River Network Structure: A Template for Understanding Predator-Prey Dynamics and Potential Anthropogenic Impacts

Catherine L. Hein
Utah State University

Follow this and additional works at: https://digitalcommons.usu.edu/etd

Part of the Life Sciences Commons

Recommended Citation

This Dissertation is brought to you for free and open access by the Graduate Studies at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.
RIVER NETWORK STRUCTURE: A TEMPLATE FOR UNDERSTANDING
PREDATOR-PREY DYNAMICS AND POTENTIAL ANTHROPOGENIC IMPACTS

by

Catherine L. Hein

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

____________________________   ____________________
Todd A. Crowl     Charles P. Hawkins
Major Professor     Committee Member

____________________________   ________________________
Phaedra Budy      Mark W. Brunson
Committee Member     Committee Member

____________________________
James A. Powell
Committee Member

____________________________
Byron R. Burnham
Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2009
Copyright © Catherine L. Hein 2009
All Rights Reserved
ABSTRACT

River Network Structure: A Template for Understanding Predator-Prey Dynamics and Potential Anthropogenic Impacts

by

Catherine L. Hein, Doctor of Philosophy
Utah State University, 2009

Major Professor: Dr. Todd A. Crowl
Department: Watershed Sciences

A landscape perspective is critically important for understanding community structure, particularly in systems dominated by migratory fauna. I aimed to understand how the structure of riverscapes in Puerto Rico mediates potential anthropogenic impacts, predator-prey interactions, and the migratory behavior of a diadromous species. I surveyed fishes and shrimps at sites throughout two watersheds, designed transplant experiments that investigated the role of natural barriers on predator-prey interactions, and developed models of shrimp migration specific to a particular river network. I did not detect an effect of anthropogenic changes to the landscape on fish and shrimp species distributions in two watersheds that drain the Luquillo Experimental Forest. These communities were primarily affected by the position of natural barriers: predatory fish distributions were limited by waterfalls and most shrimp species were found upstream from fish barriers. Thus, steep terrain mediated predator-prey interactions between fishes and shrimps, with one shrimp (*Atya lanipes*) likely avoiding predation by migrating...
above fish barriers. Lab and field experiments provided the first mechanistic evidence for landscape-level predator-avoidance behavior by *A. lanipes*. Both postlarval and adult shrimp avoided the scent of three predatory fish species in a y-maze fluvarium. In natural streams above fish barriers, adult *A. lanipes* did not respond to the addition of fish scent, but adult abundances did decline when fish were added to in-stream cages. To integrate our ideas about how shrimp behaviors scale up to observed adult *A. lanipes* distributions across the landscape, we developed a set of nested models specific to a particular river network. The best models parameterized branch choice at nodes within the river network to be heavily weighted toward particular mid-elevation tributaries above fish barriers. Our models indicated that distance traveled above and below fish barriers had little effect on adult distributions. Because the number of migrants decreases with distance upstream, the latter result was likely an artifact of the model. In montane river systems with migratory fauna, scientists would benefit by creatively designing new experiments and models that incorporate river network structure, as this is the template upon which all processes occur.
DEDICATION

I dedicate this dissertation

to my parents

Bill and Sue Hein

Thank you for supporting all of my dreams and
helping to make each one of them come true.
ACKNOWLEDGMENTS

This research was funded by the National Science Foundation through the Biocomplexity (#0308414) and Long-Term Ecological Research Programs in the Luquillo Experimental Forest (#DEB-0218039 and DEB-0620910), and a research award from the Ecology Center at Utah State University. I used facilities at El Verde Field Station (University of Puerto Rico, Río Piedras) to conduct my research in Puerto Rico.

It is truly amazing to think about the number of people who have been involved in the research presented in this dissertation. I am so grateful for the help I have received and friendships I have made.

I thank each of my committee members, Chuck Hawkins, James Powell, Phaedra Budy, and Mark Brunson, for their guidance and support through the years. I have learned a lot from each one of them and appreciate the effort they have put in to training me as a scientist. Although not on my committee, Susan Durham also provided analytical guidance on research conducted prior to my time at USU and research conducted here as a PhD student. My advisor, Todd Crowl, has provided me with many opportunities, so many more than I would expect as a typical graduate student. I thank him not only for his guidance in scientific endeavors, but mostly, I thank him for giving me the chance to see what an academic life in the sciences is all about. I was able to attend conferences around the world, help direct the research of the Biocomplexity grant, visit and give a seminar at Harvard, and teach his undergraduate ecology class.

I also acknowledge the staff at the Ecology Center and in the Department of Watershed Sciences, especially Stephanie White, Marvin Bennett, Enid Kelley, and Brian
Bailey. Thanks for dealing with receipts hand written in Spanish, a horribly costly field vehicle, and my forgetfulness in registering for classes and health insurance. I thank Chris Luecke for supporting me while I taught 77 undergraduate ecology students, for they definitely tested me at times. I also thank the permanent staff at El Verde Field Station, especially Tony Rivera Vargas, Hilda Lugo, and Francisco Perez.

Thanks to Alan Covich, Andrew Pike, Felipe Blanco, Dave Kikkert, Wyatt Cross, and Fred Scatena, who have been wonderful collaborators. I have benefited greatly from the many conversations we have shared about shrimp and rivers over the years. I thank the following people for their help in the field: Chris Blair, Andy Crowl, Ruth Kikkert, María Ocasio Torres, Enrique Marrero, Coralys Ortiz, Paul Nicholson, Kaua Fraiola, Kunal Mandal, Sarah Redd, Therese Frauendorf, and Kevin Landom. Kirk Sherrill provided land cover variables. Susan Durham and John Van Sickle provided statistical guidance and Katie McHugh, Christie Meredith, and Andy Hill provided ArcGIS support.

I would like to give special thanks to Chelse Prather, Tamara Heartsill Scalley, and Alex Sloan who became my family while living and working in Puerto Rico and provided unending support and friendship. I also received amazing support from my friends and lab mates in Logan. Thanks to Keli Goodman, Stephanie Kraft, Stephanie Miller, Kevin Landom, Brian Hines, Nick Weber, Annie Caires, Pete McHugh, Katie McHugh, and Nicol Gagstetter. I also thank Tyler Logan for his friendship, love, and support, and especially for keeping me sane over the last few months.

Lastly, I thank my family, Bill, Sue, and Christie Hein, who provide never-ending support and love.

Catherine L. Hein
## CONTENTS

<table>
<thead>
<tr>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSTRACT ................................................................. iii</td>
</tr>
<tr>
<td>DEDICATION .............................................................. v</td>
</tr>
<tr>
<td>ACKNOWLEDGMENTS ......................................................... vi</td>
</tr>
<tr>
<td>LIST OF TABLES .......................................................... ix</td>
</tr>
<tr>
<td>LIST OF FIGURES .......................................................... x</td>
</tr>
<tr>
<td>CHAPTER</td>
</tr>
<tr>
<td>1. INTRODUCTION ......................................................... 1</td>
</tr>
<tr>
<td>2. GEOMORPHIC BARRIERS STRUCTURE DIADROMOUS FAUNAL COMMUNITIES IN TROPICAL ISLAND STREAMS ................................................................. 9</td>
</tr>
<tr>
<td>3. RUNNING THE PREDATOR GAUNTLET: DO FRESHWATER SHRIMP (<em>ATYA LANIPES</em>) MIGRATE ABOVE WATERFALLS TO AVOID FISH PREDATION? ..51</td>
</tr>
<tr>
<td>4. MODELING SHRIMP (<em>ATYA LANIPES</em>) MIGRATION THROUGH TROPICAL ISLAND RIVER NETWORKS ................................................................. 87</td>
</tr>
<tr>
<td>5. SUMMARY AND DISCUSSION ........................................... 124</td>
</tr>
<tr>
<td>APPENDIX ................................................................. 132</td>
</tr>
<tr>
<td>CURRICULUM VITAE ........................................................... 138</td>
</tr>
<tr>
<td>Table</td>
</tr>
<tr>
<td>-------</td>
</tr>
<tr>
<td>2-1</td>
</tr>
<tr>
<td>2-2</td>
</tr>
<tr>
<td>2-3</td>
</tr>
<tr>
<td>3-1</td>
</tr>
<tr>
<td>3-2</td>
</tr>
<tr>
<td>4-1</td>
</tr>
<tr>
<td>4-2</td>
</tr>
<tr>
<td>4-3</td>
</tr>
<tr>
<td>A-2</td>
</tr>
<tr>
<td>A-3</td>
</tr>
<tr>
<td>Figures</td>
</tr>
<tr>
<td>---------</td>
</tr>
<tr>
<td>2-1</td>
</tr>
<tr>
<td>2-2</td>
</tr>
<tr>
<td>2-3</td>
</tr>
<tr>
<td>2-4</td>
</tr>
<tr>
<td>3-1</td>
</tr>
<tr>
<td>3-2</td>
</tr>
<tr>
<td>3-3</td>
</tr>
<tr>
<td>3-4</td>
</tr>
<tr>
<td>3-5</td>
</tr>
<tr>
<td>4-1</td>
</tr>
<tr>
<td>4-2</td>
</tr>
</tbody>
</table>
| 4-3     | Stylized diagram of the river network with stream width proportional to the net turn probabilities estimated according to the ‘same-zero’ model, direct drainage area proportions (see Table 4-3), the ‘pool area-zero’ model, and the ‘unique-two...
rates’ model. The size of each circle scales with the observed, relative abundance of adult shrimp in each tributary (denoted with a letter).
CHAPTER 1
INTRODUCTION

To fully understand many themes in ecology, a landscape perspective is critically important. Much of ecology is concerned with understanding how individual species are distributed across the landscape, with gradients in physical attributes of the landscape limiting the range of individual species. Landscape structure provides the template upon which metapopulation dynamics are understood, with interconnected patches acting as population sources or sinks (Hanski 1998). These concepts have been applied to the conservation of species in fragmented landscapes, with optimal patch locations close enough together for dispersal between patches, but far enough apart to prevent metapopulation extinction after a single stochastic event (Hanski 1998). A landscape perspective may also provide context for understanding species interactions, which occur at a single location, but may be mediated by spatial heterogeneity (Lima 2002, Woodward and Hildrew 2002). For example, lions hunt and make more kills in areas with cover and few prey than in open areas with abundant prey (Grant et al. 2005). Finally, a landscape perspective is particularly important when studying migratory species that navigate over long distances (Dingle 1996, Alerstam 2006) and connect seemingly disparate ecosystems (e.g., salmon carcasses deposit marine-derived nutrients in freshwater and terrestrial ecosystems; Ewald et al. 1998).

