

Biological and Ecological Trait Associations and Analysis of Spatial and Intraspecific Variation
in Fish Traits

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ABSTRACT

Traits provide an informative approach to examine species-environment interactions. Often, species-by-species approaches are inefficient to generate generalizable ecological relationships and do not predict species responses to environmental changes based on specific traits species possess. Multiple lines of inquiry and multi-scale approaches are best for assessing environment-trait responses. This thesis examines important questions not specifically addressed before in traits-based research. Chapter one explores biological and ecological trait associations incorporating ontogenetic diet shifts for New River fishes. Niche shift analysis as a chapter one sub-objective quantitatively support where species-specific diet shifts likely occur. Strong biological-ecological trait associations, some intuitive and others not so intuitive, were found that relate biological structure to ecological function. Improved understanding of trait associations, including what factors influence others, supports inference of ecology of fishes. Chapters two and three examine spatial and intraspecific trait variability. Chapter two specifically examines large-scale life history trait variability along latitudinal gradients for twelve widely distributed fish species, including directionality of trait variation, and hypothesizing how optimal traits change with large-scale environmental factors. Strong positive and negative patterns found include average total length of newly hatched larvae, average total length at maturation, average spawning temperature, average egg diameter, and maximum length. These five traits are correlated with other adaptive attributes (i.e. growth rate, reproductive output, and longevity/population turnover rate). In contrast to latitudinal scale, Chapter three examines trait variability of white sucker (*Catostomus commersonii*) and fantail darter (*Etheostoma flabellare*)

as a function of small-watershed scale spatial factors and anthropogenic disturbance. Toms Creek and Chestnut Creek white sucker and fantail darter displayed positive response to disturbance, contrary to past studies. Lower resource competition, and / or competitive exclusion of fishes with similar niche requirements are possible mechanisms. All three objectives support understanding of trait association and variability as a useful foundation in ecological applications and for formulating plans for conservation and management of species.

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Table of Contents

ABSTRACT	ii
Acknowledgements	iv
List of Figures.....	vii
List of Tables	ix
Introduction to Trait Associations and Variability	1

<i>Chapter 1: Identification of ontogenetic trophic niches and ecomorphological analysis of fishes of the New River, Virginia</i>	<i>5</i>
---	----------

Abstract	5
Introduction	6
Methods	9
Results	16
Discussion	20
Conclusions	25
Literature Cited.....	26
Tables and Figures	31

<i>Chapter 2: Determination of large-scale variation in life history traits within and among species for several broadly distributed North American freshwater fishes</i>	<i>48</i>
---	-----------

Abstract	48
Introduction	49
Methods	52
Results	55
Discussion	57
Conclusions	62
Literature Cited.....	63
Tables and Figures	66

<i>Chapter 3: Small-scale intraspecific variation in fish traits as a function of spatial factors and disturbance.....</i>	<i>81</i>
--	-----------

Abstract	81
Introduction	82

Methods	85
Results	92
Discussion	94
Conclusions	98
Literature Cited	99
Tables and Figures	103
Summary and Conclusions	113
APPENDIX A	116
APPENDIX B	122
APPENDIX C	124
APPENDIX D	126

List of Figures

Chapter 1 Figures

FIGURE 1. Step-wise conceptual methods model, which represents all major techniques used for niche shift and trait association analyses	31
FIGURE 2. Q-mode analysis showing the relatedness of feeding records in 2 dimensional diet space	32
FIGURE 3. Approximate diet item locations in Q-mode analysis	33
FIGURE 4. R-mode analysis showing the relatedness of food items	34
FIGURE 5. Longear sunfish trophic shift shown in Q-mode analysis	35
FIGURE 6. Greenside darter trophic niche in Q-mode analysis	36
FIGURE 7. Principal components analysis and co-inertia analysis after correction for relatedness among species	37–38
FIGURE 8. Distribution of the results of the randomization test performed to check for strength of biological and ecological trait correlation	39
FIGURE 9. Principal component analysis and co-inertia analysis before correction for relatedness among species	40–41

Chapter 2 Figures

FIGURE 1. Percent of variation explained by latitude, species effects, and random error by trait	66
FIGURE 2. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in average age at maturation versus latitude	67
FIGURE 3. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in average egg diameter versus latitude	68
FIGURE 4. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in average total length of newly hatched larvae versus latitude	69
FIGURE 5. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in longevity versus latitude	70
FIGURE 6. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in maximum length versus latitude	71
FIGURE 7. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in average spawning temperature versus latitude	72
FIGURE 8. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in length of spawning season versus latitude	73
FIGURE 9. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in average total length at age 1 versus latitude	74
FIGURE 10. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in index of egg production versus latitude	75
FIGURE 11. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in average fecundity versus latitude	76
FIGURE 12. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in average total length at maturation versus latitude	77

Chapter 3 Figures

FIGURE 1. ArcGIS map of study sites on Toms Creek, Blacksburg, VA, USA	103
---	------------

FIGURE 2. ArcGIS map of study sites on Chestnut Creek, Galax, VA, USA	104
FIGURE 3. White sucker relative condition factor between Toms Creek (n=143 specimens) and Chestnut Creek (n=103 specimens)	105
FIGURE 4. Fantail darter relative condition factor between Toms Creek (n=124 specimens) and Chestnut Creek (n=160 specimens)	105
FIGURE 5. White sucker relative condition factor according to watershed area (n=246 specimens)	106
FIGURE 6. Fantail darter relative condition factor according to watershed area (n=284 specimens)	106
FIGURE 7. Fantail darter fecundity between Toms Creek (n=74 specimens) and Chestnut Creek (n=46 specimens)	107
FIGURE 8. Fantail darter fecundity according to watershed area (n=120 specimens)	107
FIGURE 9. White sucker average egg size between Toms Creek (n=19 specimens) and Chestnut Creek (n=24 specimens)	108
FIGURE 10. Fantail darter average egg size between Toms Creek (n=74 specimens) and Chestnut Creek (n=46 specimens)	108
FIGURE 11. White sucker relative gut weight between Toms Creek (n=148 specimens) and Chestnut Creek (n=103 specimens)	109
FIGURE 12. White sucker relative condition factor between disturbed (n=51 specimens) and undisturbed (n=195 specimens) sites in Toms Creek and Chestnut Creek watersheds	109
FIGURE 13. White sucker variation in egg size between disturbed (n=8 specimens) and undisturbed (n=35 specimens) sites in Toms Creek and Chestnut Creek watersheds	110
FIGURE 14. Fantail darter relative condition factor between disturbed (n=12 specimens) and undisturbed (n=272 specimens) sites in Toms Creek and Chestnut Creek watersheds	110
FIGURE 15. Fantail darter relative gut weight between disturbed (n=10 specimens) and undisturbed (n=267 specimens) sites in Toms Creek and Chestnut Creek watersheds	111

List of Tables

Chapter 1 Tables

TABLE 1. Summary of biological traits, data scale used for each trait, and a description / note for each trait **42**

TABLE 2. Diet classifications, including diet cluster and shift means and confidence limits **43–44**

TABLE 3. Summary of positive and negative biological, ecological, and biological-ecological trait associations found in this study **45–47**

Chapter 2 Tables

TABLE 1. Life history traits used for analysis of trait variation **78**

TABLE 2. Adjusted R-square values, latitudinal direction effects, latitude coefficients, species effects, and intercept effects by trait with value significance / insignificance reported **79**

TABLE 3. Species-specific significant latitudinal direction effects by trait **80**

Chapter 3 Tables

TABLE 1. Responses, significant factors, p-values, and coefficients by species **112**

Introduction to Trait Associations and Variability

Biological and ecological relationships and trait variability in fishes have long been studied; yet, many questions remain unanswered concerning biological-ecological trait associations and spatial and intraspecific trait variability (Matthews 1998). The following thesis elucidates important trait associations, latitudinal gradients, and spatial variation mediated by scale and disturbance and sets forth useful frameworks for answering specific, trait-based questions. The results provide bases for studying broader ecological questions; these questions include ontogenetic effects on trait associations and continent-wide and watershed-specific trait variation. Trait-based studies are important since strength of correlations provide important links between structure and function and environmental gradients (Matthews 1998).

Ecological traits are specific behaviors that are easily observed and measured, but do not indicate their own driving factors. Therefore, correlation of biological traits with ecological behaviors must be identified to examine which biological traits drive specific ecological behaviors (Matthews 1998). Frimpong and Angermeier (2010) define a biological trait as “a trait that reflects physiological requirements, morphological adaptations, and life histories innate to an organism,” and an ecological trait as “a trait that reflects an organism’s environmental preferences and associated behaviors.” Many studies have reported biological and ecological trait relationships, including those which relate morphological and anatomical feeding structures and trophic ecology / niche partitioning (Moyle and Senanayake 1984; Wikramanayake 1990; Douglas and Matthews 1992; Ibanez et al. 2007). These studies provide ways to examine trait relationships, but do not account for ontogenetic diet shifts or study more than a few species when ontogeny is included (i.e. Keast 1985; Winemiller 1989; Bergman and Greenberg 1994; Eggleston et al. 1998; Scharf et al. 2000; Mol 2006; Easton and Orth 2006). Knowledge of how

ontogenetic diet shifts affect trait associations is crucial, since some fishes modify trophic patterns with growth and one cannot assume trophic behavior remains constant throughout life. I identify, quantify, and classify New River fishes' ontogenetic diet shifts and utilize this information with potentially associated biological traits to examine biological and ecological trait associations. I hypothesized New River fish species display length-based ontogenetic diet shifts, representing changes between distinct trophic classifications. Additionally, I hypothesized New River fish biological traits correlate with ecological traits, even after accounting for ontogenetic diet shifts.

Since all traits do not vary similarly, understanding how and why traits vary can help identify which traits are especially useful for making ecological predictions (Blanck and Lamouroux 2007). Spatial life history patterns provide a unique perspective to understanding trade-offs, giving insight into how species and, more specifically, populations modify their traits to fit advantageous life history strategies and maximize fitness (Pianka 1970; Stearns 1989). Few studies have assessed large-scale trait variability, and even fewer studies comprehensively examine large-scale variability to determine which traits are best for testing ecological hypotheses (Matthews 1998). Only Blanck and Lamouroux (2007) comprehensively examined large-scale spatial and intraspecific life history trait variation along a latitudinal gradient. Comparison of trait variation levels among species is informative since traits that vary more within species than between species are not well suited for mechanistic hypothesis testing (Lamouroux et al. 2002; Goldstein and Meador 2004). Herein, I support significant life history trait latitudinal relationships and identify strong correlations by adaptive attribute group (i.e. growth rate, reproductive output, and longevity / population turnover rate). Blanck and Lamouroux (2007) predicted certain life history traits are better suited than other life history

traits to address topical ecological applications, including fisheries conservation and management. I hypothesize intraspecific variation of life history traits will be less than interspecific variation.

Trait-based approaches are effective for examining disturbance-mediated species responses by disturbance type and level (McFarlane and Franzin 1978; McFarlane and Franzin 1980; Munkittrick and Dixon 1988a; Munkittrick and Dixon 1988b; Munkittrick and Dixon 1989a; Munkittrick and Dixon 1989b). Small-scale, population-level bioassessment indicates relative ecosystem condition and responses to environmental stressors (Power 2007) such as agriculture and urbanization (Paul and Meyer 2001; Scott 2006; Lussier et al. 2008). Additionally, small-scale bioassessment approaches provide site-scale insight useful in evaluating local disturbance effects (Munkittrick and Dixon 1989a). The New River drainage currently lacks specific, small-scale bioassessments of trait variability and natural spatial variation. I used small-scale bioassessment to examine spatial and disturbance-mediated influences on distribution of traits for two New River species. New River-specific spatial and disturbance effects provide a case study to address more generalizable trends. I hypothesized spatial and disturbance-mediated variation will be significant between and within watersheds. Further, I hypothesized significant variation between anthropogenically disturbed and undisturbed sites after accounting for natural variation.

Chapter one identifies New River fishes' species-specific ontogenetic niche shifts using cluster analysis by grouping food items into trophic categories, and subsequently identifying niche shifts. Biological and ecological trait associations are quantitatively tested using co-inertia analysis, showing significant patterns. Patterns of association were apparent among biological and ecological traits and often between biological and ecological traits. Chapter two investigates

life history traits related to growth rate, reproductive output, and longevity / population turnover rate and how these vary with latitude. General linear models identify trait variation in 12 widely distributed species. Chapter three examines spatial and disturbance-mediated effects on white sucker (*Catostomus commersonii*) and fantail darter (*Etheostoma flabellare*) trait variation, including implications of the use of these traits for bioassessment.

*Chapter 1: Identification of ontogenetic trophic niches and ecomorphological analysis of fishes
of the New River, Virginia*

Abstract

Biological-ecological trait associations provide a lens to view and understand how traits drive ecology. Ontogenetic diet shifts are important factors in trait-based research, but most ecomorphological studies do not or very limitedly assess their overall role in ecological interactions. The current study quantitatively assessed ontogenetic trophic shifts for a diverse group of fishes (i.e. New River basin) and incorporated these shifts into biological-ecological trait associations. I hypothesize there are ontogenetic diet shifts in feeding ecology and, biological traits correlate with ecological traits for New River fishes. Trophic-behavior (i.e. ecological-trait) data were collected from primary literature. Biological traits were obtained from 1) primary literature, 2) high resolution images, 3) measurement of field-caught specimens, and 4) existing databases. Non-metric multidimensional scaling identified overall niche breadth (i.e. Q-mode) and diet item relatedness (R-mode). Cluster and niche shift analyses identified and quantified species-specific trophic clusters and associated diet shifts from the Q-mode analysis. Several steps prepared biological data for analysis, including imputation, phylogenetic correction, and ranging. Principal component analysis summarized results from the niche shift analysis and biological dataset. Co-inertia analysis tested for correlations within and between biological and ecological traits. Niche shift analysis showed 37 species exhibited definable diet clusters by body length, and the majority (19 of 37) have ontogenetic niche shifts. Co-inertia analysis showed strong relationships based on co-variability explained by the principal components analysis (83%) and a randomization test ($p = 0.001$). Results showed many positive and negative trait associations, both between and among biological and ecological traits. This

study found some unexpected niche shift and trait association patterns; some were explainable (such as patterns involving shape, mobility, and prey consumption), and others are newly found patterns and emphasize study importance (such as patterns relating to trophic behavior between life stages). Niche shift and trait association results provide a sound basis for inferring a species' ecology from its biology.

Introduction

Frimpong and Angermeier (2010) defined a biological trait as “a trait that reflects physiological requirements, morphological adaptations, and life histories innate to an organism,” and an ecological trait as “a trait that reflects an organism's environmental preferences and associated behaviors.” Biological and ecological trait associations (i.e. ecomorphology) improve knowledge about which biological (i.e. morphological) factors drive observed ecological behaviors (Kotrschal 1989; Yamaoka 1997; Hahn and Cunha 2005). Much biological and ecological fish research exists, including several ecomorphological comparisons (see above), but none of these studies comprehensively incorporate species-specific ontogenetic niche shifts and assess their influence on ecological classifications and groupings. For example, Kotrschal (1989) examined blennioid fish trophic ecomorphology, but failed to assess how length affects these relationships. Most ecomorphology studies are site-specific and / or specifically focus on species with particular life-history types (i.e. periodic, opportunistic, etc.) (i.e. Wikramanayake 1990; Winemiller 1991; Douglas and Matthews 1992; Norton 1995; Piet 1998; Casatti and Castro 2006). I am not aware of a non-site-specific, comprehensive, quantitative assessment of biological and ecological trait relatedness that considers many species across many populations per species.

Species' biological traits and proximate environmental factors determine ecological behaviors (Wootton 1998; Frimpong and Angermeier 2010). An organism's functional traits influence growth / biomass maintenance, reproduction, and survival, contributing to performance and individual fitness (Arnold 1983; Frimpong and Angermeier 2010). Functional trait trade-off studies showed how species partition resources to co-exist and form ecological niches, linking biological traits and ecology (Dutta 1979; Liem 1980; Lauder 1983; Westneat 1994; Bremner et al. 2006; Litchman et al. 2007). McGill et al. (2006) established functional traits and trade-offs as key elements for defining species-specific ecological niches. In contrast, some studies suggest that biological traits and life histories are inadequate predictors of ecological behaviors, primarily due to factors unrelated with trait associations such as large-scale environmental patterns (Wainwright and Lauder 1992; Lasram et al. 2008).

Ecomorphological studies were first implemented in the 1970's across many taxa (Matthews 1998). Gatz (1979) initiated the ecomorphological study of fishes by examining morphological influences on community structure, including several trophic traits (i.e. mouth size, mouth position, gut length, and body shape/proportions). Subsequent studies further link biological traits to feeding behavior, including associations between trophic types and mouth position, barbel presence-absence, and gut characteristics (Moyle and Senanayake 1984; Wikramanayake 1990; Douglas and Matthews 1992; Ibanez et al. 2007). Other studies found biological traits accurately predict habitat associations at microhabitat and larger scales (Felley 1984; Moyle and Senanayake 1984; Page and Swofford 1984; Wikramanayake 1990; Douglas and Matthews 1992; Wood and Bain 1995; Lamouroux et al. 2004). Additionally, distinct biological trait-states are associated with species co-occurrence via ecological niche partitioning (Winston 1995). In studies presented above, biological-ecological trait relationships are

associated in comparative population- and community-level analyses. More studies than not provide a strong argument for biological and ecological trait association validity.

Studies of ecomorphology often do not consider phylogenetic relationships between species (i.e. Gatz 1979; Douglas 1987; Strauss 1987), which is a major confounding effect in this type of study (Matthews 1998). Douglas and Matthews (1992) warn against making broad ecomorphological comparisons between families without phylogenetic correction for relatedness (Matthews 1998). Phylogeny is part of comparative studies that must be corrected for before false assumptions from uncorrected and inaccurate results are made (Felsenstein 1985; Diniz-Filho et al. 1998). When studies correct for phylogenetic relationships, correction can be done to varying degrees. For instance, Douglas and Matthews (1992) reduced their study species to one family, effectively constraining phylogenetic influence.

Ecomorphological applications examine important topical issues in fisheries science. For instance, Goldstein and Simon (1999) classified fish trophic statuses for index of biological integrity (IBI) scores using ecomorphological comparisons. Additionally, ecomorphology was used to compare habitat quality between artificial (i.e. man-made) and natural Mediterranean reef structures (Recasens et al. 2006). Motta et al. (1995) outlined several ecomorphological applications, including combinations with and lessons learned from other disciplines (i.e. such as phylogenetics, ecophysiology, and biomechanics). In addition, Motta et al. (1995) proposed ecomorphological research topics that warrant further study such as locomotion, foraging, respiration, reproduction, and sensory mechanisms; they also suggested ways each topic should be applied. Overall, applied ecomorphology grapples with implementation of theoretical, but supported relationships, and explores how certain factors affect these processes (Motta et al. 1995).

Biological traits are frequently used to predict trophic ecology (Moyle and Senanayake 1984; Wikramanayake 1990; Douglas and Matthews 1992; Ibanez et al. 2007), but trophic niches can vary widely and change significantly with maturation. Biological changes facilitate ontogenetic diet shifts during growth and development, which are distinct switches in food items. Not accounting for ontogenetic diet shifts and resulting trophic changes throughout lifetimes is a major error when classifying species into trophic niche groups. Past studies examined ontogenetic shifts and established their importance in more accurately defining ecological relationships between and within species (i.e. Keast 1985; Winemiller 1989; Bergman and Greenberg 1994; Eggleston et al. 1998; Scharf et al. 2000; Mol 2006; Easton and Orth 2006). However, these studies fall short by not identifying universally applicable patterns in the following two ways: biological mechanisms are not well defined and / or species-specific mechanisms are not generalizable. A broader ecomorphological analysis including ontogenetic diet shifts would solve these inconsistencies. For instance, candy darter (*Etheostoma osburni*) trophic behavior and trait associations would be inferable from more common species within the same genus, such as fantail darter (*Etheostoma flabellare*). My research objectives were: 1) define ontogenetic diet shifts for New River fishes, and 2) investigate relationships between biological traits and ecological traits (trophic niches) of New River fishes. I hypothesized there are ontogenetic diet shifts in feeding ecology and, biological traits correlate with ecological traits for New River fishes.

Methods

Study System:

The New River drainage, located in North Carolina, Virginia, and West Virginia, is a northward flowing Ohio River tributary which drains 18,085 km². The New River and its tributaries support significant freshwater flora and fauna diversity, including several endemic and relatively rare species. The New also supports many introduced species and non-native populations, especially fishes (Jenkins and Burkhead 1993). For this study, the New River drainage contained sufficient species diversity for data collection obtained from specimens and literature. Virginia Tech's close proximity for specimen collection was also important. Subsequently, collected data proved analytically sufficient for hypothesis testing of biological-ecological trait relationships. Figure 1 shows details of all methodological steps used in this chapter.

Field Collections:

Fish specimens were collected during summer 2008 for biological trait assessment. These specimens were taken from throughout Toms Creek and in portions of Crooked Creek within the New River drainage in conjunction with other sampling. Samples consisted of as many fish species and individuals as possible. Primarily, average peritoneum color and average relative gut length were measured from these specimens.

Ontogenetic Diet Shift Data Collection:

Synthesizing information across many studies provides opportunities to incorporate ontogenetic shifts in trophic ecology. This is not always included in trophic studies, but provides means to answer research questions without sampling every New River fish species at every life stage. All sixty-six New River basin fish species (Jenkins and Burkhead 1993) were initially

researched for volume, count, and presence-absence of diet-at-length relationships, revealing for many species if and when length-specific ontogenetic diet shifts occur. Ontogenetic diet shift considerations enable differentiation of trophic stages, which will shed light on biological-ecological trait associations at these different stages. An extensive primary and secondary food habit literature search was conducted throughout each species' North American range; data was recorded using binary coding. Initial data collection utilized many primary journal articles, but also included many secondary sources (i.e. Wallus et al. 1990; Jenkins and Burkhead 1993; Kay et al. 1994; Simon and Wallus 2004; Simon and Wallus 2006; Wallus and Simon 2006; Wallus and Simon 2008). Citation-based literature searches helped find additional trophic information from the above sources, other state species accounts, and many journal articles. Page and Burr (1991) aided further target species data expansion using distribution maps contained within. Appendix A contains all sources used in this study. Some species ($n = 16$) were excluded due to scant diet-at-length data. All data were stored and managed before analysis in Microsoft Excel.

Data Visualization:

Non-metric multidimensional scaling visualizes spatial relationships between dissimilar descriptors and objects in n -dimensional space (Shepard 1962a; Shepard 1962b; Kruskal 1964a; Kruskal 1964b; Cox and Cox 2008). In non-metric multidimensional scaling, associations between diet items and resulting diet item classifications are crucial for trophic niche determination. Non-metric multidimensional scaling was used to find two-dimensional relationships among individual, population-level diet records (Q-mode analysis) and between diet items (R-mode analysis) (Legendre and Legendre 1998). As expected, Q-mode analysis revealed the overall niche space for studied species. All analyses were conducted in Statistical

Analysis Software (SAS, version 9.2). Jaccard similarity matrices normalized binary (in this case, diet item presence-absence), non-metric multidimensional scaling data (Jaccard 1901). Q-mode pattern interpretation used the strength of Spearman rank correlations of diet items on each ordination axis (Spearman 1904); stronger Spearman rank correlations represented stronger association of a diet with an axis or gradient (Legendre and Legendre 1998; Der and Everitt 2002). Relative Spearman rank correlation strength indicated diet item(s) significance (p-value < 0.05) based on each trophic record's Q-mode analysis placement.

Cluster and Niche Shift Analysis:

Diet records were examined by species (n = 50), utilizing raw data and species-specific Q-mode graphs produced in SAS (version 9.2). Data constraints (i.e. too few records) excluded several species (n = 13) from trophic shift analysis. Food items were condensed by phylogenetic relatedness (i.e. the more closely related, the more likely they were grouped), providing fewer, but more concise trophic classifications; this removed many redundant trophic categories. Twenty food item classifications resulted. Food items categories were divided into juvenile and adult classes to differentiate between trophic stages. Ten distinct, potential food item classifications were possible in each class (i.e. juvenile or adult); these included surface/column invertebrate, benthic macroinvertebrate, zooplankton, insect/invertebrate, large crustacean, plant material, fish, shrimp/mysis/amphipod, benthos/eggs, and undefined plankton.

Species-specific trophic niches (n = 37 species) were delineated from diet item clusters. Qualitative/visual cluster analysis determined species-specific diet shift presence-absence (if present, multiple clusters were associated with distinct length classes). By species, clusters were mapped onto one (if no shift was present) or more niches. Next, cluster-specific diet items aided

species classification into length-based feeding groups. Mean and a 95% confidence interval (representing 2 standard errors) of fish length records found in each cluster quantified species-specific niches in conjunction with diet items for each cluster. For each species showing a niche shift, the position of the shift was determined between the two cluster means using length variances:

$$(1) \text{ Niche Shift Weighting Factor } (k) = S_1^2 / (S_1^2 + S_2^2) ,$$

where S_1^2 represents variance of the lesser mean length niche and S_2^2 represents variance of the greater mean length niche. Next, niche shift mean and variance determined fish lengths at which diet shifts empirically occur:

$$(2) \text{ Niche Shift Position } (C) = M_1 \times (1 + k) ,$$

where M_1 represents mean length of the lesser length niche and k represents the variance-weighted average distance between the two niches. Niche shift location variance and standard error were calculated as follows:

$$(3) \text{ Var } C = (1 + k)^2 \times (S_1^2) ,$$

$$(4) \text{ Standard Error of } C = \sqrt{(\text{Var } C)}$$

Niche shift confidence intervals (95%) represent two standard errors from niche shift means.

Biological Trait Data Collection and Imputation:

Twelve biological traits were researched, including average age at first reproduction, average length at first reproduction, maximum known or asymptotic total length, relative eye diameter, barbel presence or absence, shape factor, swim factor, relative mouth size, average mouth position, average jaw angle, average peritoneum color, and average relative gut length (Table 1). Biological traits were hypothesized to correlate with ecological traits including diet,

feeding location, and ontogenetic changes in these traits. Biological trait values came from examining field-caught specimens, measuring high resolution images (Jenkins and Burkhead 1993), Virginia Department of Game and Inland Fisheries databases (<http://www.dgif.virginia.gov/wildlife/fish/>), the FishTraits database (Frimpong and Angermeier 2009: <http://www.cnr.vt.edu/fisheries/fishtraits/>), and Jenkins and Burkhead (1993).

A few species were missing some data and imputation was chosen to fill these gaps since it uses closely related species. Imputation expanded biological and ecological trait datasets before analysis by extrapolating 1-2 missing trait values per species from closely related species. Eliminating species missing minimal data (i.e. the 1-2 missing trait values per species) would have excluded about 20% of species and greatly reduced statistical power. Values were imputed for non-readily caught species or species with scant literature representation. Average peritoneum color and average relative gut length for logperch (*Percina caprodes*), swallowtail shiner (*Notropis procne*), and longear sunfish (*Lepomis megalotis*) are examples. Published Appalachian darter (*Percina gymnocephala*) average age at first reproduction does not exist or was not found, so it was imputed from other *Percina* species. Kanawha darter (*Etheostoma kanawhae*), Appalachian darter (*Percina gymnocephala*), and Roanoke darter (*Percina roanoka*) lacked published diet records, and were imputed from species within the same genus. Appendix B and C contain raw biological and ecological trait datasets.

Phylogenetic Correction and Ranging:

Prior to statistical analysis, phylogenetic correction for relatedness between species was needed. The FishTraits database provided family phylogenetic positions derived from Nelson (2004). Family phylogenetic position represents numerical relatedness of families based on

derived characters (Grafen 1989), which was used because the study species represent a broad phylogenetic span (Olden et al. 2006). Derived family characters are minimal when considering many species from many families, allowing family phylogenetic position to be an effective individual phylogeny proxy (Olden et al. 2006). Logistic regression of traits against family phylogenetic position provided Pearson (i.e. Chi-square) residuals and effectively removed phylogenetic constraints from data. Ranging converted data residuals into all non-negative interval values (i.e. between 0 and 1) after phylogenetic correction:

$$(5) y'_i = (y_i - y_{min}) / (y_{max} - y_{min}) ,$$

Where traits were adjusted by the most negative residual value ($y_i - y_{min}$) and divided by the data range ($y_{max} - y_{min}$) (Legendre and Legendre 1998).

Principal Component and Co-inertia Analyses of Biological and Ecological Trait Associations:

Principal component analysis (PCA) (Jolliffe 2002) prepared biological and ecological datasets for co-inertia analysis. Co-inertia analysis (Doledec and Chessel 1994; Dray et al. 2003; Dray et al. 2007) determined correlation between biological and ecological traits in R statistical analysis software (Freeware: <http://www.r-project.org/>) with the ade4 package (Thioulouse et al. 1997; Dray et al. 2007). Additionally, co-inertia analysis results are displayed in an R bi-plot. A randomization test examined significance of correlation between trait associations (Dray et al. 2007).

Trait associations (i.e. between 2 or more traits) were interpreted directly from the co-inertia analysis bi-plot. Traits positively correlated when their vectors oriented closely within the same quadrant. The closer vectors were spatially, the more positive relationships were when comparing traits within or between plots. Traits negatively correlated when their vectors oriented

in an opposite quadrant, both within or between plots. Between species comparisons follow similar patterns concerning positive and negative associations, but use species-specific vector proximity, direction, and magnitude to assess data patterns (Doledec and Chessel 1994; Dray et al. 2003; Dray et al. 2007).

Results

Trophic Shift Analysis:

A total of 879 population level trophic records for 50 species were analyzed. Species exhibited many diet choices and combinations (Figure 2), often with species-specific adult and juvenile trophic niches (Table 2). For instance, alewife (*Alosa pseudoharengus*) and largemouth bass (*Micropterus salmoides*) trophic niches differed greatly throughout each species' life cycle, but alewife exhibited a unique, species- and stage-specific planktivore / invertivore trophic niche (Table 2). Qualitative niche space partitioning showed approximate food item placement in Q-mode analysis (Figure 3). Diet-item relatedness exhibited intuitive patterns, often between diets thought to be closely related. For instance, fish and large crustacean (mainly crayfish) consumption occurred in very close diet space proximity and were observed qualitatively together in many vertebrate / invertebrate predator diet records. Conversely, benthos and zooplankton are very different, not closely related food items, reflecting distant diet space proximity due to stream bed versus water column placement (Figure 4).

Thirty-seven species displayed definable diet clusters by body length. Feeding patterns were classified as one or more trophic types, including omnivore, generalist omnivore, invertivore, generalist invertivore, vertebrate predator, and planktivore (Table 2). Trophic shifts occurred when species ($n = 19$) switched feeding patterns, which were portrayed by distinct,

body length-specific diet clusters (Figure 5). No species had greater than one distinguishable trophic shift (two clusters). Generalist feeder species maintained the same broad trophic niche throughout life (Table 2). Specialist feeder species maintained a narrow trophic niche throughout life (Figure 6). Some species appeared to make small food item changes (i.e. such as changing from one benthic macroinvertebrate to another), but did not shift food items enough to warrant calling the difference a niche shift (Table 2).

Co-Inertia Analysis of Biological and Ecological Trait Associations:

Multiple analyses exhibited strong relationships between biological and ecological traits. High co-variability (83%) was explained by principal component analyses using two axes (Figure 7). A randomization test was significant ($p=0.001$), further indicating strong relationships between biological and ecological traits (Figure 8). Co-inertia analysis, representing biological, ecological, biological-ecological, and species-specific trait correlations is shown without phylogenetic correction (Figure 9). Co-inertia analysis trait placement and vector orientation proved much different before and after correction for species relatedness, making it a significant interpretive factor (Figures 7 and 9).

Overall, traits exhibit many positive and negative correlations, both between and within biological and ecological trait datasets (Table 3). Positive biological trait correlations show three relationships within specific trait types (i.e. reproductive length and age) and between traits based on structure and function (i.e. eye diameter v. mouth and jaw traits) (Table 3). Positive ecological trait correlations exhibit nine relationships, a threefold increase over positive biological trait correlations. Seven correlations logically follow widely observed patterns. Juvenile and adult diets remain constant in three of nine instances, including no shift away from

benthic macroinvertebrate consumption. One correlation indicates incorporation of new diet items, but no shift away from previously consumed items; the lone example is juvenile insect / invertebrate consumption v. adult insect / invertebrate and adult fish consumption. Two of nine positive ecological trait correlations exhibit different diet items within the same life stage; this includes juvenile surface / column invertebrate and juvenile shrimp / mysis / amphipod consumption. Three of nine correlations show juvenile to adult food item shifts. One of three associations exhibits a logical juvenile to adult transition; the lone example is juvenile plant v. adult surface / column invertebrate. Two of nine patterns are counterintuitive, including a transition from juvenile large crustacean to adult zooplankton consumption (Table 3); longear sunfish is an example (Figure 7).

Negative biological trait correlations show two relationships between traits based on structure and function (i.e. shape factor v. mouth traits) (Table 3). Negative ecological trait correlations exhibit six relationships, a threefold increase over negative biological trait correlations. Four correlations logically follow widely observed patterns. One correlation shows a single prey type is constantly consumed and effectively excludes a drastically different prey item; this was found in juvenile and adult benthic macroinvertebrate v. juvenile zooplankton consumption. Another correlation suggests certain food items within a life stage will not be consumed; this is apparent between adult benthic macroinvertebrate v. adult large crustacean consumption. Another correlation shows certain food items between life stages will not be consumed during ontogeny; this is evident between juvenile benthos / eggs v. adult surface / column invertebrate consumption. Another correlation exhibits how some fishes retain dietary patterns throughout life and consume additional, related food types with ontogeny / growth, but do not consume vastly different food types; an example is juvenile insect / invertebrate, adult

insect / invertebrate, and adult fish v. adult plant and adult shrimp / mysis / amphipod consumption. Two of six patterns are counterintuitive, including a transition from juvenile large crustacean and adult zooplankton to juvenile fish, juvenile benthos / eggs, and adult benthos / eggs consumption (Table 3).

Eight positive biological-ecological trait correlations relate biological structure(s) to ecological function(s) (Table 3). For instance, barbel presence-absence is associated with juvenile benthic macroinvertebrate consumption. Correlations represent adult, juvenile, and adult / juvenile diet item combinations. Many biological traits have correlations, including those related to length, mobility, reproduction, body shape, and feeding apparatuses. Seven negative biological-ecological trait correlations show inverse biological and ecological trait relationships. An example is juvenile and adult planktivory v. barbel presence-absence. Correlations represent juvenile and adult diet item combinations. Many biological traits have correlations, including those related to length, mobility, reproduction, and feeding apparatuses (Table 3). Associations listed above are representative examples; Table 3 contains all the current study trait associations.

Species bi-plots from co-inertia analysis vector proximity, direction, and length show interesting interspecific biological and ecological trait relatedness patterns. Several fish species display highly divergent traits due to relatively longer, opposite facing vectors; bluntnose minnow and largemouth bass are examples (Figure 7). Several other fish species exhibit highly convergent traits due to relatively longer, same direction vectors; spotted bass and largemouth bass are examples (Figure 7). Many species show partial trait relatedness by convergent, but not precisely aligned, vectors; spottail shiner and creek chub are examples (Figure 7).

Discussion

Trophic Shifts:

Analyses effectively identify trophic patterns that support the hypothesis that length-based ontogenetic diet shifts exist and represent changes between distinct New River fish trophic classifications. Results found several general and widely applicable diet patterns, some of which fit known patterns (Table 2). Newly found diet patterns facilitate future trait research for the same and similar fish species, allowing comparisons, contrasts, and missing trait value imputations. Trophic imputations provide bases for inference on trophic ecology in given species without explicit behavior measurement. An example, first presented in the Introduction, included trophic behavior inference for candy darter from fantail darter results; this pattern is supported since fantail darter's trophic niche was definable. Reinforced interspecific or intraspecific patterns of biological-ecological trait associations provide fisheries researchers and managers useful generalizations for hypothesis testing and practical applications. For instance, managers could develop predictive, system-specific ontogenetic trophic behavior and feeding relationship models from study results. A review of current trophic modeling studies indicates they rarely assess ontogeny as an important analytical factor, which may affect study results.

Current study results were compared to Goldstein and Simon (1999), which summarized many known, species-specific, North American trophic behavior patterns. Several game fish species show multiple diet item types throughout ontogeny and very similar species-specific diet patterns between studies; examples include rock bass (*Ambloplites rupestris*), yellow perch (*Perca flavescens*), and striped bass (*Morone saxatilis*). However, the current study increases resolution and includes statistically characterized, length-specific diet shifts; Goldstein and Simon (1999) did not. Such findings emphasize need for increased food item detail and finer

trophic analysis resolution. Several species consumed single, similar prey types throughout ontogeny in Goldstein and Simon (1999) and the current study; examples include rosyside dace (*Clinostomus funduloides*), cutlips minnow (*Exoglossum maxilingua*), fantail darter (*Etheostoma flabellare*), and logperch (*Percina caprodes*). The current study provides species-specific trophic behavior bounds (mean body length and a two-standard-error confidence interval) for species without trophic shifts (Table 2); Goldstein and Simon (1999) used only expert judgment to assign niche-at-length shifts. Bounds provide useful length-based feeding information for species without trophic shifts and identify partial trophic behavior patterns if diet shifts are still suspected or later found.

Diet shift presence-absence and/or diet item types do not coincide for several species between the current study and Goldstein and Simon (1999). Two factors drive observed diet variability: 1) analyses used mostly different studies and 2) the current study uses many more diet records covering entire ranges of the study species. Cyprinids represent many species with different trophic behavior between studies, including golden shiner (*Notemigonus crysoleucas*), bluntnose minnow (*Pimephales notatus*), longnose dace (*Rhinichthys cataractae*), and creek chub (*Semotilus atromaculatus*). Cyprinids exhibit study-based differences because 1) less studies were analyzed per species (data availability problem) and 2) cyprinids represent 12 of 37 species analyzed, more than all other families (i.e. greater possibility of trophic behavior variation) (Table 2).

Trait Associations:

Results effectively identify multiple positive and negative biological and ecological trait associations per comparison (i.e. positive biological, negative biological-ecological, etc.) (Table

3). These correlations support hypothesized associations; the majority follows known or logical reasoning. Newly found trait associations facilitate future ecomorphological research through generalized and species-specific correlation-based structure and function hypothesis testing. Trait associations guide conservation and management decisions involving population / community responses to habitat modification, exotic species invasions, and species co-occurrence / community structure mechanisms (Frimpong and Angermeier 2010). For instance, managers can utilize trait associations to predict how species compositions will change due to habitat modification and exotic species invasions largely based on species presence and traits they possess. Like trophic shifts, newly found trait associations facilitate future trait research for the same and similar fish species, allowing comparisons, contrasts, and missing trait value interpolations. For example, candy darter trait associations are able to be interpolated from closely related species within the same genus, many of which are analyzed herein. Overall, trait associations provide bases for species-specific pattern prediction without explicit association assessment.

