was assumed to be open. Tag loss was assumed to occur only between primary periods. Abundance and capture probability parameters could be estimated from closed secondary period captures, whereas tag-loss and survival parameters could be estimated from open primary period captures. Modified from Kendall et al. 1997.
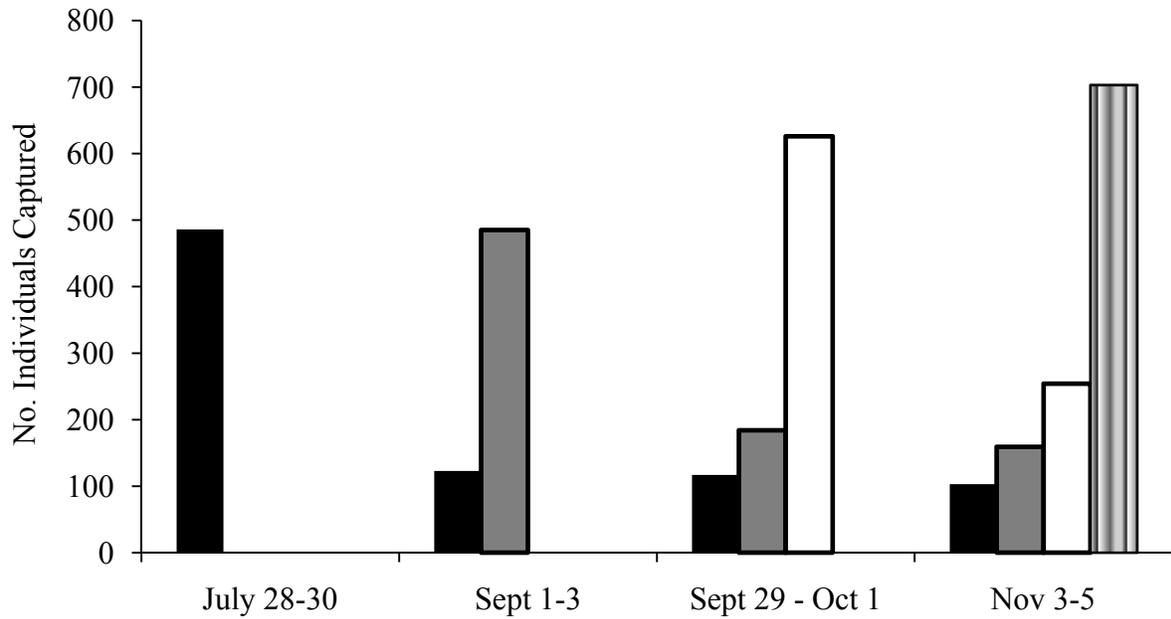
Figure 3.5. The number of fish captured in each primary period. Separate bars represent total individuals initially captured in each period: black = period one; gray = period two, open = period three, and striped = period four.
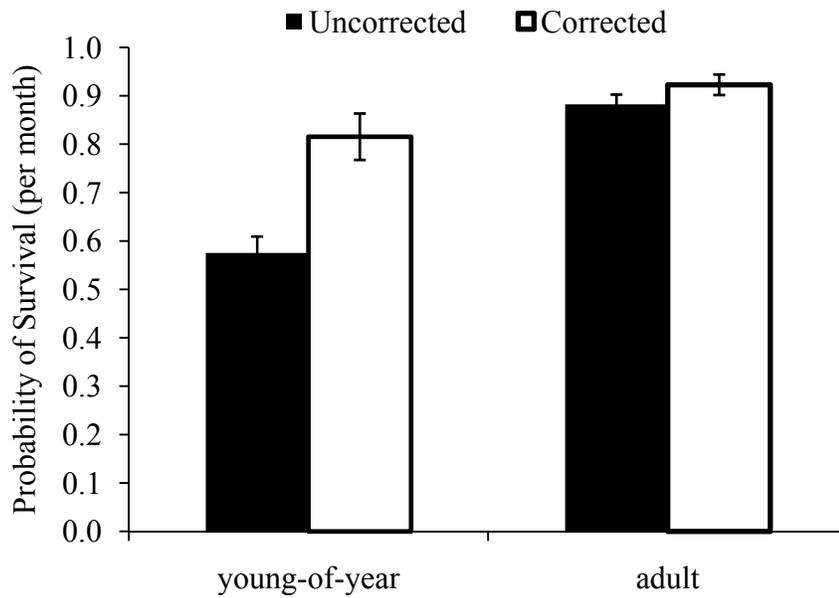
Figure 3.6. Biased (uncorrected) and corrected rate of survival for young-of-year and adult fish. Young-of-year survival was biased low by tag-loss and yoy-to-adult transitions, and adult survival was biased low by tag-loss only.

CHAPTER 4

CONCLUSION

Hydrologic changes, such as natural drought or human-induced flow manipulations, can influence the abundance and survival of aquatic biota. Studies have typically focused on macroinvertebrate and fish assemblage responses to regulated and unregulated flow regimes and large scale perturbations such as floods and droughts. However, measuring functional changes, such as production and survival, which are influenced by local abundances, can provide insight into how aquatic biota respond to environmental fluctuations. The purpose of this research was to quantify the effects of extremely low streamflow caused by drought and coupled with flow fluctuations on abundant net-spinning caddisfly taxa and a common benthic darter species.

Using a fine-scaled spatiotemporal approach, I was able to detect streamflow changes at a microhabitat scale that influenced macroinvertebrate abundances. Results from this study have shown that caddisfly production was lower than previous years and that larvae preferred habitats vulnerable to periodic exposure from water withdrawals, possibly leading to the observed decline in abundance and production. This study has demonstrated that hourly changes in flow (i.e., water withdrawals), can influence the macroinvertebrate community, with possible long-term effects on the secondary production.

Success of capture-recapture methods demonstrated that block-nets or depletion-methods were not needed to study a common darter species in a sixth-order stream. Results from this study have shown that survival of *E. inscriptum* was relatively high during drought, with animals

displaying high site fidelity in a Piedmont river shoal. Survival of young-of-year and adult fish were high, signifying that this species may have preferred shallow-swift habitat maintained in the shoal. Results from this study will allow for future comparison of functional responses of darters to interannual changes in streamflow.