Landscape ecology has primarily focused on terrestrial systems, but both landscape and stream ecology would benefit by investigating riverine landscapes (Wiens 2002). Hynes (1975) was one of the first to contextualize streams within the landscape, recognizing that the characteristics of human activities within a watershed directly affect
stream geomorphology, water chemistry, and the community structure of organisms within the stream. Also, Likens and others (1970) engaged in whole watershed experimentation, investigating the effects of deforestation on nutrient fluxes in streams. Much of the research that followed incorporated a landscape perspective, but primarily focused on longitudinal changes along rivers (e.g., Vannote et al. 1980, Newbold et al. 1982, Leopold and Maddock 1953). Lateral and vertical components of riverine landscape were emphasized as more research was conducted in floodplains and hyporheic zones (Ward 1989, Wiens 2002, Woodward and Hildrew 2002). More recent conceptual papers highlight how the fractal or dendritic nature of streams influences geomorphology, patterns in species distributions, and food web structure (Rhoads et al. 1987, Osborne and Wiley 1992, Rice et al. 2001, Power and Dietrich 2002, Benda et al. 2004, Fernandes et al. 2004, Campbell Grant et al. 2007). For example, natural barriers and/or environmental characteristics prevent predatory fishes from inhabiting some headwater streams, thereby providing refugia for prey and causing food web structure to vary with landscape position (Power and Dietrich 2002, Creed 2006).

Most paradigms in stream ecology derive from work done in temperate streams (Allan 1995), with few studies in tropical streams contributing new concepts to the field (but see Junk and others’ (1989) Flood Pulse Concept). Rivers on tropical islands are often high energy systems, with high precipitation and frequent storms causing large volumes of water to flow over steep terrain year round (Gupta 1995, Pike 2007). Thus, these stream channels have the power to flush sediments of fairly large grain size downstream, leaving behind channels dominated by boulders, cobbles, and bedrock (Pike 2007). The freshwater fauna are well-adapted to these high energy systems, with a
diadromous life history strategy and the capacity to rapidly recolonize streams at the
highest elevations (McDowall 2004, Covich 2006). In most streams on tropical islands,
biological communities are almost entirely composed of diadromous fishes, decapods,
and gastropods (McDowall 2004, Covich 2006). These organisms spend their larval life
stage in the ocean, migrate upstream as postlarvae, and either migrate to the ocean to
spawn or allow their eggs to wash downstream (McDowall 2004, Covich 2006).

Although diadromous shrimp have been well studied on the island of Puerto Rico
as part of the Long-Term Ecological Research program (Covich and McDowell 1996),
most of this research has been conducted within headwater streams protected by the
Luquillo Experimental Forest (but see Pringle 1997). Outside of the Luquillo
Experimental Forest, which protects the headwaters of nine watersheds in eastern Puerto
Rico from urban and agricultural development, logging, and hunting, most land has been
converted from forest to agricultural and urban uses (López et al. 2001). Densely
clustered human populations also result in high demands on water resources, with
approximately 70% of the water draining the Luquillo Experimental Forest diverted into
municipal water supplies before reaching the ocean (Crook et al. 2007). Studies at lower
elevations outside the Luquillo Experimental Forest may therefore change our
perspective of diadromous faunal communities in these rivers (Pringle 1997).

I aim to understand how the structure of riverscapes in Puerto Rico mediates
potential anthropogenic impacts, predator-prey interactions, and the migratory behavior
of a diadromous species. More specifically, I ask: (1) Do human activities alter
community structure in rivers with a strong, elevational gradient? (2) How do natural
barriers mediate predator-prey interactions? (3) How does the structure of river networks
influence postlarval shrimp migration and ultimately, distributions of adult shrimp? To answer these questions, I use a variety of approaches at different scales. I begin by developing empirical models based on field observations that predict the distributions of diadromous fishes and shrimps across two watersheds and assess whether roads and associated human activities alter community structure (Chapter 2). After finding that waterfalls impede the upstream migration of predatory fishes, but not shrimp (Chapter 2), I describe experiments in artificial and natural streams to investigate how waterfalls mediate predator-prey interactions between predatory fishes and a prey shrimp (Atya lanipes; Chapter 3). Lastly, I develop a series of nested models to examine how colonization of headwater streams by A. lanipes might influence patterns in adult shrimp distributions across a river network. More specifically, I model a variety of colonization scenarios based on hypotheses regarding how shrimp navigate river networks, including which branch they choose at a fork in the river and how far they migrate upstream, which depends on mortality and settling rates (Chapter 4).

LITERATURE CITED


CHAPTER 2

GEOMORPHIC BARRIERS STRUCTURE DIADROMOUS FAUNAL
COMMUNITIES IN TROPICAL ISLAND STREAMS

Abstract

Overlapping river and road networks provide a framework for studying the complex interactions between natural and social systems, with river-road intersections as focal areas of study. Roads alter the morphology of stream channels, provide easy access to streams by humans and non-native species, and guide the expansion of urban development. Here, we develop empirical models for streams in northeastern Puerto Rico to predict the distributions of diadromous fishes and shrimps and assess whether roads and associated human activities alter community structure. These species provide essential ecosystem services to Puerto Ricans who rely on streams for clean water and other services. We identified 24 sites that represent a range of river and road sizes across two watersheds that drain El Yunque National Forest in Puerto Rico. We collected information related to natural and anthropogenic features of the landscape. Using random forest models, we successfully predicted the distributions of 6 of 12 fish and shrimp species. The location of natural barriers and the size of stream pools were the most important variables for predicting these distributions. Predatory fishes were limited to areas in the river network below waterfalls, whereas the shrimp *Atya lanipes* (Atyidae) was present only above waterfalls. In general, shrimp species richness was greater above waterfalls. The fish *Awaous tajasica* was present in larger pools, whereas the shrimp

---

1 Coauthored by Catherine L. Hein, Andrew S. Pike, Juan F. Blanco, Alan P. Covich, Frederick N. Scatena, Charles P. Hawkins, and Todd A. Crowl
*Xiphocaris elongata* was present in smaller pools. Although urban and agricultural development in these watersheds was high enough to pose a threat to stream fauna, we found no indication that road crossings or urban and agricultural land cover influenced species occurrence. Several existing features of these watersheds and taxa may aid in fish and shrimp conservation. The headwaters are protected by El Yunque National Forest, connectivity within the river network has been maintained, high stream power washes out pollutants and sediments, and the diadromous life history of these organisms makes them resilient to pulsed disturbances.

**Introduction**

Linking natural and social systems within a common framework for environmental analysis requires an inter-disciplinary approach (Colwell 1998, Michener et al. 2001, Pickett et al. 2005, Liu et al. 2007). Overlapping river and road networks provide a meaningful template under which the physical, biological, and social elements of the landscape may be integrated. The road network is a conduit for the dispersal of people, providing easy access to rivers and guiding development as human populations expand outward from urban centers. Similarly, migratory fauna navigate through river networks, and materials such as sediments, organic material, and nutrients are transported downstream. We employed an analysis of river and road networks in Puerto Rico to conceptualize how the movement of people and the species they rely on for supplying essential ecosystem goods and services interact. The intersections of these networks are focal areas for study compared with similar aquatic habitats lacking road connections.
Direct connections between river and road networks have been widely studied in relation to physical and biological components of streams. Roads increase surface runoff, creating a more variable hydrograph and promoting hillslope erosion, thereby increasing sedimentation rates (Trombulak and Frissell 2000). By filling interstitial spaces, sedimentation can destroy habitat for some benthic organisms and can reduce oxygen diffusion into spawning beds of fishes (Binkley and Brown 1993, Welsh and Ollivier 1998). Roads are associated with agricultural and urban development, which cause significant declines in species diversity and increased runoff, sedimentation, and concentrations of nutrients and pollutants (Weaver and Garman 1994). Roads act as conduits for anglers and invasive species and focus the impacts of recreational uses of rivers (Trombulak and Frissell 2000). Culverts act as barriers to movement of stream fauna, particularly fishes (Trombulak and Frissell 2000).

Diadromous fauna in both tropical and temperate rivers may be especially sensitive to road building and other forms of development if connectivity between the ocean and headwater streams is not maintained. Unlike “habitat patches” in terrestrial systems, which may be colonized via many pathways, a single barrier in a river network may isolate an entire drainage area from the rest of the basin (Fagan 2002). Species that are confined to highly-disturbed streams at low elevations may disappear or have reduced abundances in these fragmented networks (McDowall 2007). Species that migrate through developed, lowland areas and spend the majority of their life cycle in headwater streams may also disappear if anthropogenic barriers impede or severely reduce migration (Benstead et al. 1999, Blanco and Scatena 2007). Anthropogenic barriers may be physical in nature (e.g., culverts, dams, water diversions, and channelized waterways).
or they may prevent passage via pollution, thermal barriers, or introduction of exotic predators (Blanco and Scatena 2006, Brasher et al. 2006, McDowall 2007).

Despite the large body of work documenting effects of roads on streams (Trombulak and Frissell 2000), few studies have been conducted in tropical regions (but see MacDonald et al. 2001, Blanco and Scatena 2005). Furthermore, few studies have been able to differentiate between anthropogenic and natural effects on species assemblages in systems in which land use is strongly confounded with natural gradients. In many mountainous landscapes, forests are concentrated on steep terrain and farms and cities lie in the valleys (Allan 2004, Brasher et al. 2006). Van Sickle (2003) and Allan (2004) warn against collinearity between land use and natural gradients when trying to understand species distributions across landscapes.

The island of Puerto Rico provides an excellent location to study the interactions between humans and the environment among intersecting river and road networks. Nearly all of the non-insect, stream fauna have a diadromous life cycle, migrating through a dense river network over steep terrain (Blanco and Scatena 2006, 2007, Kikkert et al. 2009). Waterfalls limit the upstream extent of fishes and provide upstream refugia from predation for particular prey species (Covich et al. 2009). At 438 people per km$^2$, Puerto Rico also has one of the highest population densities on the planet. Extensive road building has occurred, with high road densities in watersheds of northeastern Puerto Rico. Although El Yunque National Forest protects the headwaters of nine watersheds from urban and agricultural development, logging, and hunting, the extent and intensity of urban development continues to expand outside forest boundaries (López et al. 2001, Lugo et al. 2004). Densely clustered human populations also result in high demands on
water resources (U.S. Census Bureau 2007). Approximately 70% of the water draining El Yunque National Forest is diverted into municipal water supplies before reaching the ocean (Crook et al. 2007). Because economies in other parts of the developing world are expected to shift from agrarian to industrial bases, similar increases on water demand and potential degradation can be expected to occur (Berry 1990, Millennium Ecosystem Assessment 2005, Shaw 2005). If these trends are ubiquitous throughout the Caribbean, tropical diadromous species may be more imperiled than current management plans anticipate.