Several un-interpretable or counterintuitive correlations follow similar patterns between several comparisons, including positive and negative ecological and biological-ecological associations (Table 3). This section of discussion examines counterintuitive patterns. Several previous studies showed zooplankton consumption occurred during juvenile fish stages, followed by an ontogenetic shift to more energy-efficient prey (i.e. fish, crayfish, and/or insects) (Wainwright and Richard 1995; Hjelm et al. 2000; Hjelm et al. 2003; Johansson et al. 2006; Russo et al. 2007; Wanink and Joordens 2007; Wells et al. 2008). The current study shows large crustacean consumption during juvenile fish stages, followed by an ontogenetic shift to zooplankton during adulthood (Table 3); longear sunfish is the lone example (Figure 7). Juvenile

large crustacean and adult zooplankton consumption positively correlates with average relative gut length in the current study (Table 3); no other studies support this association either and another similar patterns exists (i.e. juvenile large crustacean, adult surface / column invertebrate, and adult zooplankton negatively correlates with average jaw angle) (Table 3). I hypothesize prey availability, especially in generalist feeders such as longear sunfish, drive unexpected trophic behavior patterns and are caused by a small subset of species and site-specific studies, rather than species-specific diet selectivity.

The current study shows associations between juvenile fish and adult benthos / egg consumption (Table 3), which is intuitively less surprising than the ontogenetic large crustacean-zooplankton transition. Several sunfish and minnow species are opportunistic benthic feeders as adults (Snyder and Peterson 1999; Garcia-Berthou and Moreno-Amich 2000), which drives this correlation herein. Many secondary-source syntheses considered benthos / egg consumption an ecological trait negatively correlated with mouth angle (Scott and Crossman 1973; Becker 1983; Jenkins and Burkhead 1993; Etnier and Starnes 1994). These syntheses sometimes mentioned opportunistic benthos and egg consumption by sunfish and minnow species. The current study found benthos / egg consumption positively correlates with mouth angle (Table 3). Sunfish and minnow trophic behavior and mouth angle drive this correlation herein as well.

The current study further supports many previously supported or assumed trait relationships, including associations within and between life stages, biological traits (i.e. structure), and ecological traits (i.e. function) (Table 3). This discussion focuses on biological and biological-ecological associations since life stage based and ecological trait relationships were analyzed in the previous section. Matthews (1998) suggested head morphology as the primary mechanism that constrains trophic behavior. Mouth position suggests where fish feed:

fish with negative mouth position are likely benthic feeders and fish with positive mouth position are likely water column feeders. Additionally, shape factor contributes to trophic behavior: fish species with lower shape factors are usually better swimmers (Jenkins and Burkhead 1993). Rincón et al. (2007) showed mouth size and position negatively associated with shape factor in several minnow species, which increased foraging success. The current study further supports the negative correlation between mouth characteristics (i.e. mouth size and position) and fish shape (Table 3). Barbels facilitate benthic trophic behavior via taste/touch feeding mechanisms (Evans 1952; Jenkins and Burkhead 1993). The current study shows barbel presence positively correlates with benthic prey consumption, and vice versa (Table 3). Past studies associated many species' eye diameter with mouth characters, including mouth size, mouth position, and jaw angle (Turner 1921; McComas and Drenner 1982; Matthews et al. 1982; Paine et al. 1982); the current study does as well (Table 3).

Several other morphological characters drive ecomorphological associations besides mouth characters. The current study shows positive associations between asymptotic total length and swim factor (Table 3). Past studies showed fish length and mobility drive trophic interactions since larger fishes require higher swim factors to fulfill higher energetic demands (Pauly 1989; Matthews 1998; Olden et al. 2006). Efficiently caught large crustaceans are great nutrient sources (Pauly 1989; Matthews 1998). Greater asymptotic total length and swim factor are correlated with large crustacean consumption in the current study (Table 3). Additionally, sight feeders positively and very strongly associate juvenile benthos / egg consumption with relative eye diameter (Table 3); visually-intensive efforts are needed to find unevenly distributed / rarer food items (Jenkins and Burkhead 1993).

The current study contains certain limitations that can affect study results. First, data collection could not assure 100% of known data for every species would be collected and included in this study. Second, diet records with very broad or no niche-at-length information could not be included herein, which reduced samples sizes for many species. However, the current study includes substantial niche-at-length records for species included in analysis; if not, species were excluded herein. Despite study limitations, future research applications can benefit from current study results. Examples include applicability of the current studies' novel approach to quantifying niche-at-length relationships and associations between structure and function. Specifically, future research studies can use the current study to quantify trophic shifts without explicit measurement of specimens or individual, literature-based data collection in each study. However, I recommend further research into multiple trophic shifts within species. The current study found, at most with the resolution used, one trophic shift per species and may not be indicative of all trophic shifts at different resolutions throughout species-specific ontogenies.

Conclusions

Novel cluster and niche shift analyses effectively identified presence-absence of and quantified ontogenetic diet shifts for many New River fish species. Current study cluster and niche shift methods increase resolution over past studies (i.e. expert opinions and quantitative species-specific studies) and provide future research and management efforts with solid bases for niche shift determination. Co-inertia analysis effectively integrated current study ontogenetic niche shifts into numerous biological, ecological, and biological-ecological trait associations, especially those related to structure-function mechanisms. The current study confirms known and provides newly found trophic niche shift and trait association relationships. Additionally, chapter

1 refined trait association resolution for future research and management scenarios, which can drastically influence future study results. Future ecological modeling studies will benefit from more defined trophic shifts and trait associations. Results from both analyses (i.e. trophic shifts and trait associations) support broad application in future site- and species-specific hypothesis testing (i.e. comparisons and contrasts) and inferences of ecology for study species or across similar species.

Literature Cited

- Arnold, S. J. 1983. Morphology, performance and fitness. *American Zoologist* 23(2):347-361.
- Becker, G. C. 1983. *Fishes of Wisconsin*. University of Wisconsin Press. Madison, WI.
- Bergman, E., and L. A. Greenberg. 1994. Competition between a planktivore, a benthivore, and a species with ontogenetic diet shifts. *Ecology* 75(5):1233-1245.
- Bremner, J., S. I. Rogers, and C. L. J. Frid. 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators* 6(3):609-622.
- Casatti, L., and R. M. C. Castro. 2006. Testing the ecomorphological hypothesis in a headwater riffles fish assemblage of the rio São Francisco, southeastern Brazil. *Neotropical Ichthyology* 4(2):203-214.
- Cox, M. A., and T. F. Cox. 2008. Multidimensional scaling. Pages 316-341 in C. Chen, W. Härdle, and A. Unwin, eds. *Handbook of data visualization*. Springer-Verlag. New York, NY.
- Der, G., and B. S. Everitt. 2002. *A handbook of statistical analyses using SAS*. CRC Press. Boca Raton, FL.
- Diniz-Filho, J. A. F., C. E. Ramos de Sant'Ana, and L. M. Bini. 1998. An eigenvector method for estimating phylogenetic inertia. *Evolution* 52(5):1247-1262.
- Doledec, S., and D. Chessel. 1994. Co-inertia analysis: an alternative method for studying species-environment relationships. *Freshwater Biology* 31(3):277-294.
- Douglas, M. E. 1987. An ecomorphological analysis of niche packing and niche dispersion in stream fish clades. Pages 144-149 in W. J. Matthews and D. C. Heins, eds. *Community and evolutionary ecology of North American stream fishes*. University of Oklahoma Press. Norman, OK.
- Douglas, M. E., and W. J. Matthews. 1992. Does morphology predict ecology – hypothesis-testing within a fresh-water stream fish assemblage. *Oikos* 65(2):213-224.
- Dray, S., D. Chessel, and J. Thioulouse. 2003. Co-inertia analysis and the linking of ecological data tables. *Ecology* 84(11):3078-3089.
- Dray, S., A. B. Dufour, and D. Chessel. 2007. The ade4 package-II: two-table and k-table methods. *R News* 7(2):47-52.

- Dutta, H. M. 1979. Form and function of jaws during feeding: *Ctenopoma acutirostre*, *Anabas testudineus* and *Macropodus opercularis*. *Acta Morphologica Neerlandico-Scandinavica* 17:119-132.
- Easton, R. S., and D. J. Orth. 2006. Ontogenetic diet shifts of age-0 smallmouth bass (*Micropterus dolomieu* Lacepede) in the New River, West Virginia, USA. *Ecology of Freshwater Fish* 1(2):86-98.
- Eggleston, D. B., J. J. Grover, and R. N. Lipcius. 1998. Ontogenetic diet shifts in Nassau grouper: trophic linkages and predatory impact. *Bulletin of Marine Science* 63(1):111-126.
- Etnier, D. A., and W. C. Starnes. 1994. The fishes of Tennessee. University of Tennessee Press. Knoxville, TN.
- Evans, H. E. 1952. The correlation of brain pattern and feeding habits in four species of cyprinid fishes. *Journal of Comparative Neurology* 97(1):133-142.
- Felley, J. D. 1984. Multivariate identification of morphological-environmental relationships within the Cyprinidae (Pisces). *Copeia* 1984:442-455.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *The American Naturalist* 125(1):1-15.
- Frimpong, E. A., and P. L. Angermeier. 2009. FishTraits: a database of ecological and life history traits of freshwater fishes of the United States. *Fisheries* 34(10):487-495.
- Frimpong, E. A., and P. L. Angermeier. 2010. Traits-based approaches in the analysis of stream fish communities.
- Garcia-Berthou, E., and R. Moreno-Amich. 2000. Food of introduced pumpkinseed sunfish: ontogenetic diet shift and seasonal variation. *Journal of Fish Biology* 57(1):29-40.
- Gatz, A. J. 1979. Community organization in fishes as indicated by morphological features. *Ecology* 60(4):711-718.
- Goldstein, R. M., and T. P. Simon. 1999. Toward a united definition of guild structure for feeding ecology of North American freshwater fishes. Pages 123-202 in T. P. Simon, ed. *Assessing the sustainability and biological integrity of water resources using fish communities*. CRC Press. New York, NY.
- Grafen, A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London, Series B* 326:119-157.
- Hahn, N. S., and F. Cunha. 2005. Feeding and trophic ecomorphology of *Satanoperca pappaterra* (Pisces, Cichlidae) in the Manso Reservoir, Mato Grosso State, Brazil. *Brazilian Archives of Biology and Technology* 48(6):1007-1012.
- Hjelm, J., L. Persson, and B. Christensen. 2000. Growth, morphological variation, and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. *Oecologia* 122(2):190-199.
- Hjelm, J., G. H. van de Weerd, and F. A. Sibbing. 2003. Functional link between foraging performance, functional morphology, and diet shift in roach (*Rutilus rutilus*). *Canadian Journal of Fisheries and Aquatic Sciences* 60(6):700-709.
- Ibanez, C., P. A. Tedesco, R. Bigorne, B. Hugueny, M. Pouilly, C. Zepita, J. Zubieta, and T. Oberdorff. 2007. Dietary-morphological relationships in fish assemblages of small forested streams in the Bolivian Amazon. *Aquatic Living Resources* 20:131-142.
- Jaccard, P. 1901. Étude comparative de la distribution florale dans une portion des Alpes et des Jura. *Société Vaudoise des Sciences Naturelles* 37:547-579.

- Jenkins, R. E., and N. M. Burkhead. 1993. Freshwater fishes of Virginia. American Fisheries Society. Bethesda, MD.
- Johansson, F., P. Radman, and J. Andersson. 2006. The relationship between ontogeny, morphology, and diet in the Chinese hook snout carp (*Opsariichthys bidens*). *Ichthyological Research* 53(1):63-69.
- Jolliffe, I. T. 2002. Principal components analysis. Springer-Verlag. New York, NY.
- Kay, L. K., R. Wallus, and B. L. Yeager. 1994. Reproductive biology and early life history of fishes in the Ohio River drainage. Volume 2: Catostomidae. CRC Press. Boca Raton, FL.
- Keast, A. 1985. The piscivore feeding guild of fishes in small freshwater ecosystems. *Environmental Biology of Fishes* 12(2):119-129.
- Kotrschal, K. M. 1989. Trophic ecomorphology in eastern Pacific blennioid fishes: character transformation of oral jaws and associated change of their biological roles. *Environmental Biology of Fishes* 24(3):199-218.
- Kruskal, J. B. 1964a. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29(1):1-27.
- Kruskal, J. B. 1964b. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29(2):115-129.
- Lamouroux, N., S. Doledec, and S. Gayraud. 2004. Biological traits of stream macroinvertebrate communities: effects of microhabitat, reach, and basin filters. *Journal of the North American Benthological Society* 23(3):449-466.
- Lasram, F. B. R., J. A. Tomasini, M. S. Romdhane, T. Do Chi, and D. Mouillot. 2008. Historical colonization of the Mediterranean Sea by Atlantic fishes: do biological traits matter? *Hydrobiologia* 607:51-62.
- Lauder, G. V. 1983. Neuromuscular patterns and the origin of trophic specialization in fishes. *Science* 219:1235-1237.
- Legendre, P., and L. Legendre. 1998. Numerical ecology. Second English edition. Elsevier Scientific Publishing Company. Amsterdam, NL.
- Liem, K. F. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *American Zoologist* 20(1):295-314.
- Litchman, E., C. A. Klausmeier, O. M. Schofield, and P. G. Falkowski. 2007. The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level. *Ecology Letters* 10(12):1170-1181.
- Matthews, W. J. 1998. Patterns in freshwater fish ecology. Kluwer Academic Publishers. Norwell, MA.
- Matthews, W. J., J. R. Bek, and E. Surat. 1982. Comparative ecology of the darters, *Etheostoma podostemone*, *E. flabellare*, and *Percina roanoka* in the upper Roanoke River drainage Virginia. *Copeia* 1982:805-814.
- McComas, S. R., and R. W. Drenner. 1982. Species replacement in a reservoir fish community: silverside feeding mechanics and competition. *Canadian Journal of Fisheries and Aquatic Sciences* 39:815-821.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21(4):178-185.
- Mol, J. H. 2006. Ontogenetic diet shifts and diet overlap among three closely related neotropical armoured catfishes. *Journal of Fish Biology* 47(5):788-807.
- Motta, P. J., S. F. Norton, and J. J. Luczkovich. 1995. Perspectives on the ecomorphology of bony fishes. *Environmental Biology of Fishes* 44(1):11-20.

- Moyle, P. B., and F. R. Senanayake. 1984. Resource partitioning among the fishes of rainforest streams in Sri-Lanka. *Journal of Zoology* 202(FEB):195-223.
- Nelson, J. S. 2004. *Fishes of the world*. John Wiley, Inc. New York, NY.
- Norton, S. F. 1995. A functional approach to ecomorphological patterns of feeding in cottid fishes. *Environmental Biology of Fishes* 44(1-3):61-78.
- Olden, J. D., N. L. Poff, and K. R. Bestgen. 2006. Life history strategies predict fish invasions and extirpations in the Colorado River basin. *Ecological Monographs* 76(1):25-40.
- Page, L. M., and B. M. Burr. 1991. *A field guide to freshwater fishes*. Houghton Mifflin Company. New York, NY.
- Page, L. M., and D. L. Swofford. 1984. Morphological correlates of ecological specialization in darters. *Environmental Biology of Fishes* 11(2):139-159.
- Paine, M. D., J. J. Dodson, and G. Power. 1982. Habitat and food resource partitioning among four species of darters Percidae: *Etheostoma* in a southern Ontario stream. *Canadian Journal of Zoology* 60:1635-1641.
- Pauly, D. 1989. Food consumption by tropical and temperate fish populations: some generalizations. *Journal of Fish Biology* 35(Supplement A):11-20.
- Piet, G. J. 1998. Ecomorphology of a size-structured tropical freshwater fish community. *Environmental Biology of Fishes* 51(1):67-86.
- Recasens, L., A. Lombarte, and P. Sánchez. 2006. Teleostean fish assemblages in an artificial reef and a natural rocky area in Catalonia (northwestern Mediterranean): an ecomorphological approach. *Bulletin of Marine Science* 78(1):71-82.
- Rincón, P. A., M. Bastir, and G. D. Grossman. 2007. Form and performance: body shape and prey-capture success in four drift-feeding minnows. *Oecologia* 152(2):345-355.
- Russo, T., C. Costa, and S. Cataudella. 2007. Correspondence between shape and feeding habit changes throughout ontogeny of gilthead sea bream *Sparus aurata* L., 1758. *Journal of Fish Biology* 71(3):629-656.
- Scharf, F. S., F. Juanes, and R. A. Rountree. 2000. Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series* 208:229-248.
- Scott, W. B., and E. J. Crossman. 1973. *Freshwater fishes of Canada*. Fisheries Research Board of Canada Bulletin 184.
- Shepard, R. N. 1962a. The analysis of proximities: multidimensional scaling with an unknown distance function I. *Psychometrika* 27(2):125-140.
- Shepard, R. N. 1962b. The analysis of proximities: multidimensional scaling with an unknown distance function II. *Psychometrika* 27(3):219-246.
- Simon, T. P., and R. Wallus. 2004. Reproductive biology and early life history of fishes in the Ohio River drainage. Volume 3: Ictaluridae – catfish and madtoms. CRC Press. Boca Raton, FL.
- Simon, T. P., and R. Wallus. 2006. Reproductive biology and early life history of fishes in the Ohio River drainage. Volume 4: Percidae – perch, pikeperch, and darters. CRC Press. Boca Raton, FL.
- Snyder, D. J., and M. S. Peterson. 1999. Foraging and prey selection by bluespotted sunfish *Enneacanthus gloriosus* (Holbrook) in backwater, vegetated ponds in coastal Mississippi. *Journal of Freshwater Ecology* 14(2):187-196.
- Spearman, C. 1904. "General intelligence," objectively determined and measured. *American Journal of Psychology* 15:201-293.

- Strauss, R. E. 1987. The importance of phylogenetic constraints in comparisons of morphological structure among fish assemblages. Pages 136-143 in W. J. Matthews and D. C. Heins, eds. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press. Norman, OK.
- Thioulouse, J., D. Chessel, S. Doleddec, J. Olivier. 1997. ADE-4: a multivariate analysis and graphical display software. *Statistics and Computing* 7:75-83.
- Turner, C. L. 1921. Food of the common Ohio darters. *Ohio Journal of Science* 22(2):41-62.
- Wainwright, P. C., and G. V. Lauder. 1992. The evolution of feeding biology in sunfishes (Centrarchidae). Pages 472-491 in R. L. Mayden, ed. Systematics, historical ecology, and North American freshwater fishes. Stanford University Press. Stanford, CA.
- Wainwright, P. C., and B. A. Richard. 1995. Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes* 44:97-113.
- Wallus, R., and T. P. Simon. 2006. Reproductive biology and early life history of fishes in the Ohio River drainage. Volume 5: Aphredoderidae through Cottidae, Moronidae, and Sciaenidae. CRC Press. Boca Raton, FL.
- Wallus, R., and T. P. Simon. 2008. Reproductive biology and early life history of fishes in the Ohio River drainage. Volume 6: Elasmobranchidae and Centrarchidae. CRC Press. Boca Raton, FL.
- Wallus, R., T. P. Simon, and B. L. Yeager. 1990. Reproductive biology and early life history of fishes in the Ohio River drainage. Volume 1: Acipenseridae through Esocidae. CRC Press. Boca Raton, FL.
- Wanink, J. H., and J. C. A. Joordens. 2007. Dietary shifts in *Brycinus sadleri* (Pisces: Characidae) from southern Lake Victoria. *Aquatic Ecosystem Health and Management* 10(4):392-397.
- Wells, R. J. D., J. H. Cowan, and B. Fry. 2008. Feeding ecology of red snapper *Lutjanus campechanus* in the northern Gulf of Mexico. *Marine Ecology-Progress Series* 361:213-225.
- Westneat, M. W. 1994. Transmission of force and velocity in the feeding mechanisms of labrid fishes (Teleostei, Perciformes). *Zoomorphology* 114(2):103-118.
- Wikramanayake, E. D. 1990. Ecomorphology and biogeography of a tropical stream fish assemblage – evolution of assemblage structure. *Ecology* 71(5):1756-1764.
- Winemiller, K. O. 1989. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. *Environmental Biology of Fishes* 26(3):177-199.
- Winemiller, K. O. 1991. Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecological Monographs* 61(4):343-365.
- Winston, M. R. 1995. Co-occurrence of morphologically similar species of stream fishes. *American Naturalist* 145(4):527-545.
- Wood, B. M., and M. B. Bain. 1995. Morphology and microhabitat use in stream fish. *Canadian Journal of Fisheries and Aquatic Sciences* 52(7):1487-1498.
- Wootton, R. J. 1998. Ecology of teleost fishes. Second edition. Kluwer Academic Publishers. Dordrecht, NL.
- Yamaoka, K. 1997. Trophic ecomorphology of Tanganyikan cichlids. Pages 25-56 in H. Kawanabe, M. Hori, and M. Nagoshi, eds. Fish communities in Lake Tanganyika. Kyoto University Press. Kyoto, JP.

Tables and Figures

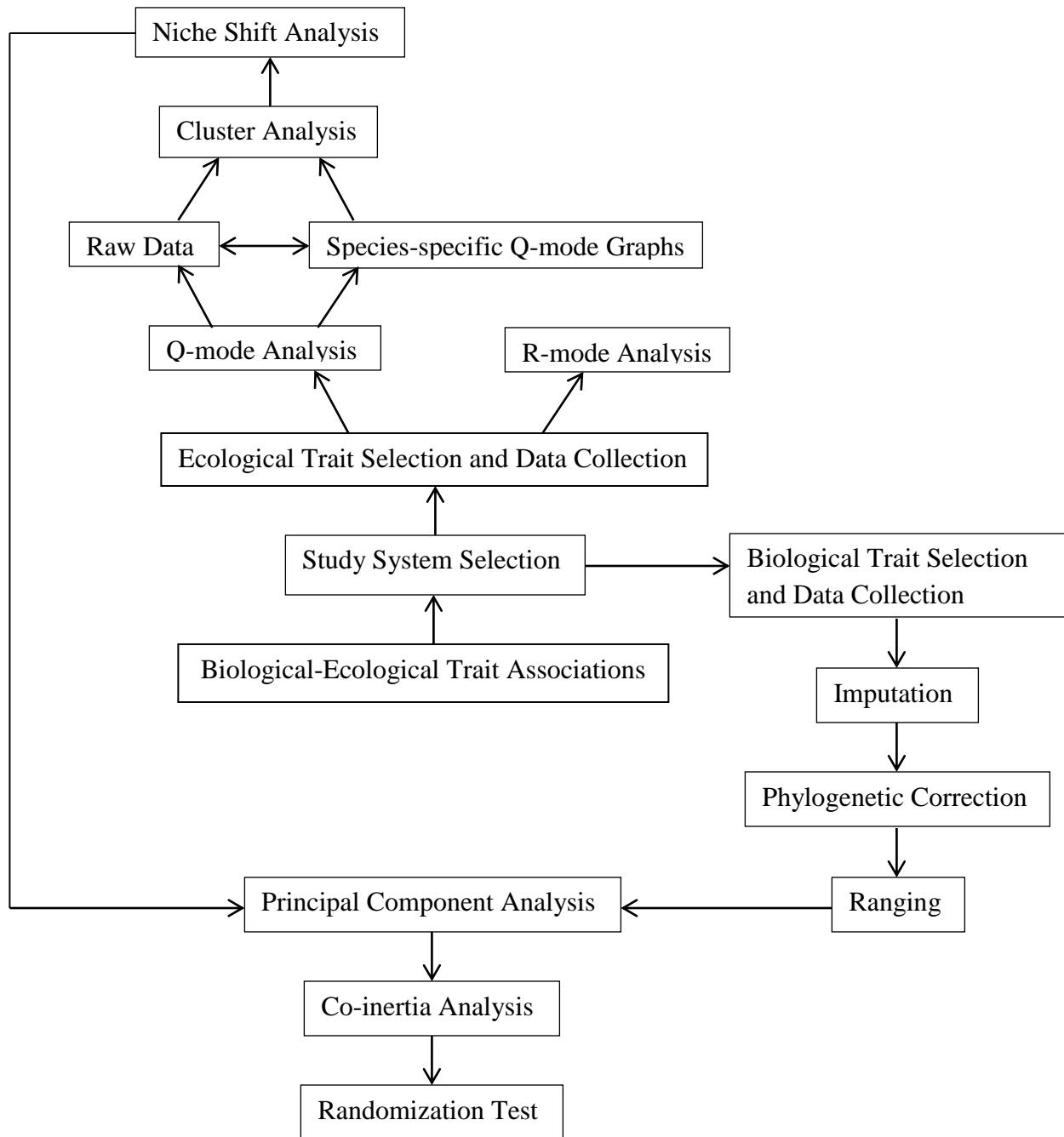


FIGURE 1. Step-wise conceptual methods model, which represents all major techniques used for niche shift and trait association analyses.

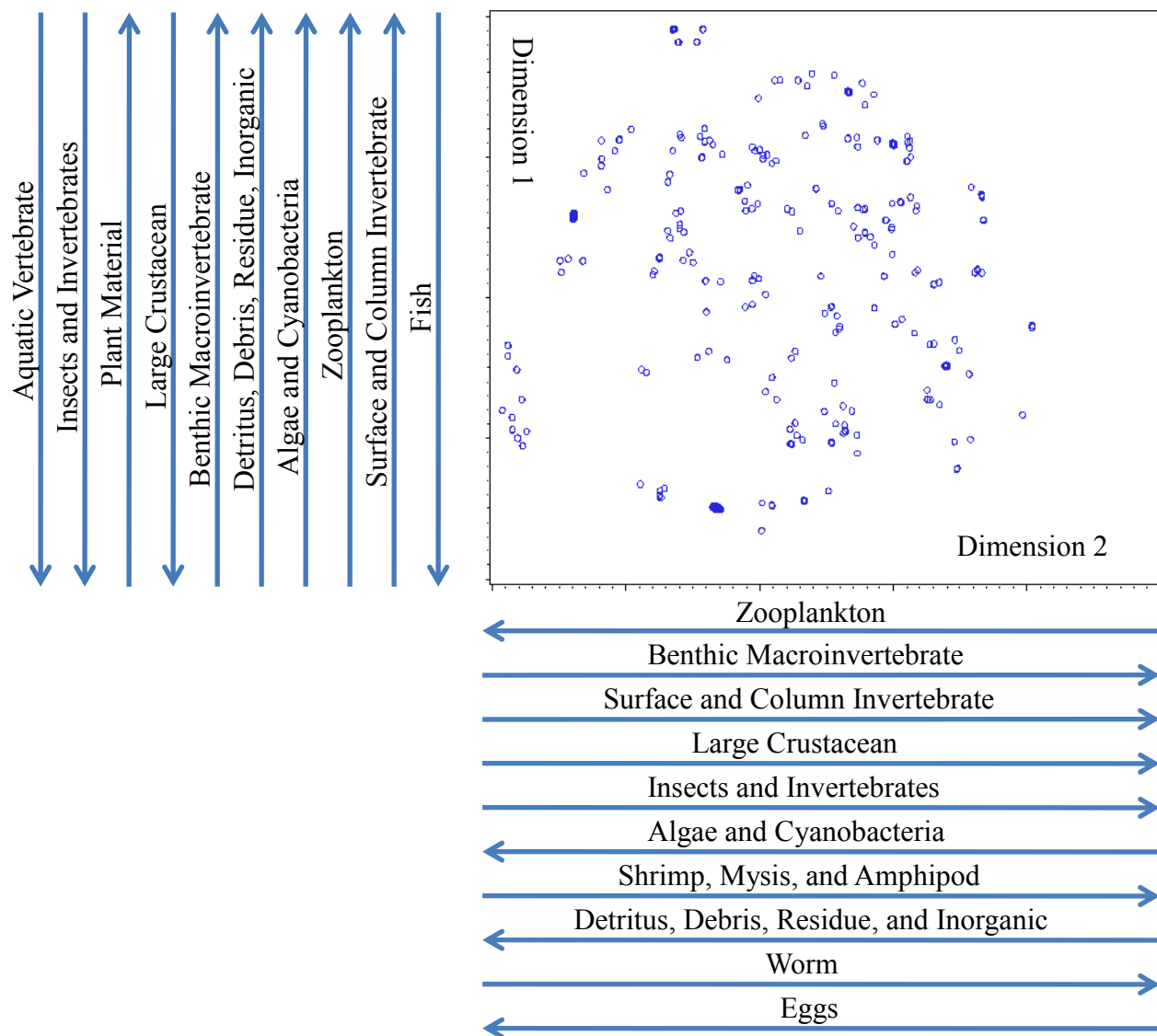


FIGURE 2. Q-mode analysis showing the relatedness of feeding records in 2 dimensional diet space. Each open circle represents a trophic record of 1 or more food items of a population. Food items displayed on the two axes represent significant relationships with each axis, with directionality indicated. Proximity of the food item label to the axis indicates relative correlation strength.

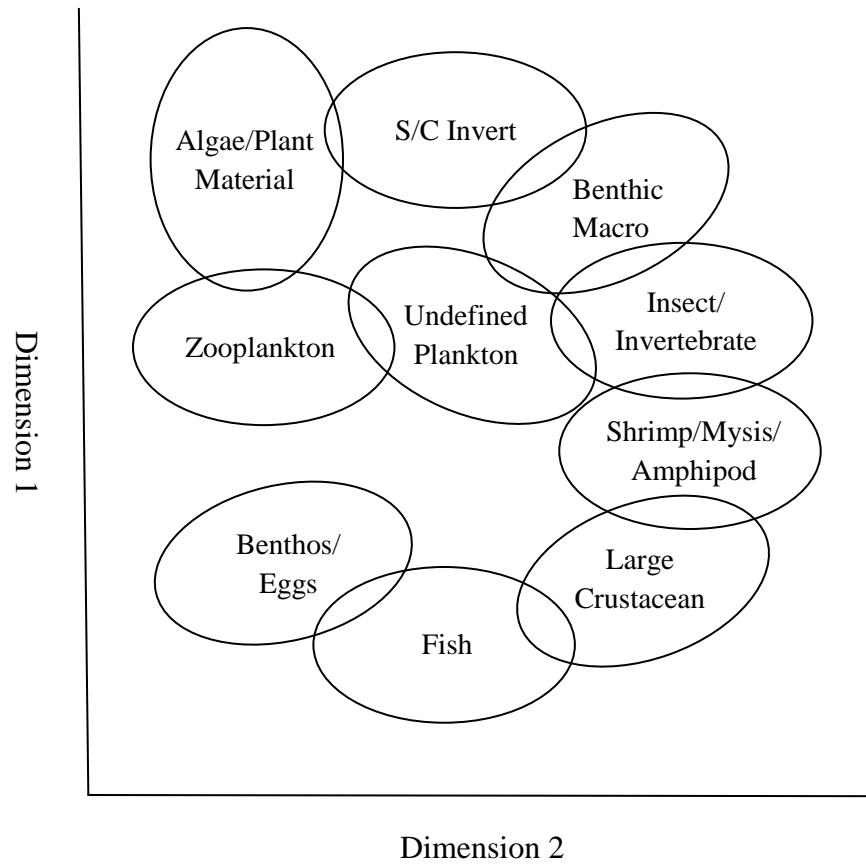


FIGURE 3. Approximate diet item locations in Q-mode analysis. Abbreviated diet space titles are as follows: S/C Invert = surface/water column invertebrate and Benthic Macro = benthic macroinvertebrate.

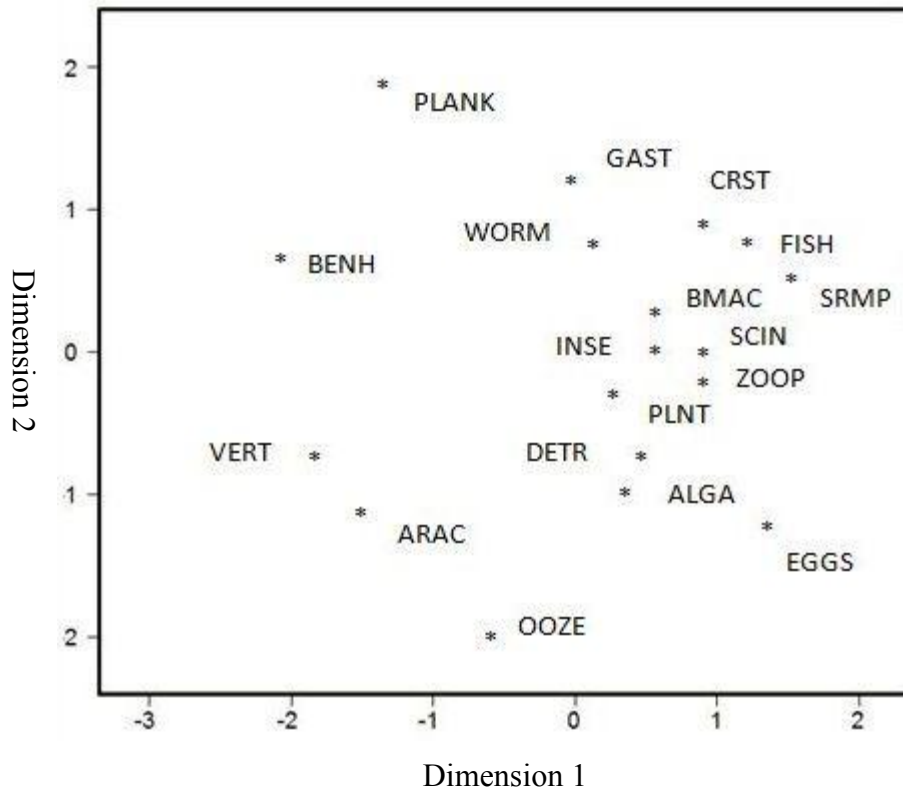


FIGURE 4. R-mode analysis showing the relatedness of food items. Closer proximity of food items indicates stronger relationships. Diet item codes are as follows: INSE = insect/invertebrate, SRMP = shrimp/mysis/amphipod, CRST = large crustacean, GAST = gastropod, BMAC = benthic macroinvertebrate, FISH = fish, EGGS = eggs, VERT = aquatic vertebrate, ALGA = algae/cyanobacteria, PLNT = plant/seed/bryozoan, SCIN = surface/water column invertebrate, WORM = worm, ARAC = arachnida, OOZE = organic matter/ooze, DETR = detritus/debris/residue/inorganic material, BENH = benthos, ZOOP = zooplankton, PLNK = unidentified plankton.

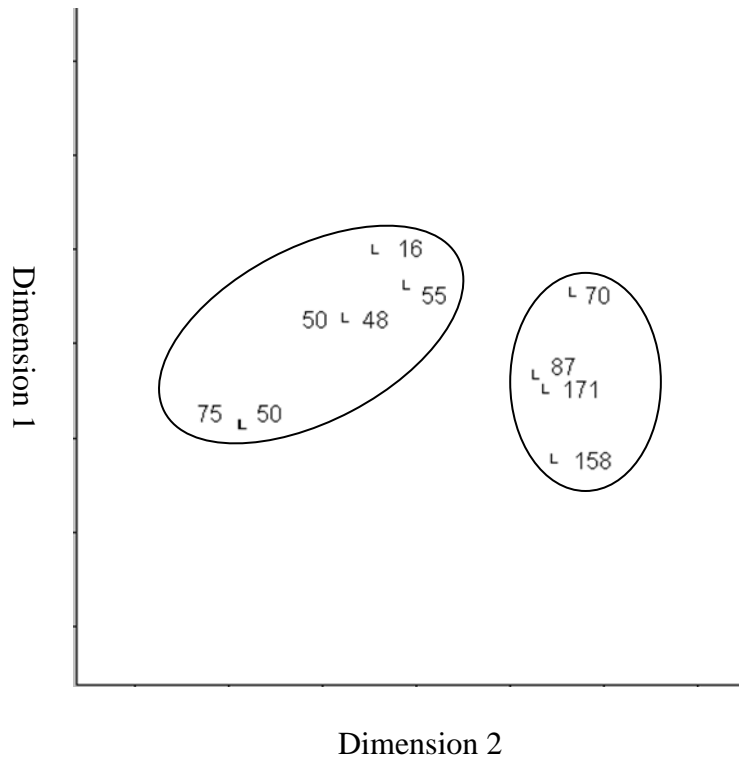


FIGURE 5. Longear sunfish trophic shift shown in Q-mode analysis. This figure is representative of a species with two diet clusters and one diet shift. Numbers within the figure represent fish lengths in millimeters (mm) associated with distinct diet records from literature.

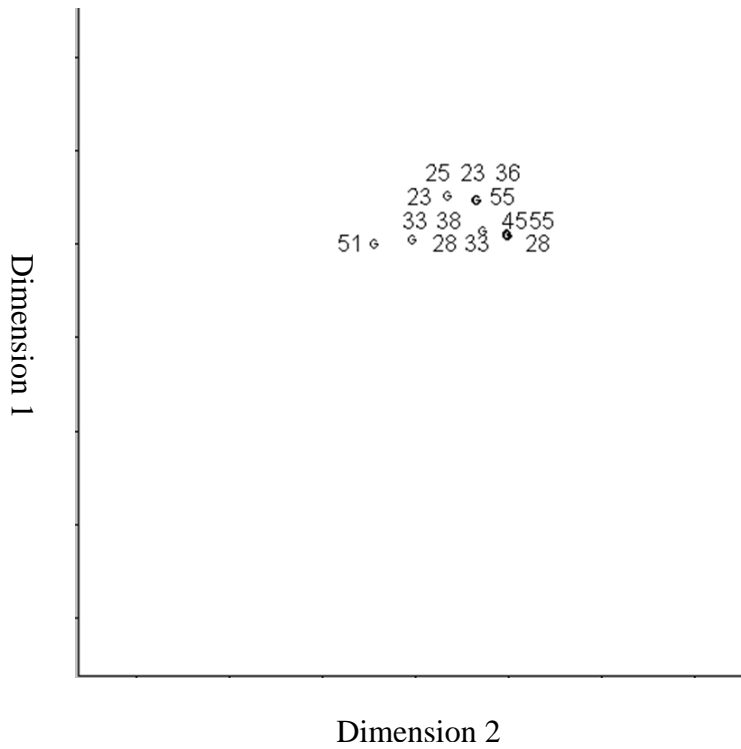


FIGURE 6. Greenside darter trophic niche in Q-mode analysis. This figure is representative of a species with one trophic cluster and no diet shift. Numbers within the figure represent fish lengths in millimeters (mm) associated with distinct diet records from literature.