Quantifying biological responses to changes in streamflow is key to understanding flow-ecology linkages. Streamflow features such as magnitude, duration, and frequency can influence aquatic biota at multiple scales and be a major driver in structuring aquatic communities. Studies that link flow to important ecological process can provide insight into the influences of streamflow in river ecosystems, which is necessary in order to meet the water needs of both aquatic systems and human populations. Extremely low flows caused by drought allowed for effective benthic sampling in a larger-stream setting because habitats were more accessible compared to higher flow years, when flows may be too deep or swift for sample collection. The coupling of drought and human-induced flow fluctuations provided a unique opportunity to study flow-ecology linkages in a sixth-order flow-altered stream and these studies together provide further insight into the effects of low streamflows on aquatic organisms

APPENDIX A: SUPPLEMENTAL MATERIAL FOR CHAPTER 2

Table1. Competing covariate model sets (n=32) for each instar. Models included up to eight parameters: day the sample was collected; day2, the squared value of day; substrate, a binomial parameter with 0 equaling unstable substrate of sand, gravel or cobble and 1 equaling stable substrate of boulder or bedrock; velocity, measured at 60% depth above sample; *P.ceratophyllum*, the ash-free dry mass of riverweed collected at the sampled location; and substrate**P.ceratophyllum*, the interaction term between substrate and *P.ceratophyllum*; an intercept and model variance term. Day and Day2 always co-occurred as a time of year factor.

Covariate Model Parameters	K
None	2
Day Day2	4
Substrate	3
Velocity	3
P.ceratophyllyum	3
Substrate**P.ceratophyllym*	3
Day Day2 Substrate	5
Day Day2 Velocity	5
Day Day2 *P.ceratophyllyum*	5
Day Day2 Substrate**P.ceratophyllym*	5
Substrate Velocity	4
Substrate *P.ceratophyllyum*	4
Substrate Substrate**P.ceratophyllym*	4
Velocity *P.ceratophyllyum*	4
Velocity Substrate**P.ceratophyllym*	4
P.ceratophyllyum Substrate**P.ceratophyllym*	4
Day Day2 Substrate Velocity	6
Day Day2 Substrate *P.ceratophyllyum*	6
Day Day2 Substrate Substrate**P.ceratophyllym*	6
Day Day2 Velocity *P.ceratophyllyum*	6
Day Day2 Velocity Substrate**P.ceratophyllym*	6
Day Day2 *P.ceratophyllyum* Substrate**P.ceratophyllym*	6
Substrate Velocity *P.ceratophyllyum*	5
Substrate Velocity Substrate**P.ceratophyllym*	5
Substrate *P.ceratophyllyum* Substrate**P.ceratophyllym*	5
Velocity *P.ceratophyllyum* Substrate**P.ceratophyllym*	5

Day Day2 Substrate Velocity *P.ceratophyllyum*	7
Day Day2 Substrate Velocity Substrate**P.ceratophyllym*	7
Day Day2 Substrate *P.ceratophyllyum* Substrate**P.ceratophyllym*	7
Day Day2 Substrate *P.ceratophyllyum* Substrate**P.ceratophyllym*	7
Substrate Velocity *P.ceratophyllyum* Substrate**P.ceratophyllym*	6
Day Day2 Substrate Velocity *P.ceratophyllyum* Substrate**P.ceratophyllym*	8

Table 2. Linear regression model set for two Hydropsychidae genera: *Hydropscyhe spp.* and *Cheumatopsyche spp.* instars (I-V). Included models were within two delta AICc values of the top model. Variables are listed in Table 1.

Instar	Model Parameters	K	ΔAICc	relative likelihood	w(i)
Hydropsyche spp.					
I	Day Day2 Velocity P.ceratophyllum	6	0.0	1.000	0.165
	Day Day2 Substrate Velocity P.ceratophyllum	7	0.8	0.682	0.113
	P.ceratophyllum	3	1.0	0.598	0.099
	Day Day2 Velocity P.ceratophyllum Substrate*P.ceratophyllum	7	1.5	0.461	0.076
	Substrate P.ceratophyllum	4	1.8	0.407	0.067
II	Day Day2 Velocity Substrate*P.ceratophyllum	6	0.0	1.000	0.389
	Day Day2 Velocity P.ceratophyllum	6	1.6	0.448	0.174
	Day Day2 Velocity P.ceratophyllum Substrate*P.ceratophyllum	7	1.9	0.378	0.147
III	Day Day2 Velocity P.ceratophyllum	6	0.0	1.000	0.306
	Day Day2 Velocity Substrate*P.ceratophyllum	6	1.8	0.410	0.125
	Day Day2 Substrate Velocity P.ceratophyllum	7	1.9	0.384	0.118
IV	Day Day2 Substrate*P.ceratophyllum	5	0.0	1.000	0.177
	Day Day2 P.ceratophyllum Substrate*P.ceratophyllum	6	0.8	0.660	0.117
	Day Day2 Substrate P.ceratophyllum	6	1.1	0.589	0.104
	Day Day2 Velocity Substrate*P.ceratophyllum	6	1.1	0.575	0.102
	Day Day2 Substrate Velocity P.ceratophyllum	7	1.9	0.384	0.068
	Day Day2 Velocity P.ceratophyllum Substrate*P.ceratophyllum	7	2.0	0.372	0.066
V	Velocity P.ceratophyllum	4	0.0	1.000	0.458
Cheumatopscyhe spp.					
I	Day Day2 Velocity Substrate*P.ceratophyllum	6	0.0	1.000	0.122
	Day Day2 Velocity P.ceratophyllum Substrate*P.ceratophyllum	7	0.3	0.878	0.108
	Day Day2 Substrate*P.ceratophyllum	5	0.3	0.842	0.103
	Day Day2 P.ceratophyllum Substrate*P.ceratophyllum	6	0.6	0.739	0.091
	Day Day2 Velocity P.ceratophyllum	6	1.3	0.533	0.065
	Substrate*P.ceratophyllum	3	1.5	0.465	0.057
	P.ceratophyllum Substrate*P.ceratophyllum	4	1.8	0.400	0.049
	Day Day2 P.ceratophyllum	5	2.0	0.369	0.045
II	Day Day2 Substrate Velocity P.ceratophyllum	7	0.0	1.000	0.132
	Day Day2 Velocity Substrate*P.ceratophyllum	6	0.3	0.844	0.111
	Day Day2 Substrate*P.ceratophyllum	5	0.4	0.807	0.107
	Day Day2 Substrate P.ceratophyllum	6	0.4	0.805	0.106
	Day Day2 Velocity P.ceratophyllum Substrate*P.ceratophyllum	7	1.0	0.594	0.078
	Day Day2 P.ceratophyllum Substrate*P.ceratophyllum	6	1.1	0.573	0.076
	Day Day2 Velocity P.ceratophyllum	6	1.3	0.522	0.069
	Day Day2 P.ceratophyllum	5	1.7	0.422	0.056
	Day Day2 Substrate Velocity P.ceratophyllum Substrate*P.ceratophyllum	8	1.9	0.389	0.051
III	Day Day2 Velocity Substrate*P.ceratophyllum	6	0.0	1.000	0.163
	Day Day2 Substrate Velocity Substrate*P.ceratophyllum	7	1.0	0.613	0.100
	Substrate*P.ceratophyllum	3	1.2	0.553	0.090
	Substrate Substrate*P.ceratophyllum	4	1.5	0.483	0.079
	Day Day2 Velocity P.ceratophyllum Substrate*P.ceratophyllum	7	1.5	0.464	0.076
IV	P.ceratophyllum	3	0.0	1.000	0.178
	Substrate P.ceratophyllum	4	0.8	0.663	0.118
	Velocity P.ceratophyllum	4	1.3	0.513	0.091
	Substrate Substrate*P.ceratophyllum	4	1.5	0.481	0.086
	Substrate P.ceratophyllum Substrate*P.ceratophyllum	5	1.5	0.463	0.082