Our goals in this study were to 1) assess whether roads and associated human activities alter the community structure of diadromous fishes and shrimps in two watersheds in northeastern Puerto Rico, and 2) differentiate anthropogenic effects from natural patterns in community structure related to the steep gradient of these watersheds. If particular road crossings cause high levels of bank erosion, sensitive taxa should be absent at these individual river-road nodes. If culverts act as physical barriers, species deletions should occur above road crossings. Conversely, we might observe species deletions from reaches at low elevations if urban and agricultural land covers alter habitat and water quality downstream. We used a variety of variables representing natural (e.g., waterfalls, pool morphology, streambed grain size) and anthropogenic (e.g., number of downstream road crossings, urban and agricultural land covers, fine sediments) features of the landscape to predict individual species distributions. We also used non-metric multidimensional scaling to look for patterns in fish and shrimp community structure.
Methods

Study Area and Fauna

From June to August of 2005, we sampled two watersheds that drain the steep terrain of the Luquillo Experimental Forest, an 11,000 ha reserve in northeastern Puerto Rico also known as El Yunque National Forest, and previously as the Caribbean National Forest (18°18’N, 65°47’W). Both the Espíritu Santo and Mameyes Rivers are steeply sloped drainages and drop approximately 950 m over a 16 to 19 km distance to the ocean (Pike 2007, Fig. 2-1). Headwater stream flow is highly variable and responds rapidly to rainfall, which averages 3600 mm per year (Covich et al. 2006). The mean annual discharge of the two watersheds is similar: 1.7 m$^3$s$^{-1}$ in the Espíritu Santo (U.S. Geological Survey (USGS) station number 50063800, gauged drainage area 22.3 km$^2$, period of record 1994-2002) and 1.5 m$^3$s$^{-1}$ in the Mameyes (50065500, 17.8 km$^2$, 1991-2004). The peak discharge recorded at each of these gauge stations was 600 m$^3$s$^{-1}$ in the Espíritu Santo (1966-2004) and 580 m$^3$s$^{-1}$ in the Mameyes (1969-2003; http://nwis.waterdata.usgs.gov/nwis).

Six species of native, diadromous freshwater fish reside in these watersheds: mountain mullet (Agonostomus monticola), bigmouth sleeper (Gobiomorus dormitor), spinycheek sleeper (Eleotris pisonis), American eel (Anguilla rostrata), river goby (Awaous tajasica), and Sirajo goby (Sicydium plumieri). All are predators except the Sirajo goby, which consumes algae and other plant material (Erdman 1986). Most native fishes are catadromous, spending their adult life in rivers and migrating to the estuary for breeding and larval development. Both gobies and all shrimp species are amphidromous: they spend adulthood in the headwaters and their eggs get washed to the estuaries.
(Covich and McDowell 1996). Five species of atyid shrimp live in these streams: *Atya lanipes*, *A. innocuous*, *A. scabra*, *Micratya poeyi*, and *Xiphocaris elongata*. *Xiphocaris spp.* are mainly detritivores (Crowl et al. 2001, Crowl et al. 2006); *Atya spp.* have modified chelae that they use to filter feed and scrape algae (Covich and McDowell 1996). Five species of predatory palaemonid shrimp inhabit these streams: *Macrobrachium carcinus*, *M. crenulatum*, *M. heterochirus*, *M. faustinum*, and *M. acanthurus*. *Macrobrachium spp.* have large chelae and consume shrimp, aquatic insects, mollusks, small fish, algae, macrophytes, and decomposing leaf litter (Crowl and Covich 1994, Covich and McDowell 1996).

**Biotic Sampling**

In 2005, we sampled 24 sites within the Espíritu Santo and Mameyes watersheds associated with road/trail networks (Fig. 2-1) to determine impacts of recreational uses of the rivers. Four sites were associated with hiking trails, one site was contiguous with a road, and the remaining sites were at river-road crossings that represented a range of combinations of road size, stream size, and level of recreational use. At each site, we sampled at least three and usually four pools for a total of 88 pools across all study sites.

We used a combination of snorkeling, electrofishing, and trapping to sample the fishes and shrimps in each pool. When water was clear, two people snorkeled pools deep enough to swim (> 0.5 m). Two people backpack electrofished pools and adjacent riffles in a single pass moving upstream. Because large pools were too deep to electrofish, adjacent riffles provided the most complete fish species occurrence data. We used three types of traps to sample all pools at all sites: wire-mesh Gee minnow traps (Cuba
Specialty Mfg. Co., Inc. Fillmore, New York) with a 3-cm diameter opening, modified Gee minnow traps with a 5-cm diameter opening, and large cylindrical traps (35-cm diameter, 65-cm long) with a 13-cm diameter opening. We scaled trap effort to pool size with one of each type of trap set in small pools (< 30 m$^2$), three of each type of minnow trap and two large traps set in medium pools (30-200 m$^2$), and five of each type of minnow trap and two large traps set in large pools (> 200 m$^2$). Each trap was baited with 22-g of dry pellets (cat food) and set over night. Larger traps were used because they are better suited for capturing large Macrobrachium spp. observed to occur in all sizes of pools.

Because of the range in sampling methods and sampling intensity across stream sizes, our analyses focused on species presence/absence (incidence functions) rather than relative abundance. We modeled the presence and absence of 12 shrimp and fish species across both watersheds. Although there are ten shrimp species, four (Atya scabra, Atya innocuous, Micratya poeyi, and Macrobrachium acanthurus) were not efficiently sampled. Both A. scabra and A. innocuous were primarily captured while electrofishing riffles with few observed in pools. Micratya poeyi were smaller than the mesh size of our traps and dip nets. Macrobrachium acanthurus were only observed at two, low elevation sites. To further reduce the likelihood of incorrectly classifying a species as absent, we aggregated the three to four pools sampled at a site for our model predictions.

**Predictor Variables**

We used a Geographic Information System (GIS) to generate a suite of variables for each site where we sampled fishes and shrimps (Table 2-1). We used road and
hydrographic data (USGS Digital Line Graphs, attributes correspond to USGS National Mapping Program Standards), land cover data (Gónzalez Ramos 2001), and a 10 x 10 m digital elevation model (Pike 2007) to calculate a number of natural and anthropogenic features of the landscape that might affect community structure. As a proxy for waterfalls, we calculated the greatest downstream vertical drop over a 10 m distance based on a 10 m digital elevation model (Pike 2007). Though direct measurements of waterfall height were available in some areas (Pike 2007), this calculation was more generally applicable to other watersheds. We calculated the land cover (percent urban, agricultural, or forest) within the upstream drainage area (Sherrill 2006), and counted the number of road crossings downstream from each site, which may also act as barriers to migratory fauna. Variables derived from field surveys provided measures of pool morphology and substrate (Table 2-1). Pike (2007) describes the methodology for the geomorphic surveys in detail. We averaged the pool morphology and grain size variables across pools within each site.

The predictor variables are highly correlated with one another. The steep gradient of these watersheds constrains the geomorphic properties of the stream channel and the spatial arrangement of land development. The slope of the channel increases rapidly at approximately 12 to 14 km inland (Pike 2007). With this increase in slope, streambed grain size increases and pool lengths and widths decrease (Pike 2007). Urban and agricultural development is primarily limited to lower elevations below the boundaries of El Yunque National Forest. The mean elevations of urban, agricultural, and protected forest lands within these watersheds are 53, 63, and 486 m above sea level (a.s.l.),
respectively. Thus, there is a distinctive physical template upon which species and land
covers are distributed.

To reduce collinearity among the predictors, we selected a subset of the variables
that were not highly correlated with one another (Table 2-1). Pearson correlation
coefficients (rho) were calculated between predictor variables. We retained variables that
represented landscape position, anthropogenic stressors, pool size, and grain size. When
several variables described a similar phenomenon (e.g., elevation, distance from ocean,
and greatest downstream vertical drop were measures of landscape position), we chose
the variable that would be most ecologically interpretable and transferable.

**Statistical Analyses**

To predict species distributions, we used both random forests and classification
trees because they make no assumptions about data distributions or the shape of response
relationships (Guisan and Zimmermann 2000, De’ath and Fabricius 2000, Breiman
2001), and they often outperform more traditional approaches (Olden and Jackson 2002,
Cutler et al. 2007). Random forests are a collection of hundreds of classification trees,
with each tree based on a bootstrap sample of the data and each split of the tree offered a
subset of the predictors (Breiman 2001). Each tree gets one vote for the out-of-bag
observations (those not used in the training data set), and the collection of votes gives the
forest class prediction for an individual observation. Unlike classification trees, random
forests cannot be over-fit and are especially useful when there are few sample sites and
many possible predictors (Breiman 2001). However, ecological interpretation of random
forest models is more difficult than that of a single classification tree. The importance of
individual predictor variables is ranked using various indices (Breiman 2002), with the most important variables closer to the tree roots. However, the combinations of tree splits and the break point values of individual predictors are not specified as in classification trees.

We used the randomForest library (Liaw and Wiener 2002) in the R statistical package (R Development Core Team 2005) to develop individual species distribution models and then examined the variable importance plots of moderate to high performing models. We used four metrics to assess model performance: 1) percent of presences correctly classified (sensitivity), 2) percent of absences correctly classified (specificity), 3) percent of all observations correctly classified (PCC), and 4) Cohen’s kappa, which corrects for chance when measuring agreement between predicted and actual class assignments (Manel et al. 2001, Cutler et al. 2007). Because species prevalence influences the values of the first three metrics but not the fourth (Manel et al. 2001, Olden et al. 2002), we used kappa to evaluate model performance, retaining moderate (0.4 - 0.6) to very high (0.8 - 1.0) performing models for further analysis (Manel et al. 2001). We used the Gini index of variable importance for our analyses (Breiman 2002, Cutler et al. 2007), with higher values indicating greater importance. To understand how the single most important variable influenced each species distribution, we created classification trees for the six species with the highest performing random forest models. We used the tree library (Ripley 1996) in the R package to carry out the classification tree analyses (Breiman et al. 1984). Because secondary splits did not improve prediction (the same class was predicted at both leaves), we pruned all trees to one split.
To understand how the fish and shrimp community structure varied across sites, we ordinated all species presence/absence data with non-metric multidimensional scaling (NMDS) in PC-ORD (McCune and Mefford 1997). We used the Sorenson distance matrix. Two pairs of sites had the exact same community assemblage, so the distances between these pairs of sites were zero. We eliminated one of these sites from analysis because NMDS does not allow null values in the distance matrix. We chose NMDS over other ordination approaches because it does not assume linear relationships, uses rank distances, and is generally recommended for analyses on ecological communities (McCune and Grace 2002).