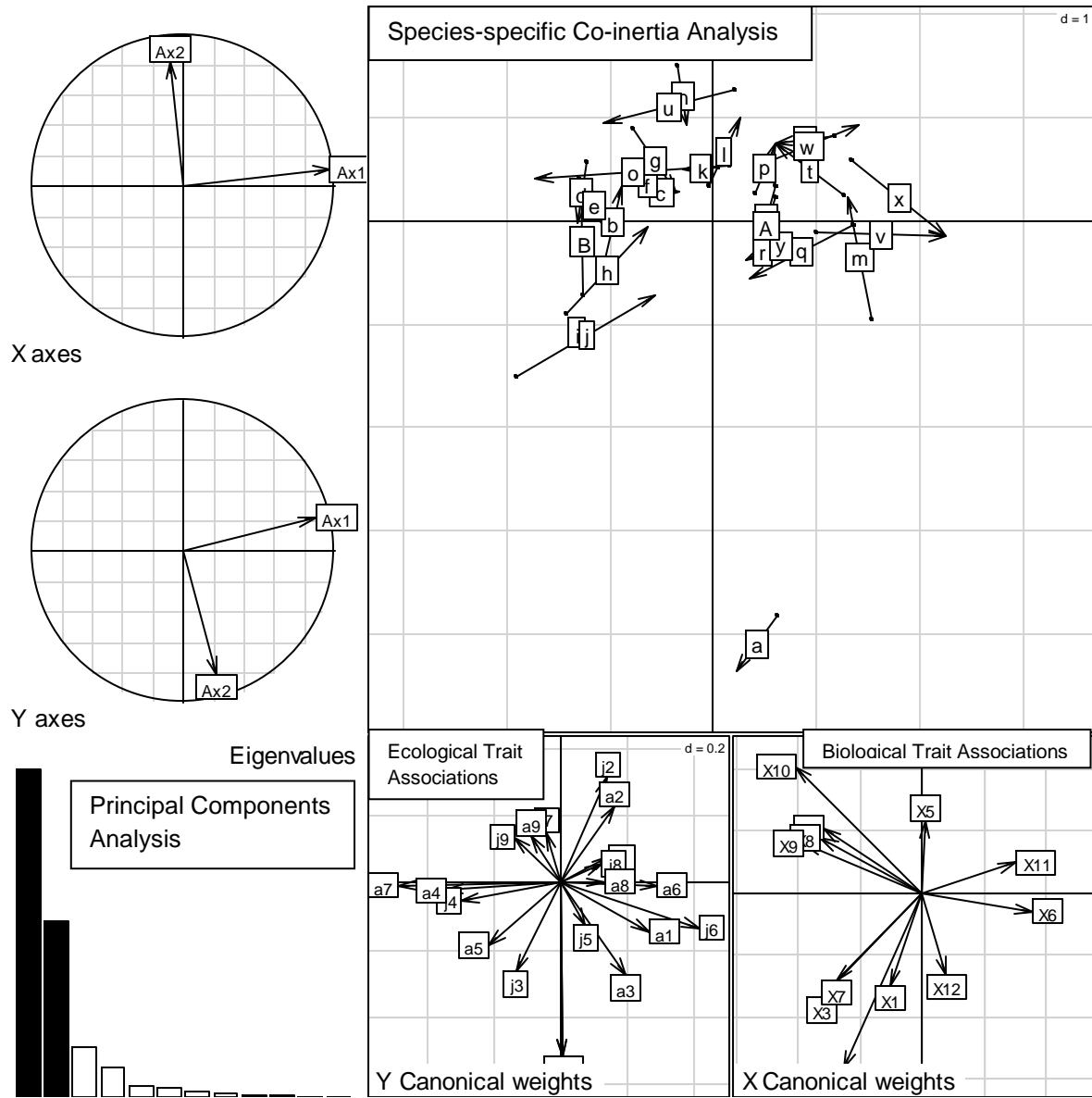


FIGURE 7. Principal components analysis and co-inertia analysis after correction for relatedness among species. Trophic niche (ecological trait) abbreviations are classified by stage food items were consumed in and the food items themselves as follows: j1 = juvenile surface/column invertebrate, j2 = juvenile benthic macroinvertebrate, j3 = juvenile zooplankton, j4 = juvenile insect/invertebrate, j5 = juvenile large crustacean, j6 = juvenile plant material, j7 = juvenile fish, j8 = juvenile shrimp/mysis/amphipod, j9 = juvenile benthos/eggs, j10 = juvenile undefined plankton, a1 = adult surface/column invertebrate, a2 = adult benthic macroinvertebrate, a3 = adult zooplankton, a4 = adult insect/invertebrate, a5 = adult large crustacean, a6 = adult plant material, a7 = adult fish, a8 = adult shrimp/mysis/amphipod, a9 = adult benthos/eggs, a10 = adult undefined plankton. Biological trait abbreviations include: X1 = average age at first reproduction, X2 = average length at first reproduction, X3 = asymptotic total length, X4 = relative eye diameter, X5 = barbel presence-absence, X6 = shape factor, X7 = swim factor, X8 = relative mouth size, X9 = average mouth position, X10 = average mouth angle, X11 = average peritoneum color, X12 = average relative gut length. Species common name abbreviations are as follows: a = white sucker, b = rock bass, c = redbreast sunfish, d = green sunfish, e = pumpkinseed, f = bluegill, g = longear sunfish, h = smallmouth bass, i = spotted bass, j = largemouth bass, k = mottled sculpin, l = banded sculpin, m = central stoneroller, n = rosyside dace, o = spottail shiner, p = swallowtail shiner, q = bluntnose minnow, r = fathead minnow, s = blacknose dace, t = longnose dace, u = creek chub, v = greenside darter, w = fantail darter, x = Kanawha darter, y = logperch, z = Appalachian darter, A = Roanoke darter, B = brook trout.

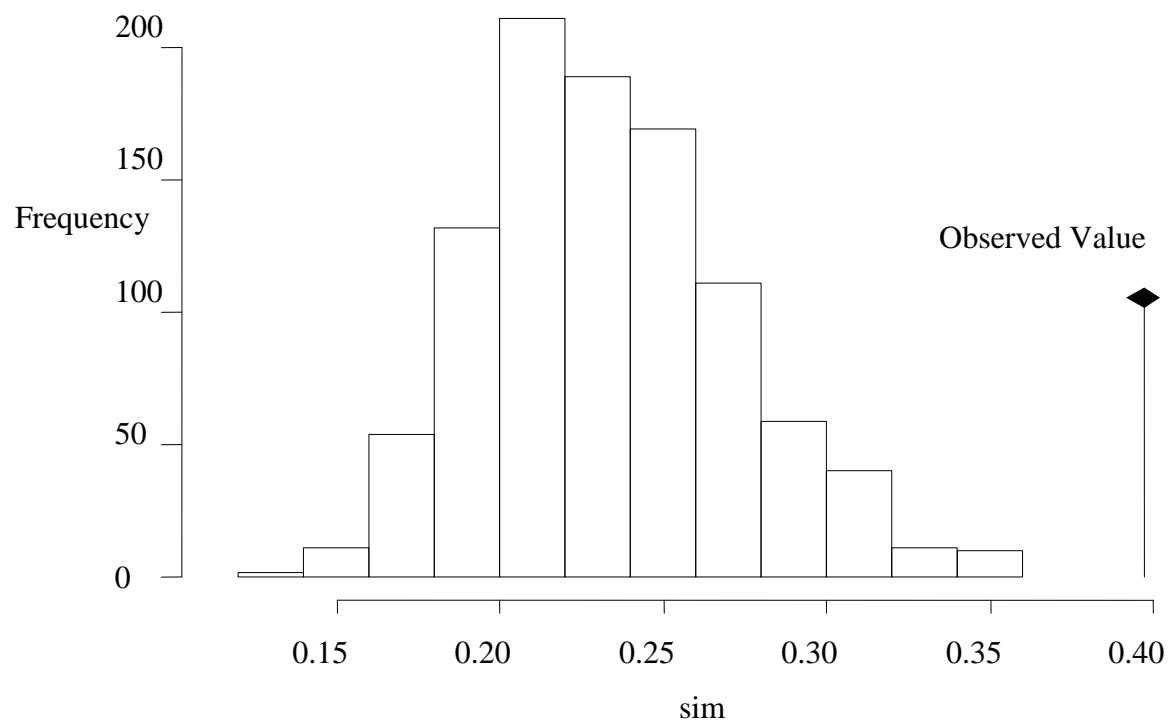
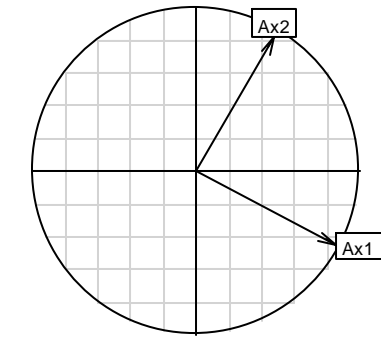
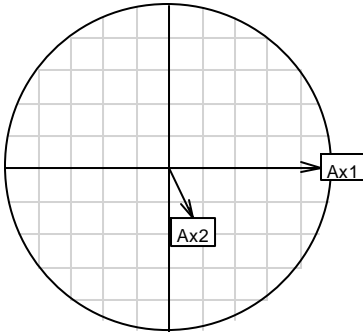


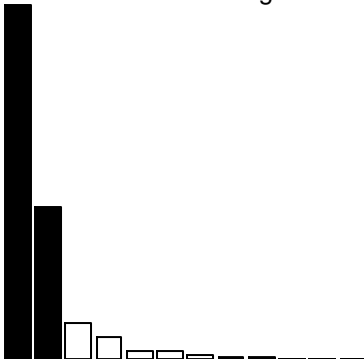
FIGURE 8. Distribution of the results of the randomization test performed to check for strength of biological and ecological trait correlation. The extreme location of the observed value shows that the relationship observed between biological and ecological traits is not by chance.



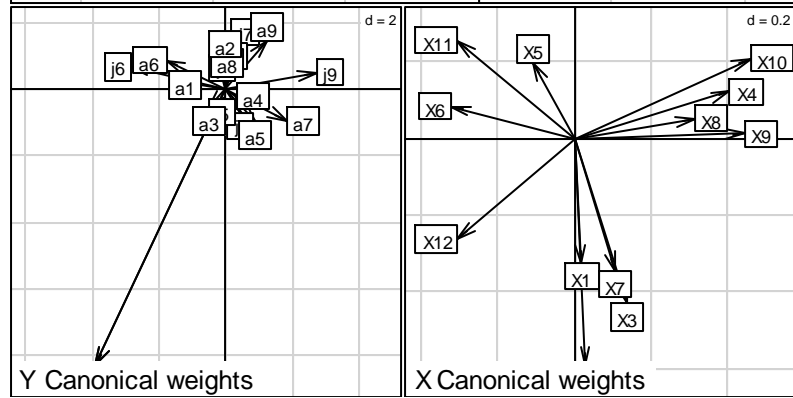
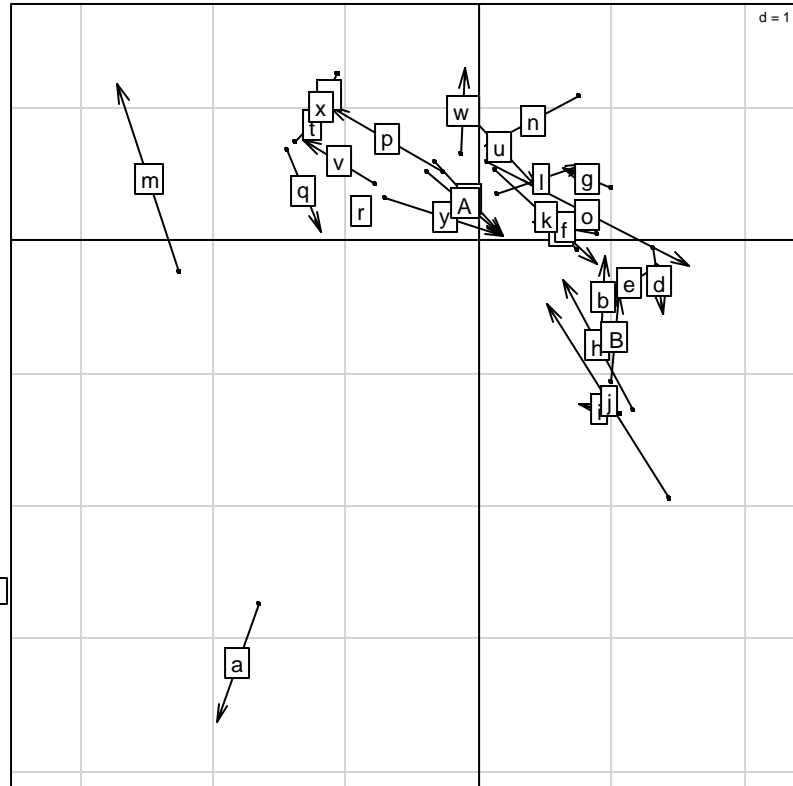
X axes



Y axes



Eigenvalues



Y Canonical weights

X Canonical weights

FIGURE 9. Principal component analysis and co-inertia analysis before correction for relatedness among species. Trophic niche (ecological trait) abbreviations are classified by stage food items were consumed in and the food items themselves as follows: j1 = juvenile surface/column invertebrate, j2 = juvenile benthic macroinvertebrate, j3 = juvenile zooplankton, j4 = juvenile insect/invertebrate, j5 = juvenile large crustacean, j6 = juvenile plant material, j7 = juvenile fish, j8 = juvenile shrimp/mysis/amphipod, j9 = juvenile benthos/eggs, j10 = juvenile undefined plankton, a1 = adult surface/column invertebrate, a2 = adult benthic macroinvertebrate, a3 = adult zooplankton, a4 = adult insect/invertebrate, a5 = adult large crustacean, a6 = adult plant material, a7 = adult fish, a8 = adult shrimp/mysis/amphipod, a9 = adult benthos/eggs, a10 = adult undefined plankton. Biological trait abbreviations include: X1 = average age at first reproduction, X2 = average length at first reproduction, X3 = asymptotic total length, X4 = relative eye diameter, X5 = barbel presence-absence, X6 = shape factor, X7 = swim factor, X8 = relative mouth size, X9 = average mouth position, X10 = average mouth angle, X11 = average peritoneum color, X12 = average relative gut length. Species common name abbreviations are as follows: a = white sucker, b = rock bass, c = redbreast sunfish, d = green sunfish, e = pumpkinseed, f = bluegill, g = longear sunfish, h = smallmouth bass, i = spotted bass, j = largemouth bass, k = mottled sculpin, l = banded sculpin, m = central stoneroller, n = rosieside dace, o = spottail shiner, p = swallowtail shiner, q = bluntnose minnow, r = fathead minnow, s = blacknose dace, t = longnose dace, u = creek chub, v = greenside darter, w = fantail darter, x = Kanawha darter, y = logperch, z = Appalachian darter, A = Roanoke darter, B = brook trout.

TABLE 1. Summary of biological traits, data scale used for each trait, and a description / note for each trait. The description/note section includes an in-depth summary of what each trait represents, literature sources that support the use of methods, data ranges, and/or where measurements were obtained from, where applicable.

Biological Trait	Data Scale	Description and Notes
Average age at first reproduction	Continuous	Mean age at first reproduction by species found in Jenkins and Burkhead (1993)
Average length at first reproduction	Continuous	Mean length at first reproduction by species found in Jenkins and Burkhead (1993)
Asymptotic total length	Continuous	Maximum reported total length found in literature
Relative eye diameter	Continuous	Eye diameter / total body length percent by species measured from pictures in Jenkins and Burkhead (1993)
Barbel presence-absence	Binary	Presence or absence of barbels by species from Jenkins and Burkhead (1993)
Shape factor	Continuous	Total body length / maximum body depth percent (Poff and Allan 1995) by species measured from pictures in Jenkins and Burkhead (1993)
Swim factor	Continuous	Maximum caudal fin depth / minimum caudal peduncle depth percent (Poff and Allan 1995) by species measured from pictures in Jenkins and Burkhead (1993)
Relative mouth size	Continuous	Mouth gape / total body length percent by species from Jenkins and Burkhead (1993)
Average mouth position	Continuous	Mean mouth position score (-1 to 1 scale, -1 = inferior and 1 = superior) of 7 individual scorers by species from pictures in Jenkins and Burkhead (1993)
Average jaw angle	Continuous	Mean jaw angle score (-1 to 1 scale, -1 = inferior and 1 = superior) of 7 individual scorers by species from pictures in Jenkins and Burkhead (1993)
Average peritoneum color	Continuous	Mean of all peritoneum color observations (1 to 6 scale, 1 = lightest and 6 = darkest) by species, with 3-24 field-caught specimen observations per species
Average relative gut length	Continuous	Mean of all gut length / total body length percent calculations by species, with 3-24 field-caught specimen observations per species

TABLE 2. Diet classifications, including diet cluster and shift means and confidence limits. Each number represents length in millimeters (mm) except for n, n1, and n2, which represent sample sizes. N1 is niche 1, N2 is niche 2, LCL is lower confidence limit (95%), UCL is upper confidence limit (95%), and vert is vertebrate. Unabbreviated species names are as follows: ALEW = alewife (*Alosa pseudoharengus*), BASC = banded sculpin (*Cottus caroliniae*), BKTR = brook trout (*Salvelinus fontinalis*), BLCR = black crappie (*Pomoxis nigromaculatus*), BLUE = bluegill (*Lepomis macrochirus*), BNDA = blacknose dace (*Rhinichthys atratulus*), BNMI = bluntnose minnow (*Pimephales notatus*), BRTR = brown trout (*Salmo trutta*), CESR = central stoneroller (*Camptostoma anomalum*), CHCA = channel catfish (*Ictalurus punctatus*), CLMI = cutlips minnow (*Exoglossum maxilingua*), CRCH = creek chub (*Semotilus atromaculatus*), FHCF = flathead catfish (*Pylodictis olivaris*), FHMI = fathead minnow (*Pimephales promelas*), FTDA = fantail darter (*Etheostoma flabellare*), GOSH = golden shiner (*Notemigonus crysoleucas*), GRSF = green sunfish (*Lepomis cyanellus*), GSDA = greenside darter (*Etheostoma blennoides*), LESF = longear sunfish (*Lepomis megalottis*), LMBA = largemouth bass (*Micropterus salmoides*), LNDA = longnose dace (*Rhinichthys cataractae*), LOPE = logperch (*Percina caprodes*), MOSC = mottled sculpin (*Cottus bairdi*), PUMP = pumpkinseed (*Lepomis gibbosus*), RBSF = redbreast sunfish (*Lepomis auritus*), RBTR = rainbow trout (*Oncorhynchus mykiss*), ROBA = rock bass (*Ambloplites rupestris*), RSDA = rosyside dace (*Clinostomus funduloides*), SMBA = smallmouth bass (*Micropterus dolomieu*), SPBA = spotted bass (*Micropterus punctulatus*), STBA = striped bass (*Morone saxatilis*), STSH = spottail shiner (*Notropis hudsonius*), SWSH = swallowtail shiner (*Notropis procne*), WALL = walleye (*Sander vitreum*), WHCR = white crappie (*Pomoxis annularis*), WHSU = white sucker (*Catostomus commersonii*), YEPE = yellow perch (*Perca flavescens*).

Species	n	N1 Type	n1	N1 Mean	N1 LCL	N1 UCL	N2 Type	n2	N2 Mean	N2 LCL	N2 UCL	Shift Mean	Shift LCL	Shift UCL
ALEW	15	planktivore/invertivore	13	35	17	54	invertivore	2	112	68	156	41	19	63
BASC	27	vert/invert predator	27	62	77	92								
BKTR	14	invertivore	7	56	33	79	vert/invert predator	7	192	102	282	59	35	84
BLCR	16	vert/invert predator	16	67	95	123								
BLUE	32	invertivore	26	43	25	61	omnivore	6	121	53	189	46	27	65
BNDA	23	generalist omnivore	23	42	36	48								
BNMI	60	generalist omnivore	60	48	45	51								
BRTR	5	vert/invert predator	5	253	132	374								
CESR	8	generalist omnivore	8	48	28	68								
CHCA	21	omnivore	11	117	52	181	omnivore/vert predator	10	217	150	285	173	76	269
CLMI	14	generalist invertivore	14	76	58	94								
CRCH	21	vert/invert predator	7	54	40	68	omnivore	14	124	90	158	62	46	78
FHCF	8	vert/invert predator	8	148	107	189								
FHMI	8	generalist omnivore	8	43	30	55								
FTDA	23	generalist invertivore	23	27	21	32								

GOSH	22	omnivore	22	61	73	85								
GRSF	10	invertivore	4	72	28	115	vert/invert predator	6	118	89	146	121	48	193
GSDA	17	generalist omnivore	17	33	27	39								
LESF	13	invertivore	7	56	37	76	omnivore	6	121	88	153	72	47	97
LMBA	61	invertivore	17	30	18	41	vert/invert predator	44	82	63	102	38	23	52
LNDA	11	generalist omnivore	11	81	56	106								
LOPE	42	generalist invertivore	42	57	47	66								
MOSC	16	invertivore	13	45	29	61	vert predator	3	74	41	107	54	35	73
PUMP	15	invertivore	13	65	40	91	vert/invert predator	2	168	124	212	82	50	115
RBSF	7	vert/invert predator	7	102	58	147								
RBTR	17	invertivore	4	51	14	87	vert/invert predator	13	277	176	378	56	16	97
ROBA	28	invertivore	9	81	49	114	vert/invert predator	19	135	113	157	136	82	191
RSDA	9	generalist invertivore	9	41	40	43								
SMBA	39	invertivore	14	37	17	57	vert/invert predator	25	106	61	152	43	19	66
SPBA	29	invertivore	8	63	47	80	vert/invert predator	21	152	112	191	72	54	91
STBA	20	invertivore	7	64	29	98	vert/invert predator	13	168	113	224	82	37	126
STSH	19	planktivore	12	42	30	54	vert/invert predator	7	83	57	109	50	36	64
SWSH	11	generalist omnivore	11	38	36	40								
WALL	46	omnivore	20	44	24	63	vert/invert predator	26	157	92	222	47	26	68
WHCR	30	invertivore	22	57	34	79	vert/invert predator	8	204	144	264	64	38	90
WHSU	20	generalist omnivore	20	112	65	160								
YEPE	36	invertivore	17	29	15	42	vert/invert predator	19	178	134	223	31	17	45

TABLE 3. Summary of positive and negative biological, ecological, and biological-ecological trait associations found in this study.

Positive Biological Trait Correlations			
asymptotic total length	swim factor		
average age at first reproduction	average length at first reproduction		
relative eye diameter	relative mouth size	average mouth position	average jaw angle
Positive Ecological Trait Correlations			
juvenile benthic macroinvertebrate	adult benthic macroinvertebrate		
juvenile insect / invertebrate	adult insect / invertebrate	adult fish	
juvenile large crustacean	adult zooplankton		
juvenile undefined plankton	adult undefined plankton		
juvenile benthos / eggs	adult benthos / eggs		
juvenile fish	adult benthos / eggs		
juvenile plant	adult surface / column invertebrate		
juvenile surface / column invertebrate	juvenile shrimp / mysis / amphipod		
adult plant	adult shrimp / mysis / amphipod		
Negative Biological Trait Correlations			
relative mouth size / average mouth position	shape factor		
average relative gut length / average age at first reproduction / average length at first reproduction	barbel presence-absence		
Negative Ecological Trait Correlations			
juvenile benthic macroinvertebrate / adult benthic macroinvertebrate	juvenile zooplankton		
adult benthic macroinvertebrate	adult large crustacean		
juvenile benthos / eggs	adult surface / column invertebrate		

juvenile surface / column invertebrate / juvenile shrimp / mysis / amphipod	juvenile insect / invertebrate
juvenile large crustacean / adult zooplankton	juvenile fish / juvenile benthos / eggs / adult benthos / eggs
juvenile insect / invertebrate / adult insect / invertebrate / adult fish	adult plant / adult shrimp / mysis / amphipod

Positive Biological-Ecological Trait Correlations

adult large crustacean	asymptotic total length / swim factor
juvenile zooplankton	average age at first reproduction / average length at first reproduction
juvenile shrimp / mysis / amphipod / juvenile surface / column invertebrate	average peritoneum color
juvenile benthic macroinvertebrate	barbel presence-absence
juvenile benthos / eggs	relative eye diameter
juvenile benthos / eggs / adult benthos / eggs	mouth angle
juvenile plant / adult plant / adult shrimp / mysis / amphipod	shape factor
juvenile large crustacean / adult zooplankton	average relative gut length

Negative Biological-Ecological Trait Correlations

juvenile unidentified plankton / adult unidentified plankton	barbel presence-absence
juvenile insect / invertebrate / adult insect / invertebrate / adult fish	average peritoneum color
juvenile fish / adult benthos / eggs	average relative gut length
juvenile benthic macroinvertebrate / adult benthic macroinvertebrate	average length at first reproduction / average age at first reproduction
juvenile benthic macroinvertebrate / adult benthic macroinvertebrate	asymptotic total length / swim factor

juvenile plant / adult surface / column invertebrate	relative eye diameter / relative mouth size / average mouth position
juvenile large crustacean / adult surface / column invertebrate / adult zooplankton	average jaw angle

*Chapter 2: Determination of large-scale variation in life history traits within and among species
for several broadly distributed North American freshwater fishes*

Abstract

Analysis of spatial and intraspecific (i.e. within species) variation of life history traits provides a key means for understanding plasticity of traits and why they vary between environments. Spatial life history patterns provide help to understand trait trade-offs that population's make. I examined trait variation with changes in environment to define life histories and their trade-offs, which provided insights with management and conservation implications (i.e. such as large-scale species distributional patterns and corresponding range expansions, constrictions, and / or shifts with climate change). I examined a suite of 11 life history traits for 10 broadly distributed North American fish species to test their associations with latitude and variation within and among species. Data were collected from 139 primary and secondary literature sources. Trait directionality (i.e. change over latitude) was assessed qualitatively by visual inspection and quantitatively with general linear models. Phylogenetic relatedness among species was corrected for in both qualitative and quantitative analyses using simple linear regression of traits against family phylogenetic position. Latitude usually explained a very low amount of variation. Random error typically explained a moderate amount of variation. Most traits had the largest amount of variation explained by species effects. All species exhibited at least one species-specific latitudinal direction effect, and either showed varied or strong affinity to latitudinal effects within species for different traits. At higher latitudes, fish matured at older ages, lived longer, grew less in the first year of life, grew to larger maximum lengths, spawned at lower temperatures, and had shorter reproductive seasons. Study results are applicable as an environmental-trait-variation framework by researchers and managers to assess thermal regime

alteration effects, many climate change scenarios, species distribution and co-occurrence, and to infer traits for understudied species or unstudied areas.

Introduction

Analysis of spatial and intraspecific (i.e. within species) variation in life history traits provides a key means for understanding trait plasticity and why traits vary between environments. Latitude-based directionality in traits are patterns seen in traits with changes in latitude, either for a group or a single species (Blanck and Lamouroux 2007). Spatial life history patterns help us to understand trade-offs that populations make (Pianka 1970; Stearns 1989). Phenotypic plasticity, as defined by Travis (2009), is “the ability of an individual to express different features under different environmental conditions.” Blanck and Lamouroux (2007) showed trait phenotypes are able to change rapidly in response to changing environmental conditions.

Traits vary narrowly, moderately, or broadly between and/or within species based on many factors including phylogeny and / or environment (Blanck and Lamouroux 2007). Species occupying similar habitats often display broad ranges of life history trait-states (Schloemer 1947; Williams and Bond 1983; Cambray 1994), which is likely due to life history trait trade-offs among species (Matthews 1998). For example, Matthews (1998) observed life history strategy trade-offs between two co-occurring sunfish species within a stream reach. Traits can have the same range of variation within a species as among species, but broad variation in one species’ traits is usually not as common as variation among species (Lamouroux et al. 2002; Goldstein and Meador 2004; Matthews 1998). For instance, Kramer (1978) concluded that temporal spawning variation between coexisting species is advantageous because it reduces competitive

pressures. Trait variation potentially increases when more species are considered, but Matthews (1998) recognized that a quantitative assessment across species is lacking.

Life history traits potentially vary by latitude. For example, Fleming and Gross (1990) found coho salmon (*Oncorhynchus kisutch*) exhibited increased fecundity, but decreased egg size and overall egg production, with increased latitude. Other coho salmon life history studies supported positive patterns between fecundity and latitude, which suggested advantages to reproductive output maximization (Drucker 1972; Crone and Bond 1976; Beacham 1982; Healey and Heard 1984). These patterns hold true for coho salmon, but do they hold true for many species encompassing a broad phylogenetic range? Life history trait latitudinal directionality provides a unique concept to determine if certain trait and life history patterns are broadly adaptive.

Many life history traits assumedly follow general latitudinal patterns by taxonomic group (Matthews 1998). In fishes, longevity, maximum body size, age at maturation, length at maturation, and fecundity assumedly increase with increased latitude. Conversely, egg size, egg production, spawning temperature, length of spawning season, and growth rate assumedly decrease with increased latitude (Matthews 1998; Wootton 1998). Life histories and trait-states are shaped by many environmental factors; environmental differences, especially temperature and photoperiod, often heavily influence life history trait expression (Wootton 1998). Additionally, life history traits themselves often have profound influences on other life history traits, such as length / body size affecting fecundity and egg production (Matthews 1998; Wootton 1998). Blanck and Lamouroux (2007) examined latitudinal directionality and intraspecific variation in European freshwater fish life history traits. Over half of the traits Blanck and Lamouroux (2007) studied had significant overall latitudinal directionality with

increased latitude, including a negative relationship between latitude and growth rate, but positive relationships with age at maturation, longevity, asymptotic length, and egg production. Additionally, Blanck and Lamouroux (2007) found traits that lacked latitudinal direction consistency when considering individual species' responses for all traits examined.

Results of the current study will provide a second comprehensive life history trait latitudinal / environmental directionality and intraspecific variation study, and the first based on North American species. However, European freshwater fish patterns (i.e. Blanck and Lamouroux 2007) will not necessarily hold true for North American fishes. This study will build on and contrast with Blanck and Lamouroux (2007) by 1) examining a different suite of fishes (i.e. North American freshwater and anadromous fishes) and 2) researching both traits they did and did not examine to support or refute previously seen patterns and recognize other patterns for North American fishes. Large-scale spatial and intraspecific trait variation results from this study will be applicable in many future research, management, and conservation situations. For example, from a spatial perspective, if climate change occurs, results could hypothesize if a species will likely evolve in place and / or compensate for changes via range shifts, expansion, or constriction. For example, current distributions and latitudinal trends can hypothesize future native and invasive species distributions and co-occurrence.

Some life history traits are better suited for testing ecological hypotheses, and these traits will be more applicable to several applied and theoretical scenarios. Traits not well suited for mechanistic hypothesis testing will vary more broadly within species than between species (Lamouroux et al. 2002; Goldstein and Meador 2004). My research objectives were: 1) to explore the presence-absence of life-history-trait latitudinal directionality in North American fishes and 2) identify such traits according to their correlative strength in future ecological

applications. I hypothesized that life history traits of North American freshwater and anadromous fishes will exhibit latitudinal directionality and that intraspecific variation of life history traits will be less than interspecific variation.

Methods

Species Selection:

Eleven life history traits were examined for 10 broadly distributed North American fish species. Study species were selected from a list of widely distributed North American bony fishes using Page and Burr (1991) range maps to maximize species diversity; a wide phylogenetic range is often desired in comparative studies (Matthews 1998). Data unavailability excluded some otherwise suitable species from this study. Species chosen for analysis include fathead minnow (*Pimephales promelas*: Cyprinidae), muskellunge (*Esox masquinongy*: Esocidae), shorthead redhorse (*Moxostoma macrolepidotum*: Catostomidae), white sucker (*Catostomus commersonii*: Catostomidae), sauger (*Sander canadensis*: Percidae), arctic char (*Salvelinus alpinus*: Salmonidae), freshwater drum (*Aplodinotus grunniens*: Sciaenidae), alewife (*Alosa pseudoharengus*: Clupeidae), channel catfish (*Ictalurus punctatus*: Ictaluridae), and largemouth bass (*Micropterus salmoides*: Centrarchidae). Two species (alewife and arctic char) had anadromous and landlocked population records; these were treated as two separate species (i.e. alewife anadromous, alewife landlocked, etc.), resulting in 12 species groups.

Data Collection and Use:

Life history trait data were collected through several primary and secondary literature searches for the selected species (Table 1). All 139 data collection sources are found in Appendix

D. Population level traits were recorded in an autecology matrix (trait and corresponding trait value by species and location) using mean published values; ranges were averaged when mean values were not reported. Many commonly reported life history traits were selected for analysis to maximize the number of species, records per trait, and amount of data per species. Also, life history traits were carefully chosen to represent reproductive, growth, and longevity / population turnover rate attributes hypothetically related to latitude. If given, latitudes used in analysis were taken from the cited sources. Otherwise, latitudes were referenced from reported geographical study areas using Google Earth (<http://www.earth.google.com>). All data were managed and stored in Microsoft Excel prior to analysis.

Large-scale spatial studies that use published literature for data collection will always contain some error. Data collection, measurement, and reporting vary across studies and contribute to uncertainty. A method does not exist that can test the extent of error found in this type of study. I assumed that if a pattern occurred over many diverse species and studies seen herein, it is a valid pattern. Additionally, significance levels can be altered by such sources of error, so consideration was given to patterns with p-values close to significance cutoffs ($\alpha < 0.05$). Studies with large sample sizes were sought, which maximized the validity of reported data. Some traits would be optimal for this study (e.g. fecundity standardized as egg count per body mass), but the amount of data across species was inconsistent. For this reason, these inconsistent life history traits were excluded from analysis and other related traits were used.

Analysis of Latitudinal Directionality in Life History Traits:

An index of egg production was included to assess latitudinal patterns for trade-offs between fecundity and egg size (i.e. diameter) (Fleming and Gross 1990):

$$(1) \text{ Index of Egg Production} = \text{Average Fecundity} * \text{Egg Size}$$

Traits were plotted individually against latitude in Minitab (version 15) before and after correction for species relatedness to assess presence-absence of linear and non-linear positive, negative, and dome shaped patterns. Relatedness constraints were corrected for by simple linear regression of traits against family phylogenetic position (Diniz-Filho et al. 1998). Family phylogenetic position is the numerical relatedness of fish families based on derived characters (Grafen 1989) and was used because the study species represented a broad phylogenetic span (Olden et al. 2006). Derived characters within families are minimal with a broad phylogenetic span of species; this allows family-level phylogenies to be an approximate qualitative proxy for individual phylogenetic tree positions (Olden et al. 2006). Therefore, resulting residual values used in analysis represent “independent evolution of each species” (Diniz-Filho et al. 1998). Family phylogenetic positions were obtained from the FishTraits database (Frimpong and Angermeier 2009: <http://www.cnre.vt.edu/fisheries/fishtraits/>) based on Nelson (2006).

General linear models (McCullagh and Nelder 1989; Dobson and Barnett 2008) were conducted in Minitab (version 15) with latitude as a covariate and species as a random effect on phylogenetically corrected residual values. General linear models tested the presence or absence of significantly different relationships for traits between species, within species, and by latitude ($\alpha = 0.05$). Adjusted sum of squares were partitioned between species, latitude, and random error to determine between and within species variability. The model is as follows:

$$(2) y_{ij} = \beta_0 + \beta_1 x_j + \alpha_i + \gamma_i x_j + \varepsilon_{ij} ,$$

Where y_{ij} is the life history trait response for species i and observation j , β_0 is the intercept for all species combined, β_1 is the slope coefficient for the relationship between trait and latitude, x_j is the latitude associated with observation j , α_i is the random intercept for species i , γ_i is the random

slope coefficient between the response and latitude for species i , and ϵ_{ij} is random error (Der and Everitt 2002). The number of species examined for each trait range 8 to 12, since 12 species maximum were studied, but some species lacked data for particular traits.

General linear model adjusted sum of squares were used to calculate relative variance in each trait explained by latitude, species effects, and random error. Trait variability sums were necessary to identify factors driving specific data patterns. Species effects were expected to have high variation since the species used were phylogenetically diverse. Greater phylogenetic breadth usually means more varied trait-states and ranges. For example, muskellunge and fathead minnow will not have similar fecundities. Latitude was typically expected to explain relatively low amounts of variation, but can explain relatively high amounts of variation when traits have high latitudinal affinity. High latitudinal variability and high amounts of random error were undesirable; these patterns make traits less useful for understanding life history trade-offs between species. High amounts of species adjusted sum of squares were desired and give insight into interspecific and intraspecific trait relationships (Blanck and Lamouroux 2007).

Results

Latitude frequently explained little variation (usually less than 5%), but average age at maturation, longevity, and average total length at age-1 had $>5\%$ (8.6%-25.8%) of variation explained by latitude (Figure 1). Species effects usually explained the majority of variation for each trait, but exceptions were found when random error was high, including longevity, length of spawning season, average total length at age-1, and average fecundity. Latitude never explained more variation for a trait than species effects or random error (Figure 1), which showed that strong species-specific and overall trends were apparent in the data.

All life history traits had at least one species with a significant ($p \leq 0.05$) latitudinal directionality (i.e. increase or decrease), except index of egg production, which remained constant across latitudes. Strong species-specific life history trait latitudinal patterns indicate much intraspecific variation and support latitudinal variation validity. Adjusted R-square values ranged 32.0% to 86.9% (Table 2). Traits with more than one species exhibiting an individual significant latitudinal direction effect (10 of 11) always contained a combination of latitudinal increases and decreases. A majority of species displayed more than two significant latitudinal direction effects; within species, most traits displayed the same directionality. The other species experienced both latitudinal trait increases and decreases. All species had at least one species-specific latitudinal direction effect (Table 3).

Several traits linearly increased with increased latitude, including average age at maturation (Figure 2), average egg diameter (Figure 3), average total length of newly hatched larvae (Figure 4), and longevity (Figure 5). Several traits quantitatively increased linearly with increased latitude, including average age at maturation ($p = 0.000$, latitudinal coefficient = 0.140) (Figure 2), longevity ($p = 0.000$, latitudinal coefficient = 0.529) (Figure 5), and maximum length ($p = 0.021$, latitudinal coefficient = 6.870) (Figure 6). Several weak to moderate decreases with increased latitude occurred, including average spawning temperature (Figure 7), length of spawning season (Figure 8), average total length at age 1 (Figure 9), and index of egg production (Figure 10). Several traits quantitatively decreased linearly with increased latitude, including average spawning temperature ($p = 0.026$, latitudinal coefficient = -0.251) (Figure 7), length of spawning season ($p = 0.046$, latitudinal coefficient = -0.032) (Figure 8), and average total length at age 1 ($p = 0.005$, latitudinal coefficient = -4.572) (Figure 9).

Maximum length (Figure 6), average fecundity (Figure 11), and average total length at maturation (Figure 12) visually appeared to neither increase nor decrease significantly with increased latitude. Average fecundity (Figure 11) declined slightly with increased latitude, but the data contained much variation and only a slightly negative slope ($p = 0.145$). Maximum length (Figure 6) increased with increased latitude for all species combined ($p = 0.021$ and latitudinal coefficient = 6.870) and showed a clear increase for individual species such as muskellunge (Table 3). Average total length at maturation (Figure 12) had no clear latitudinal patterns ($p = 0.895$).

All traits had their p-values compared before and after correction for relatedness to determine if this process changed significance levels. Correction for relatedness among species played a significant, but not very important role in study outcomes. Only average fecundity ($p = 0.002$ before, $p = 0.145$ after) exhibited a significant difference in latitudinal directionality before and after relatedness was corrected for.

Discussion

Average total length of newly hatched larvae, average total length at maturation, average spawning temperature, average egg diameter, and maximum length exhibited the greatest variation among species within adaptive attribute groups (Figure 1). Herein, adaptive attribute groups represent groups of correlated traits that serve as proxies for each other according to Winemiller's (1992) triangular, adaptive life history model. Table 1 arrangement represents adaptive attribute groupings. Between-species variation was determined by percent variation explained by species; higher percent variation makes the trait better for testing ecological hypotheses. Accordingly, fish will show different, but predictable patterns by location and

between species for the best ecologically applicable traits, allowing broad applications of such traits. Index of egg production would be good for ecological hypothesis testing as well. Egg production showed only slightly less variation explained by species than average egg diameter, which was the reproductive-investment adaptive attribute with the greatest variation between species (Figure 1).