V	Substrate Velocity P.ceratophyllum Substrate*P.ceratophyllum	6	0.0	1.000	0.235
	Day Day2 Substrate Velocity P.ceratophyllum Substrate*P.ceratophyllum	8	0.7	0.718	0.169
	Substrate Velocity P.ceratophyllum	5	1.4	0.488	0.115
	Day Day2 Substrate Velocity P.ceratophyllum	7	1.8	0.411	0.097

Table 3. Linear regression confidence model set for each instar (I-V) of *Hydropsyche spp.* in streamflow analysis. Models included up to thirteen parameters: an intercept and variance term, combinations of the five habitat covariates listed in Table 1, and either: frequency, many or few, which represented the total number of hours samples spend with water depths less than 5cm over the prior 30day period; duration, many or few, which represented the total number of hours of the longest single continuous time samples spent with water depths less than 5cm over the prior 30-day period; depth, the mean depth of a sample measured at 1-hr intervals over the prior 30-day period; variability, the standard deviation of depths measured at 1-hr intervals over the prior 30-day period; and depth*variability, the interaction term between depth and variability with respect to variability. Day and Day2 always co-occurred as a time of year factor. Depth*Variability interaction term was used in models with variability.

	Hydropsyche spp.				
Instar (#models)	**Model Parameters**	**K**	**ΔAICc**	**relative likelihood**	**w(i)**
I (30)	Day Day2 Vel Pod Depth	7	0.0	1.000	0.110
	Day Day2 Sub Vel Pod Depth	8	0.3	0.860	0.094
	Day Day2 Vel Pod	6	0.4	0.803	0.088
	Day Day2 Sub Vel Pod	7	1.2	0.548	0.060
	Pod Depth	4	1.3	0.513	0.056
	Pod	3	1.5	0.480	0.053
	Day Day2 Vel Pod Sub*Pod Depth	8	1.5	0.474	0.052
	Day Day2 Vel Pod Depth* Variability	8	1.6	0.449	0.049
	Sub Pod Depth	5	1.6	0.446	0.049
	Day Day2 Vel Pod Sub*Pod	7	2.0	0.371	0.041
	Day Day2 Sub Vel Pod Depth* Variability	9	2.2	0.330	0.036
	Pod Depth* Variability	5	2.2	0.327	0.036
	Sub Pod	4	2.2	0.327	0.036
	Day Day2 Vel Pod Variability	7	2.7	0.254	0.028
	Sub Pod Depth* Variability	6	3.0	0.223	0.024
	Pod FewF ManyF	5	3.1	0.210	0.023
	Day Day2 Vel Pod Sub*Pod Depth* Variability	9	3.2	0.205	0.022
	Day Day2 Sub Vel Pod Variability	8	3.4	0.181	0.020
	Pod Variability	4	3.5	0.173	0.019
	Day Day2 Vel Pod FewF ManyF	8	3.8	0.152	0.017
	Day Day2 Vel Pod Sub*Pod Variability	8	4.3	0.118	0.013
	Sub Pod FewF ManyF	6	4.4	0.111	0.012
	Sub Pod Variability	5	4.4	0.108	0.012
	Pod FewD ManyD	5	4.7	0.094	0.010
	Day Day2 Vel Pod FewD ManyD	8	4.8	0.091	0.010
	Day Day2 Sub Vel Pod FewF ManyF	9	4.9	0.084	0.009
	Day Day2 Vel Pod Sub*Pod FewF ManyF	9	5.8	0.056	0.006
	Sub Pod FewD ManyD	6	5.9	0.053	0.006
	Day Day2 Sub Vel Pod FewD ManyD	9	5.9	0.053	0.006
	Day Day2 Vel Pod Sub*Pod FewD ManyD	9	6.6	0.036	0.004
II (18)	Day Day2 Vel Pod FewF ManyF	8	0.0	1.000	0.404
	Day Day2 Vel Sub*Pod FewF ManyF	8	0.2	0.893	0.361
	Day Day2 Vel Pod Sub*Pod FewF ManyF	9	2.1	0.348	0.141
	Day Day2 Vel Sub*Pod Variability	7	4.8	0.093	0.038
	Day Day2 Vel Sub*Pod Depth* Variability	8	7.1	0.029	0.012
	Day Day2 Vel Pod Sub*Pod Variability	8	7.2	0.028	0.011
	Day Day2 Vel Sub*Pod FewD ManyD	8	8.2	0.017	0.007