Results

Incidence Functions

Natural variables were most important for predicting the distributions of two shrimp and four fish species (Fig. 2-2). The greatest downstream vertical drop was most important for predicting distributions of *A. lanipes* and the fishes *A. rostrata*, *A. monticola* and *G. dormitor* (Fig. 2-2). *Atya lanipes* was only present at high elevations above waterfalls, whereas the fishes were only present below these points in the river network (Table 2-2). These four species shared the same threshold in greatest downstream vertical drop, which was 3.5 m (Table 2-2). Base flow pool width was the most important predictor for the distributions of one shrimp and one fish species (Fig. 2-2). *Xiphocaris elongata* was predicted to be present in pools less than 10.4 m wide, whereas *A. tajasica* was predicted present in pools larger than 11.6 m wide (Table 2-2).
Anthropogenic variables were among the three most important variables predicting five species distributions (Fig. 2-2), but predicted incidence patterns counter to those hypothesized. We hypothesized species absences at sites downstream from urban and agricultural lands. Classification tree models based on a single land-cover-variable predicted the fishes *A. rostrata*, *A. monticola*, and *G. dormitor* to be present at sites downstream from catchments composed of more than 0.05 – 0.8% urban land cover or 2 – 4.8% agricultural land cover. Similarly, we expected species absences to occur upstream from road crossings. Counter to our hypothesis, *Xiphocaris elongata* were predicted to be present at sites upstream from more than two road crossings. Models of *A. lanipes’* distribution did fit our expectation, with this shrimp species predicted to be absent at sites with more than 0.8% urban or 2% agricultural land cover upstream. These models of *A. lanipes’* distribution misclassified two more sites than did the model based on greatest downstream vertical drop.

Anthropogenic variables were among the most important variables for predicting species distributions because they were highly correlated with the natural gradient. Both urban and agricultural land covers decreased with increasing elevation (rho = -0.60 and -0.52, respectively), and the number of downstream road crossings increased with distance from the ocean (rho = 0.45). Most natural barriers were near the boundaries of El Yunque National Forest. Therefore, break points near 0% urban or agricultural land in upstream catchments corresponded well with the location of waterfalls.

To differentiate anthropogenic effects from natural patterns in species distributions, we examined areas where the location of the forest boundary did not exactly match that of barriers to fish dispersal. Three sites within the forest boundary
were downstream from natural barriers, and one site downstream from the forest boundary, which contained 36% agricultural and 6% urban land in the upstream catchment, was upstream from a potential barrier to fishes (i.e., 4 m vertical drop as determined by GIS). If distribution patterns truly reflect natural dispersal abilities rather than anthropogenic effects, fishes should be present and *A. lanipes* should be absent from the three forest sites below natural barriers. This was the pattern observed, and these three sites were a common source of error for distribution models based on land cover. Furthermore, fishes should be absent and *A. lanipes* should be present at the site upstream from a natural barrier and downstream from urban and agricultural lands. This pattern was only partially true: *A. monticola* and *G. dormitor* were absent at this site, but *A. rostrata* was present and *A. lanipes* was absent.

Half of the random forest models performed moderately to excellently well, with kappa values greater than 0.5 and more than 80% of observations correctly classified (Table 2-3). We focused on the six best models for further analysis, interpreting variable importance plots and running classification trees with a single candidate predictor variable and one split (Table 2-2). The classification trees were very robust, with more than 91% of observations correctly classified and kappa values greater than 0.8 (Table 2-2).

However, six of the random forest models poorly predicted species presence/absence, with kappa values less than 0.27 (Table 2-3). These models had fairly high percentages of sites correctly classified as present or absent (50 to 83.3%), but these values were not higher than expected given the high prevalence of some species and low
prevalence of others (Table 2-2, Manel et al. 2001, Olden et al. 2002). For example, 95% of Eleotris pisonis absences were correctly classified, but only one of the four presences was correctly classified.

**Community Composition**

The most striking pattern in fish and shrimp community structure across the landscape was the distinction between sites with and without predatory fishes (Fig. 2-3). Shrimp species richness was higher at sites without predatory fishes (mean of 6.6 species compared to 3.5 species, post-hoc t-test, p<0.001). The vector representing the location of waterfalls (greatest downstream vertical drop) pointed toward the upper left corner of the ordination, perpendicular to the break between sites with and without predatory fishes. This pattern also shows that predatory fishes were absent at steep gradient, high elevation sites above waterfalls, whereas shrimp were present at these sites (Figs. 2-3, 2-4). All predatory fishes abruptly dropped out of the stream community at approximately 12 km from the ocean, which was within the range of distances (9 – 14 km) where the stream gradient rapidly increases (Fig. 2-4). Most predatory fishes were limited to elevations below 270 m a.s.l., but A. monticola were observed at one site 380 m a.s.l. The only herbivorous fish (S. plumieri) was present at sites ranging from the highest to lowest elevations (Fig. 2-4). Below barriers to predatory fishes, decapod species richness declined with increasing pool width (Fig. 2-3). Only M. carcinus or M. faustinum were present at the two sites with the widest pools to the far right of the plot (Fig. 2-3).
Discussion

The Espíritu Santo and Mameyes are relatively healthy river systems in terms of water quantity, quality, and their diadromous faunal communities. The Río Mameyes is one of the few free-flowing rivers on the island and was recently designated as a Wild and Scenic River under the U.S. National Wild and Scenic River System (Ortiz-Zayas and Scatena 2004). Compared to 14 other watersheds across the island, some of which have very poor water quality, the Río Espíritu Santo is classified as a densely forested watershed with good water quality (Santos-Román et al. 2003). Furthermore, nutrient concentrations do not differ with elevation in the Río Mameyes (Ortiz-Zayas et al. 2005). Compared to other watersheds with high head dams, few exotic species have been introduced and abundant, native taxa inhabit the Espíritu Santo and Mameyes watersheds (Blanco and Scatena 2006, Greathouse et al. 2006). Given the high levels of human activities in these watersheds, we were surprised that we did not find anthropogenic effects on fish and shrimp communities. The levels of urban development in the Espíritu Santo (21%) and Mameyes (18%) watersheds (based on land cover data from Gónzalez Ramos 2001) were higher than levels of development (8 – 15%) in other locations worldwide where urbanization has been associated with declines in the abundance and diversity of stream organisms (Limburg and Schmidt 1990, Booth and Jackson 1997, Paul and Meyer 2001, Riley et al. 2005, Stanfield et al. 2006).

The steep gradient, intense rainfall, and extended duration of storms make river networks in northeastern Puerto Rico fairly resilient. At mid elevations, steep slopes combined with high discharge result in high stream power and stable substrates dominated by boulders (Pike 2007). Pollutants would rapidly be diluted and sediment
loads would be carried downstream. Therefore, particular road crossings did not cause local species deletions by increasing erosion and fine sediment deposition, as has been documented in other systems (Bilby et al. 1989, Wemple et al. 2001, Angermeier et al. 2004). Effects of erosion on bank stability and fish and shrimp habitat were observed at a few road crossings that used culverts on alluvial substrates (Sherrill 2006), but these habitat alterations were of limited downstream extent and were not associated with changes in species composition. Similarly, alterations to streams associated with urban and agricultural lands did not influence species distributions. However, between 1830 and 1950, most land was cleared for agriculture; high erosion rates resulted in coarse sediment deposits that still remain in the lower reaches of rivers running through alluvial valleys (Clark and Wilcock 2000). Currently, forest covers the headwaters and steeply-sloped mid-elevation areas of these watersheds, thereby minimizing input of coarse sediment. Puerto Rico is prone to landslides (Larsen and Simon 1993, Larsen and Torres-Sanchez 1998). Although our study did not document landslide effects, many landslides occur near roads and other construction (Larsen and Simon 1993, Larsen and Torres-Sanchez 1998) and greatly increase local sediment loading.

Contrary to our second hypothesis, repeated road crossings did not inhibit upstream migration. The number of downstream road crossings was potentially important for predicting the distribution of X. elongata (Fig. 2-2), but when modeled, predicted presences rather than absences upstream from multiple road crossings. In the Espíritu Santo and Mameyes watersheds, culverts are primarily limited to small river-road crossings at high elevations above waterfalls. Although culverts often limit dispersal of fishes (Trombulak and Frissell 2000), five of eight culverts at our sites were located
above waterfalls where fish cannot gain access. Shrimp can climb waterfalls and also pass through most culverts. Road crossings at most of the low elevation sites are pylon bridge structures that have free flowing water beneath and do not obstruct fish or shrimp passage. Thus, these roads did not pose artificial barriers to movement of diadromous fauna and only diverted the flow.

In Puerto Rico, the diadromous life history of shrimps and fishes make them resilient to pulsed human disturbances. These species are adapted to a high natural disturbance regime, with hurricanes of magnitude similar to Hurricane Hugo every 60 years (Lugo 2000) and frequent flooding year round (http://nwis.waterdata.usgs.gov/nwis). They have the ability to find refugia during storm events and/or rapidly recolonize, enabling recovery after severe declines. For example, some people have used chlorine bleach to harvest shrimp in headwater streams, killing all shrimps within approximately a 500 m reach (Greathouse et al. 2005). Three months after one particular bleaching event, Greathouse et al. (2005) found complete recovery of the palaemonid and xiphocarid populations and nearly complete recovery of the atyid populations. These species demonstrate the ability to rapidly colonize and recover from pulsed disturbances. However, if connectivity between larval and adult habitats is broken by poorly designed, high dams (i.e., without spill water and effective by-pass structures) or other barriers (e.g., exotic species invasions and water withdrawal), diadromy will no longer be advantageous and species extirpations may occur.

In high-gradient river networks dominated by diadromous fauna, the location of natural barriers (i.e., waterfalls) is critical for understanding patterns in community structure. For example, fish communities in New Zealand rivers, which are dominated by
diadromous species, are best explained by the location of barriers and the swimming or climbing ability of individual taxa (Hayes et al. 1989, McDowall 1998). Like fishes in many other systems (Townsend and Crowl 1991, Gilliam et al. 1993, Power and Dietrich 2002), the ranges of three predatory fishes in Puerto Rico were limited to stream reaches below waterfalls (Table 2-2, Figs. 2-3, 2-4). Our models indicated that a 3.5 m vertical drop within a 10 m distance best predicted these species’ distributions. Although this GIS-derived proxy for waterfall location performed well, A. monticola and A. rostrata were each found at one site above a 3.5 m drop, indicating that one must know the specific structure of steeply-sloped channels to accurately place all natural barriers. Unlike the three predatory fishes discussed, one goby (Sicydium plumieri) and nearly all shrimps can surpass waterfalls (Fig. 2-4). Sicydium plumieri has modified pelvic fins that form a suction cup and allow this gobiid fish to climb vertical cliffs (Erdman 1986).