Life history trait latitudinal directionality exhibited interesting patterns between species and traits. Contrasts between muskellunge and fathead minnow were particularly interesting; species had eight life history traits in common with species-specific latitudinal patterns, but mostly opposite directionality. In total, muskellunge and fathead minnow had all except one significant, species-specific life history trait directionality in common (Table 3). Results signified both species have strong, but opposite latitudinal direction effects likely due to life history trait trade-off constraints. As expected, all other species exhibited either predominately positive, negative, or a mix of latitudinal directionality (Table 3). Each species showed directionality for at least 1 life history trait examined (Table 3), but directionality was not necessarily the same as overall latitudinal patterns (Table 2).

All latitudinal patterns quantitatively supported herein were strongly linked to temperature and/or photoperiod as a function of latitude. Spawning season was abbreviated and spawning occurred at lower temperatures in more northerly locations; photoperiod and temperature are strong influences (Wootton 1998). Growth-related life history traits affected in more northerly locations include maturation at older ages (Figure 2), increased maximum length (Figure 6), and reduced first year growth (Figure 9). Longevity was greater in northern locations because lower temperatures slow growth and other life processes. Trait relationships shed light on environmental interactions: for instance, slower growth causes older age at maturation, but

slow growth increases longevity and allows greater maximum length attainment. Length at maturation did not have significant latitudinal directionality or variation; it remained relatively constant, regardless of latitude (Matthews 1998). Shorter spawning seasons and lower spawning temperatures explain these phenomena. Less spawning time and cooler spawning temperatures mean spawning occurs later in northern species range locations, and this provides less opportunity to attain lengths comparable to southerly populations for a given age. Prime northern growth periods will be consistently less, causing longer periods and older ages before maturation. Lengthier temporal growth processes influenced by temperature will yield greater longevity and maximum length since growth is slower and fishes have more time to grow, respectively.

Braaten and Guy (2002) showed decreased growth rates (mm/day) for some species with increased latitude moving northward from the equator. For all species, von Bertalanffy growth coefficients decreased when latitude increased, which indicated growth is slower in more northerly locations. Heibo et al. (2005) found a negative relationship between growth rate and latitude. Herein, slower growth rates led to latitudinal directionalities in growth-related traits, including a negative relationship with increased latitude of average total length at age 1 (Figure 9), and positive relationships with increased latitude of average age at maturation (Figure 2), longevity (Figure 5), and maximum length (Figure 6). These life history trait latitudinal directionalities were previously associated with differences in temperature regimes (Braaten and Guy 2002). My data further supports the Braaten and Guy (2002) latitudinal temperature-regime argument with significant negative relationships for temperature-related traits, including average spawning temperature (Figure 7) and length of spawning season (Figure 8).

Conover (1990) found latitudinal constraints on growing season did not significantly influence certain species' length at age 1; this was termed "countergradient variation." Current study results suggest otherwise, as average total length at age 1 decreased with increased latitude (Figure 9). Three other studies supported reduced length / growth in the first year of life at higher latitudes as well (L'abee-Lund et al. 1989; Braaten and Guy 2002; Heibo et al. 2005). Conover (1990) claimed growth rates must be proportionately greater in northern latitudes since shorter growing seasons and potential for proportionately higher mortality in younger, smaller fishes caused by harsher environmental conditions exist. Three laboratory studies concluded more northerly fish had higher growth capacities and took advantage of briefer prime growth periods (Conover and Present 1990; Schultz et al. 1996; Conover et al. 1997). Later, Yamahira and Conover (2002) recognized and incorporated environmental condition adaptations into earlier countergradient variation ideas. Lessened average total length at age 1 with increased latitude (Figure 9) and reduced northerly growth seen by L'abee-Lund et al. (1989), Braaten and Guy (2002), and Heibo et al. (2005) are due to environmental factors overriding genetic selection pressures (Conover et al. 1997), which resulted when more than a few select species were examined (i.e. as the countergradient variation studies always did).

Age and length at maturation patterns were positively influenced by increased latitude in L'abee-Lund et al. (1989), Morrison and Hero (2003), and Heibo et al. (2005), but the current study exhibited varying patterns. For instance, average age at maturation (Figure 2) exhibited positive, significant relationships with increased latitude (Table 2), but average total length at maturation (Figure 12) displayed non-significant latitudinal patterns (Table 2). Results suggest age at maturation increases positively with increased latitude and length at maturation does not.

This is likely due to fairly constant, large-scale and length-specific maturation patterns (Matthews 1998).

Like growing season, length of spawning season constricted as latitude increased (Gotelli and Pyron 1991; Morrison and Hero 2003). In the current study, length of spawning season decreased with increased latitude (Figure 8) and was explained by lower temperatures and shortened photoperiods (Wootton 1998). In previous studies, reproductive traits such as clutch size, gonadosomatic index (GSI), and / or egg production decreased with increased latitude (Fleming and Gross 1990; Morrison and Hero 2003; Heibo et al. 2005). Average fecundity decreased herein with increased latitude (Figure 11), but was not statistically significant (Table 2). Average egg diameter increased herein with increased latitude (Figure 3), but was not statistically significant (Table 2). Visual relationship confirmations are probably best in these cases.

Reduced reproductive investment (i.e. production of fewer, but larger eggs likely to develop into more viable offspring) likely drives average egg diameter increases with increased latitude. Conversely, larger maximum length with increased latitude (Figure 6) may override needs for larger eggs by producing more offspring than southerly populations. Morrison and Hero (2003) noticed amphibian egg size increased with increased latitude and noted egg size increases led to positive relationships between latitude, lengthier larval periods, and average total length of newly hatched larvae. In the current study, average total length of newly hatched larvae versus latitude results showed positive (Figure 4), but statistically insignificant patterns (Table 2). Lengthier larval periods are typically caused by lower temperatures at higher latitudes (Morrison and Hero 2003).

Other studies showed that longevity increases positively with increased latitude (Braaten and Guy 2002; Heibo et al. 2005), which agrees with the overall longevity pattern herein (Figure 5). Heibo et al. (2005) observed mortality rates decreased with increased latitude, which supports a positive longevity versus latitude relationship. Decreased mortality contributed to increased longevity, but factors not discussed by Heibo et al. (2005) such as fecundity, size of eggs / offspring, egg production, temperature regimes, etc. could significantly affect longevity too. Braaten and Guy (2002) showed freshwater drum do not have a latitudinal longevity pattern, which is also found herein (Table 3).

The current study exhibited generalized and species-specific life history trait latitudinal directionality patterns, indicated which patterns act predictably across latitudes, and identified which latitudinal patterns are optimal in many future research and management scenarios. For instance, results showed latitudinal trait responses to climatic conditions. Such responses display how thermal regime alteration and climate change may affect certain fish species and cause these species to either shift ranges or survive and evolve in-place, thus hypothesizing future distributional patterns. For example, current distributions and latitudinal trends found in this study can hypothesize future native and invasive species distributions and co-occurrence. Results provide important trait interpolation or imputation ability for closely-related species or for the same species in unstudied locations.

Conclusions

Study results effectively identify general and species-specific patterns of large-scale life history trait variability for North American fishes. Additionally, this study shows which traits are best for testing hypotheses involving life history tradeoffs as environmental factors change

according to strength of correlation with latitude. Based on questions being asked and / or the species in question, I recommend average total length of newly hatched larvae, average total length at maturation, average spawning temperature, average egg diameter, maximum length, and egg production for future ecological hypothesis testing. Most general and species-specific patterns identified in the current study supported known patterns, especially those found in Blanck and Lamouroux (2007). Agreement of patterns between Blanck and Lamouroux (2007) and the current study suggest widely applicable, universal patterns, including those related to growth rate, age at maturation, longevity, and maximum length. Different reproductive life history trait patterns found between Blanck and Lamouroux (2007) and the current study also provided bases for future hypothesis testing of among-study life history trait patterns. Future application in several research and management areas are apparent, including predicting effects of future large-scale thermal regime / climate change situations and modeling future species' distributional patterns.

Literature Cited

- Beacham, T. D. 1982. Fecundity of coho salmon (*Oncorhynchus kisutch*) and chum salmon (*O. keta*) in the northeast Pacific Ocean. *Canadian Journal of Zoology* 60(6):1463-1469.
- Blanck, A., and N. Lamouroux. 2007. Large-scale intraspecific variation in life-history traits of European freshwater fish. *Journal of Biogeography* 34:862-875.
- Braaten, P. J., and C. S. Guy. 2002. Life history attributes of fishes along the latitudinal gradient of the Missouri River. *Transactions of the American Fisheries Society* 131:931-945.
- Cambray, J. A. 1994. The comparative reproductive styles of two closely related African minnows (*Pseudobarbus afer* and *P. asper*) inhabiting two different sections of the Gamtoos River system. *Environmental Biology of Fishes* 41:247-268.
- Conover, D. O. 1990. The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. *Transactions of the American Fisheries Society* 119:416-430.
- Conover, D. O., and T. M. C. Present. 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia* 83:316-324.

- Conover, D. O., J. J. Brown, and A. Ehtisham. 1997. Countergradient variation in growth of young striped bass (*Morone saxatilis*) from different latitudes. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2401-2409.
- Crone, R. A., and C. E. Bond. 1976. Life history of coho salmon, *Oncorhynchus kisutch*, in Sashin Creek, southeastern Alaska. *United States National Atmospheric Administration Fishery Bulletin* 74:897-923.
- Der, G., and B. S. Everitt. 2002. A handbook of statistical analyses using SAS. CRC Press. Boca Raton, FL.
- Diniz-Filho, J. A. F., C. E. Ramos de Sant'Ana, and L. M. Bini. 1998. An eigenvector method for estimating phylogenetic inertia. *Evolution* 52(5):1247-1262.
- Dobson, A. J., and A. Barnett. 2008. An introduction to generalized linear models. Third edition. Chapman and Hall. London, UK.
- Drucker, B. 1972. Some life history characteristics of coho salmon of the Karluk River, Kodiak Island, Alaska. *United States National Atmospheric Administration Fishery Bulletin* 70:79-94.
- Fleming, I. A., and M. R. Gross. 1990. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. *Ecology* 71(1):1-11.
- Frimpong, E. A., and P. L. Angermeier. 2009. FishTraits: a database of ecological and life history traits of freshwater fishes of the United States. *Fisheries* 34(10):487-495.
- Goldstein, R. M., and M. R. Meador. 2004. Comparisons of fish species traits from small streams to large rivers. *Transactions of the American Fisheries Society* 133:971-983.
- Gotelli, N. J., and M. Pyron. 1991. Life history variation in North American freshwater minnows: effects of latitude and phylogeny. *Oikos* 62(1):30-40.
- Grafen, A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London, Series B* 326:119-157.
- Healey, M. C., and W. R. Heard. 1984. Inter- and Intra- population variation in the fecundity of Chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. *Canadian Journal of Fisheries and Aquatic Sciences* 41:476-483.
- Heibo, E., C. Magnhagen, and L. A. Vollestad. 2005. Latitudinal variation in life-history traits in Eurasian perch. *Ecology* 86(12):3377-3386.
- Kramer, D. L. 1978. Reproductive seasonality in the fishes of a tropical stream. *Ecology* 59(5):976-985.
- L'Abée-Lund, J. H., B. Jonsson, A. J. Jensen, L. M. Sættem, T. G. Heggberget, B. O. Johnsen, and T. F. Naesje. 1989. Latitudinal variation in life-history characteristics of sea-run migrant brown trout *Salmo trutta*. *Journal of Animal Biology* 58(2):525-542.
- Lamouroux, N., N. L. Poff, and P. L. Angermeier. 2002. Intercontinental convergence of stream fish community traits along geomorphic and hydrologic gradients. *Ecology* 83(7):1792-1807.
- Matthews, W. J. 1998. Patterns in freshwater fish ecology. Kluwer Academic Publishers. Norwell, MA.
- McCullagh, P., and J. A. Nelder. 1989. Generalized linear models. Second edition. Chapman and Hall. London, UK.
- Morrison, C., and J. M. Hero. 2003. Geographic variation in life-history characteristics of amphibians: a review. *Journal of Animal Ecology* 72(2):270-279.
- Nelson, J. S. 2006. Fishes of the world. Fourth edition. John Wiley, Inc. New York, NY.

- Olden, J. D., N. L. Poff, and K. R. Bestgen. 2006. Life history strategies predict fish invasions and extirpations in the Colorado River basin. *Ecological Monographs* 76(1):25-40.
- Page, L. M., and B. M. Burr. 1991. A field guide to freshwater fishes. Houghton Mifflin Company. New York, NY.
- Pianka, E. R. 1970. On 'r' and 'K' selection. *The American Naturalist* 104(940):592-597.
- Schloemer, C. L. 1947. Reproductive cycles of five species of Texas centrarchids. *Science* 106:85.
- Schultz, E. T., K. E. Reynolds, and D. O. Conover. 1996. Countergradient variation in growth among newly hatched *Fundulus heteroclitus*: geographic differences revealed by common-environment experiments. *Functional Ecology* 10(3):366-374.
- Stearns, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3(3):259-268.
- Travis, J. 2009. Phenotypic plasticity. *In*: The Princeton Guide to Ecology (S. A. Levin, ed.). Princeton University Press. Princeton, NJ.
- Williams, J. E., and C. E. Bond. 1983. Status and life history notes on the native fishes of the Alvord basin, Oregon and Nevada. Department of Fisheries and Wildlife, Oregon State University. Corvallis, OR.
- Winemiller, K. O. 1992. Life-history strategies and the effectiveness of sexual selection. *Oikos* 63(2):318-327.
- Wootton, R. J. 1998. Ecology of teleost fishes. Second edition. Kluwer Academic Publishers. Dordrecht, NL.
- Yamahira, K., and D. O. Conover. 2002. Intra- vs. interspecific latitudinal variation in growth: adaptation to temperature or seasonality? *Ecology* 83(5):1252-1262.

Tables and Figures

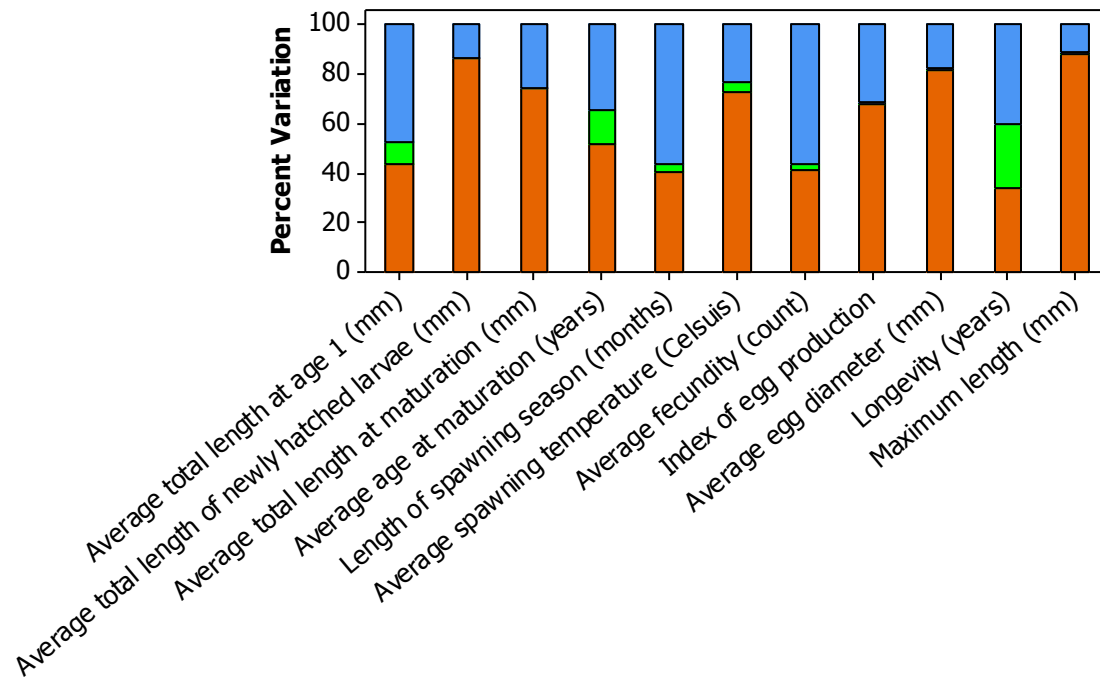


FIGURE 1. Percent of variation explained by latitude, species effects, and random error by trait. Orange bars represent % variation explained by species effects (lower portion), green bars represent % variation explained by latitude (middle portion), and blue bars represent % variation explained by random error (top portion) per trait.

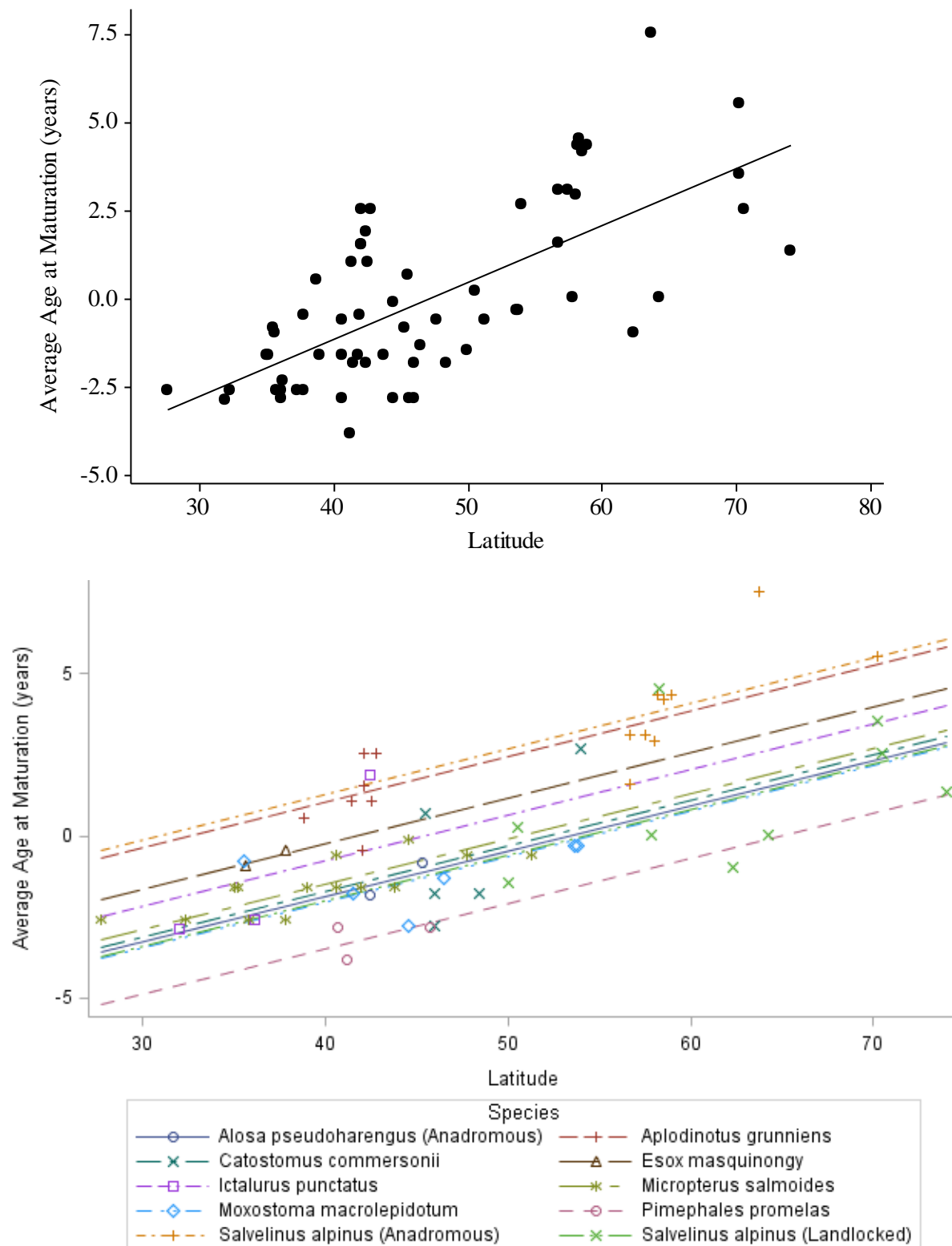


FIGURE 2. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in average age at maturation versus latitude. The axis representing a life history trait has been corrected for phylogeny and represents residual values.

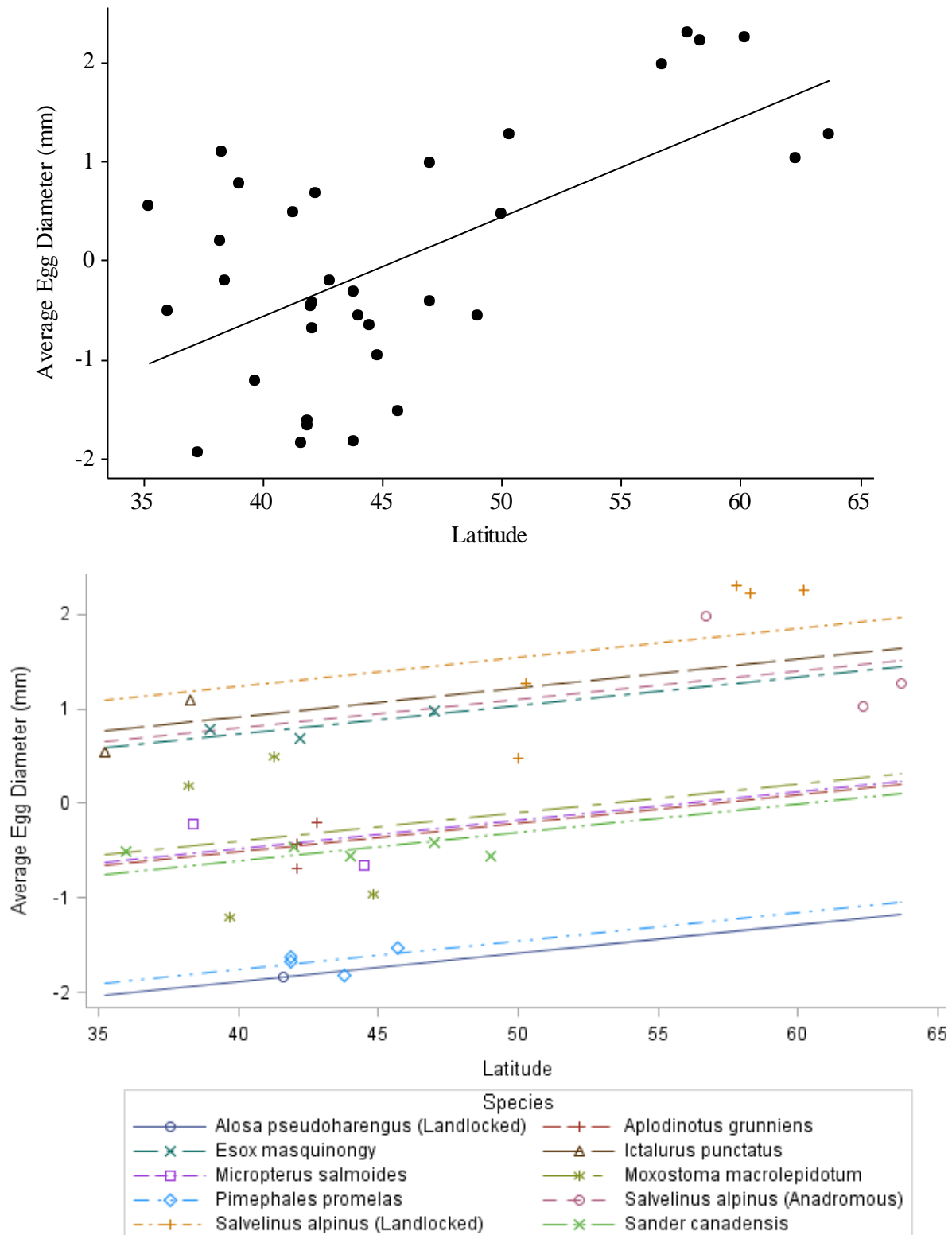


FIGURE 3. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in average egg diameter versus latitude. The axis representing a life history trait has been corrected for phylogeny and represents residual values.

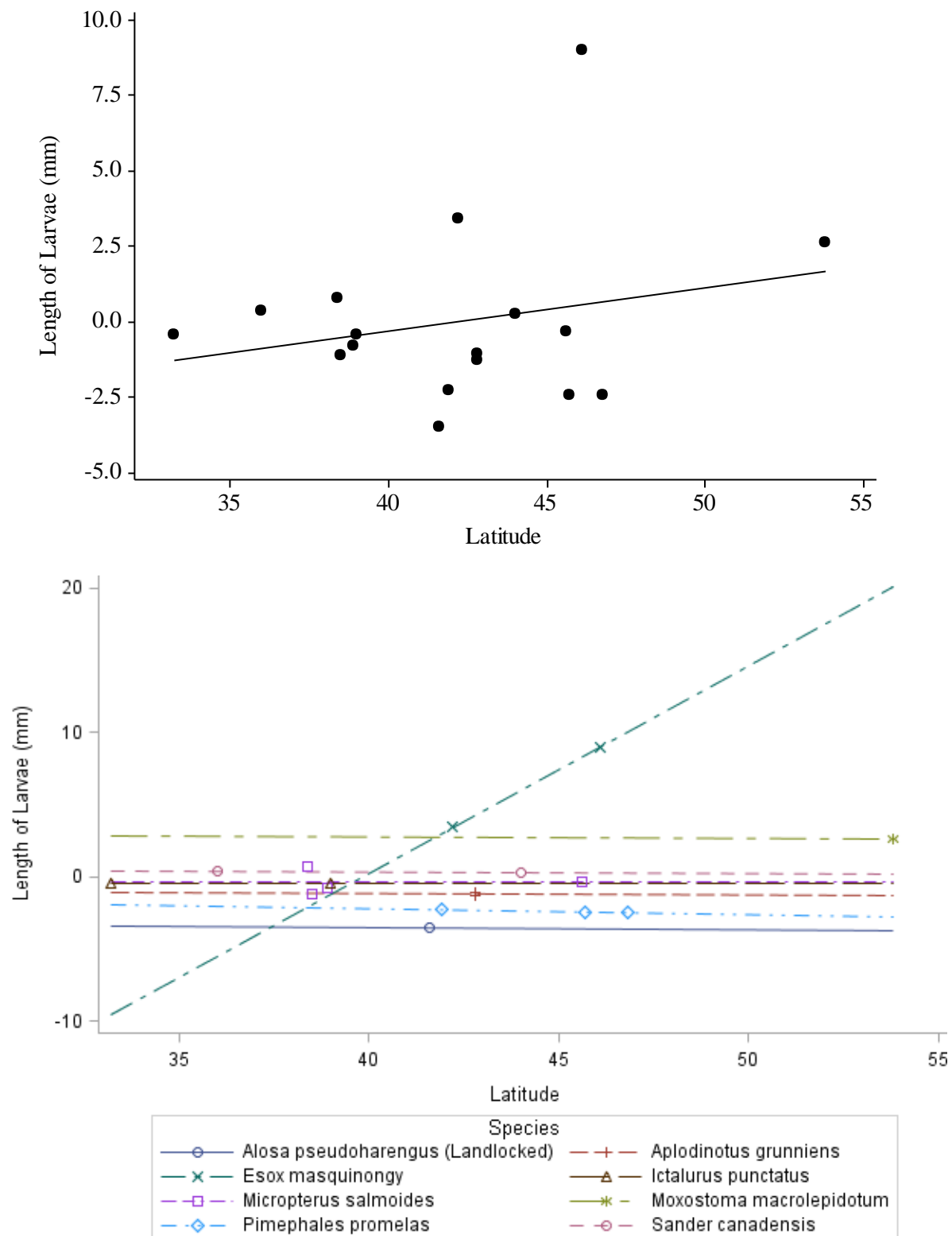


FIGURE 4. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in average total length of newly hatched larvae versus latitude. The axis representing a life history trait has been corrected for phylogeny and represents residual values.

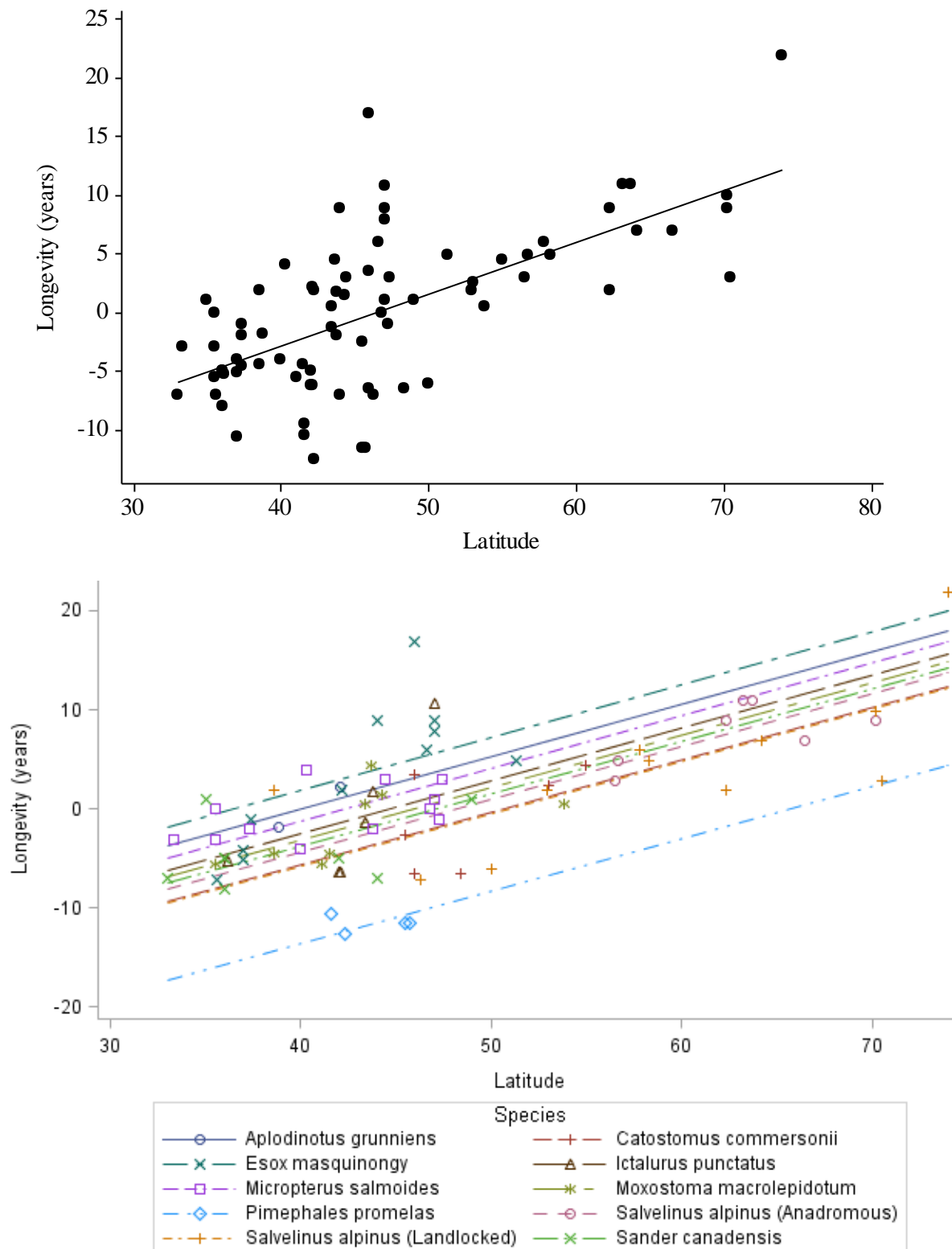


FIGURE 5. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in longevity versus latitude. The axis representing a life history trait has been corrected for phylogeny and represents residual values.

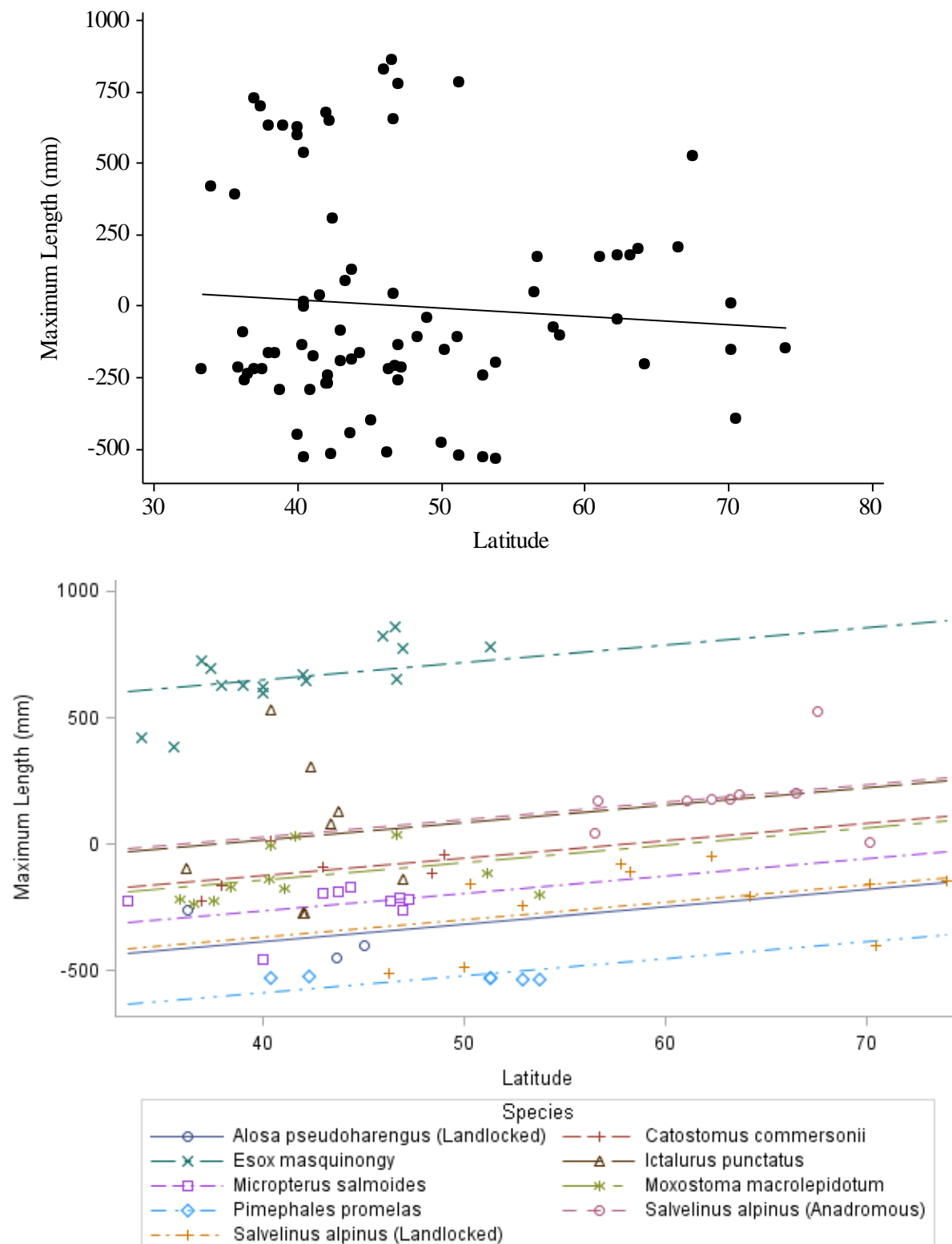


FIGURE 6. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in maximum length versus latitude. The axis representing a life history trait has been corrected for phylogeny and represents residual values.

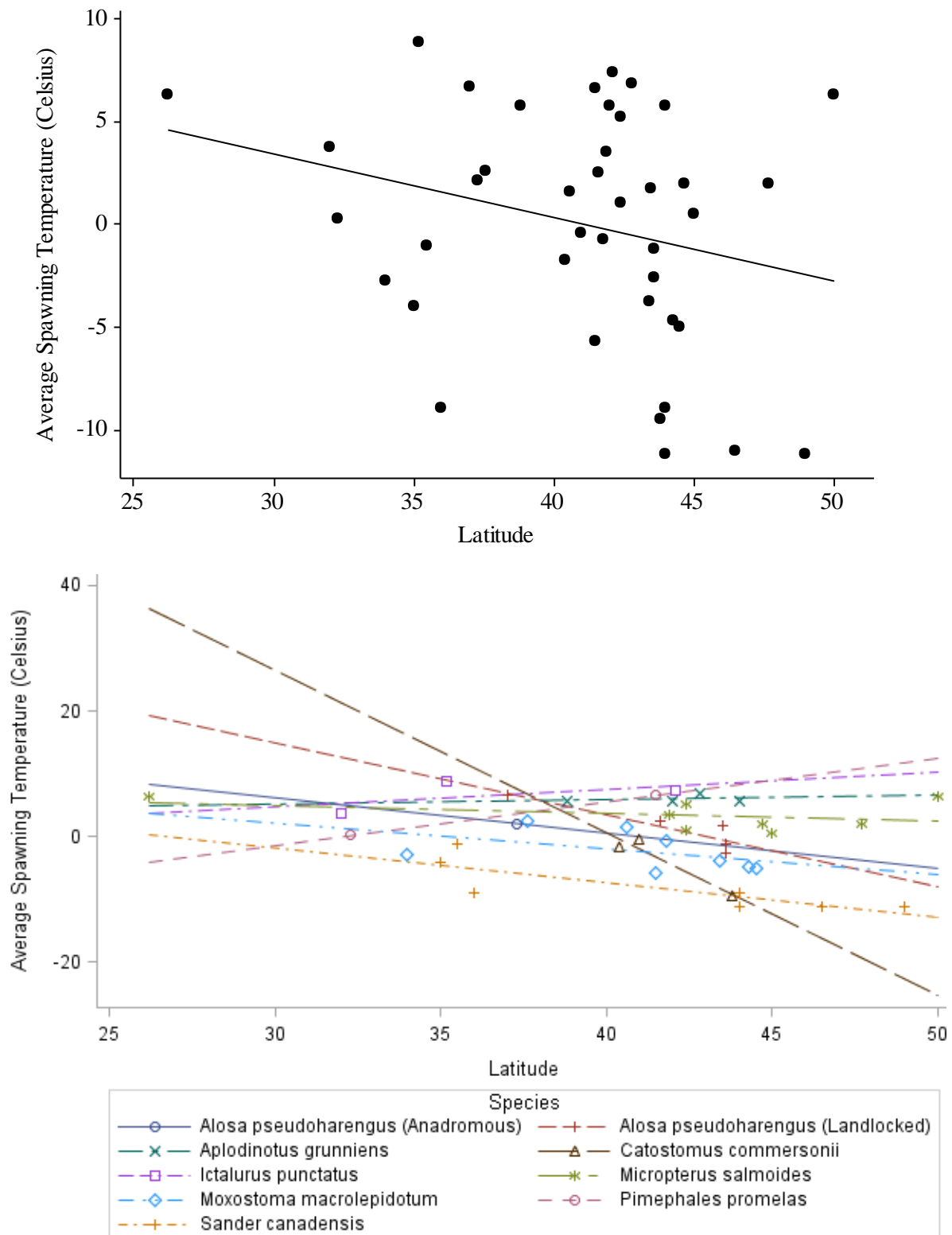


FIGURE 7. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in average spawning temperature versus latitude. The axis representing a life history trait has been corrected for phylogeny and represents residual values.