109

	Day Day2 Vel Pod FewD ManyD	8	8.2	0.016	0.007
	Day Day2 Vel Pod Variability	7	8.2	0.016	0.007
	Day Day2 Vel Pod Sub*Pod Depth* Variability	9	9.5	0.008	0.003
	Day Day2 Vel Pod Sub*Pod FewD ManyD	9	10.0	0.007	0.003
	Day Day2 Vel Pod Depth* Variability	8	10.6	0.005	0.002
	Day Day2 Vel Sub*Pod	6	11.2	0.004	0.002
	Day Day2 Vel Sub*Pod Depth	7	11.7	0.003	0.001
	Day Day2 Vel Pod	6	12.8	0.002	0.001
	Day Day2 Vel Pod Sub*Pod	7	13.1	0.001	0.001
	Day Day2 Vel Pod Depth	7	13.4	0.001	0.000
	Day Day2 Vel Pod Sub*Pod Depth	8	13.7	0.001	0.000
III (18)	Day Day2 Vel Pod	6	0.0	1.000	0.179
	Day Day2 Vel Pod Variability	7	1.2	0.560	0.100
	Day Day2 Vel Pod FewF ManyF	8	1.2	0.554	0.099
	Day Day2 Vel Pod FewD ManyD	8	1.5	0.465	0.083
	Day Day2 Vel Sub*Pod	6	1.8	0.410	0.073
	Day Day2 Sub Vel Pod	7	1.9	0.384	0.069
	Day Day2 Vel Sub*Pod Variability	7	2.1	0.346	0.062
	Day Day2 Vel Pod Depth	7	2.2	0.329	0.059
	Day Day2 Sub Vel Pod Variability	8	2.8	0.244	0.044
	Day Day2 Vel Sub*Pod FewF ManyF	8	3.2	0.200	0.036
	Day Day2 SubVel Pod FewF ManyF	9	3.4	0.179	0.032
	Day Day2 Vel Pod Depth* Variability	8	3.5	0.176	0.031
	Day Day2 Vel Sub*Pod FewD ManyD	8	3.7	0.161	0.029
	Day Day2 SubVel Pod FewD ManyD	9	3.9	0.146	0.026
	Day Day2 Vel Sub*Pod Depth	7	4.0	0.135	0.024
	Day Day2 Sub Vel Pod Depth	8	4.1	0.126	0.022
	Day Day2 Vel Sub*Pod Depth* Variability	8	4.5	0.107	0.019
	Day Day2 Sub Vel Pod Depth* Variability	9	5.2	0.075	0.013
IV (36)	Day Day2 Sub*Pod Variability	6	0.0	1.000	0.165
	Day Day2 Vel Sub*Pod Variability	7	0.3	0.879	0.145
	Day Day2 Sub Vel Pod Variability	8	1.7	0.425	0.070
	Day Day2 Sub Pod Variability	7	1.8	0.399	0.066
	Day Day2 Pod Sub*Pod Variability	7	1.8	0.399	0.066
	Day Day2 Vel Sub*Pod Depth* Variability	8	2.0	0.367	0.061
	Day Day2 Sub*Pod Depth* Variability	7	2.0	0.366	0.061
	Day Day2 Vel Pod Sub*Pod Variability	8	2.2	0.333	0.055
	Day Day2 Sub Vel Pod Depth* Variability	9	3.4	0.184	0.030
	Day Day2 Sub*Pod	5	3.5	0.176	0.029
	Day Day2 Sub Pod Depth* Variability	8	3.8	0.147	0.024
	Day Day2 Pod Sub*Pod Depth* Variability	8	3.8	0.147	0.024
	Day Day2 Vel Pod Sub*Pod Depth* Variability	9	3.9	0.140	0.023
	Day Day2 Pod Sub*Pod	6	4.3	0.116	0.019
	Day Day2 Sub*Pod Depth	6	4.4	0.111	0.018
	Day Day2 Sub Pod	6	4.5	0.104	0.017
	Day Day2 Vel Sub*Pod	6	4.6	0.101	0.017
	Day Day2 Vel Sub*Pod Depth	7	5.0	0.080	0.013
	Day Day2 Sub Pod Depth	7	5.2	0.074	0.012
	Day Day2 Pod Sub*Pod Depth	7	5.3	0.072	0.012
	Day Day2 Sub Vel Pod	7	5.4	0.067	0.011
	Day Day2 Sub Vel Pod Depth	8	5.5	0.066	0.011
	Day Day2 Vel Pod Sub*Pod	7	5.5	0.065	0.011
	Day Day2 Vel Pod Sub*Pod Depth	8	5.9	0.051	0.008
	Day Day2 Sub*Pod FewD ManyD	7	7.5	0.024	0.004
	Day Day2 Sub Pod FewD ManyD	8	7.7	0.021	0.004
	Day Day2 Sub*Pod FewF ManyF	7	7.7	0.021	0.003

	Day Day2 Pod Sub*Pod FewD ManyD	8	8.1	0.017	0.003
	Day Day2 Sub Pod FewF ManyF	8	8.2	0.017	0.003
	Day Day2 Pod Sub*Pod FewF ManyF	8	8.5	0.015	0.002
	Day Day2 Sub Vel Pod FewD ManyD	9	8.6	0.013	0.002
	Day Day2 Vel Sub*Pod FewD ManyD	8	8.6	0.013	0.002
	Day Day2 Vel Sub*Pod FewF ManyF	8	9.0	0.011	0.002
	Day Day2 Sub Vel Pod FewF ManyF	9	9.2	0.010	0.002
	Day Day2 Vel Pod Sub*Pod FewD ManyD	9	9.3	0.009	0.002
	Day Day2 Vel Pod Sub*Pod FewF ManyF	9	9.7	0.008	0.001
V (6)	Vel Pod FewD ManyD	6	0.0	1.000	0.323
	Vel Pod Depth	5	0.5	0.768	0.248
	Vel Pod FewF ManyF	6	0.8	0.655	0.212
	Vel Pod	4	2.3	0.322	0.104
	Vel Pod Variability	5	2.8	0.250	0.081
	Vel Pod Depth* Variability	6	4.6	0.100	0.032