By excluding predatory fishes, waterfalls may provide upstream refugia to freshwater shrimps. Waterfalls can limit the dispersal of predators and competitors and provide refuge for poor competitor and prey species (Townsend and Crowl 1991, Feminella and Hawkins 1994, Brasher et al. 2006). Released from their competitors, predators, and parasites, organisms that have the ability to access these headwater reaches should be much more abundant than they are downstream (Power and Dietrich 2002, Creed 2006). We observed this pattern in Puerto Rico, with greater shrimp species richness above waterfalls (Figs. 2-3, 2-4). Higher A. lanipes abundance in fishless streams also occurs in streams within the Espiritu Santo and Mameyes watersheds that have been monitored since 1987 (Covich et al. 2009). Shrimps may avoid fish predation
by migrating above barriers to fish dispersal and by altering their morphology where fish are present (*sensu* Townsend and Crowl 1991, Godin and McDonough 2003).

*Atya lanipes* may be more vulnerable to fish predation than other species, but predatory mechanisms have not been explicitly tested. *A. lanipes* is relatively small (4-28 mm carapace length (CL)), lacks morphological defenses, and perches on top of rocks or logs to filter feed (Chace and Hobbs 1969, Cross et al. 2008, Covich et al. 2009). Other shrimp species shared part of their range with predatory fishes and may not be as vulnerable to fish predation (Fig. 2-4). *Xiphocaris spp.* is also fairly small (8-28 mm CL), but its long, sharp rostrum and transparent body may aid in avoiding predation (Chace and Hobbs 1969, Covich et al. 2009). Most adult *Macrobrachium spp.* are relatively large (40-99 mm maximum CL across species) and they all have chelae that can be used to defend against predatory fishes (Chace and Hobbs 1969).

Although species abundance patterns may have been a more sensitive measure, disturbance in other mountainous landscapes has been shown to affect assemblage patterns based on presence/absence data. In Chile’s Biobío River, sewage and paper mill effluent inputs, hydropower plants, and irrigation diversions have severely reduced the water quality in the lower portions of the river drainage and extirpated native fishes that would otherwise be present at these sites (Habit et al. 2006). In Hawaii, exotic fishes have excluded native fishes from sites low in the river drainage (Brasher et al. 2006). Like our analysis of shrimp presence/absence, shrimp abundance was also best predicted by natural factors in the Espíritu Santo and Mameyes watersheds (Pike 2007, Covich et al. 2009).
More severe human activities (e.g., high head dams, exotic species introductions, and high rates of water withdrawal) would likely result in species extirpations from portions of the Espíritu Santo and Mameyes watersheds. The low head dam on the Espíritu Santo River is not a barrier to fish or shrimp passage, but a large percentage of larval shrimp drifting downstream are entrained by the water intake structure (Benstead et al. 1999). On average, 42% of first-stage larvae die due to entrainment, and 100% of larvae are entrained during low flow (Benstead et al. 1999). Still, we observed high abundances of shrimps in headwater streams of the Espíritu Santo watershed. Elsewhere on the island, high head dams without spill water eliminate all native fishes and shrimps upstream, and shrimp are very rare in streams above large dams with spill water (Holmquist et al. 1998, Greathouse et al. 2006).

Water withdrawal for human use could also threaten diadromous fauna if flows are reduced below a critical level (Scatena and Johnson 2001, Pringle 1997). Extremely low stream flow reduces habitat and resource availability, disconnects migratory pathways as streams dry, and reduces the reproductive rate of shrimp as competition increases and mortality during migration increases (Covich et al. 2003). Although these effects were documented during drought periods, similar effects might occur in response to water withdrawal for human uses (Covich et al. 2003). The water supply system is already in deficit with two new regional aqueducts under development and increasing water demands as the human population grows (Ortiz-Zayas and Scatena 2004). The human population surrounding El Yunque National Forest increased by 37% from 1980-2000 (Ortiz-Zayas and Scatena 2004) and is predicted to continue growing at a similar
rate or faster through 2025 (Puerto Rico Planning Board 1995, Ortiz-Zayas and Scatena 2004).

By considering expected and observed fauna on a site-specific basis, we were able to tease out the otherwise confounding effects of natural gradients and land use. Fishes were present at three forested sites below barriers. If these fishes were only present in streams altered by human activities, we would not expect them to be present at high-elevation sites within El Yunque National Forest. If *A. lanipes* were not influenced by the distribution of predatory fishes, then they should have been present at the three forested sites below barriers. Although *A. lanipes* were absent at the agricultural site above a fish barrier, this site did contain American eels. To assess whether urban and agricultural development could cause extirpations of this shrimp species, one would need to survey developed sites above barriers to all predatory fishes.

We also highlight our method of using random forest models to predict species distributions and classification trees to interpret the variables that were most important for the random forest models. We warn that the variable importance metric could be misleading if the specific relationship between the response and predictor variable is not investigated further. For example, we may have erroneously concluded that urban and agricultural land covers impacted the three fish distributions had we not observed that these fishes were present at sites downstream from developed land.

Although all diadromous fauna in northeastern Puerto Rico, except *A. lanipes*, are widespread throughout the West Indies, and some distributions even include parts of North, Central, and South America (Chace and Hobbs 1969, Robins and Ray 1986, McDowall 1988, Page and Burr 1991, Harrison 1995, Bowles et al. 2000), species
extirpations may accumulate regionally and result in risk of extinction. Similar trends of urban development and human population growth are occurring worldwide (Millennium Ecosystem Assessment 2005), but if urban growth is planned carefully to avoid fragmenting river corridors, diadromous fauna may still be conserved. On islands where surface waters provide the only freshwater resources, conserving the habitats and organisms that provide clean water is especially important. Most freshwater fauna that inhabit tropical island streams are diadromous, and these organisms, particularly atyid shrimps, influence ecosystem processes such as sedimentation, nutrient cycling and leaf decomposition (Pringle et al. 1999, March et al. 2002, Greathouse et al. 2006). The Espiritu Santo and Mameyes Rivers provide hope that human development can occur while maintaining native diversity, and in turn, the ecosystem processes they influence.

Literature Cited


Bilby, R. E., K. Sullivan, and S. H. Duncan. 1989. The generation and fate of road-
surface sediment in forested watersheds in southwestern Washington. Forest
Science 35:453-468.

Binkley, D., and T. C. Brown. 1993. Forest practices as nonpoint sources of pollution in

Blanco, J. F., and F. N. Scatena. 2005. Floods, habitat hydraulics and upstream migration
of *Neritina virginea* (Gastropoda: Neritidae) in northeastern Puerto Rico.

connectivity, water chemistry, hydraulics and substrate to the distribution of
diadromous snails in Puerto Rico streams. Journal of the North American
Benthological Society 25: 82-98.

Blanco, J. F., and F. N. Scatena. 2007. Hydraulics and spatial arrangement of neritid
snails (*Neritina virginea*, Gastropoda: Neritidae) during upstream migration under

thresholds, stormwater detection, and the limits of mitigation. Journal of the
American Water Resources Association 33:1077-1090.

Palaemonidae) in the contiguous United States: a review of the species and an


Michener, W. K., T. J. Baerwald, P. Firth, M. A. Palmer, J. L. Rosenberger, E. A.


Pike, A. P. 2007. Longitudinal patterns in stream channel geomorphology and aquatic
habitat in the Luquillo Mountains of Puerto Rico. University of Pennsylvania,
Philadelphia, USA.

Research 17:451-471.

Pringle, C. M. 1997. Exploring how disturbance is transmitted upstream: Going against

Linking species and ecosystems: different biotic assemblages cause interstream

Area de Planificación Económica y Social (San Juan: Oficina del Gobernador).

R Development Core Team. 2007. R: A language and environment for statistical

distribution and abundance of amphibians and invasive species in southern

Press, Cambridge, UK.

America. Houghton Mifflin Company, Boston, Massachusetts, USA.


Table 2-1. Potential predictor variables used in the random forest modeling.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Median value</th>
<th>Range of values</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Derived from GIS</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>greatest downstream vertical drop*</td>
<td>3.5 m</td>
<td>0.1 - 9 m</td>
</tr>
<tr>
<td>urban (upstream drainage)</td>
<td>0.1%</td>
<td>0 – 17%</td>
</tr>
<tr>
<td>agriculture (upstream drainage)</td>
<td>0%</td>
<td>0 – 76%</td>
</tr>
<tr>
<td>number of downstream road crossings</td>
<td>4</td>
<td>1 – 9</td>
</tr>
<tr>
<td><strong>Derived from geomorphic field surveys</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>base flow channel width</td>
<td>7.1 m</td>
<td>2.2 – 22.3 m</td>
</tr>
<tr>
<td>coefficient of variation of depth</td>
<td>0.36</td>
<td>0.21 – 0.65</td>
</tr>
<tr>
<td>median grain size (d50)</td>
<td>131.8 mm</td>
<td>13.4 – 1327.2 mm</td>
</tr>
<tr>
<td>bedrock</td>
<td>7%</td>
<td>0 – 53%</td>
</tr>
<tr>
<td>cobble</td>
<td>21%</td>
<td>6 – 40%</td>
</tr>
<tr>
<td>fine sediment</td>
<td>0.1%</td>
<td>0 – 40%</td>
</tr>
</tbody>
</table>

*see definition in methods section
Table 2-2. Classification trees built using the most important predictor variable as determined by random forest models (see Fig. 2-2). Classification trees were only built for those species whose random forest models performed moderately to very well (kappa ≥ 0.5). The split indicates the conditions necessary for the species to be present. ‘Sens’ refers to the sensitivity of the model (percent of presences correctly classified), ‘Spec’ is the specificity of the model (percent of absences correctly classified), ‘PCC’ is the overall percent of observations correctly classified, and ‘Kappa’ is a measure of agreement between predicted and actual class assignments that corrects for chance.