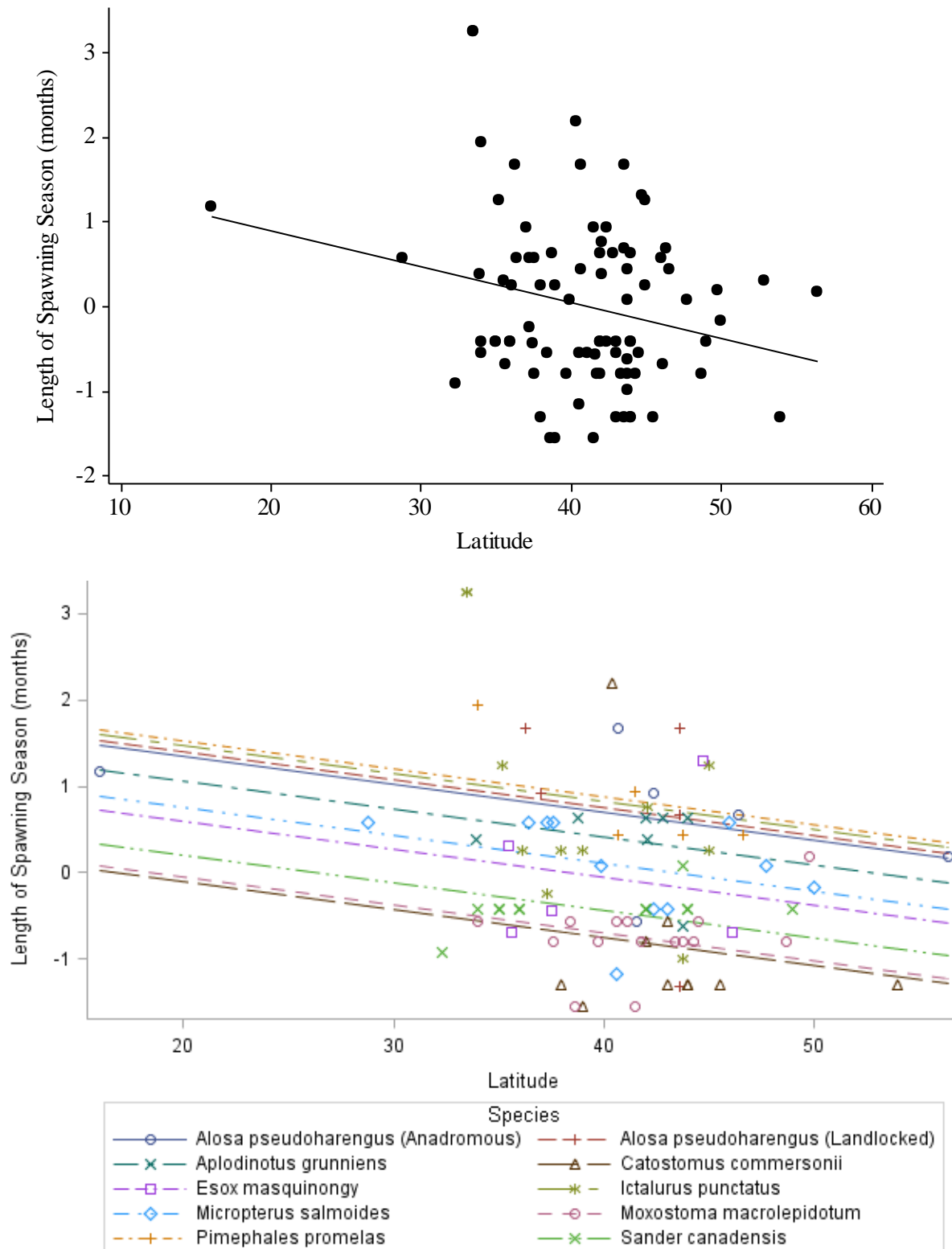


FIGURE 8. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in length of spawning season versus latitude. The axis representing a life history trait has been corrected for phylogeny and represents residual values.

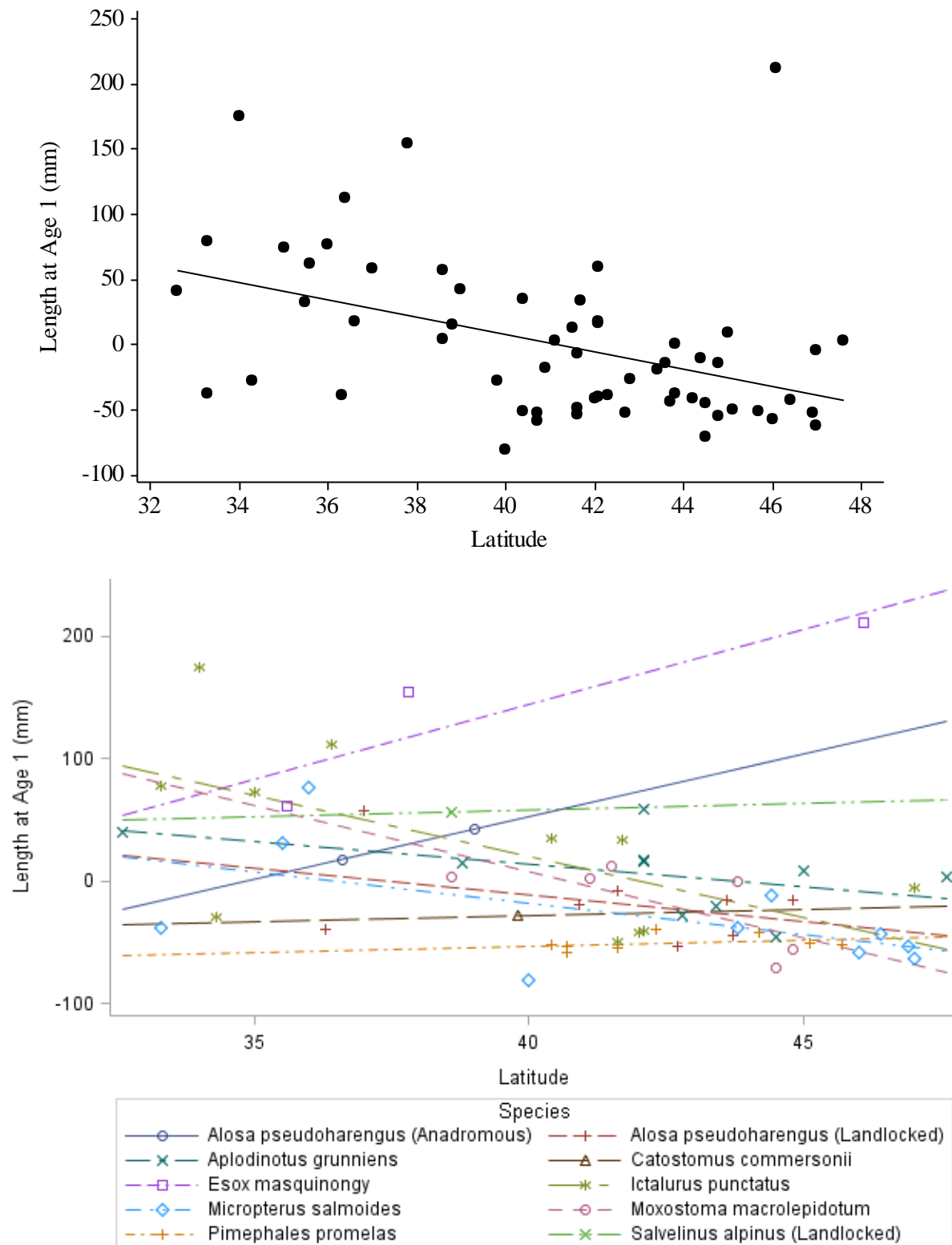


FIGURE 9. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in average total length at age 1 versus latitude. The axis representing a life history trait has been corrected for phylogeny and represents residual values.

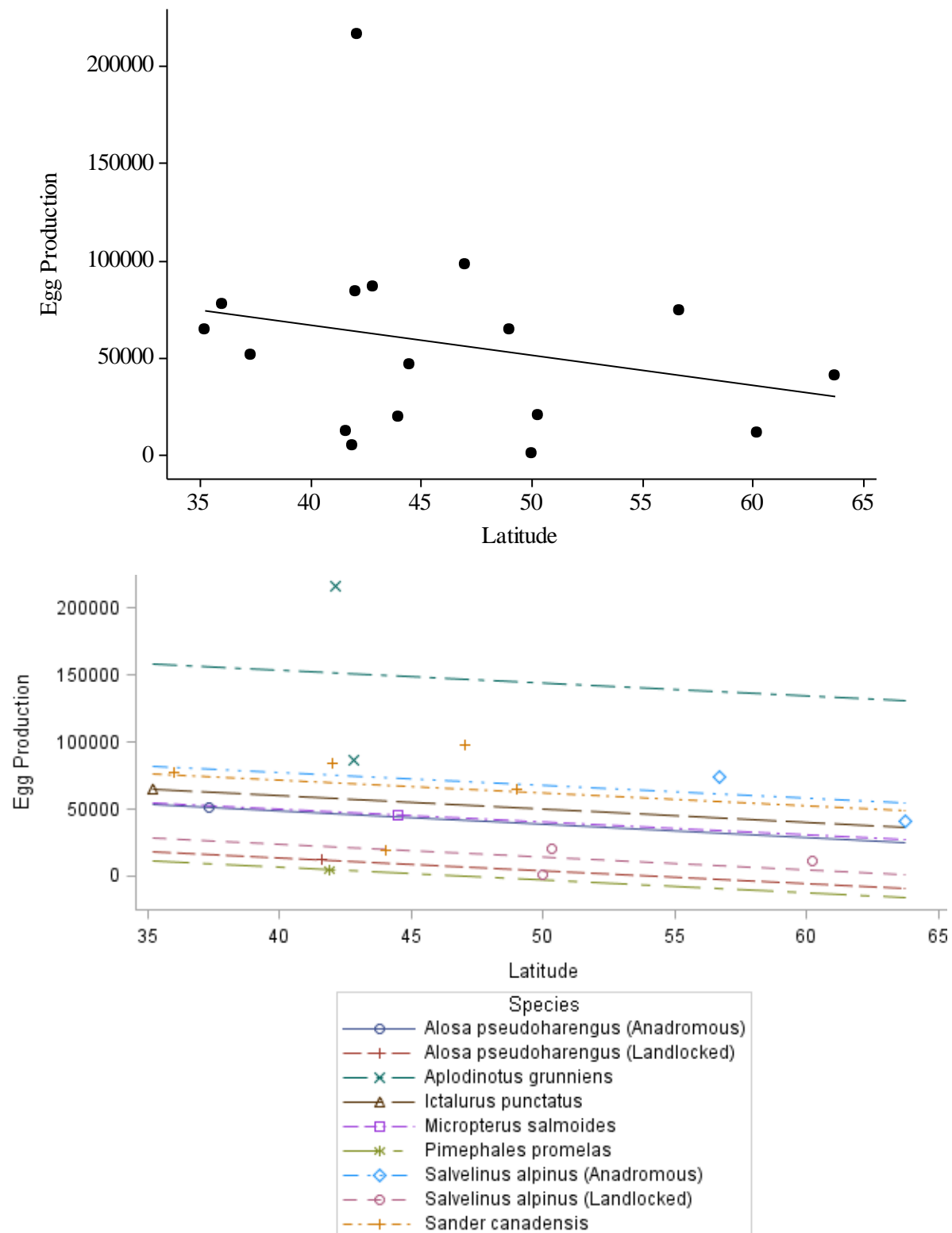


FIGURE 10. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in index of egg production versus latitude. The axis representing a life history trait has been corrected for phylogeny and represents residual values.

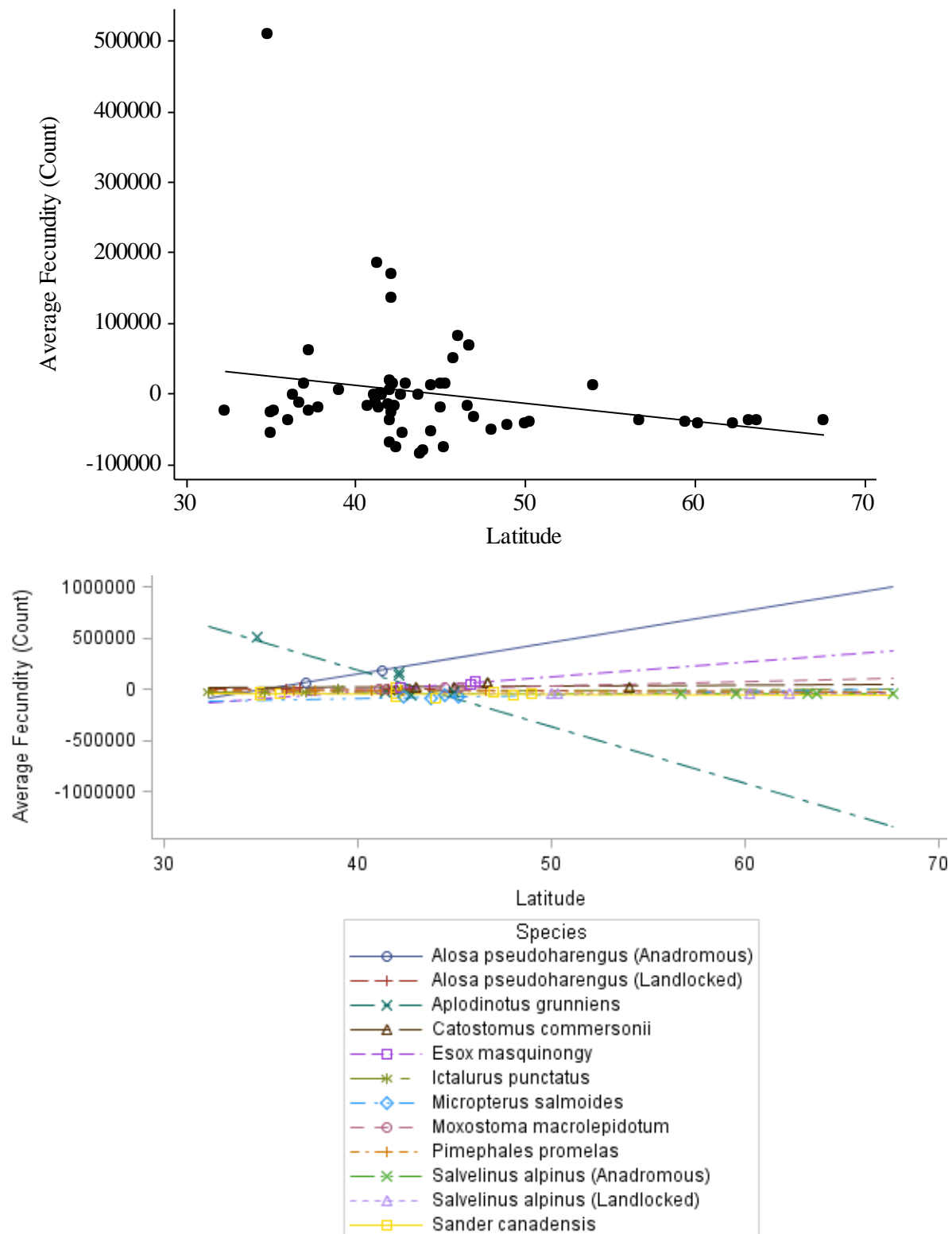


FIGURE 11. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in average fecundity versus latitude. The axis representing a life history trait has been corrected for phylogeny and represents residual values.

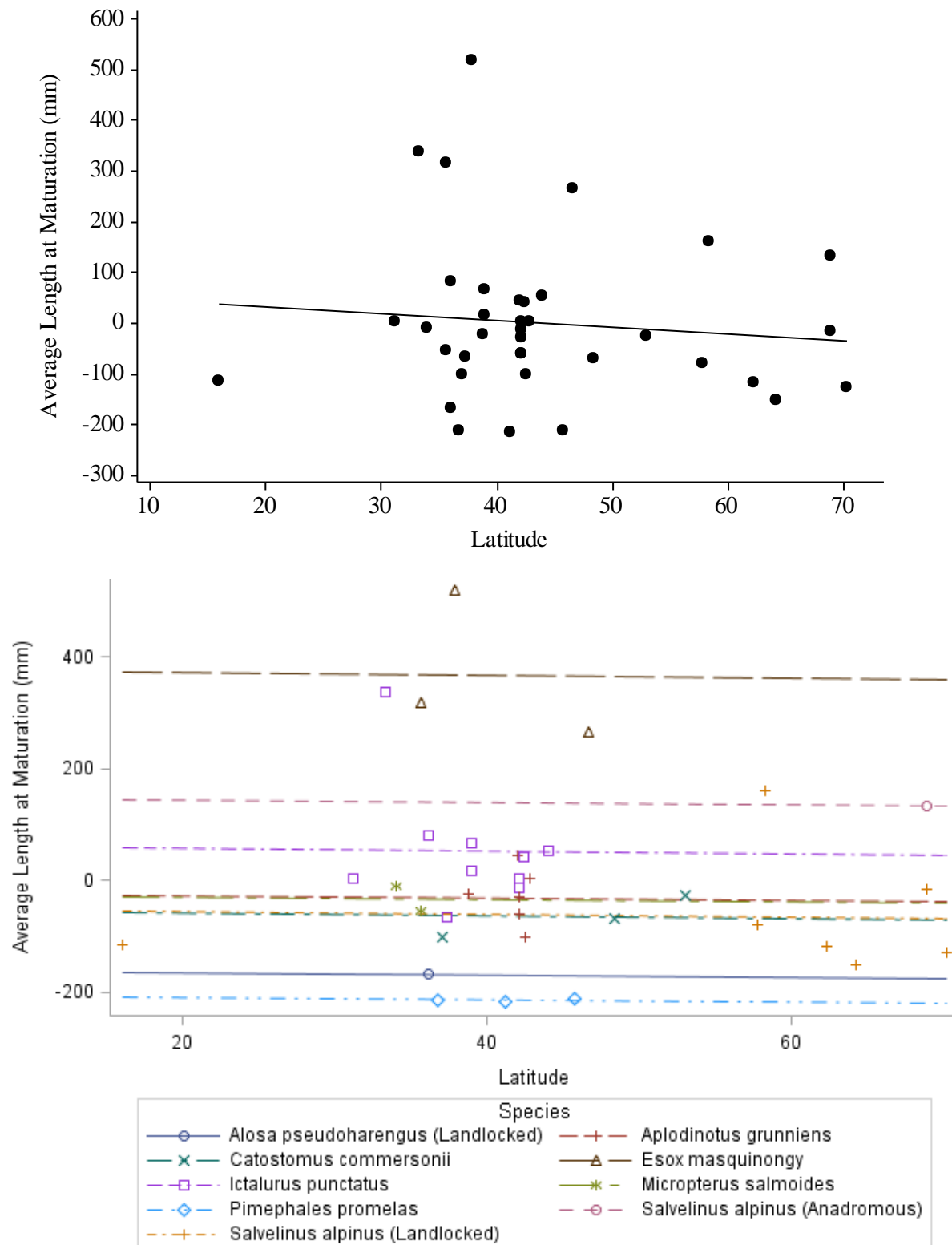


FIGURE 12. Scatter (upper) and ANCOVA (analysis of covariance - lower) plots showing patterns in average total length at maturation versus latitude. The axis representing a life history trait has been corrected for phylogeny and represents residual values.

TABLE 1. Life history traits used for analysis of trait variation.

Life History Trait	Adaptive Attribute
Average total length at age 1 (mm)	Juvenile growth
Average total length of newly hatched larvae (mm)	Juvenile growth
Average total length at maturation (mm)	Juvenile growth
Length of spawning season (months)	Reproductive timing
Average spawning temperature (°C)	Reproductive timing
Average fecundity (count)	Reproductive investment and output
Index of egg production	Reproductive investment and output
Average egg diameter (mm)	Reproductive investment and output
Average age at maturation (years)	Longevity/population turnover rate
Longevity (years)	Longevity/population turnover rate
Maximum length (mm)	Longevity/population turnover rate

TABLE 2. Adjusted R-square values, latitudinal direction effects, latitude coefficients, species effects, and intercept effects by trait with value significance / insignificance reported. Latitudinal direction effect, species effect, and intercept effect are p-values with a 0.05 significance level. Adj R Sq % is the abbreviation for adjusted R-square percent.

Life History Trait	Adj R Sq %	Latitudinal Direction Effect	Latitude Coefficient	Species Effect	Intercept Effect
Average age at maturation (years)	74.2	0.000	0.140	0.000	0.000
Average egg diameter (mm)	83.3	0.305	0.030	0.000	0.233
Average total length of newly hatched larvae (mm)	75.2	0.526	0.093	0.005	0.541
Longevity (years)	62.6	0.000	0.529	0.000	0.000
Average spawning temperature (Celsius)	71.1	0.026	-0.251	0.000	0.017
Length of spawning season (months)	37.0	0.046	-0.032	0.000	0.028
Average total length at age 1 (mm)	49.2	0.005	-4.572	0.000	0.003
Index of egg production	32.4	0.761	-966	0.204	0.510
Average fecundity (count)	32.0	0.145	-3662	0.002	0.129
Maximum length (mm)	86.9	0.021	6.870	0.000	0.002
Average total length at maturation (mm)	65.8	0.895	-0.246	0.000	0.928

TABLE 3. Species-specific significant latitudinal direction effects by trait. Positive numerical values represent a significant positive relationship and negative numerical values represent a significant negative relationship with latitude. Species names are as follows: P. p = *Pimephales promelas* (Fathead Minnow), E. m. = *Esox masquinongy* (Muskellunge), M. m. = *Moxostoma macrolepidotum* (Shorthead Redhorse), C. c. = *Catostomus commersonii* (White Sucker), I. p. = *Ictalurus punctatus* (Channel Catfish), M. s. = *Micropterus salmoides* (Largemouth Bass), A. g. = *Aplodinotus grunniens* (Freshwater Drum), S. a. (A) = *Salvelinus alpinus* (Arctic Char Anadromous), S. a. (LL) = *Salvelinus alpinus* (Arctic Char Landlocked), A. p. (A) = *Alosa pseudoharengus* (Alewife Anadromous), A. p. (LL) = *Alosa pseudoharengus* (Alewife Landlocked), and S. c. = *Sander canadensis* (Sauger).

Life History Trait	P. p	E. m	M. m	C. c	I. p	M. s	A. g	S. a (A)	S. a (LL)	A. p (A)	A. p (LL)	S. c
Average total length of newly hatched larvae (mm)	-2.73	5.95									-3.55	
Average total length at age 1 (mm)	-53.34	126.41				-33.66						
Maximum length (mm)	-430.17	809.16			176.29	-104.10		185.26	-207.58		-224.61	
Longevity (years)	-9.33	6.18				3.05						
Minimum total length at maturation (mm)	-169.83	350.03							-84.50		-134.47	
Average total length at maturation (mm)	-212.24	369.62										
Minimum age at maturation (years)									-2.10			
Average age at maturation (years)	-2.21						2.35	2.59				
Length of spawning period (months)			-0.92	-0.98	0.61							-0.66
Minimum spawning temperature (Celsius)	3.12	-4.23	-2.13	-4.68	6.18							
Average spawning temperature (Celsius)			-3.08	-4.47	4.76	2.99	5.50					-8.69
Maximum fecundity (count)		141421				-134205	156958					-94237
Average fecundity (count)						-84339	98856					-60796
Average egg diameter (mm)	-1.41	1.08			1.27				1.60	-1.51	-1.54	
Egg production							97677					

Chapter 3: Small-scale intraspecific variation in fish traits as a function of spatial factors and disturbance

Abstract

Small-scale bioassessment is usually the means to study effects of localized, anthropogenic disturbances on fish communities. For instance, benthic species often exhibit species-specific and general responses to many anthropogenic disturbances due to strong substrate affinity. The current study utilizes white sucker (*Catostomus commersonii*) and fantail darter (*Etheostoma flabellare*) traits to examine small-scale (i.e. between small watersheds) natural and disturbance-mediated variation in traits. Effective bioassessment traits would provide signals of anthropogenic effect beyond natural spatial variation. My objectives were 1) to identify traits that are useful for distinguishing the effect of spatial factors and disturbances on New River basin white sucker and fantail darter, and 2) to identify trait-disturbance relationships that would be useful in the future for bioassessment applications. I hypothesize traits will not vary significantly on a small-scale, watershed level, but variation due to anthropogenic disturbance will be detectable. White sucker and fantail darter were collected from Toms Creek and Chestnut Creek sites characterized by similar land use gradients. Chestnut Creek and Toms Creek exhibit urbanized and agricultural disturbances, respectively. Fishes were analyzed for reproductive, trophic, and age-related traits and trait variation due to spatial and disturbance effects. Step-wise general linear models identified significant trait-disturbance relationships. White sucker and fantail darter showed similar, type 1 responses consistent with positive disturbance-mediated, exploitive competitor responses in Munkittrick and Dixon (1989a). The current study results are contrary to past white sucker studies, which showed negative disturbance effects on traits associated with fish condition, but did not incorporate spatial factors

such as watershed and watershed area. I propose spatial factors, along with disturbance, drive current and past white sucker bioassessment study differences. Spatial and disturbance-mediated signals show egg size variation, relative condition factor, and relative gut weight are optimal white sucker and fantail darter bioassessment traits and indices; this is due to general linear model correlation strength. Additionally, paired t-tests showed relative weight to be an optimal white sucker bioassessment index. Current study results represent peculiar patterns for white sucker and fantail darter, and support importance of spatial factors and disturbances as they influence trait distributions within the New River basin, and potentially elsewhere.

Introduction

Traits vary within and between species and exhibit directionality on various scales and along different habitat gradients. Large, continent-wide analyses exhibited much variation and directionality in certain species and traits (Lamouroux et al. 2002; Blanck and Lamouroux 2007; Chapter 2 of this thesis). Blanck et al. (2007) examined small- and large-scale trait variation with habitat template and hierarchical landscape filter approaches, which related specific habitat preferences and life history traits. Additionally, Goldstein and Meador (2005) found various levels of small-scale habitat modification adversely affected stream fishes through population trait-state alteration. Traits are used extensively in bioassessment applications and generally vary with spatial factors (Doherty et al. 2005), but natural spatial variability in traits should be separated from disturbance-mediated variation; this poses a greater challenge for some traits than others since spatial and disturbance-mediated affiliations with individual traits varies.

Population-level bioassessment indicates changes in populations in response to one or more environmental stressors. Compare-and-contrast bioassessment examines differences among

study areas and is especially useful for between-site comparisons and before-and-after disturbance scenarios (Power 2007). Field-based bioassessment provides an effective method to examine suites of stressor-response relationships without having to tease apart individual stressor effects on physiological condition (Munkittrick and Dixon 1989a; Power 2007). Additionally, small-scale bioassessment approaches gives information on site condition and are more applicable for understanding localized disturbance effects than more generalized large-scale approaches (Munkittrick and Dixon 1989a).

Certain fishes are more susceptible to environmental contaminants. Many contaminants build up in benthos, so close benthic association speeds up and / or amplifies contaminant problems (Munkittrick and Dixon 1989b). The white sucker (*Catostomus commersonii*) is ubiquitous and spends significant time associated with stream beds, especially during feeding and reproduction (Jenkins and Burkhead 1993). Strong benthic affinity makes white sucker an ideal contaminant-disturbance-effect study species (Munkittrick and Dixon 1989b). Fantail darter (*Etheostoma flabellare*) is ubiquitous and has a strong benthic affinity, which makes it an excellent contaminant-disturbance-effect study species as well. Fantail darters and white suckers have different trophic behavior in the New River (Jenkins and Burkhead 1993), so comparative analysis of trait-mediated disturbance responses between these species is instructive and may show different patterns based on trophic type.

Land use and resulting disturbances can significantly influence aquatic and terrestrial watershed conditions. Urbanization is an anthropogenic environmental disruption with high, potentially negative biotic and abiotic effects, both aquatic and terrestrial, via land modifications; increased human population densities drive this process (Paul and Meyer 2001; Scott 2006; Lussier et al. 2008). Agriculture is an anthropogenic environmental disruption that causes

negative biotic and abiotic effects to terrestrial and aquatic systems due to farming activities. Agriculture and urbanization are the two leading causes of stream degradation. Urbanization results in higher degradation and environmental impact per unit area than agriculture (Paul and Meyer 2001). Urbanization is characterized by high impervious surface proportions relative to other land cover types (Paul and Meyer 2001). Impervious surfaces cause decreased infiltration and increased runoff, which increases storm-water over-land flow rates and decreases water transport time to streams (Leopold et al. 2005; Fleming 2007). Also, reduced riparian vegetative cover is associated with urbanization (Arnold and Gibbons 1996), which decreases natural riparian nutrient and toxin buffering capabilities.

White sucker exhibits small-scale anthropogenic disturbance responses, including those related to growth, reproductive traits, and population structure (McFarlane and Franzin 1978; McFarlane and Franzin 1980; Munkittrick and Dixon 1988a; Munkittrick and Dixon 1988b; Munkittrick and Dixon 1989b; Doherty et al. 2005). Munkittrick and Dixon (1989a) established a bioassessment system using trait states to assess how different species typically react positively or negatively to different disturbance types and intensities. Species consistently exhibit reduced performance (i.e. reduced fecundity, growth, condition, etc.) when disturbance increases physical stress or competition versus undisturbed areas (i.e. type 3-4 response). Likewise, resilient fish species usually exhibit increased fitness (i.e. increased fecundity, growth, condition, etc.) when disturbances decrease physical stress and competition (i.e. type 1 response) (Munkittrick and Dixon 1989a). Other typologies within Munkittrick and Dixon (1989a) include type 2 responses (i.e. recruitment failure and subsequent negative, disturbance-mediated effects) and type 5 responses (i.e. niche shift and population suppression by disturbance). Traits help researchers identify population and community structure changes caused by land-use patterns (Poff and

Allan 1995). Changes in species traits are driven by habitat degradation, which makes traits the basis for biological integrity assessment (Goldstein and Meador 2005; Haddad et al. 2008). Effective and defensible bioassessment requires traits to provide a signal of anthropogenic effects beyond variation explained by natural spatial factors.

The current study examines how several life history traits vary on the small-scale (i.e. watershed level) between sites, within sites, between watersheds, and by disturbance level. My objectives were 1) to identify traits that are useful for distinguishing the effect of spatial factors and disturbances on New River basin white sucker and fantail darter, and 2) to identify trait-disturbance relationships that would be useful in the future for bioassessment applications. I hypothesize traits will not vary significantly on a small-scale, watershed level, but variation due to anthropogenic disturbance will be detectable.

Methods

Study Organisms:

The white sucker (Lacepède, 1803) is a benthic insectivore/herbivore (omnivore) of family Catostomidae that inhabits a wide spatial range and many lentic and lotic habitats. White suckers spawn earlier than most other species in Virginia, typically in March and April (Jenkins and Burkhead 1993). The fantail darter (Rafinesque, 1819) is a primarily insectivorous perciform of family Percidae. Fantail darters occur mostly in small- to medium-sized streams, but are known to inhabit larger rivers and lake shallows. Fantail darters are serial spawners, spawning multiple times from April to June (Jenkins and Burkhead 1993). The introduction provides details of reasons for species inclusion in this study.

Site Selection:

Five sampling reaches per stream were established on Toms Creek (Figure 1) and Chestnut Creek (Figure 2) (both New River tributaries). Sampled reaches were upstream of periodic sampling sites established during summer 2008 by Brandon Peoples and Jeremy Pritt. Each reach represented different anthropogenic disturbance levels. Land-use classes included downstream forested, downstream transitional, heavy urbanization / agriculture, upstream transitional, and upstream forested; one of each land use type was sampled per stream. Heavy urbanization / agriculture sites were considered disturbed and were analyzed in comparison with all other sites. Agriculture versus urbanization effects were not testable within this study and limit conclusions based on disturbance type. Sites were chosen through analysis with ArcView GIS software and the National Land Cover Database (NLCD). Agricultural Toms Creek sites and urbanized Chestnut Creek sites were selected by percent agricultural land and percent impervious surface cover, respectively. Fish habitat data collected previously by Brandon Peoples and Jeremy Pritt aided exact site selection from a larger pool of possible sites.

Fish Sampling:

Field collections were conducted to catch approximately 30 gravid female specimens and up to 30 immature fish of both species per 150-250 meter site. Sampling occurred 7-10 March 2009 for white suckers and 9, 17, and 20 April 2009 for fantail darters. Sampling dates insured capture of gravid, pre-spawn female specimens useful for all analyses. Several sampling efforts within 1-2 months of expected spawning initiation (referenced from Jenkins and Burkhead 1993) confirmed both species had increased gonadal development and remained pre-spawn. Fantail darters were collected by seining and backpack electrofishing, whereas white suckers were

collected via barge electrofishing. If needed, targeted fish sampling was conducted after initial reaches were sampled to collect more specimens. Additional fish sampling extended to the next 1-2 upstream or downstream pools/riffles from ending and starting points of each reach, respectively. Fantail darters were not sampled at the heavily disturbed agriculture site on Toms Creek; none were captured here on numerous other fish community sampling efforts by Brandon Peoples and Jeremy Pritt in summer 2008 due to habitat limitations.

Most (approximately 95%) white suckers and fantail darters caught during sampling were kept for laboratory analysis; a few fish occasionally escaped. Gravid adult females of both species were kept for fecundity analysis. White suckers of both sexes and all catchable sizes were kept for age analysis. All specimens of both species were kept for trophic analysis. White sucker total lengths and whole weights were measured in the field. Fantail darters were not measured in the field due to time constraints. All fish were euthanized streamside in MS-222 (tricaine methanesulfonate). Subsequent laboratory identification required minimum reproductive size white suckers (i.e. around 150mm total length: Jenkins and Burkhead 1993) to be uniquely tagged streamside. All white sucker specimens were cut before fixation behind the right pectoral fin base with a straight 1-inch incision; this cut improved fluid infiltration into the abdominal cavity. All specimens were fixed in 10% buffered (neutral pH) formalin before leaving each field site.

Laboratory Analysis:

Fecundity, trophic behavior, and age analyses were conducted in the laboratory. Fish remained in ca. 10% buffered (neutral pH) formalin for five days, were water soaked and rinsed several times over the next two days, and placed in ca. 70% ethanol for final preservation for at

least a week before examination. Following preservation, white suckers were re-measured (to the nearest mm total length) and re-weighed (to ± 0.001 grams for smaller fish and the nearest gram for larger fish) to determine preservation-induced shrinkage. Fantail darters were measured (to the nearest mm total length) and weighed (to ± 0.001 grams) for the first time. Next, all abdominal cavities were opened with a lateral incision at about the septum transversum and a longitudinal cut along the right abdominal body wall. Fish were completely eviscerated and re-weighed wet. Whole digestive tracts were cut as far anteriorly as possible and at the anus, then extracted. Gonads were extracted simultaneously from the remaining visceral anatomy. After fat removal, guts and gonads were stored in specimen-specific vials before analysis. For white suckers, sagittal otolith pairs were extracted using through-the-gills methodology (Devries and Frie 1996). Opercles were extracted from each fish and hand-cleaned under hot water to loosen tissue. Scales were hand-cleaned and pressed between two microscope slides. All aging structures from individual fishes were stored in specimen-specific envelopes prior to examination.

Full (i.e. contents still inside), dried guts were examined for weight. Most white sucker guts were dried at approximately 40°C (Fisher Scientific IsoTemp Oven) to remove all liquids. Small white sucker guts and all fantail darter guts were air dried. Brief experimentation showed oven drying versus air drying similarly removed gut moisture for both species (fishes < 100mm total length, ± 0.001 grams). Dried guts and contents were weighed together to ± 0.001 grams with an electronic Fisher Scientific balance.

White sucker otoliths, opercles, and scales were independently aged. Otoliths and opercles are reliable aging structures (Devries and Frie 1996), especially for suckers (McCarthy and Minckley 1987; Hewitt et al. 2009; R.E. Jenkins, pers. comm.). Scales are problematic aging

structures because scale loss/regeneration and re-absorption of annuli occur in older fishes (Devries and Frie 1996). Additionally, scales consistently underestimate age in older suckers (McCarthy and Minckley 1987; Hewitt et al. 2009; R.E. Jenkins, pers. comm.). All aging structures were completely cleaned and dried before examination. Otoliths were hand-polished down the sagittal plane using fine grit sand paper. Three people independently aged all otoliths, scales and opercles under a dissecting microscope at varying magnifications, light intensities, and angles. Variance components analysis quantified age variation attributable to human error (i.e. ager), methodological error (i.e. aging structure), and random error, which verified ages (Searle et al. 2006); use of median age as the overall age is acceptable if random error dominates total variance (Chang 1982; Kimura and Lyons 1991). Median age per individual represents final age across both readers and structures. Within-study age validation was not attempted with known-age fishes due to time constraints. Another study suggested suckers form annual growth rings that correspond with annuli (Hewitt et al. 2009).

Fecundity was assessed gravimetrically by subsampling mature white sucker oocytes and counting all fantail darter oocytes. Ovaries of both species were dried at 40°C (Fisher Scientific IsoTemp Oven) until fully dry. Ovaries were considered fully dry when weight changes ceased between 15 minute weighing intervals. Dry weights of whole ovaries to +/- 0.001 grams and individual eggs to +/- 0.0001 grams were measured using two different precision level Fisher Scientific electronic balances. Ovary and egg weights (n=10) per female quantified ovary and egg weight variability and estimated fecundity in both species:

$$(1) \text{ Dry Ovary Weight} / \text{Average Dry Egg Weight} = \text{Fecundity}$$

Calculations and Statistical Analyses:

Certain traits correlate with and constrain other traits. Thus, some traits in this study were both responses and explanatory variables. Traits include total length (mm), eviscerated weight (g), maturity (mature/immature), gonadosomatic index (GSI), fecundity (count), average egg weight (g), coefficient of variation in egg size, and median age (years). Related indices include relative (i.e. full) gut weight (% body weight) and relative condition factor (K_n). Spatial factors encompass watershed (Toms/Chestnut) and watershed area (m^2), while disturbance includes site quality (disturbed / undisturbed). Gonadosomatic index (GSI) was used to assess gonad condition relative to body weight (Strange 1996):

$$(2) \text{ Gonadosomatic Index (GSI)} = (\text{Gonad Weight} / \text{Eviscerated Body Weight}) * 100$$

Relative condition factor enabled condition comparisons between sites. Relative weight, a more precise, species-specific condition estimator, was only used and compared with relative condition factor for white sucker because fantail darter species-specific slopes and intercepts necessary for calculation were unknown (i.e. see Bister et al. 2000). Relative condition factor compares individual condition with overall population condition (Anderson and Neumann 1996):

$$(3) \text{ Relative Condition Factor } (K_n) = (W/W'),$$

where W' is the length-specific mean weight for all individuals in the population of interest and W is the weight of an individual fish from the population of interest. Relative condition factor shows individual fish length to weight ratios in relation to other fishes in the population of interest. Similarly, relative weight shows population condition in comparison to the overall, species-specific average condition (Anderson and Neumann 1996):

$$(4) \text{ Relative Weight } (W_r) = (W/W_s) \times 100,$$

where W_s is the species- and length-specific standard weight and W is the weight of an individual fish from the population of interest. Paired, one sample t-tests with equal variance

were conducted to identify the presence of relative weight trends that significantly differed from overall white sucker length-specific averages (i.e. 75th percentile). Manual Bonferroni corrections were done to insure $\alpha = 0.05$ was maintained. Species- and site-specific length-weight regression gave length-specific mean weight equations in Microsoft Excel.