Table 4. Linear regression confidence model set for each instar (I-V) of *Cheumatopsyche spp.* in streamflow analysis. Models included up to thirteen parameters: an intercept and variance term, combinations of the five habitat covariates listed in Table 1, and either: frequency, many or few, which represented the total number of hours samples spend with water depths less than 5cm over the prior 30day period; duration, many or few, which represented the total number of hours of the longest single continuous time samples spent with water depths less than 5cm over the prior 30-day period; depth, the mean depth of a sample measured at 1-hr intervals over the prior 30-day period; variability, the standard deviation of depths measured at 1-hr intervals over the prior 30-day period; and depth*variability, the interaction term between depth and variability with respect to variability. Day and Day2 always co-occurred as a time of year factor. Depth*Variability interaction term was used in models with variability.

	Cheumatopsyche spp.				
Instar (# models)	Model Parameters	K	ΔAICc	relative likelihood	w(i)
I (48)	Day Day2 Vel Sub*Pod Variability	7	0.0	1.000	0.068
	Day Day2 Vel Sub*Pod Depth	7	0.4	0.825	0.056
	Day Day2 Vel Pod Sub*Pod Depth	8	0.6	0.725	0.050
	Day Day2 Vel Sub*Pod	6	0.7	0.709	0.049
	Day Day2 Vel Pod Sub*Pod	7	0.9	0.622	0.043
	Day Day2 Sub*Pod	5	1.0	0.597	0.041
	Day Day2 Sub*Pod Variability	6	1.1	0.582	0.040
	Day Day2 Vel Pod Sub*Pod Variability	8	1.2	0.547	0.037
	Day Day2 Vel Sub*Pod Depth* Variability	8	1.2	0.546	0.037
	Day Day2 Pod Sub*Pod	6	1.3	0.524	0.036
	Sub*Pod Depth	4	1.4	0.492	0.034
	Day Day2 Sub*Pod Depth	6	1.6	0.454	0.031
	Pod Sub*Pod Depth	5	1.7	0.421	0.029
	Day Day2 Vel Pod Depth	7	1.8	0.398	0.027
	Day Day2 Pod Sub*Pod Depth	7	1.9	0.395	0.027
	Day Day2 Vel Pod	6	1.9	0.378	0.026
	Day Day2 Pod Sub*Pod Variability	7	2.2	0.340	0.023
	Sub*Pod	3	2.2	0.330	0.023
	Day Day2 Vel Pod Sub*Pod Depth* Variability	9	2.3	0.318	0.022
	Pod Sub*Pod	4	2.5	0.284	0.019
	Day Day2 Pod	5	2.7	0.261	0.018
	Day Day2 Sub*Pod Depth* Variability	7	2.8	0.246	0.017
	Sub*Pod Variability	4	2.9	0.239	0.016
	Day Day2 Vel Pod Variability	7	2.9	0.232	0.016
	Sub*Pod Depth* Variability	5	3.2	0.206	0.014
	Day Day2 Pod Depth	6	3.5	0.178	0.012
	Pod Sub*Pod Variability	5	3.8	0.152	0.010
	Day Day2 Vel Pod Sub*Pod FewD ManyD	9	3.8	0.150	0.010
	Day Day2 Pod Sub*Pod Depth* Variability	8	3.8	0.150	0.010
	Pod Sub*Pod Depth* Variability	6	3.9	0.141	0.010
	Day Day2 Vel Sub*Pod FewD ManyD	8	4.0	0.137	0.009
	Day Day2 Vel Pod FewD ManyD	8	4.0	0.137	0.009
	Day Day2 Vel Pod Depth* Variability	8	4.0	0.135	0.009
	Day Day2 Vel Pod FewF ManyF	8	4.0	0.135	0.009
	Pod Sub*Pod FewD ManyD	6	4.0	0.133	0.009
	Sub*Pod FewD ManyD	5	4.1	0.129	0.009
	Day Day2 Vel Pod Sub*Pod FewF ManyF	9	4.1	0.128	0.009