<table>
<thead>
<tr>
<th>Species</th>
<th>Split</th>
<th>Sens</th>
<th>Spec</th>
<th>PCC</th>
<th>Kappa</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Atya lanipes</em></td>
<td>Drop ≥ 3.5</td>
<td>100.0</td>
<td>92.3</td>
<td>95.8</td>
<td>0.917</td>
</tr>
<tr>
<td>Anguilla rostrata</td>
<td>Drop &lt; 3.5</td>
<td>92.3</td>
<td>100.0</td>
<td>95.8</td>
<td>0.917</td>
</tr>
<tr>
<td>Agonostomus monticola</td>
<td>Drop &lt; 3.5</td>
<td>92.3</td>
<td>100.0</td>
<td>95.8</td>
<td>0.917</td>
</tr>
<tr>
<td>Gobiomorus dormitor</td>
<td>Drop &lt; 3.5</td>
<td>100.0</td>
<td>85.7</td>
<td>91.7</td>
<td>0.833</td>
</tr>
<tr>
<td>Awaous tajasica</td>
<td>Pool width &gt; 11.6</td>
<td>75.0</td>
<td>100.0</td>
<td>91.7</td>
<td>0.800</td>
</tr>
<tr>
<td><em>Xiphocaris elongata</em></td>
<td>Pool width &lt; 10.4</td>
<td>88.9</td>
<td>100.0</td>
<td>91.7</td>
<td>0.800</td>
</tr>
</tbody>
</table>

* denotes a shrimp species
Table 2-3. Accuracy measures for fish and shrimp species presence/absence random forest models. There were a total of 24 sites. Model ‘sensitivity’ is percent of presences correctly classified, ‘specificity’ is the percent of absences correctly classified, ‘PCC’ is the overall percent of observations correctly classified, and ‘Kappa’ is a measure of agreement between predicted and actual class assignments that corrects for chance.

<table>
<thead>
<tr>
<th>Species</th>
<th>Observed Presences</th>
<th>Sensitivity</th>
<th>Specificity</th>
<th>PCC</th>
<th>Kappa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atya lanipes*</td>
<td>11</td>
<td>90.9</td>
<td>100.0</td>
<td>95.8</td>
<td>0.915</td>
</tr>
<tr>
<td>Anguilla rostrata</td>
<td>13</td>
<td>100.0</td>
<td>90.9</td>
<td>95.8</td>
<td>0.915</td>
</tr>
<tr>
<td>Agonostomus monticola</td>
<td>13</td>
<td>92.3</td>
<td>90.9</td>
<td>91.7</td>
<td>0.832</td>
</tr>
<tr>
<td>Gobiomorus dormitor</td>
<td>10</td>
<td>80.0</td>
<td>85.7</td>
<td>83.3</td>
<td>0.657</td>
</tr>
<tr>
<td>Awaous tajasica</td>
<td>8</td>
<td>62.5</td>
<td>93.8</td>
<td>83.3</td>
<td>0.600</td>
</tr>
<tr>
<td>Xiphocaris elongata*</td>
<td>18</td>
<td>94.4</td>
<td>50.0</td>
<td>83.3</td>
<td>0.500</td>
</tr>
<tr>
<td>Sicydium plumieri</td>
<td>17</td>
<td>82.4</td>
<td>42.9</td>
<td>70.8</td>
<td>0.263</td>
</tr>
<tr>
<td>Eleotris pisonis</td>
<td>4</td>
<td>25.0</td>
<td>95.0</td>
<td>83.3</td>
<td>0.25</td>
</tr>
<tr>
<td>Macrobrachium crenulatum*</td>
<td>10</td>
<td>60.0</td>
<td>64.3</td>
<td>62.5</td>
<td>0.239</td>
</tr>
<tr>
<td>Macrobrachium heterochirus*</td>
<td>9</td>
<td>22.0</td>
<td>66.7</td>
<td>50.0</td>
<td>-0.116</td>
</tr>
<tr>
<td>Macrobrachium carcinus*</td>
<td>20</td>
<td>90.0</td>
<td>0.0</td>
<td>75.0</td>
<td>-0.125</td>
</tr>
<tr>
<td>Macrobrachium faustinum*</td>
<td>20</td>
<td>90.0</td>
<td>0.0</td>
<td>75.0</td>
<td>-0.125</td>
</tr>
</tbody>
</table>

* denotes a shrimp species
Figure 2-1. Map of study sites in the Espiritu Santo and Mameyes watersheds, which drain El Yunque National Forest in northeastern Puerto Rico.
Figure 2-2. Variable importance plots of the four fish and two shrimp species (denoted with *) whose random forest models of presence/absence were robust (kappa ≥ 0.5). Note that axes are not constant across plots.
Figure 2-3. Non-metric multidimensional scaling plot of all sites in the Espiritu Santo and Mameyes watersheds. Each point represents the assemblage of fish and shrimp species at a site. Larger points indicate greater shrimp species richness, and the color of the point indicates the presence (black) or absence (white) of predatory fishes. Vectors represent the correlations of two environmental variables with the ordination; vector length is proportional to the strength of the interaction.
Figure 2-4. Distributions of fish and shrimp (*) species in relation to the elevation gradient. The upper plot shows the elevation and distance from the ocean of each site. Lines in the upper plot depict the connectivity of sites in the Mameyes (solid) and Espíritu Santo (dotted) watersheds. The filled circles in the lower plot depict the sites where each species was present.
CHAPTER 3

RUNNING THE PREDATOR GAUNTLET: DO FRESHWATER SHRIMP (*ATYA LANIPES*) MIGRATE ABOVE WATERFALLS TO AVOID FISH PREDATION?  

Abstract. Predation may be responsible for the disparate distributions observed between fish and shrimp in Puerto Rican streams. Adult shrimp (*Atya lanipes*) are only present above waterfalls that pose barriers to predatory fishes. Because we have not found *Atya* in fish stomachs, we believe that these amphidromous shrimp avoid predation by migrating to locations above waterfalls. We designed experiments in artificial, y-maze streams and in natural streams to test whether shrimp avoid predatory fishes. In artificial streams, adult shrimp avoided 2 fishes (*Gobiomorus dormitor* and *Agonostomus monticola*) whether or not they had recently consumed shrimp, but they only avoided eels (*Anguilla rostrata*) recently fed shrimp. Postlarval shrimp also avoided the scent of *G. dormitor* fed shrimp and crushed conspecifics. We then tested whether adult shrimp in 4, natural, headwater streams would redistribute if exposed to the chemical scent and/or the physical presence (a combination of visual, mechanical and chemical cues) of *G. dormitor*. We expected that shrimp from the manipulated pool would move upstream, resulting in increased emigration from and lower shrimp abundance in the manipulated pool. Shrimp abundances did not decline significantly in the pool where fish scent was added, but abundances did decline significantly in the same pools when fish were added to in-stream cages. Emigration from the manipulated pool also increased, but the change was not statistically significant. Reduced abundances could also result from emigration to pools beyond our study reaches or reduced activity levels within manipulated pools. Our

---

2 Coauthored by Catherine L. Hein and Todd A. Crowl
study provides the first mechanistic evidence that predatory fishes alter the behavior of *Atya lanipes* and may be responsible for this species’ distribution across the landscape.

**Introduction**

Predation structures communities in a wide variety of ecosystems through both direct consumptive and indirect behavioral effects (Brooks and Dodson 1965, Paine 1966, Flecker and Allan 1984, Sih et al. 1985). By studying behavioral responses, scientists can identify the mechanisms at work and more fully understand why predators cause large declines in prey abundances in some instances but not in others. Although behavioral responses of prey were rarely studied 2 decades ago (Sih et al. 1985), more recent work highlights nonconsumptive effects of predators, including changes in life history strategies (Crowl and Covich 1990, Reznick et al. 1997, Peckarsky et al. 2002), morphological defenses (Dodson et al. 1994, Kats and Dill 1998), emigration rates from predator patches, activity levels, and use of refugia (Sih et al. 1992, Crowl and Covich 1994, Feminella and Hawkins 1994, Sih and Wooster 1994, Englund 1999, Gilliam and Fraser 2001, McIntosh et al. 2002).

Prey are rarely able to achieve complete segregation from their predators, causing prey to seek temporal or spatial refuge within the same lake or stream reach. For example, when fish are present, mayfly larvae drift at night (Flecker 1992), crayfish hide under rocks or logs (Stein and Magnuson 1976), and minnows move from deep to shallow water in stream pools (Power et al. 1985). However, isolated lakes and stream reaches above waterfalls often prevent colonization by predatory fishes, thereby providing complete spatial refugia to organisms that can access these areas (Townsend...

Distinct community patterns across entire watersheds are often observed when waterfalls limit the distribution of predators. For example, introduced salmonids (*Salmo trutta, Oncorhynchus mykiss*) eliminate native *Galaxias vulgaris* from reaches below waterfalls in New Zealand (Townsend and Crowl 1991, McIntosh et al. 1992, Lintermans 2000). Tadpoles (*Ascaphus truei*) are limited to stream reaches above waterfalls due to predation by shorthead sculpin (*Cottus confuses*, Feminella and Hawkins 1994), and young-of-the-year crayfish (*Cambarus chasmodactylus*) are eliminated by rock bass (*Ambloplites rupestris*) in a fourth-order stream, but are abundant in its tributaries (Fortino and Creed 2007). Prey fish (*Rivulus hartii*) move into streamside, artificial tributaries with the addition of predatory fish (*Hoplias malabaricus*) to the main channel of a natural stream (Gilliam et al. 1993, Fraser et al. 1995). Conversely, when predatory fish are removed from the main channel of the natural stream, prey fish return to the main channel (Gilliam et al. 1993, Fraser et al. 1995).

In Puerto Rico, an adult freshwater shrimp (*Atya lanipes*) is only found in high-elevation streams above natural barriers to predatory fishes (Chapter 2). All freshwater fishes and shrimps inhabiting the watersheds in northeastern Puerto Rico have a diadromous life cycle, spending a portion of their larval stage in the ocean or estuarine environment and migrating upstream as postlarvae (Covich and McDowell 1996). Although mountain mullet (*Agonostomus monticola*), American eel (*Anguilla rostrata*),
and bigmouth sleeper (*Gobiomorus dormitor*) have the ability to migrate up fairly steep slopes, only freshwater shrimp and an herbivorous goby (*Sicydium plumieri*) climb over steep waterfalls (Chapter 2). We hypothesize that *A. lanipes* run the predator gauntlet, migrating upstream from the ocean as juveniles until they arrive at fishless reaches above waterfalls, which presumably provide greater survivorship and overall fitness.

Although others have arrived at the same hypothesis based on similar observations of disparate fish and shrimp distributions at waterfalls (Covich and McDowell 1996, Greathouse et al. 2006, Covich et al. 2009, Chapter 2), no one has experimentally tested whether *A. lanipes* abundances are greater above waterfalls due to lack of predation. Atyid shrimps dramatically declined in abundance when a predatory fish (*Kuhlia rupestris*) was added to stream reaches above waterfalls in Guam, but the authors were unable to distinguish whether behavioral responses or consumption by fish caused the decline (Leberer and Nelson 2001).