Total length, eviscerated weight, and fecundity were \log_{10} transformed and watershed area was natural log transformed before analysis for approximate normal distributions. General linear models (McCullagh and Nelder 1989; Dobson and Barnett 2008) showed biotic and abiotic relationship significance ($\alpha = 0.05$) in Minitab (version 15). Site quality was a fixed factor, watershed was a random factor, and total length, eviscerated weight, median age, and watershed area were covariates. Fixed, random, and covariate designations were driven by data structure and questions posed by this study. The individual species model was adapted from Der and Everitt (2002):

$$(5) y_{ij} = \beta_0 + \gamma_i x_{1j} + \beta_2 x_{2j} + \beta_3 x_{3j} + \beta_4 x_{4j} + \beta_5 x_{5j} + \beta_6 x_{6j} + \alpha_i + \epsilon_{ij} ,$$

where y_{ij} is the trait response for watershed i and observation j , β_0 is the intercept, γ_i is the random slope coefficient between the response and watershed i for observation j , x_{1j} is the watershed for observation j , β_2 is the slope coefficient for the relationship between trait and site quality, x_{2j} is the site quality for observation j , β_3 is the slope coefficient for the relationship between trait and length, x_{3j} is the length for observation j , β_4 is the slope coefficient for the relationship between trait and weight, x_{4j} is the weight for observation j , β_5 is the slope coefficient for the relationship between trait and age, x_{5j} is the age for observation j , β_6 is the slope coefficient for the relationship between trait and watershed area, x_{6j} is the watershed area for observation j , α_i is the random intercept for watershed, and ϵ_{ij} is random error. β_5 and x_{5j} were excluded from the general linear model since fantail darters were not aged.

Stepwise model procedure helped identify factors that most significantly influenced each life history trait. The general linear model was fit initially with all factors to be considered, and then the most insignificant (i.e. highest p-value) factor was removed before re-running the model until all remaining values were significant. If a correlated factor was retained, other factors were excluded to minimize co-linearity and counterintuitive coefficients. Coefficients of multiple determination and graphical interpretations helped determine significant responses.

Results

Variance components analysis explains relatively little total age variance (approximately 6%) for age and aging structure combined. The remaining variance represents random error; this justifies mean or median age use for final age determination from all agers ($n = 3$) and structures (i.e. scale, opercle, and otolith) ($n = 3$) per specimen. Discrete, median age values out of 9 ages (i.e. 3×3) were obtained per specimen for use in subsequent analysis.

Study results showed significant, small-scale trait variation in the New River basin within and between watersheds, within the same species and site, and between anthropogenically disturbed and undisturbed sites (Table 1). White sucker and fantail darter exhibit similar patterns spatially, between traits, and based on disturbance. Table 1 contains a complete species-specific account of all significant results, which displays only minor differences between species. Trait relationships coincide largely with well-known patterns, including size v. reproductive traits (i.e. fecundity, gonadosomatic index, average egg size, and egg size variation for both species) and size / age (i.e. total length and median age for white sucker, and eviscerated weight for fantail darter) v. relative gut weight patterns. As expected, maturity was positively related to age and length in white sucker and fantail darter, respectively.

Spatial patterns include trait and performance measure variation between watersheds and according to watershed area (Table 1). White sucker condition factor was higher in Toms Creek (Figure 3; Table 1), but fantail darter condition factor appeared to be higher in Chestnut Creek (Figure 4). Both white sucker and fantail darter condition factor increased with watershed area (Figures 5-6). Fantail darter fecundity was higher in Toms Creek (Figure 7) and increased with watershed area (Figure 8). White sucker average egg size was higher in Toms Creek (Figure 9), but fantail darter average egg size was higher in Chestnut Creek (Figure 10). White sucker relative gut weight was higher in Chestnut Creek (Figure 11).

The current study suggests responses to anthropogenic disturbance with signals above natural spatial variation (Table 1). White sucker populations showed higher condition factor (Figure 12) and greater egg size variation in disturbed areas (Figure 13). Likewise, fantail darter populations showed condition factor (Figure 14) and relative gut weight increases in disturbed areas (Figure 15). White sucker relative weight results had values similar to the overall species average by length (i.e. 75th percentile). T-test results showed white suckers in disturbed sites had relative weights significantly higher than the 75th percentile ($p = 0.020$), while white suckers in undisturbed sites had relative weights significantly lower than the 75th percentile ($p = 0.019$). Study results support trait variability driven by anthropogenic disturbance after models have accounted for biological (size) and spatial factors. Additionally, study results suggest that white sucker and fantail darter display largely positive disturbance-mediated responses (Table 1; Figures 12-15; relative weight t-test results).

Discussion

Analysis identified potentially useful bioassessment traits and performance indices, which include egg size variation, condition factor, and relative gut weight for white sucker and fantail darter (Table 1), as well as relative weight for white sucker. This trait (egg size variation) and performance indices (condition factor, relative weight, and relative gut weight) each displayed positive associations with disturbance. Previous studies showed overwhelming negative effects of chronic land and water resource degradation on local scales, especially for white sucker (McFarlane and Franzin 1978; McFarlane and Franzin 1980; McMaster et al. 1992; Van der Kraak et al. 1992; Gagnon et al. 1994; McMaster et al. 1995). Munkittrick and Dixon (1989a) provide a functional framework for low-level white sucker habitat degradation responses. Frameworks are useful, but low-level system- and species-specific anthropogenic disturbance effects require additional research to develop accurate, condition-based assessments (Munkittrick and Dixon 1989a). The current study effectively applies Munkittrick and Dixon's (1989a) framework to classify white sucker and fantail darter as exploitative competitors (i.e. type 1 response) due to positive condition factor (Figures 12 and 14) and relative weight responses. White sucker and fantail darter occupy a wide variety of habitats (Jenkins and Burkhead 1993) and have wide geographic ranges (Page and Burr 1991) due to their hardy and adaptable nature.

Reproductive life history theory states environmental pressures, such as natural changes in environmental conditions, cause shifts in offspring production to fewer, but relatively larger progeny (Parker and Begon 1986; McGinley et al. 1987; Roff 1992). Past studies showed smaller eggs provide less viable offspring and decrease survival rate in larval and / or juvenile stages (Miller et al. 1988; Hutchings 1991; Heath et al. 1999). Resource competition and predation

drive size-mediated fitness dynamics in sub-optimal environments (Parker and Begon 1986). Maternal size (i.e. adult female length and weight) and fitness interact with environmental factors, selecting for optimal egg size (Smith and Fretwell 1974; Sargent et al. 1987; Johnston and Leggett 2002). Occasionally, site- and species-specific reproductive trait patterns display vastly different relationships (Johnston and Leggett 2002). Increased, habitat-based, stressor-induced egg size variation conferred negative reproductive effects on egg production (Parker and Begon 1986) and is consistent with the current study's white sucker populations (Figure 13). Little additional information exists on stressor-induced egg size variation. I speculate that disturbances drive egg size variation and cause reproductive abnormalities since white sucker and fantail darter egg size correlated significantly with eviscerated weight (as expected) (Table 1), but natural spatial factors had no effect (Table 1).

Many fish species respond negatively through sub-optimal trait states to turbid water conditions caused by anthropogenically driven siltation (Onorato et al. 1998; Sweka and Hartman 2001). Fantail darter relative gut weight positively correlated with stream reach disturbance, indicating increased prey consumption (Figure 15). High prey consumption rates drive accelerated organismal growth rates (Jensen et al. 2006) and relative condition (Rice et al. 1983). These past results are consistent with current study findings; fantail darter condition increased with disturbance (Figure 14). Fantail darters are insectivore sight-feeders (Jenkins and Burkhead 1993); study results indicate disturbance is either 1) light enough to not affect fantail darter prey consumption rates or 2) strong enough to exclude fantail darter competitors and predators. Additional research should further identify and support the exact mechanisms of fantail darter condition factor and relative gut weight increases. Currently, condition factor is a more convincing measure of population condition over relative gut weight; both species

exhibited positive, disturbance-driven condition factor patterns between disturbed and undisturbed sites for the streams examined. Since fantail darter habitat limitations limited specimen collection at the disturbed site on Toms Creek; observations were from 1 disturbed site only (i.e. on Chestnut Creek) and could be an artifact of sampling time.

Within and between watershed (i.e. small-scale spatial variation) comparisons largely focus on community and population change mechanisms or disturbance-mediated responses to land use (Jackson et al. 2001; see above examples on chronic land and water resource degradation), but often do not integrate effects of natural spatial variation such as watershed and watershed area. Herein, life history traits show benthic species exhibit strong patterns of variation within and between watersheds (Table 1; Figures 3-11). White sucker is particularly interesting for between and within watershed analysis, since it has been well studied for watershed-based comparisons (McFarlane and Franzin 1978; McFarlane and Franzin 1980; McMaster et al. 1992; Van der Kraak et al. 1992; Gagnon et al. 1994; McMaster et al. 1995). Study results show relationships through between-watershed and watershed area correlations with relative condition factor (Figures 3-6), fecundity (Figures 7-8), average egg size (Figures 9-10), and relative gut weight (Figure 11). Results are relatively consistent with past studies and indicate traits differ between watersheds and by watershed area (Marchetti et al. 2004; Santoul et al. 2005). In particular, watershed area is important to life history trait variation (Figures 5-6, 8), which could drastically alter inferences about anthropogenic disturbance effects if not accounted for in research and bioassessment designs.

Additional site- and species-specific research can strengthen study results, but were beyond the current study scope. First, this study provides a temporal “snapshot,” not a long-term, population-level assessment. Second, results were only intended to provide detailed spatial and

disturbance-mediated responses within the New River basin. Third, factors not tested herein likely interact with and influence studied traits and indices. However, the current study incorporated many important traits and indices and minimized exclusion of important factors. Fourth, before and after disturbance comparisons were not possible since study streams were significantly altered long before study initiation and long-term, New River white sucker and fantail darter bioassessment data are scant. Lack of long-term data were corrected for in the current study by substitution of space (i.e. examining disturbed v. undisturbed sites) for time (i.e. before v. after disturbance comparisons). Fifth, study focus was restricted to spatial and disturbance effects on eggs, juveniles, and adults, so no comment is made on indirect or larval stage effects. Munkittrick and Dixon (1989a; 1989b) state that not all levels of bioassessment are needed to formulate accurate conclusions. Several lines of inquiry (i.e. such as egg, juvenile, and adult effects) provide substantial support for site- and species-specific patterns (Munkittrick and Dixon 1989a; Munkittrick and Dixon 1989b). Lastly, future studies can incorporate more disturbance-mediated resolution, including differences between disturbance types.

Current study results provide information for future bioassessment-related research, conservation, and management applications. Results elucidate importance of land-use mediated habitat disturbance and resulting benthic fish responses, which enable future spatial and temporal comparisons for these benthic species. For example, significant correlations provide a basis for testing future hypotheses about disturbance effects on fantail darter, white sucker, or other benthic fish species in similar disturbance scenarios. The current study shows various contrasts with past studies, possibly due to inclusion of spatial factors. The limited scope of the current study restricts broad applicability beyond white sucker and fantail darter populations in the New River, VA or in similarly-disturbed streams with similar benthic species. However, current study

results allow syntheses with past (i.e. summarized for study species above in Discussion) and future studies to answer broader small-scale, spatial and disturbance-mediated questions between study and non-study species. For example, fantail darter results can be used to predict habitat degradation responses for rarer and / or imperiled, but similar benthic fish species, such as candy darter (*Etheostoma osburni*) and kanawha darter (*Etheostoma kanawhae*).

Conclusions

Results emphasize inclusion and importance of spatial factors and disturbance in small-scale trait studies. From study result correlations, I recommend critical analysis of watershed, watershed area, egg size variation, condition factor, relative weight, and relative gut weight to elucidate site- and species-specific responses to spatial factors and disturbance-based regimes in future, similar bioassessment studies. Overall, current study correlations indicate white sucker and fantail darter display positive, disturbance-mediated responses consistent with exploitative competitor behavior within the New River drainage, which is contrary to previous studies in other locations (i.e. especially for white sucker). Therefore, due to current and past study result differences, care must be taken in future studies to assess disturbance quality and type for white sucker and fantail darter condition and trophic- and fecundity-related indices. Since chapter 3 showed different patterns than previous studies, results are applicable beyond the relatively-narrow scope of the current study for comparisons and contrasts with other bioassessments. However, caution must be taken to individually assess site- and species-specific responses of natural spatial factors and anthropogenic trait and performance index variation.

Literature Cited

- Anderson, R. O., and R. M. Neumann. 1996. Length, weight, and associated structural indices. Pages 447-482 in B. R. Murphy and D. W. Willis, eds. Fisheries techniques. American Fisheries Society. Bethesda, MD.
- Arnold, C. L., and C. J. Gibbons. 1996. Impervious surface coverage: the emergence of a key environmental indicator. *American Planners Association Journal* 62(2):243-258.
- Bister, T. J., D. W. Willis, M. L. Brown, S. M. Jordan, R. M. Neumann, M. C. Quist, and C. S. Guy. 2000. Proposed standard weight (W_s) equations and standard length categories for 18 warmwater nongame and riverine fish species. *North American Journal of Fisheries Management* 20(2):570-574.
- Blanck, A., and N. Lamouroux. 2007. Large-scale intraspecific variation in life-history traits of European freshwater fish. *Journal of Biogeography* 34:862-875.
- Blanck, A., P. A. Tedesco, and N. Lamouroux. 2007. Relationships between life-history strategies of European freshwater fish species and their habitat preferences. *Freshwater Biology* 52(5):843-859.
- Chang, W. Y. B. 1982. A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* 39(8):1208-1210.
- Der, G., and B. S. Everitt. 2002. A handbook of statistical analyses using SAS. CRC Press. Boca Raton, FL.
- Devries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483-512 in B. R. Murphy and D. W. Willis, eds. Fisheries techniques. American Fisheries Society. Bethesda, MD.
- Dobson, A. J., and A. Barnett. 2008. An introduction to generalized linear models. Third edition. Chapman and Hall. London, UK.
- Doherty, C. A., B. Galloway, R. A. Curry, and K. R. Munkittrick. 2005. Performance of white sucker populations along the Saint John River main stem, New Brunswick, Canada: an example of effects-based cumulative effects assessment. *Water Quality Research Journal of Canada* 40(3):361-373.
- Fleming, S. W. 2007. Quantifying urbanization-associated changes in terrestrial hydrologic system memory. *Acta Geophysica* 55(3):359-368.
- Gagnon, M. M., J. J. Dodson, P. V. Hodson, G. J. Van der Kraak, and J. H. Carey. 1994. Seasonal effects of bleached kraft mill effluent on reproductive parameters of white sucker (*Catostomus commersoni*) populations of the St. Maurice River, Quebec, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 51:337-347.
- Goldstein, R. M., and M. R. Meador. 2005. Multilevel assessment of fish species traits to evaluate habitat degradation in streams of the upper Midwest. *North American Journal of Fisheries Management* 25(1):180-194.
- Haddad, N. M., M. Holyoak, T. M. Mata, K. F. Davies, B. A. Melbourne, and K. Preston. 2008. Species' traits predict the effects of disturbance and productivity on diversity. *Ecology Letters* 11(4):348-356.
- Heath, D. D., C. W. Fox, and J. W. Heath. 1999. Maternal effects on offspring size: variation through early development in Chinook salmon. *Evolution* 53(5):1605-1611.
- Hewitt, D. A., R. P. Braham, and M. A. Johnson. 2009. Methods for aging catostomids from upper Klamath Lake, Oregon. United States Geological Survey Klamath Falls Field Station.

- Hutchings, J. A. 1991. Fitness consequences of variation in egg size and food abundance in brook trout *Salvelinus fontinalis*. *Evolution* 45(5):1162-1168.
- Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities: the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58:157-170.
- Jenkins, R. E., and N. M. Burkhead. 1993. *Freshwater fishes of Virginia*. American Fisheries Society. Bethesda, MD.
- Jensen, H., P. A. Amundsen, J. M. Elliott, T. Bøhn, and P. E. Aspholm. 2006. Prey consumption rates and growth of piscivorous brown trout in a subarctic watercourse. *Journal of Fish Biology* 68(3):838-848.
- Johnston, T. A., and W. C. Leggett. 2002. Maternal and environmental gradients in the egg size of an iteroparous fish. *Ecology* 83(7):1777-1791.
- Kimura, D. K., and J. J. Lyons. 1991. Between-reader bias and variability in the age-determination process. *Fishery Bulletin* 89(1):53-60.
- Lamouroux, N., N. L. Poff, and P. L. Angermeier. 2002. Intercontinental convergence of stream fish community traits along geomorphic and hydrologic gradients. *Ecology* 83(7):1792-1807.
- Leopold, L. B., R. Huppman, and A. Miller. 2005. Geomorphic effects of urbanization in forty-one years of observation. *Proceedings of the American Philosophical Society* 149(3):349-371.
- Lussier, S. M., S. N. da Silva, M. Charpentier, J. F. Heltshe, S. M. Cormier, D. J. Klemm, M. Chintala, and S. Jayaraman. 2008. The influence of suburban land use on habitat and biotic integrity of coastal Rhode Island streams. *Environmental Monitoring and Assessment* 139(1-3):119-136.
- Marchetti, M. P., P. B. Moyle, and R. Levine. 2004. Alien fishes in California watersheds: characteristics of successful and failed invaders. *Ecological Applications* 14(2):587-596.
- McCarthy, M. S., and W. L. Minckley. 1987. Age estimation for razorback sucker (Pisces: Catostomidae) from Lake Mohave, Arizona and Nevada. *Journal of the Arizona-Nevada Academy of Science* 21:87-97.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized linear models*. Second edition. Chapman and Hall. London, UK.
- McGinley, M. A., D. H. Temme, and M. A. Gerber. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. *The American Naturalist* 130(3):370-398.
- McFarlane, G. A., and W. G. Franzin. 1978. Elevated heavy metals: a stress on population of white sucker, *Catostomus commersoni*, in Hamell Lake, Saskatchewan. *Journal of the Fisheries Research Board of Canada* 35:963-970.
- McFarlane, G. A., and W. G. Franzin. 1980. An examination of Cd, Cu and Hg concentrations in livers of northern pike, *Esox lucius* and white sucker, *Catostomus commersoni*, from five lakes near a base level smelter at Flin Flon, Manitoba. *Canadian Journal of Fisheries and Aquatic Sciences* 37:1573-1578.
- McMaster, M. E., C. B. Portt, K. R. Munkittrick, and D. G. Dixon. 1992. Milt characteristics, reproductive performance, and larval survival and development of white sucker exposed to bleached kraft mill effluent. *Ecotoxicology and Environmental Safety* 23(1):103-117.
- McMaster, M. E., G. J. Van der Kraak, and K. R. Munkittrick. 1995. Exposure to bleached kraft pulp mill effluent reduces the steroid biosynthetic capacity of white sucker ovarian

- follicles. *Comparative Biochemistry and Physiology Part C: Comparative Pharmacology and Toxicology* 112(2):169-178.
- Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* 45(9):1657-1670.
- Munkittrick, K. R., and D. G. Dixon. 1988a. Evidence for a maternal yolk factor associated with increased tolerance and resistance of feral white sucker (*Catostomus commersoni*) to waterborne copper. *Ecotoxicology and Environmental Safety* 15(1):7-20.
- Munkittrick, K. R., and D. G. Dixon. 1988b. Growth, fecundity and energy stores of white sucker (*Catostomus commersoni*) from lakes containing elevated levels of copper and zinc. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1355-1365.
- Munkittrick, K. R., and D. G. Dixon. 1989a. A holistic approach to ecosystem health assessment using fish population characteristics. *Hydrobiologia* 188-189(1):123-135.
- Munkittrick, K. R., and D. G. Dixon. 1989b. Use of white sucker (*Catostomus commersoni*) populations to assess the health of aquatic ecosystems exposed to low-level contaminant stress. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1455-1462.
- Onorato, D., K. R. Marion, and R. A. Angus. 1998. Longitudinal variations in the ichthyofaunal assemblages of the upper Cahaba River: possible effects of urbanization in a watershed. *Journal of Freshwater Ecology* 13(2):139-154.
- Page, L. M., and B. M. Burr. 1991. A field guide to freshwater fishes. Houghton Mifflin Company. New York, NY.
- Parker, G. A., and M. Begon. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. *The American Naturalist* 128(4):573-592.
- Paul, M. J., and J. L. Meyer. 2001. Streams in the urban landscape. *Annual Review of Ecology and Systematics* 32:333-365.
- Poff, N. L., and J. D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* 76(2):606-627.
- Power, M. 2007. Fish population bioassessment. Pages 561-624 in C. S. Guy and M. L. Brown, eds. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society. Bethesda, MD.
- Rice, J. A., J. E. Breck, S. M. Bartell, and J. F. Kitchell. 1983. Evaluating the constraints of temperature, activity, and consumption on growth of largemouth bass. *Environmental Biology of Fishes* 9(3-4):263-275.
- Roff, D. A. 1992. *The evolution of life histories: theory and analysis*. Chapman and Hall. New York, NY.
- Santoul, F., J. Cayrou, S. Mastrorillo, and R. Céréghino. 2005. Spatial patterns of the biological traits of freshwater fish communities in south-west France. *Journal of fish Biology* 66(2):301-314.
- Sargent, R. C., P. D. Taylor, and M. R. Gross. 1987. Parental care and the evolution of egg size in fishes. *The American Naturalist* 129(1):32-46.
- Scott, M. C. 2006. Winners and losers among stream fishes in relation to land use legacies and urban development in the southeastern United States *Biological Conservation* 127(3):301-309.
- Searle, S. R., G. Casella, and C. E. McCulloch. 2006. *Variance components*. John Wiley and Sons, Inc. Hoboken, NJ.

- Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. *The American Naturalist* 108(4):499-506.
- Strange, R. J. 1996. Field examination of fishes. Pages 433-446 *in* B. R. Murphy and D. W. Willis, eds. *Fisheries techniques*. American Fisheries Society. Bethesda, MD.
- Sweka, J. A., and K. J. Hartman. 2001. Effects of turbidity on prey consumption and growth in brook trout and implications for bioenergetics modeling. *Canadian Journal of Fisheries and Aquatic Sciences* 58(2):386-393.
- Van der Kraak, G. J., K. R. Munkittrick, M. E. McMaster, C. B. Portt, and J. P. Chang. 1992. Exposure to bleached kraft pulp mill effluent disrupts the pituitary-gonadal axis of white sucker at multiple sites. *Toxicology and Applied Pharmacology* 115(2):224-233.

Tables and Figures

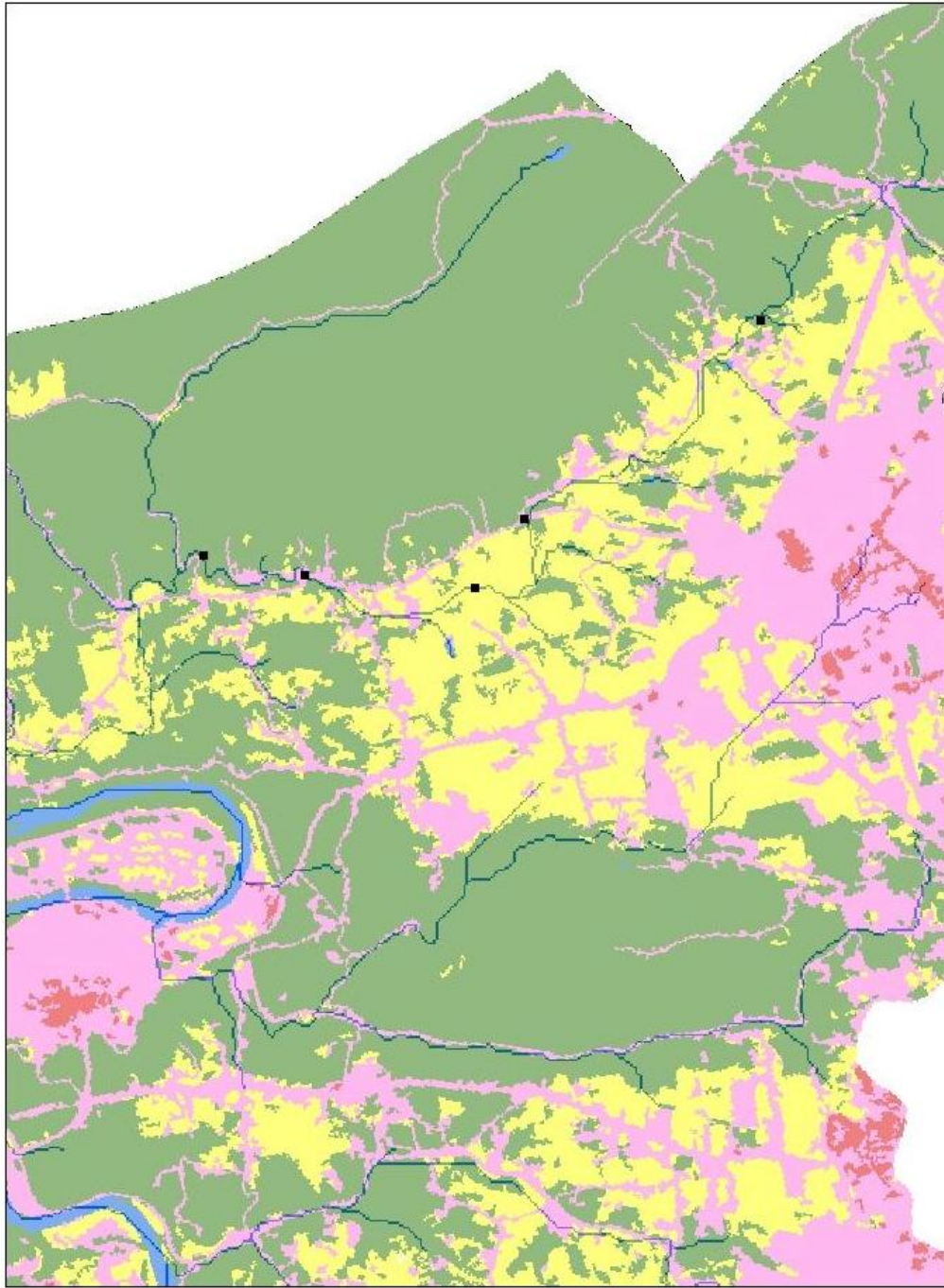


FIGURE 1. ArcGIS map of study sites on Toms Creek, Blacksburg, VA, USA. Sites are represented by black squares and become progressively more downstream right to left (i.e. upstream forested, upstream transitional, heavy agriculture, downstream transitional, and downstream forested). Red represents high density urban development, pink represents low density urban development, yellow represents low density residential/agricultural land, and green represents forested areas.

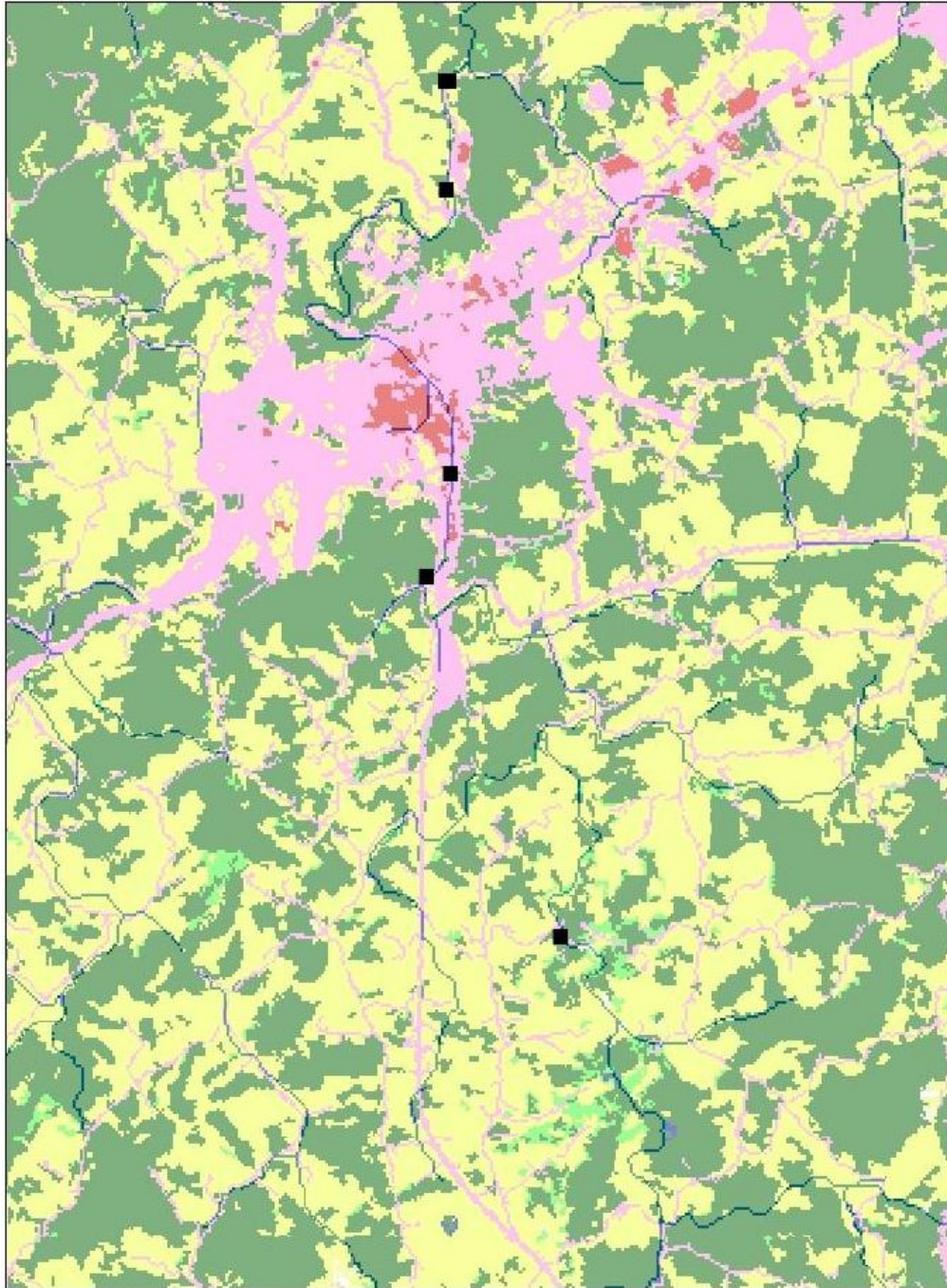


FIGURE 2. ArcGIS map of study sites on Chestnut Creek, Galax, VA, USA. Sites are represented by black squares and become progressively more downstream bottom to top (i.e. upstream forested, upstream transitional, heavy agriculture, downstream transitional, and downstream forested). Red represents high density urban development, pink represents low density urban development, yellow represents low density residential/agricultural lands, and green represents forested areas.

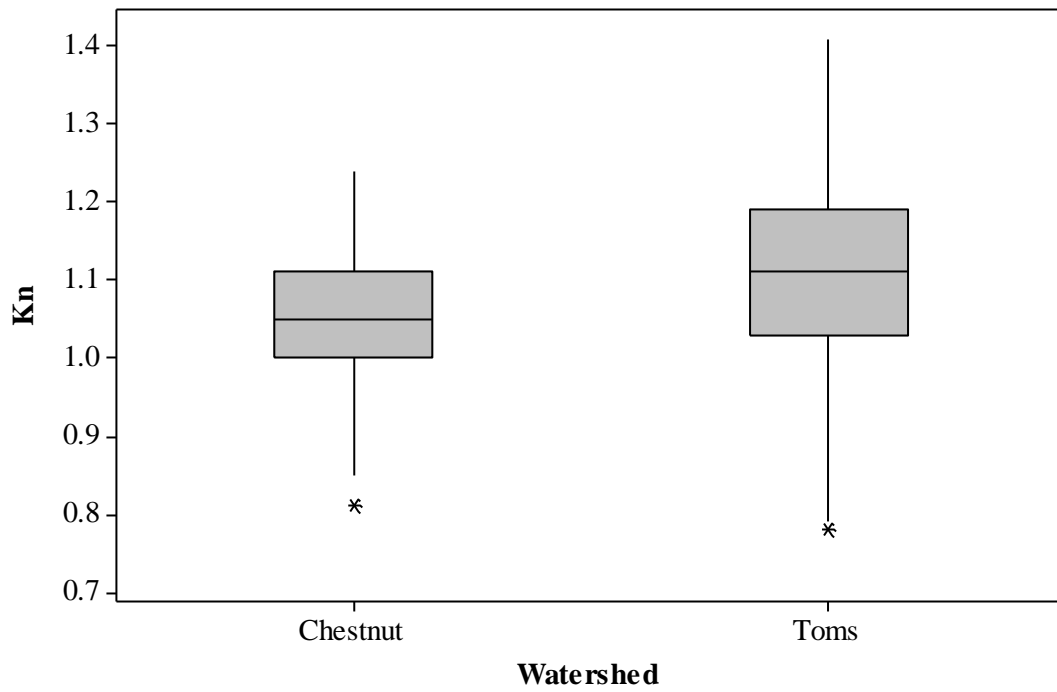


FIGURE 3. White sucker relative condition factor between Toms Creek (n=143 specimens) and Chestnut Creek (n=103 specimens).

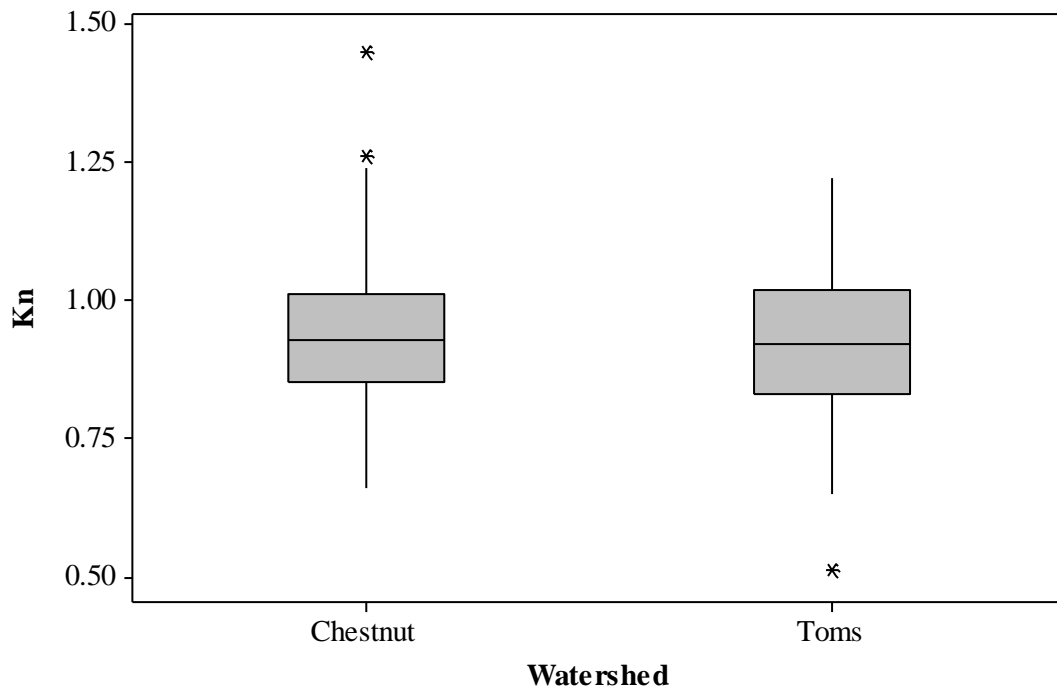


FIGURE 4. Fantail darter relative condition factor between Toms Creek (n=124 specimens) and Chestnut Creek (n=160 specimens).

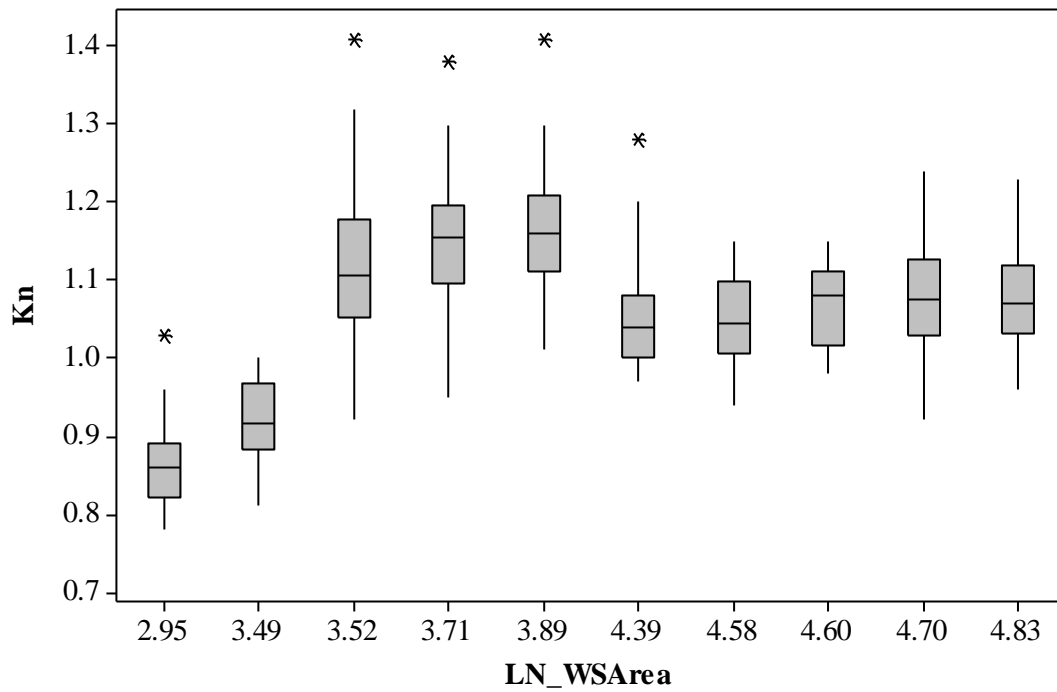


FIGURE 5. White sucker relative condition factor according to watershed area (n=246 specimens).

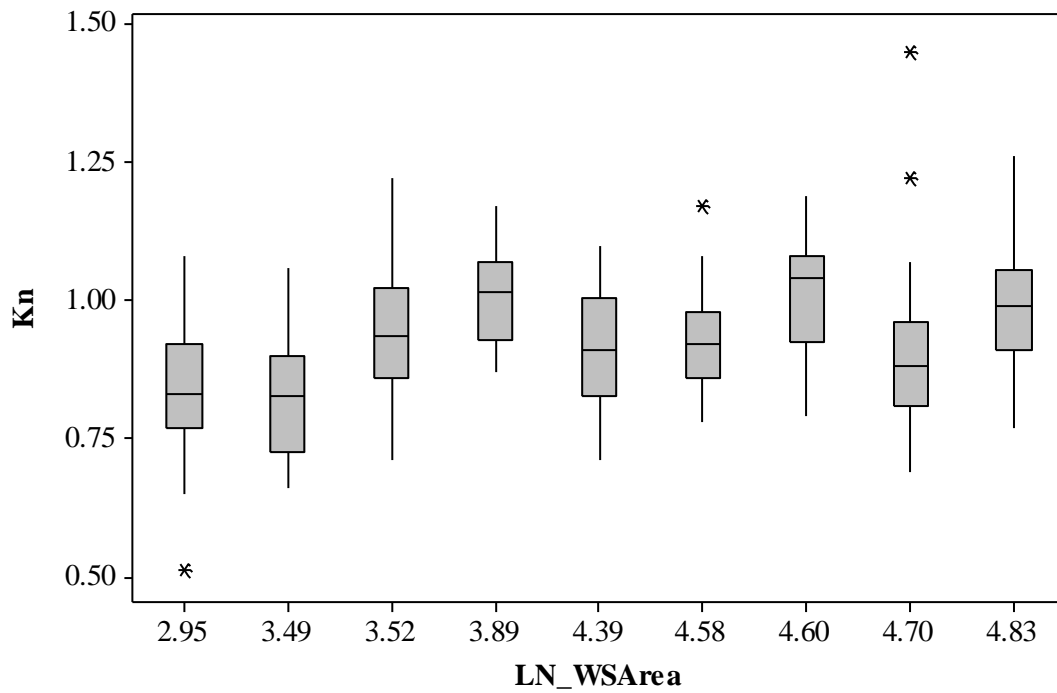


FIGURE 6. Fantail darter relative condition factor according to watershed area (n=284 specimens).