	Day Day2 Pod Sub*Pod FewD ManyD	8	4.1	0.127	0.009
	Day Day2 Pod Variability	6	4.2	0.125	0.009
	Day Day2 Pod Vel Sub*Pod FewF ManyF	8	4.2	0.122	0.008
	Sub*Pod FewF ManyF	5	4.2	0.121	0.008
	Day Day2 Pod Sub*Pod FewF ManyF	8	4.2	0.120	0.008
	Pod Sub*Pod FewF ManyF	6	4.2	0.119	0.008
	Day Day2 Sub*Pod FewD ManyD	7	4.3	0.117	0.008
	Day Day2 Sub*Pod FewF ManyF	7	4.3	0.116	0.008
	Day Day2 Pod FewF ManyF	7	4.3	0.114	0.008
	Day Day2 Pod FewD ManyD	7	4.6	0.098	0.007
	Day Day2 Pod Depth* Variability	7	5.8	0.055	0.004
II (54)	Day Day2 Vel Sub*Pod Variability	7	0.0	1.000	0.058
	Day Day2 Sub Vel Pod Depth	8	0.0	0.997	0.058
	Day Day2 Sub Vel Pod Variability	8	0.1	0.940	0.055
	Day Day2 Sub Vel Pod Depth* Variability	9	0.9	0.623	0.036
	Day Day2 Vel Sub*Pod Depth* Variability	8	1.0	0.603	0.035
	Day Day2 Vel Sub*Pod Depth	7	1.0	0.593	0.034
	Day Day2 Sub*Pod Variability	6	1.0	0.593	0.034
	Day Day2 Sub Vel Pod FewD ManyD	9	1.3	0.520	0.030
	Day Day2 Sub Pod Variability	7	1.6	0.445	0.026
	Day Day2 Sub Pod Depth	7	1.7	0.428	0.025
	Day Day2 Vel Pod Sub*Pod Variability	8	1.7	0.425	0.025
	Day Day2 Vel Pod Sub*Pod Depth	8	1.7	0.420	0.024
	Day Day2 Sub Pod FewD ManyD	8	1.8	0.410	0.024
	Day Day2 Sub Vel Pod Sub*Pod Variability	9	1.9	0.396	0.023
	Day Day2 Sub Vel Pod FewF ManyF	9	1.9	0.388	0.023
	Day Day2 Sub Pod FewF ManyF	8	2.0	0.374	0.022
	Day Day2 Sub Vel Pod Sub*Pod Depth	9	2.0	0.365	0.021
	Day Day2 Sub Vel Pod	7	2.1	0.352	0.020
	Day Day2 Sub*Pod Depth	6	2.2	0.341	0.020
	Day Day2 Vel Pod Depth	7	2.2	0.330	0.019
	Day Day2 Vel Sub*Pod	6	2.4	0.297	0.017
	Day Day2 Sub*Pod	5	2.5	0.284	0.016
	Day Day2 Sub Pod	6	2.5	0.283	0.016
	Day Day2 Sub*Pod Depth* Variability	7	2.6	0.270	0.016
	Day Day2 Vel Pod Sub*Pod Depth* Variability	9	2.6	0.269	0.016
	Day Day2 Pod Sub*Pod Variability	7	2.6	0.268	0.016
	Day Day2 Pod FewF ManyF	7	2.7	0.262	0.015
	Day Day2 Vel Pod FewF ManyF	8	2.7	0.259	0.015
	Day Day2 Vel Pod FewD ManyD	8	2.7	0.254	0.015
	Day Day2 Sub Vel Pod Sub*Pod Depth* Variability	10	2.7	0.254	0.015
	Day Day2 Pod Sub*Pod Depth	7	2.8	0.241	0.014
	Day Day2 Vel Pod Variability	7	2.9	0.233	0.014
	Day Day2 Sub Pod Depth* Variability	8	3.1	0.211	0.012
	Day Day2 Vel Pod Sub*Pod	7	3.1	0.209	0.012
	Day Day2 Pod FewD ManyD	7	3.1	0.208	0.012
	Day Day2 Pod Sub*Pod	6	3.2	0.202	0.012
	Day Day2 Vel Pod	6	3.4	0.184	0.011
	Day Day2 Sub*Pod FewF ManyF	7	3.5	0.176	0.010
	Day Day2 Vel Pod Sub*Pod FewD ManyD	9	3.5	0.175	0.010
	Day Day2 Vel Sub*Pod FewD ManyD	8	3.5	0.173	0.010
	Day Day2 Pod Sub*Pod FewF ManyF	8	3.6	0.167	0.010
	Day Day2 Pod Sub*Pod FewD ManyD	8	3.6	0.165	0.010
	Day Day2 Sub*Pod FewD ManyD	7	3.6	0.163	0.009
	Day Day2 Vel Sub*Pod FewF ManyF	8	3.7	0.158	0.009

	Model				
	Day Day2 Pod Depth	6	3.7	0.157	0.009
	Day Day2 Sub Vel Pod Sub*Pod FewD ManyD	10	3.7	0.156	0.009
	Day Day2 Vel Pod Sub*Pod FewF ManyF	9	3.8	0.151	0.009
	Day Day2 Pod	5	3.8	0.149	0.009
	Day Day2 Vel Pod Depth* Variability	8	3.8	0.148	0.009
	Day Day2 Sub Vel Pod Sub*Pod	8	4.0	0.137	0.008
	Day Day2 Pod Variability	6	4.1	0.128	0.007
	Day Day2 Pod Sub*Pod Depth* Variability	8	4.1	0.126	0.007
	Day Day2 Sub Vel Pod Sub*Pod FewF ManyF	10	4.3	0.114	0.007
	Day Day2 Pod Depth* Variability	7	5.6	0.060	0.003
III (30)	Day Day2 Vel Sub*Pod Variability	7	0.0	1.000	0.198
	Day Day2 Vel Sub*Pod Depth* Variability	8	0.2	0.899	0.178
	Day Day2 Sub Vel Sub*Pod Variability	8	2.0	0.371	0.073
	Day Day2 Sub Vel Sub*Pod Depth* Variability	9	2.2	0.331	0.065
	Day Day2 Vel Pod Sub*Pod Variability	8	2.3	0.315	0.062
	Day Day2 Vel Pod Sub*Pod Depth* Variability	9	2.5	0.285	0.056
	Day Day2 Vel Sub*Pod Depth	7	2.6	0.278	0.055
	Sub*Pod Depth* Variability	5	3.9	0.140	0.028
	Day Day2 Sub Vel Sub*Pod Depth	8	3.9	0.139	0.027
	Day Day2 Vel Pod Sub*Pod Depth	8	4.1	0.128	0.025
	Sub*Pod Depth	4	4.1	0.127	0.025
	Sub*Pod Variability	4	4.1	0.127	0.025
	Sub Sub*Pod Depth	5	4.9	0.086	0.017
	Sub*Pod FewD ManyD	5	5.1	0.079	0.016
	Sub Sub*Pod Depth* Variability	6	5.2	0.074	0.015
	Day Day2 Vel Sub*Pod	6	5.3	0.071	0.014
	Day Day2 Vel Sub*Pod FewD ManyD	8	5.3	0.071	0.014
	Sub Sub*Pod Variability	5	5.3	0.069	0.014
	Sub Sub*Pod FewD ManyD	6	5.6	0.061	0.012
	Sub*Pod FewF ManyF	5	6.0	0.050	0.010
	Day Day2 Sub Vel Sub*Pod	7	6.3	0.044	0.009
	Sub Sub*Pod FewF ManyF	6	6.3	0.044	0.009
	Day Day2 Vel Pod Sub*Pod FewD ManyD	9	6.3	0.043	0.009
	Sub*Pod	3	6.5	0.039	0.008
	Day Day2 Vel Sub*Pod FewF ManyF	8	6.5	0.038	0.008
	Day Day2 Sub Vel Sub*Pod FewD ManyD	9	6.6	0.038	0.007
	Sub Sub*Pod	4	6.7	0.034	0.007
	Day Day2 Vel Pod Sub*Pod	7	6.8	0.033	0.007
	Day Day2 Sub Vel Sub*Pod FewF ManyF	9	7.6	0.023	0.005
	Day Day2 Vel Pod Sub*Pod FewF ManyF	9	7.6	0.022	0.004
IV (30)	Pod FewD ManyD	5	0.0	1.000	0.115
	Vel Pod FewD ManyD	6	0.1	0.940	0.108
	Vel Pod Depth	5	0.7	0.697	0.080
	Sub Pod FewD ManyD	6	1.0	0.605	0.070
	Pod Depth	4	1.0	0.599	0.069
	Pod Variability	4	1.8	0.405	0.047
	Vel Pod Depth* Variability	6	1.9	0.382	0.044
	Pod Depth* Variability	5	2.0	0.376	0.043
	Sub Pod Depth	5	2.4	0.301	0.035
	Pod FewF ManyF	5	2.4	0.299	0.034
	Sub Pod Sub*Pod FewD ManyD	7	2.5	0.280	0.032
	Sub Pod FewF ManyF	6	2.8	0.245	0.028
	Vel Pod Variability	5	2.9	0.231	0.027
	Vel Pod FewF ManyF	6	2.9	0.229	0.026
	Sub Sub*Pod Variability	5	3.0	0.226	0.026
	Sub Pod Sub*Pod Depth	6	3.2	0.202	0.023