Although most predator-transplant experiments only test whether prey densities change (Schofield et al. 1988, Sih et al. 1992, Fraser et al. 1995, Englund 1999), a few transplant experiments do demonstrate changes in prey behavior (Sih et al. 1992, McIntosh et al. 1999) and life history strategies (Reznick et al. 1997, Peckarsky et al. 2002). Prey use a variety of visual, mechanical, and tactile cues to detect predators and modify their behavior (Dodson et al. 1994, Dicke and Grostal 2001). Two classes of chemical cues related to predation have been identified: kairomones and alarm cues (Dodson et al. 1994, Dicke and Grostal 2001). Kairomones are substances that come from one species (e.g., predator) and benefit the receiving species (e.g., prey), whereas alarm
cues warn conspecifics of danger and are generally released when an organism is injured or eaten (Dodson et al. 1994, Dicke and Grostal 2001).

To test whether fish predation drives the distribution of *Atya lanipes*, hereafter simply referred to as shrimp, we designed a series of experiments in artificial and natural environments to answer the following questions: 1) Do postlarval and adult shrimp chemically detect and avoid predatory fishes (bigmouth sleeper, mountain mullet, and American eel)? Do they respond equally to starved fish and to those recently fed shrimp? 2) If shrimp do detect and avoid their predators in the artificial environment, do adults also seek refugia by moving to a pool upstream when fish are added to natural, fishless streams? We tested the behavioral response of adults to the addition of fish chemical cues via streamside, flow-through tanks and to the addition of fish to in-stream cages, which exposed shrimp to a combination of visual, mechanical, and chemical cues. We expected a stronger behavioral response to the in-stream fish addition than to the addition of fish chemical cues alone. We monitored the abundance and movement of shrimp in 7 contiguous pools in each of 4 streams, enabling us to answer spatially specific questions, such as how far downstream shrimp respond to the predator addition.

**Methods**

**Study area**

Both the artificial and natural stream experiments took place in the Espíritu Santo watershed, which drains the Luquillo Experimental Forest (18°18’N, 65°47’W) in northeastern Puerto Rico. Abundant waterfalls and cascades characterize the rivers in this watershed as they drop from peaks greater than 1000 m above sea level (a.s.l.) over a 19-
km distance to the Atlantic Ocean (Pike 2007). Stream flow is highly variable and responds rapidly to heavy rainfall events; the discharge can increase 10-fold within 1 hour (Covich and McDowell 1996). Within the Luquillo Experimental Forest, the average annual rainfall is 3600 mm and is only slightly seasonal, with more rainfall from January through April (García-Martinó et al. 1996).

All freshwater shrimp, including *Atya lanipes*, are amphidromous: they spend adulthood in the headwaters and their eggs get washed to the estuaries. The postlarvae migrate from the ocean to headwater streams year round throughout the night (Kikkert et al. 2009). Most predatory fishes are catadromous: they also spend adulthood in the headwaters, but migrate to the estuary to spawn (Covich and McDowell 1996). Five of 6 fish species in this watershed consume shrimp: *Gobiomorus dormitor*, *Agonostomus monticola*, *Anguilla rostrata*, *Awaous tajasica*, and *Eleotris pisonis* (Aiken 1998, Nieves 1998). Because *A. tajasica* and *E. pisonis* are relatively small and *E. pisonis* is not widely distributed (Chapter 2), we limited our study to interactions between *A. lanipes* and the first 3 fishes listed above. Non-native fishes are rare in these watersheds, with only a few occurrences of *Oreochromis mossambicus* in the estuary and *Poecilia spp.* in freshwater (Smith et al. 2008, personal observation).

**Artificial stream experiment**

To test whether shrimp respond to kairomones and/or alarm cues, we exposed shrimp to water treated with: starved fish, fish fed shrimp, and crushed shrimp. We constructed a Y-maze fluvarium (Fig. 3-1) and observed shrimp behavior when exposed to fishless water flowing down one arm and treated water flowing down the other arm.
We expected shrimp to avoid the arm with treated water and expected no
differentiation between arms when fishless water flowed down both arms. We used rain
gutter materials to construct the channels of the fluvarium and glued Plexiglas reinforced
with wood onto each end. One tank (67-L volume) contained source water for the left
arm of the fluvarium and a 2nd tank contained source water for the right arm. Gravity-fed
water from a fishless, headwater stream flowed continuously through the source tanks
and into the fluvarium. We maintained equal discharges between both arms of the
fluvarium (~0.024 L sec⁻¹). Because shrimp are nocturnal, trials were run after dark. Dim
red lights evenly lit the fluvarium to allow visual observations.

We tested 8 treatments: starved predatory fishes (mountain mullet, bigmouth
sleeper, and eel), each fish species fed shrimp, crushed adult shrimp, and a control
(fishless stream water). We added approximately 200 g of fish (or shrimp) to 1 of the 2
tanks (determined by flipping a coin) 20 minutes before trials began. We starved fish for
2 days prior to the fish only treatments and fed fish both postlarval and small adult
shrimp for 2 days prior to the fish fed shrimp treatments. During the latter treatments, we
also added 50 postlarval shrimp and 10 small adult shrimp to the tank with fish, but fish
rarely ate shrimp during the trials.

We tested both postlarvae and adult shrimp, but treated each life stage separately.
We only exposed postlarvae to the bigmouth sleeper fed shrimp and crushed adult shrimp
treatments, but exposed adults to all treatments except the crushed adult shrimp
treatment. We netted postlarvae as they migrated up a reach of the Río Espíritu Santo that
contains predatory fishes, and trapped adults from a tributary of the Río Espíritu Santo
that does not contain predatory fishes. Migrating postlarvae are rare above fish barriers
(D. A. Kikkert, Utah State University, personal communication), and adults are rare below fish barriers (Chapter 2). We placed shrimp in a rectangular, holding pen (16.5 X 12.1 X 13.3 cm) at the bottom of the fluvarium for 1 minute (adults) or 0.5 minute (postlarvae). After removing the holding pen, we recorded the shrimp’s location (left arm, right arm, or bottom) at 30-second intervals for a total of 5 minutes. We removed the shrimp after a trial ended and repeated this process with 25 naïve individuals, allowing the water to flow continuously between trials.

We used individual G-tests for each treatment to determine whether shrimp spent different amounts of time in the arms with or without fish scent. We summed the total number of times shrimp were observed in each arm across all 25 individuals. During the control trials, adults spent an equal amount of time in each arm of the fluvarium, showing no inherent bias toward one arm of the fluvarium. Therefore, we compared the observed frequencies of each treatment to the expected under control conditions, with 50% of observations portioned to either arm. We also did a test for heterogeneity among the treatments that induced a significant behavioral response in adult shrimp (bigmouth sleeper + Attya, bigmouth sleeper, mullet + Attya, mullet, eel + Attya) to determine whether shrimp responded more strongly to particular treatments. Unlike adults, postlarval shrimp preferred one arm over the other during the control trials, so the expected value for each treatment was based on this proportion (69% of observations in one arm and 31% in the other).
Field experiment

The field experiments took place in 4 streams within the Espíritu Santo watershed; 2 were tributaries of the Espíritu Santo River (18°19’45.63” N, 65°49’15.88” W and 18°19’46.00” N, 65°49’15.88” W) and 2 were tributaries of Jimenez Stream (18°19.933 N, 65°46.956 W and 18°19.916 N, 65°46.857 W). All stream reaches occurred at approximately 300 m a.s.l. and were of similar size. The ranges of average pool lengths, widths, and depths within each stream were 2.8—3.8 m, 1.3—2.0 m, and 0.1—0.2 m, respectively. In hopes of minimizing the number of flood events during the manipulations, we conducted experiments from late March through early June of 2007.

To test whether adult shrimp avoided fish in the natural environment, we used a completely randomized block design under which we added bigmouth sleepers to 4 fishless streams and observed changes in shrimp abundances and movement patterns. This experiment included 3 periods: pre-manipulation, exposure to fish chemical cues (“chemical”), and exposure to in-stream fish (a combination of chemical, mechanical, and visual cues: “all”). During the pre-manipulation period in late March and early April, we sampled shrimp in each stream to determine baseline abundances and distributions. We added 2 fish (~193 g total) to streamside, flow-through tanks during the chemical period and added 1 fish (~130 g) to a cylindrical, wire mesh, in-stream cage (65-cm long and 35-cm diameter) during the all period. Each stream was manipulated (fish present) and served as a control (fish absent), but at alternating times. For 18 days beginning 19 and 20 April, water flowed through empty tanks in 2 streams (“chemical-absent”) and flowed through tanks containing fish in the other 2 streams (“chemical-present”). On 6 and 7 May, we switched which streamside tanks contained fish and continued running the
experiment for 24 days. For 5 days beginning 29 and 30 May, 2 streams contained in-stream cages with fish (“all-present”) while 2 streams served as controls (“all-absent”). Fish were moved to cages in the other 2 streams on 6 and 7 June and remained for 6 days. Thus, the treatments tested in this experiment were: pre-manipulation, chemical-absent, chemical-present, all-absent, and all-present (Fig. 3-2).

In each of the 4 streams, we located 7 contiguous pools; fish were added to the center pool (pool 0) with 3 pools upstream (pools 1, 2, and 3) and 3 downstream (pool -1, -2, and -3). The study reaches ranged in length from 68—94 m (Fig. 3-2). To add fish scent to the streams, we built gravity-fed, flow-through tanks. PVC elbows caught water beneath a small cascade; water flowed through PVC pipe (0.5-inch diameter) to the 80.75-L tank located on the stream bank and then flowed out of the tank through 3 garden hoses into the upstream end of pool 0. The average volume of water flowing through the tanks and into the streams was 0.35-L water per second. The volume of water flowing through the tanks fluctuated with stream discharge: less water flowed through the tanks during periods of low discharge, more water flowed through the tanks at high discharge, and, because the water collecting elbows were knocked out of place, no water flowed through tanks during flood events.

We used cylindrical, wire-mesh, Gee-minnow traps (Cuba Specialty Mfg. Co., Inc. Fillmore, New York) with a 3-cm diameter opening to sample shrimp in each pool. We baited traps with 22-g of dry cat food and set them overnight at a density of 0.5 traps/m² of pool surface area. The relative abundance of shrimp was calculated as the total number of shrimp caught in a pool divided by the number of traps set in the pool.
We averaged catch rates across dates (5 dates during pre-manipulation, 3—4 dates during each phase of the chemical period, and 1—2 dates during each phase of the all period).

To track emigration of shrimp from pool 0, we marked shrimp in pool 0 with Visible Implant Elastomer (VIE) Tags (Northwest Marine Technologies, Inc., http://www.nmt.us). We inserted the elastomer on the underside of the telson, which was easily visible and is retained past 15 years (shrimp marked in 1991 by T.A. Crowl, S.L. Johnson, and A. P. Covich are still recaptured). We marked 417 shrimp in the 4 streams during the pre-manipulation period, with an average recapture rate of 65% in pool 0 once marking was completed.