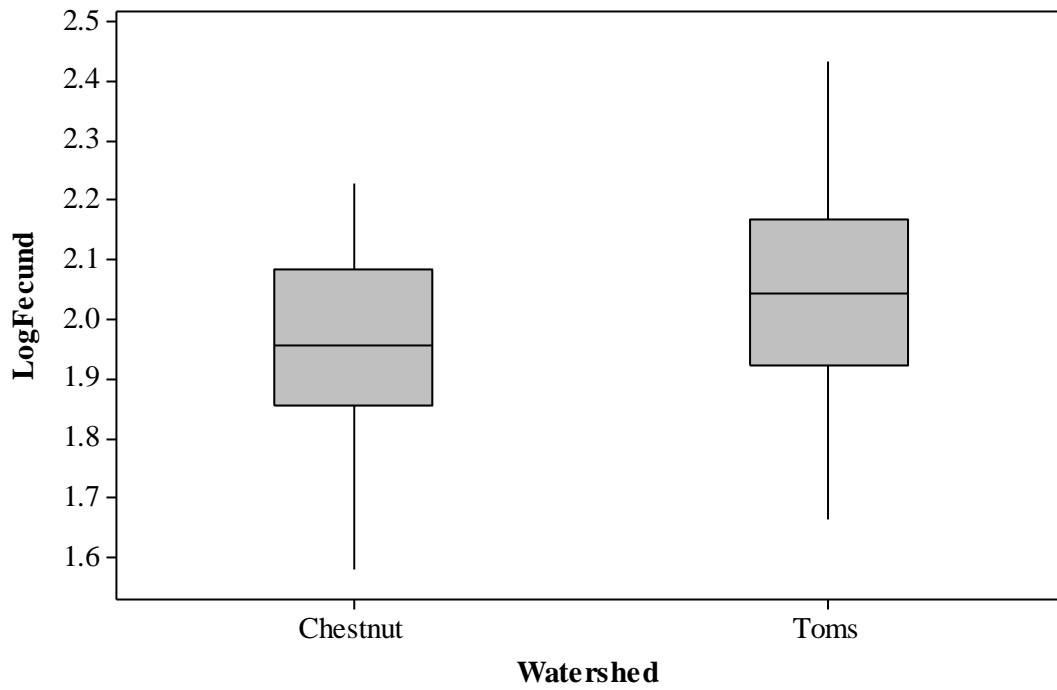


FIGURE 7. Fantail darter fecundity between Toms Creek (n=74 specimens) and Chestnut Creek (n=46 specimens).

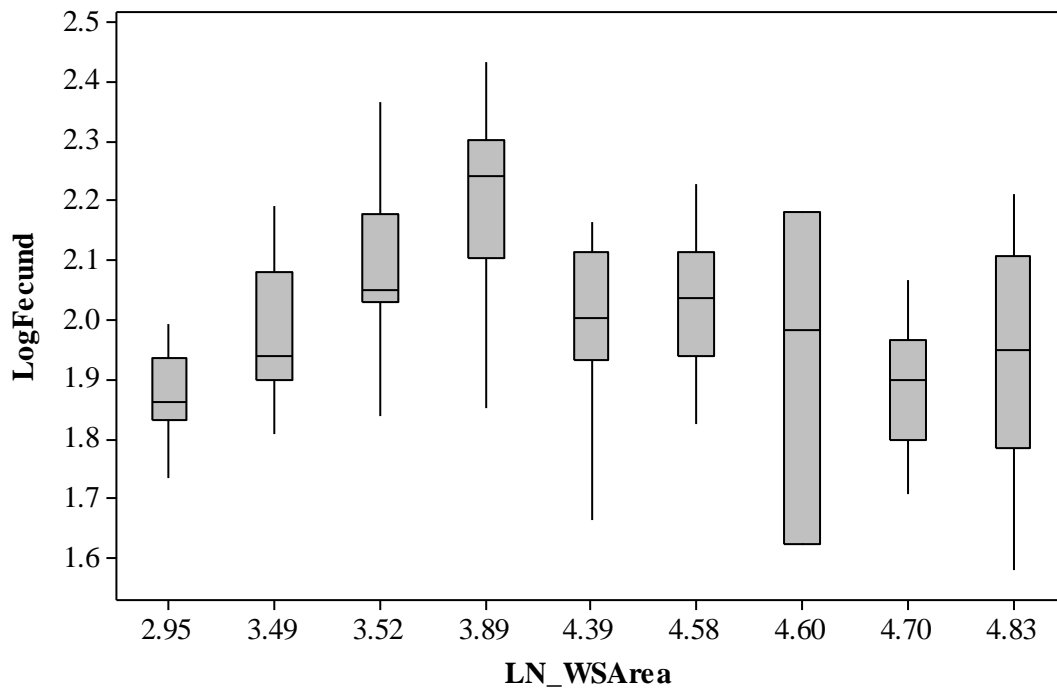


FIGURE 8. Fantail darter fecundity according to watershed area (n=120 specimens).

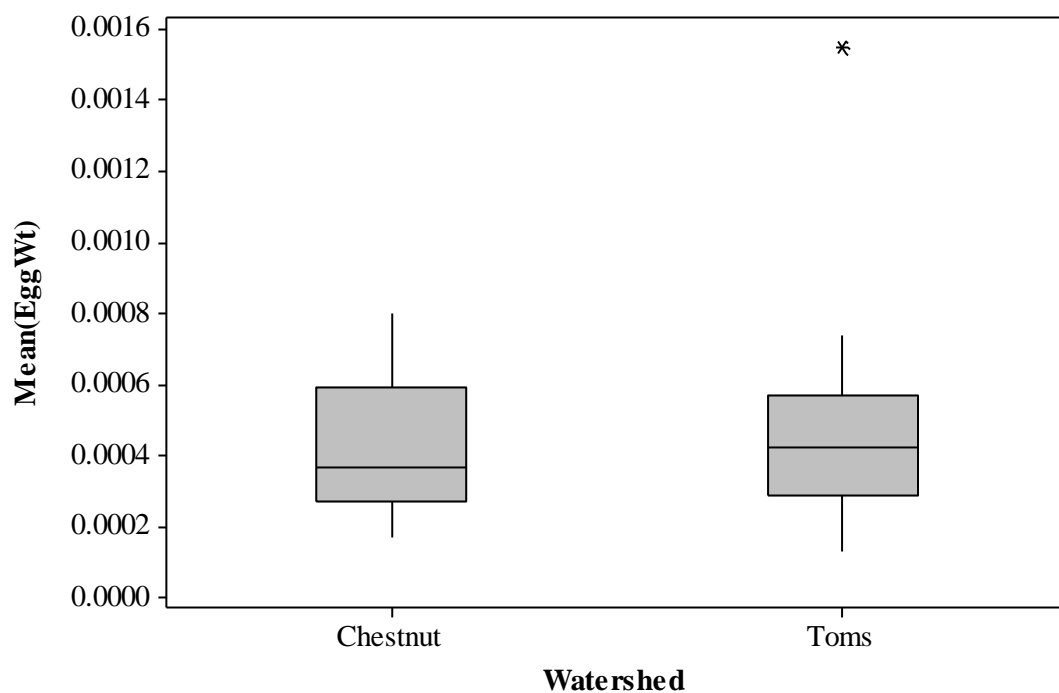


FIGURE 9. White sucker average egg size between Toms Creek (n=19 specimens) and Chestnut Creek (n=24 specimens).

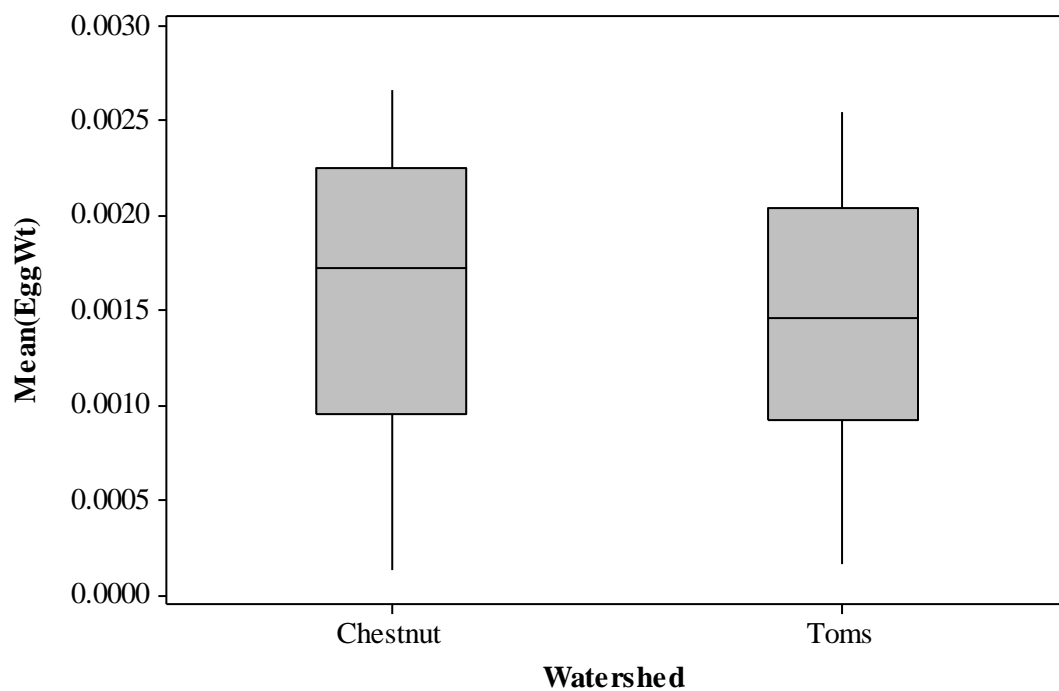


FIGURE 10. Fantail darter average egg size between Toms Creek (n=74 specimens) and Chestnut Creek (n=46 specimens).

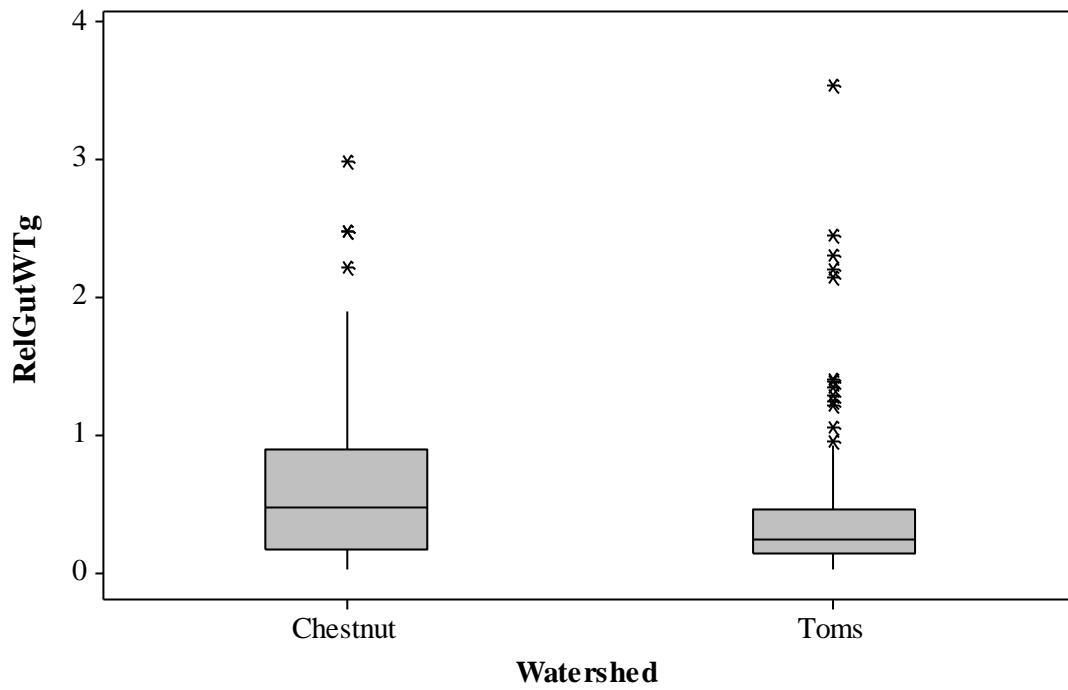


FIGURE 11. White sucker relative gut weight between Toms Creek (n=148 specimens) and Chestnut Creek (n=103 specimens).

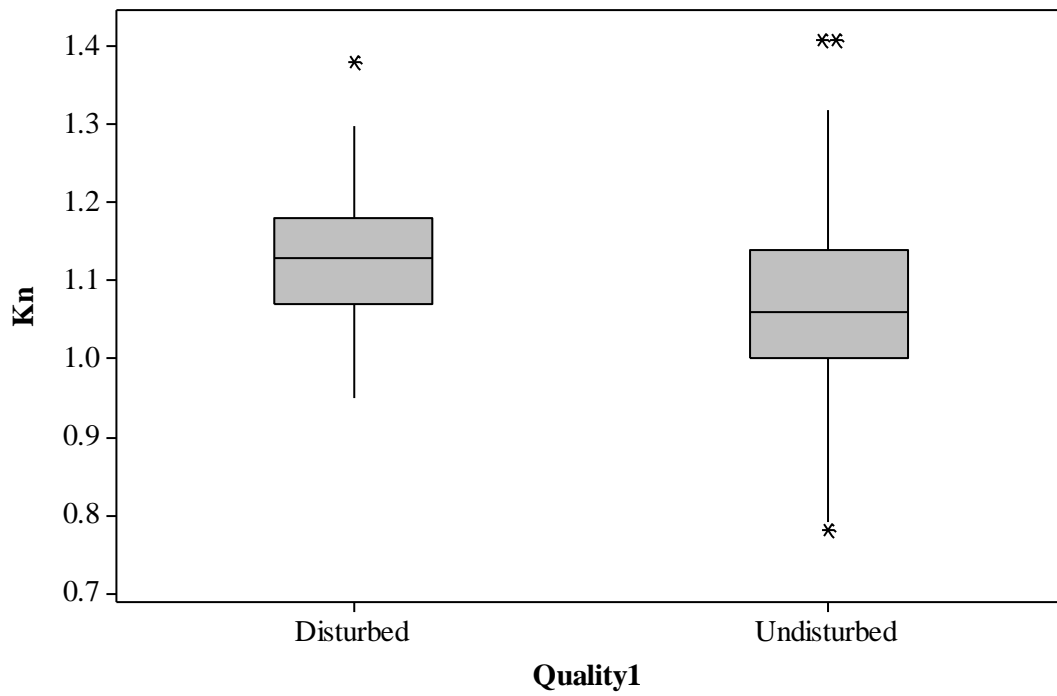


FIGURE 12. White sucker relative condition factor between disturbed (n=51 specimens) and undisturbed (n=195 specimens) sites in Toms Creek and Chestnut Creek watersheds.

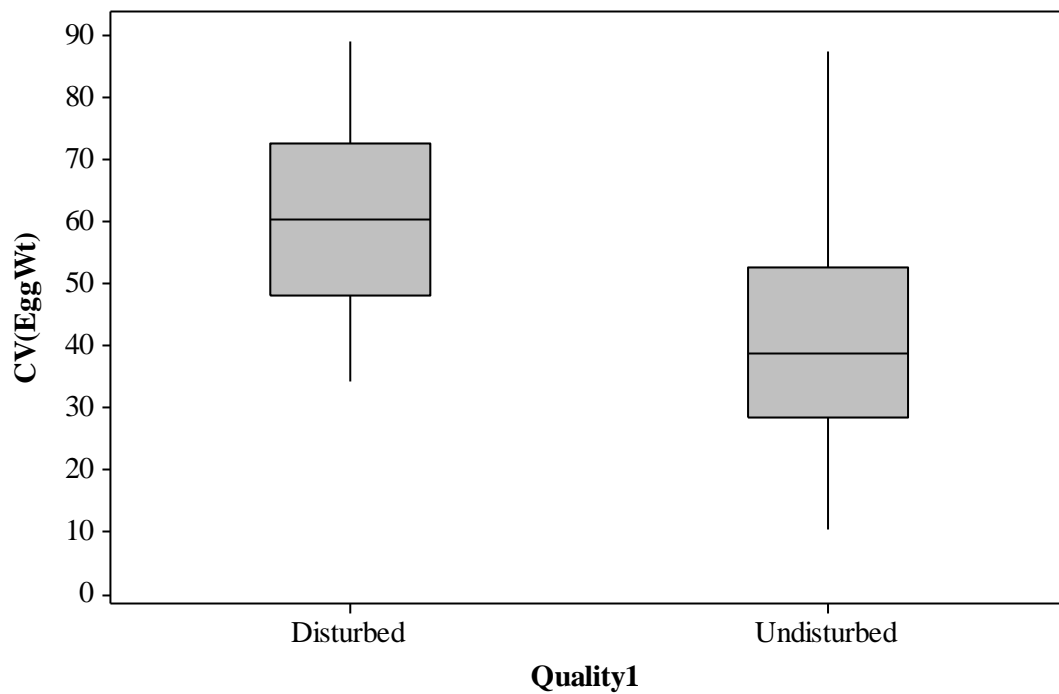


FIGURE 13. White sucker variation in egg size between disturbed (n=8 specimens) and undisturbed (n=35 specimens) sites in Toms Creek and Chestnut Creek watersheds.

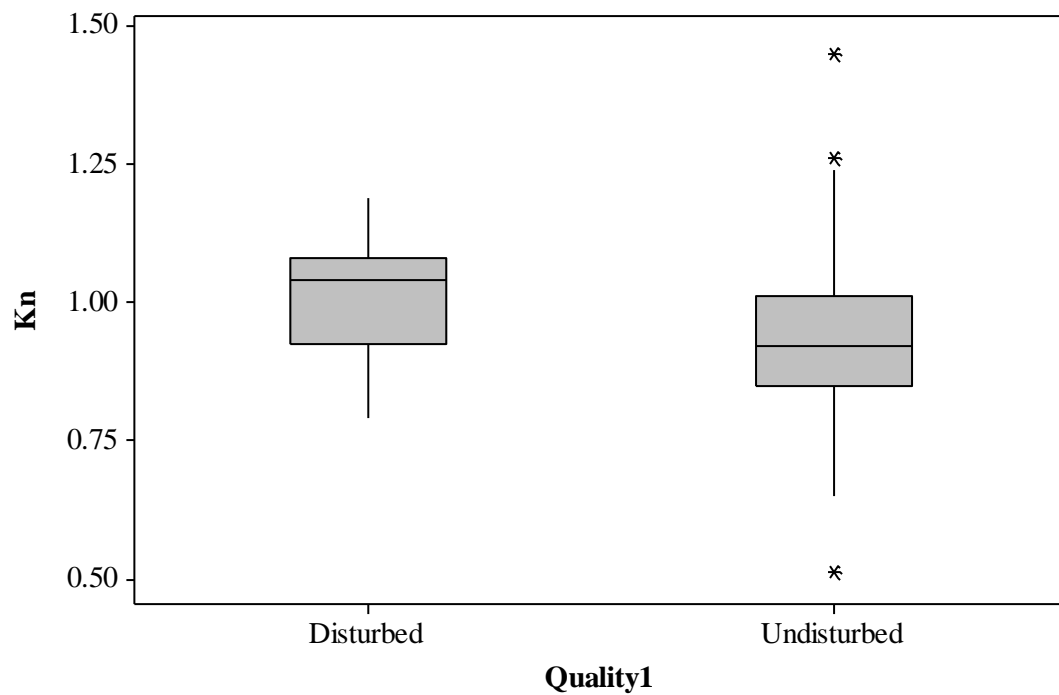


FIGURE 14. Fantail darter relative condition factor between disturbed (n=12 specimens) and undisturbed (n=272 specimens) sites in Toms Creek and Chestnut Creek watersheds.

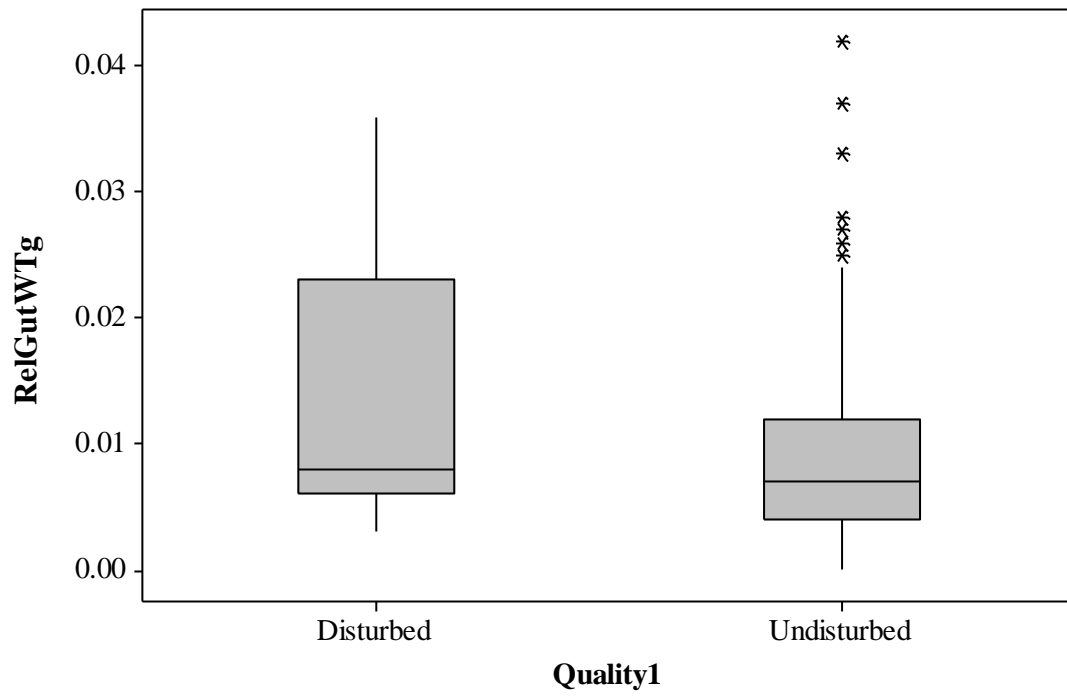


FIGURE 15. Fantail darter relative gut weight between disturbed (n=10 specimens) and undisturbed (n=267 specimens) sites in Toms Creek and Chestnut Creek watersheds.

TABLE 1. Responses, significant factors, p-values, and coefficients by species. WHSU = white sucker and FTDA = fantail darter. Watershed and site quality do not have coefficients because they were random and binary factors, respectively. Refer to previous graphs (Figures 8-11) for interpretations, if distinguishable.

Species	Response	Significant Factor	n	p-value	Coefficient
WHSU	Fecundity	Eviscerated weight	43	0.000	1.039
WHSU	Total length	Watershed area	246	0.000	0.164
WHSU	Average egg size	Eviscerated weight	43	0.004	0.001
WHSU		Watershed	43	0.022	
WHSU	Variation in egg size	Eviscerated weight	43	0.020	-30.470
WHSU		Site quality	43	0.027	
WHSU	Relative gut weight	Total length	246	0.000	2.001
WHSU		Watershed	251	0.004	
WHSU		Age	251	0.000	
WHSU	Gonadosomatic index	Eviscerated weight	43	0.003	3.304
WHSU	Condition factor	Watershed area	246	0.000	13.763
WHSU		Watershed	246	0.000	
WHSU		Site quality	246	0.004	
WHSU	Maturity	Age	251	0.000	3.590
FTDA	Fecundity	Eviscerated weight	120	0.000	0.756
FTDA		Watershed area	120	0.007	
FTDA		Watershed	120	0.003	
FTDA	Total length	Watershed	284	0.001	
FTDA	Average egg size	Eviscerated weight	120	0.000	0.002
FTDA		Watershed	120	0.008	
FTDA	Variation in egg size	Eviscerated weight	120	0.000	-30.783
FTDA	Relative gut weight	Eviscerated weight	280	0.000	0.014
FTDA		Site quality	277	0.019	
FTDA	Gonadosomatic index	Eviscerated weight	120	0.000	10.547
FTDA	Condition factor	Watershed area	284	0.000	8.856
FTDA		Watershed	284	0.001	
FTDA		Site quality	284	0.016	
FTDA	Maturity	Total length	282	0.000	29.229

Summary and Conclusions

Chapter 1 defined ontogenetic trophic niches for New River fishes and integrated these niches into a comprehensive assessment of biological-ecological trait relationships. Chapter 1 trophic niche shift results emphasize inclusion of quantitative niche shifts into studies, which the current study incorporates with greater resolution. Quantitative trophic niche shifts in the current study go beyond previous methods for trophic niche shift determination (i.e. expert opinions and quantitative species-specific studies) and provide future research and management efforts with solid bases for niche shift determination. Co-inertia analysis quantitatively supported previously known trait association patterns and identified new patterns, within and between biological and ecological trait datasets. From this, results provide increased knowledge and resolution of how biological traits and ontogeny drive trophic behavior. Within-dataset biological trait associations showed relationships between structures involved in trophic behavior, such as eye diameter and mouth-jaw traits. Such relationships show how biological traits influence one another and are useful for future predictions involving feeding-related structures. Prey type presence-absence was apparent within ecological data, where consumption of particular prey types effectively caused other prey types to go unconsumed within and between life stages. Future prey selectivity and related trophic behavior research will benefit from the understanding of ecological trait associations developed in this study. Chapter 1 trait associations provide researchers and managers with information for future ecological hypothesis testing. These hypotheses will help assess site-, species-, and stage-specific responses linked to structure-function relationships. In future studies, structure-function responses found herein will reduce effort needed to draw accurate conclusions for species included in chapter 1. Current study results support trophic shift and trait association extrapolation for similar species due to strong similarities found within

families. For instance, fantail darter (*Etheostoma flabellare*) and other genus *Etheostoma* species in this study have similar biological, ecological, and biological-ecological associations. These associations indicate trophic behavior for closely related, relatively rare and / or imperiled fish species, such as candy darter (*Etheostoma osburni*) and kanawha darter (*Etheostoma kanawhae*). Therefore, trophic behavior and trait associations can be extrapolated from fantail darter and other *Etheostoma* species for candy darter and kanawha darter.

Chapter 2 examined large scale, continent-wide latitudinal life history trait variation and provided a comprehensive life history trait-pattern characterization for North American fishes. General linear models showed average total length of newly hatched larvae, average total length at maturation, average spawning temperature, average egg diameter, and maximum length had highest correlative strengths with latitude within respective adaptive attribute groups and, therefore, would be the best-suited traits among those examined in this study for future ecological hypothesis testing. Some overall latitudinal patterns were similar between the current study and European patterns, including those related to growth rate, age at maturation, longevity, and maximum length. Species-specific patterns displayed similarities between studies as well, especially for muskellunge (*Esox masquinongy*). Chapter 2 patterns that are similar with European patterns provide reasonable bases for future large-scale studies. Chapter 2 results also suggested some different, non-transferrable latitudinal patterns between North America and Europe, including those related to reproduction (i.e. spawning temperature and length of spawning season). Different latitudinal patterns between studies are likely due to differences in species compositions. In conclusion, the current study elucidated universally applicable, as well as continent- and species-specific life history trait latitudinal patterns. I suggest use of universally applicable and continent- and species-specific patterns found within this thesis

chapter in future research scenarios involving latitudinal life history trait variation. For example, results herein could be applied to studies of native and invasive species interactions in climate change and species distribution / co-occurrence contexts.

Chapter 3 provided a small scale, watershed-level bioassessment trait-response characterization of significant spatial factors and disturbance for two New River drainage benthic species (i.e. white sucker, *Catostomus commersonii*, and fantail darter). Past bioassessment studies rarely accounted for natural spatial variation, which often affected study results and provided motivation for the current study. General linear models in the current study showed disturbance had multiple positive effects on white sucker and fantail darter above natural spatial variation. Study results contained one trait and two performance indices significantly correlated with spatial factors and disturbance for both white sucker and fantail darter; these factors included egg size variation, condition factor, and relative gut weight. Additionally, white sucker relative weight showed significantly higher values at disturbed sites, which indicated trends consistent with condition factor and further supported white sucker as an exploitative competitor. Overall, chapter 3 results generally disagree with previous benthic fish disturbance studies (i.e. especially white sucker), which I suggest is due to drainage-specific white sucker and fantail darter resilience to outcompete and occupy areas unfit for less-tolerant species within the New River drainage. Chapter 3 results increase knowledge of how spatial and disturbance regimes influence white sucker and fantail darter life history characteristics. Overall, chapter 3 elucidated small scale, site- and species-specific biological differences for both study species. I suggest due to correlative strength of traits and performance indices with spatial factors and disturbance found herein, trait patterns are useful for biological assessments and applications in same or similar species and disturbance-mediated scenarios.

Appendices

APPENDIX A. Literature used to find trophic information for trophic shift analysis for all New River fishes. Author(s), year, title, journal / publication / publisher, volume, and page numbers are given above.

Source	Title	Journal/Publication/Publisher	Volume	Page(s)
Applegate et al 1966	Food and growth of six centrarchids from shoreline areas of Bull Shoals Reservoir	Proceedings of the 20th Annual Conference of the Southeastern Association of Game and Fish Commissioners	20	469-482
Bailey 1952	Life history and ecology of the sculpin <i>C. bairdi punctulatus</i> in southwestern Montana	Copeia	1952	243-255
Bailey and Harrison 1948	Food habits of the southern channel catfish in the Des Moines River, Iowa	Transactions of the American Fisheries Society	75	110-138
Barber and Minckley 1971	Summer foods of the cyprinid fish <i>S. atromaculatus</i>	Transactions of the American Fisheries Society	100	283-289
Barton 1980	Spawning migrations, age and growth, and summer feeding of white and longnose suckers in a irrigation reservoir	Canadian Field-Naturalist	94	300-304
Becker 1983	Fishes of Wisconsin	The University of Wisconsin Press, Madison		
Boesel 1938	The food of nine species of fish from the western end of Lake Erie	Transactions of the American Fisheries Society	67	215-223
Boschung and Mayden 2004	Fishes of Alabama	HarperCollins Publishers		
Brazo et al 1978	Life history of the longnose dace in the surge zone of eastern Lake Michigan near Ludington, Michigan	Transactions of the American Fisheries Society	107	550-556
Breder and Crawford 1922	The food of certain minnows	Zoologica	2	287-327
Bridges and Mullan 1958	A compendium of the life history of the eastern brook trout	Massachusetts Division of Fisheries and Game, Fisheries Bulletin, Boston	23	
Carlander 1969	Handbook of Freshwater Fishery Biology, Volume 1	Iowa State University Press, Ames		
Carlander 1977	Handbook of Freshwater Fishery Biology, Volume 2	Iowa State University Press, Ames		
Carlander 1997	Handbook of Freshwater Fishery Biology, Volume 3	Iowa State University Press, Ames		
Clemens et al 1923	The food of Lake Nipigon fishes	University of Toronto Studies, Biological Series	22	173-188
Coble 1975	Smallmouth bass	pp 21-33 in Stroud and Clepper, eds. Black Bass Biology and Management. Sport Fishing Institute, Washington DC		
Copes 1978	Ecology of the creek chub	University of Wisconsin, Stevens Point, Museum of Natural History Reports Fauna and Flora of Wisconsin	12	1-21

Couey 1935	Fish food studies of a number of northeastern Wisconsin lakes	Transactions of the Wisconsin Academy of Science, Arts, and Letters	29	131-172
Craddock 1965	Some aspects of the life history of the banded sculpin in Doe Run, Meade County, Kentucky	Doctoral Dissertation, University of Louisville, Kentucky		
Dendy 1946	Food of several species of fish, Norris Reservoir, Tennessee	Journal of the Tennessee Academy of Science	21	105-127
DeRyke 1922	Foods of the common fishes of Winona Lake in Kosciusko County, Indiana	Division of Fish and Game, Department of Conservation, Indiana		7-48
Dewey et al 1997	Patterns of foraging and distribution of bluegill sunfish in a Mississippi River backwater: influence of macrophytes and predation	Ecology of Freshwater Fish	6	8-15
Dill 1944	The fishery of the lower Colorado River	California Fish and Game	30	109-211
Dinsmore 1962	Life history of the creek chub, with emphasis on growth	Proceedings of the Iowa Academy of Science	69	296-301
Divine 1968	A study of the smallmouth bass in ponds with special consideration of minnows and decapods as forage	M.S. Thesis, University of Missouri, Columbia		
Dobie 1959	Note on food of northern logperch	Transactions of the American Fisheries Society	88	213
Eder and Carlson 1977	Food habits of carp and white suckers in the South Platte and St. Vrain Rivers and Goosequill Pond, Weld County, Colorado	Transactions of the American Fisheries Society	106	339-346
Elrod et al 1981	Food of white perch, rock bass, and yellow perch in eastern Lake Ontario	New York Fish and Game Journal	28	191-207
Ewers 1933	Summary report of the crustacea used as food by the fishes of the western end of Lake Erie	Transactions of the American Fisheries Society	63	379-390
Ewers and Boesel 1935	The food of some Buckeye Lake fishes	Transactions of the American Fisheries Society	65	57-70
Flemer and Woolcott 1966	Food habits and distribution of the fishes of Tuckahoe Creek, Virginia, with special emphasis on the bluegill	Chesapeake Science	7	75-89
Gerald 1966	Food habits of the longnose dace	Copeia	1966	478-485
Greeley 1927	Fishes of the Genesee region with annotated list	pp 47-66 in A Biological Survey of the Genesee River System		
Guier et al 1984	Biological investigations of flathead catfish in the Cape Fear River	Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies	35	607-621
Hacker 1966	An analysis of the muskellunge fishery of Little Green Lake, Green Lake County, Wisconsin, 1957-65	Wisconsin Conservation Department Division of Fisheries Management Report No. 4		
Hambrick et al 1975	Distribution, habitat, and food of the cyprinid fish <i>Phenacobius teretulus</i> , a New River endemic	Copeia	1975	172-176
Hayes 1956	Life history studies of two species of suckers in Shadow Mountain Reservoir, Grand County, Colorado	M.S. Thesis, Colorado AM College, Fort Collins, Colorado		
Hazzard 1935	A preliminary study of an exceptionally productive trout water, Fish Lake, Utah	Transactions of the American Fisheries Society	65	122-128

Heidinger et al 1985	Evidence of two feeding subpopulations of white crappie in Rend Lake, Illinois	Journal of Freshwater Ecology	3	133-139
Held and Peterka 1974	Age, growth, and food habits of the fathead minnow in North Dakota saline lakes	Transactions of the American Fisheries Society	103	743-756
Hildebrand and Schroeder 1928	Fishes of the Chesapeake Bay	U.S. Bureau of Fisheries Bulletin	43	
Hodson and Strawn 1969	Food of young-of-the-year largemouth and spotted bass during the filling of Beaver Reservoir, Arkansas	Proceedings of the 22nd Annual Conference of the Southeastern Association of Game and Fish Commissioners	22	510-516
Holland 1964	Ecology of the bowfin in southeastern Missouri	M.S. Thesis, University of Missouri, Columbia		
Jenkins and Burkhead 1993	Freshwater Fishes of Virginia	American Fisheries Society, Bethesda, Maryland		
Johnson 1981	The summer diets of the cutlips minnow in a central New York stream	Copeia	1981	484-487
Johnson 1982	Summer feeding ecology of the blacknose dace in a tributary of Lake Ontario	Canadian-Field Naturalist	96	282-286
Johnson and Dropkin 1991	Summer food habits of spotfin shiner, mimic shiner, and subyearling fallfish in the Susquehanna River Basin	Journal of Freshwater Ecology	6	35-42
Johnson and Johnson 1982	Diel foraging in relation to available prey in an Adirondack Mountain stream fish community	Hydrobiologia	96	97-104
Kay et al 1994	Reproductive Biology and Early Life History of Fishes in the Ohio River Drainage. Volume 2: Catostomidae	CRC Press, Boca Raton, FL		
Keast 1965	Resource subdivision amongst cohabiting fish species in a bay, Lake Opinicon, Ontario	University of Michigan Great Lakes Research Division Publication	13	106-132
Keast 1966	Trophic interrelationships in the fish fauna of a small stream	University of Michigan Great Lakes Research Division Publication	15	51-79
Keast 1970	Food specializations and bioenergetic interrelations in the fish fauna of some small Ontario waterways	pp 377-411 in J.H. Steele, ed. Marine Food Chains. Oliver and Boyd, Edinburgh, UK		
Keast and Webb 1966	Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario	Journal of the Fisheries Research Board of Canada	23	1845-1874
Keeton 1963	Growth of fishes in the Des Moines River, Iowa, with particular reference to water levels	Doctoral Dissertation, Iowa State University, Ames		
Kendall and Goldsborough 1908	The Fishes of the Connecticut Lakes and Neighboring Waters, with Notes on the Plankton Environment	Department of Commerce and Labor Bureau of Fisheries Document No. 633, Washington Government Printing Office		
Kidd 1927	The food of Minnesota fishes with special reference to the algae	Transactions of the American Fisheries Society	57	85-91
Kohler 1980	Trophic ecology of an introduced, land-locked alewife population and assessment of alewife impact on resident sport fish and crustacean zooplankton communities in Claytor Lake, Virginia	Doctoral Dissertation, Virginia Polytechnic Institute and State University, Blacksburg		