	Sub Pod Variability	5	3.4	0.183	0.021
	Sub Sub*Pod Depth* Variability	6	3.4	0.179	0.021
	Sub Sub*Pod Depth	5	3.5	0.174	0.020
	Sub Sub*Pod FewD ManyD	6	3.6	0.165	0.019
	Sub Pod Depth* Variability	6	3.7	0.160	0.018
	Sub Pod Sub*Pod Variability	6	3.8	0.152	0.017
	Sub Pod Sub*Pod Depth* Variability	7	4.1	0.131	0.015
	Pod	3	4.4	0.111	0.013
	Sub Pod Sub*Pod FewF ManyF	7	4.5	0.106	0.012
	Sub Sub*Pod FewF ManyF	6	5.1	0.076	0.009
	Sub Pod	4	5.2	0.074	0.008
	Vel Pod	4	5.7	0.057	0.007
	Sub Sub*Pod	4	5.9	0.054	0.006
	Sub Pod Sub*Pod	5	5.9	0.052	0.006
V (24)	Sub Vel Pod Sub*Pod Variability	7	0.0	1.000	0.423
	Sub Vel Pod Sub*Pod Depth* Variability	8	1.9	0.387	0.163
	Day Day2 Sub Vel Pod Sub*Pod Variability	9	2.4	0.296	0.125
	Sub Vel Pod Variability	6	2.6	0.272	0.115
	Sub Vel Pod Depth* Variability	7	4.5	0.104	0.044
	Day Day2 Sub Vel Pod Variability	8	4.5	0.104	0.044
	Day Day2 Sub Vel Pod Sub*Pod Depth* Variability	10	4.5	0.103	0.044
	Day Day2 Sub Vel Pod Depth* Variability	9	6.6	0.037	0.016
	Sub Vel Pod Sub*Pod	6	8.4	0.015	0.006
	Day Day2 Sub Vel Pod Sub*Pod	8	9.0	0.011	0.005
	Sub Vel Pod	5	9.8	0.007	0.003
	Day Day2 Sub Vel Pod	7	10.2	0.006	0.003
	Sub Vel Pod Sub*Pod Depth	7	10.4	0.006	0.002
	Day Day2 Sub Vel Pod Sub*Pod Depth	9	11.0	0.004	0.002
	Sub Vel Pod Depth	6	11.7	0.003	0.001
	Day Day2 Sub Vel Pod Depth	8	12.0	0.002	0.001
	Sub Vel Pod Sub*Pod FewD ManyD	8	12.6	0.002	0.001
	Sub Vel Pod Sub*Pod FewF ManyF	8	12.6	0.002	0.001
	Day Day2 Sub Vel Pod Sub*Pod FewD ManyD	10	14.0	0.001	0.000
	Day Day2 Sub Vel Pod Sub*Pod FewF ManyF	10	14.0	0.001	0.000
	Sub Vel Pod FewF ManyF	7	14.2	0.001	0.000
	Sub Vel Pod FewD ManyD	7	14.3	0.001	0.000
	Day Day2 Sub Vel Pod FewF ManyF	9	14.9	0.001	0.000
	Day Day2 Sub Vel Pod FewD ManyD	9	15.0	0.001	0.000

APPENDIX B: SUPPLEMENTAL MATERIAL FOR CHAPTER 3

Table 1. MARK output from the best supported model [S(age) p=c(t) N(age+t)]for robust design model (using all fish from all periods) showing estimates for all parameters in the model. Parameters estimates are shown for survival (S) and abundance (N) of for both young-of-year (first estimate) and adults (second estimate within each period). Probability of capture (p) is estimated for all individuals, regardless of age. Parameters that could not be estimated are listed as fixed (gamma = temporary emigration).

Parameter	Period	Estimate	Standard Error	Lower	Upper	
1:Gamma"		0	0	0	0	Fixed
2:S	1	0.575177	0.034099	0.50737	0.640267	
3:S	2	0.575177	0.034099	0.50737	0.640267	
4:S	3	0.575177	0.034099	0.50737	0.640267	
5:S	1	0.882332	0.020274	0.836439	0.916632	
6:S	2	0.882332	0.020274	0.836439	0.916632	
7:S	3	0.882332	0.020274	0.836439	0.916632	
8:p	1	0.102334	0.01287	0.079721	0.130453	
9:p	1	0.102334	0.01287	0.079721	0.130453	
10:p	1	0.102334	0.01287	0.079721	0.130453	
11:p	1	0.102334	0.01287	0.079721	0.130453	
12:p	1	0.102334	0.01287	0.079721	0.130453	
13:p	1	0.102334	0.01287	0.079721	0.130453	
14:p	2	0.109899	0.007703	0.095685	0.12593	
15:p	2	0.109899	0.007703	0.095685	0.12593	
16:p	2	0.109899	0.007703	0.095685	0.12593	
17:p	2	0.109899	0.007703	0.095685	0.12593	
18:p	2	0.109899	0.007703	0.095685	0.12593	
19:p	2	0.109899	0.007703	0.095685	0.12593	
20:p	3	0.133655	0.007114	0.120315	0.148223	
21:p	3	0.133655	0.007114	0.120315	0.148223	
22:p	3	0.133655	0.007114	0.120315	0.148223	
23:p	3	0.133655	0.007114	0.120315	0.148223	
24:p	3	0.133655	0.007114	0.120315	0.148223	
25:p	3	0.133655	0.007114	0.120315	0.148223	
26:p	4	0.147243	0.007492	0.133156	0.162541	
27:p	4	0.147243	0.007492	0.133156	0.162541	

28:p	4	0.147243	0.007492	0.133156	0.162541
29:p	4	0.147243	0.007492	0.133156	0.162541
30:p	4	0.147243	0.007492	0.133156	0.162541
31:p	4	0.147243	0.007492	0.133156	0.162541
32:N	1	259.7489	39.2039	197.2355	353.4668
33:N	1	1495.934	179.5289	1197.273	1908.472
34:N	2	698.3	59.62614	594.6044	829.6659
35:N	2	1363.178	102.1531	1182.892	1585.086
36:N	3	1223.194	73.59297	1091.535	1380.979
37:N	3	1306.109	77.52507	1167.243	1472.125
38:N	4	1318.338	73.2988	1186.831	1475.06
39:N	4	1584.211	85.06352	1431.132	1765.553

Table 2. MARK output from multistate model [S(age) Psi$_T$(age) Psi$_G$(t) p=c(t) N(age+t)]. Parameters that could not be estimated are listed as fixed (transitions from adult to yoy). Estimates for all parameters in the model are shown with corresponding time (primary period). Parameters estimates are shown for both adults (A2, A1, and the first estimates in each group). young-of-year (Y2 and Y1, second estimate in each group). Probability of capture (p) is estimated for all individuals, regardless of age group.

Parameter		Time	Estimate	Standard Error	Lower	Upper	
1:Psi	A:Y,etc		0	0	0	0	Fixed
2:S	A2	1	0.749336	0.024759	0.697774	0.79469	
3:S	A2	2	0.749336	0.024759	0.697774	0.79469	
4:S	A2	3	0.749336	0.024759	0.697774	0.79469	
5:S	A1	1	0.749336	0.024759	0.697774	0.79469	
6:S	A1	2	0.749336	0.024759	0.697774	0.79469	
7:S	A1	3	0.749336	0.024759	0.697774	0.79469	
8:S	Y2	1	0.544066	0.06229	0.421784	0.661256	
9:S	Y2	2	0.544066	0.06229	0.421784	0.661256	
10:S	Y2	3	0.544066	0.06229	0.421784	0.661256	
11:S	Y1	1	0.544066	0.06229	0.421784	0.661256	
12:S	Y1	2	0.544066	0.06229	0.421784	0.661256	
13:S	Y1	3	0.544066	0.06229	0.421784	0.661256	
14:Psi$_T$	A:B	1	0.069308	0.011901	0.049314	0.096584	
15:Psi$_T$	A:B	2	0.069308	0.011901	0.049314	0.096584	
16:Psi$_T$	A:B	3	0.069308	0.011901	0.049314	0.096584	
17:Psi$_G$	Y:A	1	0.172108	2.81E-04	0.171557	0.17266	
18 Psi$_G$	Y:A	2	0.596071	0.054023	0.48734	0.696121	
19:Psi$_G$	Y:A	3	0.701014	4.97E-04	0.70004	0.701987	
20:Psi$_G$	Y:A	1	0.022926	6.79E-05	0.022793	0.023059	
21:Psi$_G$	Y:B	2	0.142775	0.027462	0.096895	0.205438	
22:Psi$_G$	Y:B	3	0.209256	5.08E-04	0.208261	0.210254	
23:Psi$_T$	Y:Z	1	0.08973	2.81E-04	0.089181	0.090282	
24:Psi$_T$	Y:Z	2	0.08973	2.81E-04	0.089181	0.090282	
25:Psi$_T$	Y:Z	3	0.08973	2.81E-04	0.089181	0.090282	
26:p		1	0.102643	0.014284	0.077833	0.13421	
27:p		1	0.098388	0.013764	0.07451	0.128851	
28:p		1	0.092129	0.012995	0.069627	0.120957	
29:p		2	0.141732	0.013358	0.117512	0.169984	
30:p		2	0.136102	0.01297	0.112621	0.163578	
31:p		2	0.127784	0.012386	0.10541	0.15409	
32:p		3	0.199118	0.019948	0.162876	0.241103	
33:p		3	0.191718	0.019434	0.156475	0.232708	
34:p		3	0.180712	0.018651	0.146987	0.220178	
35:p		4	0.236171	0.028453	0.184985	0.29637	
36:p		4	0.227785	0.027773	0.177946	0.286716	

37:p		4	0.21526	0.026725	0.167481	0.272214
38:N	A2	1	1577.25	200.6483	1245.565	2041.073
39:N	A2	2	298.9523	31.39832	246.5966	370.9441
40:N	A2	3	190.3779	20.65425	157.4802	239.8037
41:N	A2	4	151.0101	17.37225	124.8532	194.7766
42:N	A1	1	22.274	12.53009	7.970085	62.24917
43:N	A1	2	11.67236	2.218727	9.230595	18.95913
44:N	A1	3	21.88213	1.229418	20.5851	26.05438
45:N	A1	4	17.24375	0.851201	16.3691	20.19105
46:N	Y2	1	220.8204	32.95514	169.075	300.7288
47:N	Y2	2	32.2066	4.872064	24.37975	43.77341
48:N	Y2	3	16.40618	2.922432	11.86727	23.56374
49:N	Y2	4	8.198254	2.318515	4.760006	14.12002
50:N	Y1	1	4.64E-07	0.001175	1.98E-10	0.001088
51:N	Y1	2	7.65E-08	1.94E-04	3.26E-11	1.79E-04
52:N	Y1	3	1	9.93E-05	1	1.000092
53:N	Y1	4	1	6.56E-05	1	1.000061