Kraatz 1923	A study of the food of the minnow <i>Campostoma anomalum</i>	Ohio Journal of Science	23	265-283
Kraatz 1928	Study of the food of the blunt-nosed minnow	Ohio Journal of Science	28	86-98
Krska and Applegate 1982	Food of young muskellunge in a power plant cooling reservoir	Progressive Fish-Culturist	44	172-173
Kwain 1983	Downstream migration, population size, and feeding of juvenile rainbow trout	Journal of Great Lakes Research	9	52-59
Leonard 1940	Further observations on the feeding habits of the Montana grayling (<i>Thymallus montanus</i>) and the bluegill (<i>Lepomis macrochirus</i>) in Ford Lake, Michigan	Transactions of the American Fisheries Society	69	244-256
McAfee 1966	Rainbow trout and eastern brook trout	pp 192-215 and 242-271 in Calhoun 1966		
McLane 1955	The fishes of the St. Johns River system	Doctoral Dissertation, University of Florida, Gainesville		
McNicol et al 1985	Quantitative field investigations of feeding and terrestrial behavior of young-of-the-year brook char	Environmental Biology of Fishes	12	219-229
Minckley 1963	The ecology of a spring stream Doe Run, Meade County, Kentucky	Wildlife Monographs	11	
Minckley and Deacon 1959	Biology of the flathead catfish in Kansas	Transactions of the American Fisheries Society	88	344-355
Miner 1978	The feeding habits of smallmouth bass and largemouth bass in the Shenandoah River, Virginia	M.S. Thesis, University of Virginia, Charlottesville		
Moffett and Hunt 1943	Winter feeding habits of bluegills, <i>Lepomis macrochirus</i> Rafinesque, and yellow perch <i>Perca flavescens</i> (Mitchell), in Cedar Lake, Washetenaw County, Michigan	Transactions of the American Fisheries Society	73	231-242
Morsell and Norden 1968	Food habits of the alewife, <i>Alosa pseudoharengus</i> (Wilson), in Lake Michigan	Proceedings of the Annual Conference of Great Lakes Research	1968	96-102
Moshenko and Gee 1973	Diet, time, place of spawning, and environments occupied by the creek chub in the Mink River, Manitoba	Journal of the Fisheries Research Board of Canada	30	357-362
Moyle 1969	Ecology of the fishes of a Minnesota lake with special reference to the Cyprinidae	Doctoral Dissertation, University of Minnesota, Minneapolis		
Mullan et al 1968	Food of the logperch and brook silverside	Transactions of the American Fisheries Society	97	300-305
Newsome and Gee 1978	Preference and selection of prey by creek chub inhabiting the Mink River, Manitoba	Canadian Journal of Zoology	56	2486-2497
Nigro and Ney 1982	Reproduction and early-life accommodations of landlocked alewives to a southern range extension	Transactions of the American Fisheries Society	111	559-569
Noble 1965	Life history and ecology of western blacknose dace, Boone County, Iowa, 1963-1964	Proceedings of the Iowa Academy of Science	72	282-293
Nurnberger 1928	A list of the plant and animal food of some fishes of Jay Cooke park	Transactions of the American Fisheries Society	58	175-177

Nurnberger 1930	The plant and animal food of the fishes of Big Sandy Lake	Transactions of the American Fisheries Society	1930	253-259
Olmsted and Kilambi 1971	Interrelationships between environmental factors and feeding biology of white bass of Beaver Reservoir, Arkansas	American Fisheries Society Special Publication	8	397-409
Outten 1958	Studies of the life history of the cyprinid fishes <i>Notropis galacturus</i> and <i>rubricroceus</i>	Journal of the Elisha Mitchell Scientific Society	74	122-134
Pappantoniou et al 1984	Aspect of the life history of the cutlips minnow from two eastern Pennsylvania streams	Journal of Freshwater Ecology	2	449-458
Parsons 1958	Fishery management problems and possibilities on large southeastern reservoirs	Transactions of the American Fisheries Society	87	333-355
Pate 1933	Studies of fish food in selected areas	New York Conservation Department, Biological Survey	7	130-156
Pate 1934	Studies on the fish food supply in selected areas of the Raquette Watershed	<i>In</i> A Biological Survey of the Upper Hudson Watershed, Supplement of the 22nd Annual Report, New York Conservation Department		130-156
Pearse 1918	The food of the shore fishes of certain Wisconsin lakes	U.S. Bureau of Fisheries Bulletin	35	246-292
Pearse 1921	Distribution and food of the fishes of three Wisconsin lakes in summer	University of Wisconsin Studies in Science	3	1-61
Pfeiffer 1955	Studies on the life history of the rosyface shiner	Copeia	1955	95-104
Power and Matthews 1983	Algae-grazing minnows, piscivorous bass, and the distribution of attached algae in a small prairie-margin stream	Oecologia	60	328-332
Raney 1952	The life history of the striped bass	Bulletin of the Bingham Oceanographic Collection, Yale University	14	5-97
Raney and Lachner 1942	Studies of the summer food, growth, and movements of young yellow pike-perch, in Oneida Lake, New York	Journal of Wildlife Management	6	1-16
Reed 1957	Phases of the life history of the rosyface shiner in northern Pennsylvania	Copeia	1957	286-290
Ricker 1930	Feeding habits of speckled trout in Ontario waters	Transactions of the American Fisheries Society	60	64-72
Rohde and Arndt 1981	Life history of a Coastal Plain population of the mottled sculpin	Brimleyana	7	69-94
Rosebery 1950	Game fisheries investigations of Claytor Lake, a mainstream impoundment of New River, Pulaski County, Virginia	Doctoral Dissertation, Virginia Polytechnic Institute and State University, Blacksburg		
Ross 2001	Inland Fishes of Mississippi	University Press of Mississippi, Oxford		
Sadzikowski and Wallace 1976	A comparison of the food habits of size classes of three sunfishes	American Midland Naturalist	95	220-225
Scott and Crossman 1973	Freshwater Fishes of Canada	Fisheries Research Board of Canada Bulletin	184	
Sibley 1929	The food of certain fishes of the Lake Erie drainage basin	Supplement of the 18th Annual Report, New York Conservation Department		180-188

Siefert 1972	First food of larval yellow perch, white sucker, bluegill, emerald shiner, and rainbow smelt	Transactions of the American Fisheries Society	101	219-225
Simon and Wallus 2004	Reproductive Biology and Early Life History of Fishes in the Ohio River Drainage. Volume 3: Ictaluridae – catfish and madtoms	CRC Press, Boca Raton, FL		
Simon and Wallus 2006	Reproductive Biology and Early Life History of Fishes in the Ohio River Drainage. Volume 4: Percidae – perch, pikeperch, and darters	CRC Press, Boca Raton, FL		
Smith 1977	The biology of three species of Moxostoma in Clear Creek, Hocking and Fairfield Counties, Ohio, with emphasis on the golden redbreast	Doctoral Dissertation, Ohio State University, Columbus		
Smith and Kramer 1964	The spottail shiner in lower Red Lake, Minnesota	Transactions of the American Fisheries Society	93	35-45
Starnes and Starnes 1985	Ecology and life history of the mountain madtom	American Midland Naturalist	114	331-341
Sule 1981	First-year growth and feeding of largemouth bass in a heated reservoir	Illinois Natural History Survey Bulletin	32	520-535
Sule et al 1981	Food habits of some common fishes from heated and unheated areas of Lake Sangchris	Illinois Natural History Survey Bulletin	32	500-519
Summerfelt et al 1970	Food habits of the carp in five Oklahoma reservoirs	Proceedings of the 24th Annual Conference of the Southeastern Association of Game and Fish Commissioners	24	352-377
Traver 1929	The habits of the black-nosed dace	Journal of the Elisha Mitchell Scientific Society	45	101-129
Turner 1921	Food of the common Ohio darters	Ohio Journal of Science	22	41-62
Vogele 1975	The spotted bass	pp 34-45 in Stroud and Clepper, eds. Black Bass Biology and Management. Sport Fishing Institute, Washington DC		
Wallus et al 1990	Reproductive Biology and Early Life History of Fishes in the Ohio River Drainage. Volume 1: Acipenseridae through Esocidae	CRC Press, Boca Raton, FL		
Wallus and Simon 2006	Reproductive Biology and Early Life History of Fishes in the Ohio River Drainage. Volume 5: Aphredoderidae through Cottidae, Moronidae, and Sciaenidae	CRC Press, Boca Raton, FL		
Wallus and Simon 2008	Reproductive Biology and Early Life History of Fishes in the Ohio River Drainage. Volume 6: Elasmobranchii and Centrarchidae	CRC Press, Boca Raton, FL		
Whitaker 1977	Seasonal changes in food habits of some cyprinid fishes from the White River at Petersburg, Indiana	American Midland Naturalist	97	411-418
Wickliff 1921	Food of young small-mouth black bass in Lake Erie	Transactions of the American Fisheries Society	50	364-371

APPENDIX B. Raw biological trait data by species. Biological trait abbreviations include: avgage1repro = average age at first reproduction, avglen1repro = average length at first reproduction, maxtl = asymptotic total length, releyedia = relative eye diameter, barbel = barbel presence-absence, shpfact = shape factor, swmfact = swim factor, relmthsize = relative mouth size, avgmthpos = average mouth position, avgmthang = average mouth angle, peritavg = average peritoneum color, rglavg = average relative gut length. Species common name abbreviations are as follows: WHSU = white sucker, ROBA = rock bass, RBSF = redbreast sunfish, GRSF = green sunfish, PUMP = pumpkinseed, BLUE = bluegill, LESF = longear sunfish, SMBA = smallmouth bass, SPBA = spotted bass, LMBA = largemouth bass, MOSC = mottled sculpin, BASC = banded sculpin, CESR = central stoneroller, RSDA = rosieside dace, STSH = spottail shiner, SWSH = swallowtail shiner, BNMI = bluntnose minnow, FHMI = fathead minnow, BNDA = blacknose dace, LNDA = longnose dace, CRCH = creek chub, GSDA = greenside darter, FTDA = fantail darter, KADA = Kanawha darter, LOPE = logperch, APDA = Appalachian darter, RODA = Roanoke darter, BKTR = brook trout. SppAb is species abbreviation and famnum is family number.

SppAb	famnum	avgage1repro	avglen1repro	maxtl	releyedia	barbel	shpfact	swmfact	relmthsize	avgmthpos	avgmthang	peritavg	rglavg
APDA	350	1.5	64.0	9.6	0.48	0	6.0	2.0	0.55	-0.21	0.21	1.00	0.49
BASC	320	2.0	91.5	18.0	0.50	0	4.8	2.3	1.04	0.00	0.57	3.00	0.61
BKTR	175	2.5	233.5	86.0	0.48	0	3.9	2.1	1.89	0.07	0.64	1.00	0.61
BLUE	349	1.5	138.0	41.0	0.56	0	2.6	2.2	0.75	0.29	0.93	1.86	0.70
BNDA	102	2.0	55.0	10.0	0.40	1	5.5	1.6	0.75	-0.79	0.14	2.67	0.64
BNMI	102	1.0	49.5	11.0	0.48	0	6.3	2.3	0.47	-0.79	0.00	5.00	1.28
CESR	102	2.0	51.0	22.0	0.33	0	4.9	1.9	0.56	-0.79	0.07	5.38	3.25
CRCH	102	1.5	65.0	30.0	0.40	1	4.6	1.6	0.93	-0.07	0.71	1.00	0.75
FHMI	102	2.0	40.0	10.0	0.48	0	4.6	2.5	0.67	-0.43	0.21	4.50	1.47
FTDA	350	2.0	39.5	8.4	0.47	0	5.5	1.9	0.55	-0.07	0.43	1.00	0.52
GRSF	349	2.0	173.0	31.0	0.63	0	2.8	2.1	1.50	0.29	0.93	1.00	0.77
GSDA	350	2.0	63.0	17.0	0.47	0	5.8	1.8	0.36	-0.71	-0.07	1.22	0.47
KADA	350	2.0	55.5	7.2	0.48	0	5.7	1.6	0.46	-0.43	0.14	5.50	0.53
LESF	349	2.0	107.0	24.0	0.63	0	2.6	1.9	0.95	0.21	0.93	1.42	0.78
LMBA	349	3.5	382.5	97.0	0.56	0	4.2	2.1	1.60	0.79	0.86	1.00	0.83
LNDA	102	2.0	72.5	22.5	0.31	1	5.8	1.7	0.71	-1.00	0.07	2.00	0.73
LOPE	350	2.0	102.5	18.0	0.47	0	6.4	1.8	0.62	-0.71	0.00	1.00	0.49
MOSC	320	2.0	57.0	15.0	0.47	0	4.1	2.2	0.95	0.00	0.50	2.88	0.48
PUMP	349	2.0	135.0	40.0	0.71	0	2.5	2.4	0.86	0.36	0.93	1.42	0.78
RBSF	349	2.0	146.0	30.5	0.60	0	2.5	2.1	0.10	0.36	0.93	1.40	0.86

ROBA	349	3.0	142.5	43.0	0.63	0	2.8	2.4	0.14	0.36	1.00	1.00	0.99
RODA	350	1.0	48.0	7.8	0.51	0	5.8	2.4	0.45	-0.50	0.14	1.00	0.49
RSDA	102	1.0	49.0	11.0	0.64	0	5.4	2.1	1.00	0.43	0.93	1.80	0.65
SMBA	349	3.5	220.5	69.0	0.56	0	4.2	2.3	1.38	0.64	0.71	1.00	0.79
SPBA	349	2.5	250.0	63.5	0.55	0	4.2	2.6	1.28	0.64	0.64	1.00	0.87
STSH	102	1.5	55.0	15.0	0.63	0	5.8	2.3	0.71	-0.36	0.50	1.83	0.67
SWSH	102	2.0	39.0	7.2	0.60	0	5.9	2.5	0.49	-0.43	0.43	3.00	0.66
WHSU	105	3.0	400.0	64.0	0.31	0	5.3	2.4	0.04	-1.00	-0.57	1.00	1.72

APPENDIX C. Raw ecological trait data representing presence or absence of food items by species. Food item (ecological trait) abbreviations are classified by stage food items were consumed and food items themselves as follows: j1 = juvenile surface/column invertebrate, j2 = juvenile benthic macroinvertebrate, j3 = juvenile zooplankton, j4 = juvenile insect/invertebrate, j5 = juvenile large crustacean, j6 = juvenile plant material, j7 = juvenile fish, j8 = juvenile shrimp/mysis/amphipod, j9 = juvenile benthos/eggs, j10 = juvenile undefined plankton, a1 = adult surface/column invertebrate, a2 = adult benthic macroinvertebrate, a3 = adult zooplankton, a4 = adult insect/invertebrate, a5 = adult large crustacean, a6 = adult plant material, a7 = adult fish, a8 = adult shrimp/mysis/amphipod, a9 = adult benthos/eggs, a10 = adult undefined plankton. Species common name abbreviations are as follows: WHSU = white sucker, ROBA = rock bass, RBSF = redbreast sunfish, GRSF = green sunfish, PUMP = pumpkinseed, BLUE = bluegill, LESF = longear sunfish, SMBA = smallmouth bass, SPBA = spotted bass, LMBA = largemouth bass, MOSC = mottled sculpin, BASC = banded sculpin, CESR = central stoneroller, RSDA = rosyzide dace, STSH = spottail shiner, SWSH = swallowtail shiner, BNMI = bluntnose minnow, FHMI = fathead minnow, BNDA = blacknose dace, LNDA = longnose dace, CRCH = creek chub, GSDA = greenside darter, FTDA = fantail darter, KADA = Kanawha darter, LOPE = logperch, APDA = Appalachian darter, RODA = Roanoke darter, BKTR = brook trout. SppAb is species abbreviation and famnum is family number.

SppAb	famnum	j1	j2	j3	j4	j5	j6	j7	j8	j9	j10	a1	a2	a3	a4	a5	a6	a7	a8	a9	a10
APDA	350	1	1	1	1	1	0	0	1	0	0	1	1	1	1	1	0	0	1	0	0
BASC	320	1	1	0	0	1	0	1	1	0	0	0	1	0	0	1	0	1	1	0	0
BKTR	175	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
BLUE	349	1	1	1	1	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0
BNDA	102	1	1	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	0	0	0
BNMI	102	1	0	1	1	0	1	0	0	0	0	1	0	1	1	0	1	0	0	0	0
CESR	102	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0
CRCH	102	1	1	0	1	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0
FHMI	102	0	0	1	1	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	0
FTDA	350	1	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0
GRSF	349	1	1	1	1	0	0	0	0	1	0	0	0	1	1	1	0	1	0	0	0
GSDA	350	1	1	1	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0
KADA	350	1	1	1	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0
LESF	349	1	0	1	1	0	0	0	0	1	0	1	1	0	1	1	1	0	1	1	0
LMBA	349	1	0	1	1	0	0	0	0	0	0	1	1	1	1	1	0	1	1	0	0
LNDA	102	1	1	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	0	0	0
LOPE	350	1	1	1	1	1	0	0	1	0	0	1	1	1	1	1	0	0	1	0	0

MOSC	320	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
PUMP	349	1	1	1	1	1	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0
RBSF	349	1	1	1	1	0	0	1	0	0	0	1	1	1	1	0	0	1	0	0	0
ROBA	349	1	1	1	1	0	0	0	1	0	0	0	1	0	1	1	0	1	0	0	0
RODA	350	1	1	1	1	1	0	0	1	0	0	1	1	1	1	1	0	0	1	0	0
RSDA	102	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0
SMBA	349	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	1	0	0	0
SPBA	349	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0
STSH	102	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0
SWSH	102	1	1	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	0	0	0
WHSU	105	1	0	1	1	1	1	0	0	0	1	1	0	1	1	1	1	0	0	0	1

APPENDIX D. Comprehensive list of literature used to collect life history data for all species studied. Author(s), year, title, journal/publication/publisher, volume, and page numbers are given above.

Author	Year	Title	Journal/Publication/Publisher	Volume	Pages
Andrews and Flickinger	1974	Spawning requirements and characteristics of the fathead minnow	Proceedings of the Twenty-Seventh Annual Conference of the Southeastern Association of Game and Fish Commissioners	27	759-766
Applegate and Smith	1951	The determination and rate of growth from vertebrae of the channel catfish, <i>Ictalurus lacustris punctatus</i>	Transactions of the American Fisheries Society	80	119-139
Backus	1951	New and rare records of fishes from Labrador	Copeia	4	288-294
Barton	1980	Spawning migrations, age and growth, and summer feeding of white and longnose suckers in an irrigation reservoir	Canadian Field-Naturalist	94	300-304
Bauman	1946	Bait minnow production in ponds	Missouri Conservationist	7	2-5
Beamish	1973	Determination of age and growth of populations white sucker (<i>Catostomus commersonii</i>) exhibiting a wide range of size at maturity	Journal of the Fisheries Research Board of Canada	30	607-616
Beamish and Crossman	1977	Validity of the subspecies designation for the dwarf white sucker (<i>Catostomus commersonii utawana</i>)	Journal of the Fisheries Research Board of Canada	34	371-378
Becker	1983	Fishes of Wisconsin	University of Wisconsin Press, Madison, WI		
Braaten and Guy	2002	Life history attributes along the latitudinal gradient of the Missouri River	Transactions of the American Fisheries Society	131	931-945
Brewer	1980	A study of native muskellunge populations in eastern Kentucky streams	Kentucky Department of Fish and Wildlife Resources Fisheries Bulletin Number 64, Frankfort, KY		
Brown	1968	Population characteristics and physical condition of alewives in a massive dieoff in Lake Michigan, 1967	Great Lakes Fisheries Commission Technical Report No. 13		
Burr	1984	Growth, reproduction, mortality, distribution, and biomass of freshwater drum in Lake Erie	Journal of Great Lakes Research	10	48-58
Burr and Morris	1977	Spawning Behavior of the shorthead redhorse, <i>Moxostoma macrolepidotum</i> , in Big Rock Creek, Illinois	Transactions of the American Fisheries Society	106	80-82
Butler	1965	Freshwater drum, <i>Aplodinotus grunniens</i> , in the navigational impoundments of the upper Mississippi River	Transactions of the American Fisheries Society	94	339-349
Buynak and Mohr	1979	Larval development of the shorthead redhorse (<i>Moxostoma macrolepidotum</i>), in Big Rock Creek, Illinois	Transactions of the American Fisheries Society	108	161-165

Campbell	1935	A study of the common sucker, <i>Catostomus commersoni</i> (Lacepede), of Waskesiu Lake	Master's Thesis. University of Saskatchewan, Saskatoon, Canada		
Carlander	1950	Handbook of Freshwater Fishery Biology, Volume 1	The Iowa State University Press, Ames, IA		
Carlander	1969	Handbook of Freshwater Fishery Biology, Volume 1	The Iowa State University Press, Ames, IA		
Carlander and Sprugel	1957	Fishes of Little Wall Lake, Iowa prior to dredging	Proceedings of the Iowa Academy of Science	62	555-566
Carlson	1967	Fathead minnow, <i>Pimephales promelas</i> Rafinesque, in the Des Moines River, Boone County, Iowa, and the Skunk River drainage, Hamilton and Story Counties, Iowa	Iowa State Journal of Science	41	363-374
Carroll and Hall	1964	Growth of catfishes in Norris Reservoir, Tennessee	Journal of the Tennessee Academy of Science	39	86-91
Casselman et al.	1999	Growth and ultimate length of muskellunge from Ontario water bodies	North American Journal of Fisheries Management	19	271-290
Chambers	1963	Lake of the Woods survey. Northern sector – 1963 (Preliminary report)	Ontario Department of Lands and Forests, Maple, ON		
Clay	1975	The Fishes of Kentucky	Kentucky Department of Fish and Wildlife Resources, Frankfort, KY		
Clemons and Sneed	1957	The spawning behavior of the channel catfish <i>Ictalurus punctatus</i>	U.S. Fish and Wildlife Service Special Scientific Report No. 219		
Corbett and Powles	1983	Spawning and early-life ecological phases of the white sucker in Jack Lake, Ontario	Transactions of the American Fisheries Society	112	308-313
Corbett and Powles	1986	Spawning and larva drift of sympatric walleyes and white suckers in an Ontario stream	Transactions of the American Fisheries Society	115	41-46
Cross	1951	Early limnological and fish population conditions of Canton Reservoir, Oklahoma, and fishery management recommendations	Doctoral Dissertation, Oklahoma State University, Stillwater, OK		
Cross	1967	Handbook of Fishes of Kansas	Museum of Natural History, University of Kansas, Misc. Publication	45	1-357
Curry and Spacie	1984	Differential use of stream habitat by spawning catostomids	American Midland Naturalist	111	267-279
Daiber	1953	Notes on the spawning population of the freshwater drum (<i>Aplodinotus grunniens</i> Rafinesque) in western Lake Erie	American Midland Naturalist	50	159-171
Dempson	1981	Identification of anadromous arctic charr stocks in coastal areas of northern Labrador	L. B. Johnson, and B. Burns, editors. Biology of the arctic charr: Proceedings of the international symposium on arctic charr, volume 1984. The University of Manitoba Press, Winnipeg, Manitoba		143-162

Dempson and Green	1985	Life-history of anadromous arctic charr, <i>salvelinus-alpinus</i> , in the Raser-River, northern Labrador	Canadian Journal of Zoology-Revue Canadienne de Zoologie	63	315-324
Dobie et al.	1956	Raising bait fishes	U.S. Fish and Wildlife Service No. 35		
Dymond	1926	The Fishes of Lake Nipigon	University of Toronto Studies in Biology Series 27	27	1-108
Eberley	1975	Spawning behavior of major fish species in the Monticello area of the....			
Eddy and Surber	1947	Northern fishes with special reference to the upper Mississippi Valley	C. T. Branford Company, Newton Centre, MA		
Edsall	1967	Biology of the freshwater drum in western Lake Erie	Ohio Journal of Science	67	321-340
Etnier and Starnes	1993	The Fishes of Tennessee	University of Tennessee Press, Knoxville, TN		
Everhart and Waters	1965	Life history of the blueback trout (arctic char, <i>Salvelinus alpinus</i> (Linnaeus)) in Maine	Transactions of the American Fisheries Society	94	393-397
Farrel et al.	1996	Egg distribution and spawning habitat of northern pike and muskellunge in a St. Lawrence River marsh, New York	Transactions of the American Fisheries Society	125	127-131
Finke	1964	The channel catfish	Wisconsin Conservation Bulletin	29	18-19
Fish	1932	Contribution to the early life history of sixty-two species of fish from Lake Erie and its tributary waters	Bulletin of the United States Fish Commission		
Forney	1957	Raising bait fish and crayfish in New York ponds			
Fraser and Power	1981	The interactive segregation of landlocked arctic charr (<i>Salvelinus alpinus</i>) from lake charr (<i>S. namaycush</i>) and brook charr (<i>S. fontinalis</i>) in two lakes of subarctic Quebec, Canada	L. B. Johnson, and B. Burns, editors. Biology of the arctic charr: Proceedings of the international symposium on arctic charr, volume 1984. The University of Manitoba Press, Winnipeg, Manitoba		163-181
Frohnauer et al.	2007	Population dynamics and angler exploitation of the unique muskellunge population in Shoepack Lake, Voyageurs National Park, Minnesota	North American Journal of Fisheries Management	27	63-76
Fuiman	1979	Descriptions and comparisons of catostomid fish larvae: northern Atlantic drainage species	Transactions of the American Fisheries Society	108	560-603
Galat	1973	Normal embryonic development of the muskellunge (<i>Esox masquinongy</i>)	Transactions of the American Fisheries Society	102	384-391
Gale and Buynak	1982	Fecundity and spawning frequency of the fathead minnow-a fractional spawner	Transactions of the American Fisheries Society	111	220-229
Geen et al.	1966	Life histories of two species of catostomid fishes in Sixteenmile Lake, British Columbia, with particular reference to inlet stream spawning	Journal of the Fisheries Research Board of Canada	23	1761-1788

Goeman	1983	Freshwater drum spawning and fecundity in the upper Mississippi River	Proceedings of the Iowa Academy of Science	90	132-133
Graeb et al.	2009	Shifts in sauger spawning locations after 40 years of reservoir ageing: influence of a novel delta ecosystem in the Missouri River, USA	River Research and Applications	25	153-159
Grainger	1953	On the age, growth, migration, reproductive potential and feeding habits of arctic char (<i>salvelinus alpinus</i>) of Frobisher Bay, Baffin Island	Journal of the Fisheries Research Board of Canada	10	326-369
Gulseth and Nilssen	2001	Life-history traits of char, <i>salvelinus alpinus</i> , from a high Arctic watercourse on Svalbard	Arctic	54	1-11
Hankinson	1919	Notes on life-histories of Illinois fishes	Transactions of the Illinois State Academy of Science	12	132-150
Harrison and Hadley	1979	Biology of muskellunge (<i>Esox masquinongy</i>) in the upper Niagara River	Transactions of the American Fisheries Society	108	444-451
Hart	1978	Smith Mountain Reservoir research study	Virginia Commission of Game and Inland Fisheries, Federal Aid in Sport Fish Restoration, Project F-30-R, April 16, 1973-April 15, 1976, Project Completion Report, Richmond, VA		
Hasler and Wisby	1958	The return of displaced largemouth bass and green sunfish to a "home" area	Ecology	39	289-293
Hedges and Ball	1953	Production and harvest of bait fishes in Michigan	Michigan Department of Conservation Miscellaneous Publication	6	1-30
Holland-Bartels	1988	Variations in abundance of young-of-the-year channel catfish in a navigation pool of the upper Mississippi River	Transactions of the American Fisheries Society	117	202-208
Isaak	1961	The ecological life history of the fathead minnow, <i>Pimephales promelas</i> (Rafinesque)	University of Michigan, Ann Arbor, MI		
Jenkins and Burkhead	1994	Freshwater Fishes of Virginia	American Fisheries Society, Bethesda, MD		
Johnson	1954	And it didn't get away	Wisconsin Conservation Bulletin	19	16-17
June. 1977	1977	Reproductive patterns in seventeen species of warmwater fishes in a Missouri River reservoir	Environmental Biology of Fishes	2	285-296
Kapuscinski et al.	2007	Population dynamics of muskellunge in Wisconsin waters of Green Bay, Lake Michigan, 1989-2005	Environmental Biology of Fishes	79	27-36
Kay et al.	1994	Reproductive Biology and Early Life History of Fishes in the Ohio River Drainage Volume 2	Tennessee Valley Authority, Chattanooga, TN		102-111
Keleher	1961	Comparison of the largest Great Slave Lake fish with North American records	Journal of the Fisheries Research Board of Canada	18	417-421

Kelley	1962	Sexual maturity and fecundity of the largemouth bass, <i>Micropterus salmoides</i> (Lacepede) in Maine	Transactions of the American Fisheries Society	91	23-38
Kramer and Smith	1962	Formation of year classes in largemouth bass	Transactions of the American Fisheries Society	91	29-41
Krieger	1980	Ecology of catostomids in Twin Lakes, Colorado, in relation to a pumped storage powerplant	United States Department of the Interior Bureau of Land and Recreation Publication REC-ERC-80-2		
Lebeau et al.	1986	The muskellunge as a multiple spawner: an adaptive strategy for production of a large number of eggs	American Fisheries Society Special Publication	15	
Lippson and Moran	1974	Manual for identification of early developmental stages of fishes of the Potomac River estuary	Power Plant Siting Program of the Maryland Department of Natural Resources Publication PPSP-MP-13, Baltimore, MD		
Lord	1927	Notes on the use of the blackhead minnow, <i>Pimephales promelas</i> , as a forage fish	Transactions of the American Fisheries Society	57	92-99
MacCallum and Reiger	1981	The biology and bioenergetics of arctic charr in Char Lake, N.W.T., Canada	L. B. Johnson, and B. Burns, editors. Biology of the arctic charr: Proceedings of the international symposium on arctic charr, volume 1984. The University of Manitoba Press, Winnipeg, Manitoba		329-340
Mansueti and Hardy	1967	Development of fishes of the Chesapeake Bay Region. Part 1	Natural Resources Institution, University of Maryland, Baltimore, MD		
Markus	1932	The extent to which temperature changes influence consumption in largemouth bass	Transactions of the American Fisheries Society	62	202-210
Markus	1934	Life history of the blackheaded minnow (<i>Pimephales promelas</i>)	Copeia	1934	116-122
Marzolf	1957	The reproduction of channel catfish in Missouri ponds	Journal of Wildlife Management	21	22-28
McCarracher and Thomas	1968	Some ecological observations on the fathead minnow, <i>Pimephales promelas</i> , in the alkaline waters of Nebraska	Transactions of the American Fisheries Society	97	52-55
McClellan	1954	A study of the southern spotted channel catfish, <i>Ictalurus punctatus</i> (Rafinesque)	Master's Thesis, North Texas State College, Denton, TX		
McCrimmon and Berst	1961	The native fish population and trout harvests in an Ontario farm pond	Progressive Fish-Culturist	23	106-113
McHugh and Steinkoenig	1980	Northeast Virginia sport fishery study	Virginia Commission of Game and Inland Fisheries, Federal Aid Sport Fish Restoration, Project F-37-R, January 1, 1977-December 31, 1979. Project Completion Report, Richmond, VA		
Meyer	1962	Life history of three redhorse (<i>Moxostoma</i>) in the Des Moines River, Iowa	Transactions of the American Fisheries Society	91	412-419

Meyer	1970	Development of some larval centrarchids	Progressive Fish-Culturist	32	130-136
Miles	1978	A life history study of the muskellunge in West Virginia	Selected Coolwater Fishes of North America, American Fisheries Society Special Publication No. 11		140-145
Moore and Moore	1974	Food and growth of arctic char, <i>salvelinus alpinus</i> (L.), in the Cumberland Sound area of Baffin Island	Journal of Fish Biology	6	79-92
Moshenko et al.	1981	The arctic charr sport fishery at Tree River, Northwest Territories, Canada 1964-1978	L. B. Johnson, and B. Burns, editors. Biology of the arctic charr: Proceedings of the international symposium on arctic charr, volume 1984. The University of Manitoba Press, Winnipeg, Manitoba		349-369
Mraz	1964	Observations on large and smallmouth bass nesting and early life history	Wisconsin Conservation Department Fisheries Resources Report No. 11		
Mraz et al.	1961	The largemouth bass, its life history, ecology and management	Wisconsin Conservation Department Publication 232		
Muncy	1959	Age and growth of channel catfish from the Des Moines River, Boone County, Iowa, 1955 and 1956	Iowa State Journal of Science	34	127-137
Nilsen and Klemetsen	1981	Anadromous, resident and landlocked arctic charr on the coast of Finnmark, N. Norway	L. B. Johnson, and B. Burns, editors. Biology of the arctic charr: Proceedings of the international symposium on arctic charr, volume 1984. The University of Manitoba Press, Winnipeg, Manitoba		79-89
Norden	1967	Age, growth and fecundity of the alewife, <i>Alosa pseudoharengus</i> (Wilson), in Lake Michigan	Transactions of the American Fisheries Society	96	387-393
Odell	1934	The life history and ecological relationships of the alewife (<i>Pomolobus pseudoharengus</i> (Wilson)), in Seneca Lake, New York	Transactions of the American Fisheries Society	64	118-126
Oehmecke et al.	1965	The Wisconsin muskellunge, its life history, ecology and management	Wisconsin Conservation Department Publications No. 225		
Osterberg	1985	Habitat partitioning by muskellunge and northern pike in the international portion of the St. Lawrence River	New York Fish and Game Journal	32	158-166
Padfield	1951	Age and growth differentiation between the sexes of the largemouth bass, <i>Micropterus salmoides</i> (Lacepede)	Journal of the Tennessee Academy of Science	26	42-54
Parsons	1959	Muskellunge in Tennessee streams	Transactions of the American Fisheries Society	88	136-140

Perry and Carver	1972	Length at maturity and total length-collarbone length conversions for channel catfish, <i>Ictalurus punctatus</i> , and blue catfish, <i>Ictalurus furcatus</i> , collected from the marshes of southwest Louisiana	Proceedings of the Twenty-Sixth Annual Conference of the Southeastern Association of Game and Fish Commissioners		541-553
Pflieger	1975	The Fishes of Missouri	Missouri Department of Conservation, Jefferson City, MO		
Prather	1957	Preliminary experiments on winter feeding small fathead minnows	Proceedings of the Eleventh Annual Conference of the Southeastern Association of Game and Fish Commissioners	11	249-253
Priegel	1969	Age and growth of the freshwater drum in Lake Winnebago, Wisconsin	Transactions of the American Fisheries Society	98	116-118
Quinn and Ross	1985	Non-annual spawning in the white sucker, <i>Catostomus commersoni</i>	Copeia	1985	613-618
Raney and Webster	1942	The spring migration of the common white sucker, <i>Catostomus c. commersonii</i> (Lacepede), in Skaneateles Lake inlet, New York	Copeia	1942	139-148
Reid	2006	Timing and demographic characteristics of redhorse spawning runs in three Great Lakes basin rivers	Journal of Freshwater Ecology	21	249-258
Reighard	1920	The breeding behavior of the suckers and minnows	Biological Bulletin (Woods Hole)	38	1-32
Robison and Buchanan	1988	Fishes of Arkansas	University of Arkansas Press, Fayetteville, AR		
Rombough et al.	1978	Life-history and taxonomic status of an isolated population of arctic char, <i>salvelinus-alpinus</i> , from Gros Morne National Park, Newfoundland	Journal of the Fisheries Research Board of Canada	35	1537-1541
Ross	2001	Inland Fishes of Mississippi	University Press of Mississippi, Oxford, MS		
Sandlund et al.	1992	The arctic charr <i>salvelinus-alpinus</i> in Thingvallavatn	Oikos	64	305-351
Saunders and Power	1969	The arctic char, <i>salvelinus alpinus</i> (Linnaeus), of Mamatek Lake, Quebec	Le Naturaliste Canadien	96	919-934
Scott and Crossman	1973	Freshwater Fishes of Canada	Fisheries Research Board of Canada Bulletin 184		
Simon and Wallus	2004	Reproductive Biology and Early Life History of Fishes in the Ohio River Drainage Volume 3	CRC Press, Boca Raton, FL		100-107
Simon and Wallus	2006	Reproductive Biology and Early Life History of Fishes in the Ohio River Drainage Volume 4	CRC Press, Boca Raton, FL		571-583
Smith	1979	The Fishes of Illinois	University of Illinois Press, Urbana, IL		
Smith	1985	The Inland Fishes of New York	New York State Department of Environmental Conservation, Albany, NY		

Sparholt	1985	The population, survival, growth, reproduction and food of arctic charr, <i>salvelinus-alpinus</i> (I), in 4 unexploited lakes in Greenland	Journal of Fish Biology	25	313-330
Spoor	1935	On the sexual dimorphism of <i>Catostomus commersoni</i> (Lacepede)	Copeia	1935	167-171
Spoor	1938	Age and growth of the sucker <i>Catostomus commersoni</i> (Lacepede), in Muskellunge Lake, Vilas County, Wisconsin	Transactions of the Wisconsin Academy of Sciences, Arts and Letters	31	457-505
Sprules	1952	The arctic char of the west coast of Hudson Bay	Journal of the Fisheries Research Board of Canada	9	1-15
Stevens	1959	The white and channel catfishes of the Santee-Cooper Reservoir and tailrace sanctuary	Proceedings of the Thirteenth Annual Conference of the Southeastern Association of Game and Fish Commissioners		203-219
Stewart	1926	Development, growth, and food habits of the white sucker, <i>Catostomus commersonii</i> Lesueur	United States Bureau of Fisheries Bulletin	42	147-184
Stocek et al.	1999	The Muskellunge, <i>Esox masquinongy</i> , distribution and biology of a recent addition to the ichthyofauna of New Brunswick	Canadian Field-Naturalist	113	230-234
Strange et al.	1987	Age and growth, food habits, and forage value of the alewife in Watauga Reservoir, Tennessee	Proceeding of the Thirty-Ninth Annual Conference of the Southeast Association of Fisheries and Wildlife Agencies		157-165
Sule and Skelly	1985	The life history of the shorthead redhorse, <i>Moxostoma macrolepidotum</i> , in the Kankakee River drainage, Illinois	Illinois Natural History Survey Biological Notes 123, Champaign, IL		
Swedburg and Walburg	1970	Spawning and early life history of the freshwater drum in Lewis and Clark Lake, Missouri River, South Dakota	Transactions of the American Fisheries Society	99	560-570
Thompson	1959	Fecundity of the arctic char, <i>salvelinus alpinus</i> , of the Wood River Lakes, Bristol Bay, Alaska	Copeia	4	345-346
Thomsen and Hasler	1944	The minnow problem in Wisconsin	Wisconsin Conservation Bulletin	9	6-8
Trautman	1981	The Fishes of Ohio	The Ohio State University Press, Columbus, OH		
Vessel and Eddy	1941	A preliminary study of the egg production of certain Minnesota fishes	Minnesota Bureau of Fisheries Research Investigations Report 26, St. Paul, MN		
Wahlquist	1974	Fecundity and maturity of channel catfish, <i>Ictalurus punctatus</i> (Rafinesque), from Alabama	Journal of the Alabama Academy of Science	45	23-29
Walburg	1976	Changes in fish populations of Lewis and Clark Lake, 1956-74, and their relation to water management and the environment	U.S. Fish and Wildlife Service Report No. 69		

Wallus and Simon	2006	Reproductive Biology and Early Life History of Fishes in the Ohio River Drainage Volume 5	CRC Press, Boca Raton, FL		281-302
Wallus and Simon	2008	Reproductive Biology and Early Life History of Fishes in the Ohio River Drainage Volume 6	CRC Press, Boca Raton, FL		310-350
Wallus et al.	1990	Reproductive Biology and Early Life History of Fishes in the Ohio River Drainage Volume 1	Tennessee Valley Authority, Chattanooga, TN		243-249
Wang	1981	Taxonomy of early life stages of fishes — fishes of the Sacramento-San Joaquin Estuary and Moss Landing Harbor-Elkhorn Slough, California	Ecological Analysts, Concord, CA		
Wang and Kernehan	1979	Fishes of the Delaware estuaries, a guide to the early life histories	Ecological Analysts, Towson, MD		
Winemiller and Rose	1992	Patterns of life-history diversification in North American fishes: Implications for population regulation	Canadian Journal of Fisheries and Aquatic Sciences	49	2196-2218
Wydoski and Whitney	2003	Inland Fishes of Washington	American Fisheries Society, The University of Washington Press, Singapore		
Wynne-Edwards	1932	The breeding habits of the black-headed minnow (<i>Pimephales promelas</i> Raf.)	Transactions of the American Fisheries Society	62	382-383