We expected shrimp to relocate when exposed to fish chemical cues or a combination of fish cues, but we did not know how far downstream the chemical cues would travel. Therefore, we only analyzed the relative abundance of shrimp in pool 0 and the proportion of marked shrimp that moved. We calculated the latter metric as the total number of marked shrimp recaptured in a different pool divided by the total number of marked shrimp recaptured in all 7 pools during each period of the experiment. The abundance metric was analyzed using a completely randomized block ANOVA with 5 levels: pre-manipulation, chemical-absent, chemical-present, all-absent, and all-present. We blocked by stream to account for among stream variability in shrimp abundance and to minimize Type II error. We used the same design to analyze the proportion moved metric. Because shrimp abundances did not decline in response to the fish scent addition, we only tested 3 treatments: pre-manipulation, all-absent, and all-present. For both analyses, we used SAS PROC MIXED (SAS version 9.1; SAS Institute, Cary, North
Carolina) to fit our models. Our analyses met the assumptions of normality and homogeneity of variance without transformations. We also assumed that there was: 1) no underlying trend in shrimp abundance or movement patterns through time, 2) no carryover effect when fish-absent treatments followed fish-present treatments, and 3) independence between streams.

**Results**

*Artificial streams*

Adult shrimp avoided the treated arm of the fluvarium when exposed to bigmouth sleeper and mountain mullet, regardless of whether or not the fish had eaten shrimp (Table 3-1, Fig. 3-3). Adult shrimp avoided the scent of eel fed shrimp, but they portioned their time equally among arms when exposed to the scent of eels alone (Table 3-1, Fig. 3-3). No single treatment, among those that induced a significant response, caused stronger avoidance behavior (test for heterogeneity, $G = 3.8$, $df = 4$, $p < 0.5$). Adult shrimp were observed at an equal frequency in each arm of the fluvarium during the control, indicating that there was no underlying preference or bias for either arm (Table 3-1, Fig. 3-3).

Postlarval shrimp showed similar avoidance behavior toward bigmouth sleeper fed shrimp and also avoided the arm scented with crushed shrimp (Table 3-1, Fig. 3-3). However, postlarval shrimp did prefer one arm of the fluvarium during the control treatment, indicating an underlying bias toward one arm (Table 3-1). We assumed that this bias remained consistent through the other treatments and adjusted the expected frequency in each arm to match that of the control treatment. Even after accounting for
this bias, avoidance of bigmouth sleeper fed shrimp and avoidance of crushed shrimp were significantly greater than baseline preferences during the control (Table 3-1).

Field experiments

Adult shrimp in natural streams changed their behavior when bigmouth sleeper were added to in-stream cages, but they did not respond to addition of fish scent only (Table 3-2, Fig. 3-4). Manipulation of predator cues in 4 natural streams significantly affected the relative abundance of shrimp in pool 0 (randomized block 1-way ANOVA, treatment effect, df = 4, 12, F = 7.8, p = 0.0025). Post-hoc comparisons showed that shrimp abundances were lower during the all period than the chemical period; abundances were also lower when fish were present than absent, but the interaction between type of predator cue and fish presence/absence was not significant (Table 3-2). The decline in shrimp abundance when fish were added to in-stream cages was primarily responsible for the significant main effects, with approximately 4 shrimp per trap during this treatment compared to 10 to 14 shrimp per trap during the other treatments (Table 3-2, Fig. 3-4). Abundances were slightly lower during the chemical-absent and all-absent treatments than during the pre-manipulation period, but the difference was not significant and the magnitude of change was half that of the change induced by adding fish to cages (Table 3-2).

Although shrimp abundances significantly declined in the pool where fish were added to in-stream cages, we did not observe large declines in pools downstream from the manipulation nor did we observe large increases in pools upstream from pool 0 (Fig. 3-5). Shrimp responded to a combination of visual, chemical, and mechanical cues when
exposed to fish in pool 0, but they did not respond to chemical cues that potentially travelled to pools downstream. In addition, shrimp did not move en masse to any single 1 of the 3 pools directly upstream.

There is evidence that shrimp did move out of pool 0 in response to the in-stream fish addition. On average, 82% of marked shrimp were recaptured in pool 0 prior to manipulation (Fig. 3-5). Even after approximately 7 weeks had passed (during the all-absent treatment), only 25% of shrimp from pool 0 had moved into another pool. When fish were added to in-stream cages, this percentage nearly doubled, with 47% of shrimp from pool 0 found in other pools. Most emigrants entered the pool immediately upstream, but some moved to the 3 downstream pools as well (Fig. 3-5). Although we observed a tendency for more shrimp to emigrate from pool 0 during the all-present treatment, there was not a statistically significant treatment effect on the proportion of marked shrimp that moved between pre-manipulation, all-absent, and all-present (randomized block ANOVA, df = 2, 6, F = 1.04, p = 0.4). In 1 of the 4 streams, shrimp abundances in pool 0 did not decline when fish were added to in-stream cages. In that stream, fewer shrimp from pool 0 moved out of the pool during the all-present treatment than the pre-manipulation and all-absent treatments. In the other 3 streams, abundances in pool 0 declined and consistently more shrimp from pool 0 moved into other pools when fish were added to in-stream cages (62%, 10%, and 13% of recaptured shrimp had moved out of pool 0 during the all-present, all-absent, and pre-manipulation treatments, respectively).
Discussion

Our experiments in artificial and natural streams provide the first line of evidence for a mechanistic explanation of disparate predatory fish and prey shrimp distributions in streams on the island of Puerto Rico. Rather than attribute direct consumption to the observed patterns, we believe that postlarval *Atya* run the predator gauntlet until they migrate above waterfalls. These upstream reaches provide refugia from predatory fishes (Chapter 2) and should ultimately result in high survivorship and overall reproductive output. Our experiments showed that postlarval and adult shrimp avoided chemical cues from predatory fish in artificial stream experiments (Table 3-1, Fig. 3-3, see also Kikkert et al. 2009), and that adults altered their behavior when fish were added to cages in natural streams.

Our experiments did not directly test whether predator-avoidance behavior by migrating postlarval shrimp leads to disparate fish and adult shrimp distributions. When scaling up to the natural environment, we might expect predatory fishes to induce different types of behavioral responses by postlarval and adult shrimp. We assumed that postlarvae continue migrating upstream until they surpass barriers to fishes. Ideally, we would have tested whether postlarval migration changes if we add fish above barriers and remove fish below. Due to the low number of migrants at high elevations (2-4 individuals per hour, D. A. Kikkert, Utah State University, personal communication), we would lack the power to observe migratory stopping points further upstream. Because *Atya* are slow growing with a long life span (Cross et al. 2008), reaches below barriers would need to remain fishless for several years to observe higher postlarval recruitment. Therefore, we
only tested the behavioral response of adult shrimp in the natural environment. Unlike our expectation for postlarval shrimp, we found that adults either reduced activity levels or relocated to pools up and downstream from the pool where fish were added to in-stream cages (Table 3-2, Figs 3-4 and 3-5). Similarly, when exposed to predatory shrimp (*Macrobrachium* spp.) in natural streams, adult *Atya* moved up and downstream from the manipulated pool (Crowl and Covich 1994). More research is necessary to determine how postlarval colonization influences adult distributions and population dynamics (Chapter 4).

*Atya* have either evolved an innate response to kairomones or learned to associate danger with the kairomones of bigmouth sleeper and mountain mullet (Table 3-1, Fig. 3-3, Dicke and Grostal 2001). Adult shrimp avoided bigmouth sleeper and mountain mullet whether they were starved or fed shrimp, and postlarvae avoided isolated alarm cues, which were tested using crushed adult shrimp (Table 3-1, Fig. 3-3). Observing the behavior of naïve postlarval shrimp would clarify whether the shrimps’ response to kairomones is learned or innate. Although crayfish avoid kairomones of other eel species (Shave et al. 1994, Hirvonen et al. 2007), adult *Atya* did not avoid the scent of starved American eel (Table 3-1, Fig. 3-2). They did, however, avoid eels fed shrimp, indicating that *Atya* avoided alarm cues but perhaps have not learned to associate eel kairomones with danger. Similarly, naïve brook trout do not avoid kairomones from American eels, not even after they have been exposed 3 times to eels fed trout (Keefe 1992).

Avoidance of fish scent by adult shrimp in the artificial environment did not scale up to experiments conducted in natural streams. The abundance of adult *Atya* did not change in response to addition of bigmouth sleeper chemical cues in 4 natural, headwater...
streams (Table 3-2, Fig. 3-4). However, the concentration of chemical cues added to natural streams may have been too dilute for detection (McIntosh et al. 1999, Brönmark and Hansson 2000, Brown et al. 2006). The concentration of chemical cues used in the fluvarium, which had an equal volume of fishless and fish-scented water, was much higher than that added to natural streams. The concentration of chemical cues during our natural field experiment also fluctuated with discharge. Because the identities of most kairomones are unknown (Brönmark and Hansson 2000, Dicke and Grostal 2001), including those emitted by bigmouth sleepers, it is difficult to control and/or measure the concentration actually released into natural streams. Little is known about how kairomones and/or alarm cues travel through natural streams (Brönmark and Hansson 2000, Dicke and Grostal 2001). Turbulence, degradation time, water velocity, and water volume may act to create the chemical landscape that an organism perceives (Brönmark and Hansson 2000). Although we expected shrimp several pools downstream from the chemical cue input to respond, shrimp abundance did not change in the pool immediately downstream from the input nor did it change in pools downstream from the in-stream fish addition. Still, another study successfully manipulated the drift behavior of mayfly larvae (Baetis) by adding fish scent to natural streams (McIntosh et al. 1999)

Alternatively, the concentration of chemical cues we added to the stream may have been high enough for shrimp to detect, but not high enough to alter their behavior. The “threat-sensitive predator avoidance hypothesis” states that prey are able to assess the degree of risk associated with a predator in a specific situation and adjust their response in a way that will balance gains (e.g., higher survivorship) with losses (e.g., energy lost due to less foraging time, Helfman 1989). Higher concentrations of chemical
cues may communicate greater risk. Prey behavior only changes once the chemical cue concentration is above a “minimum response threshold” in the laboratory (Brown et al. 2006) or above background levels found in stream water that naturally contains predatory fish (Kikkert et al. 2009, McIntosh et al. 1999). To relocate, *Atya* would have to expend energy moving to a new pool already occupied by shrimp. Thus, we posit that the concentration of chemical cues in our natural stream experiments were either too low to detect or too low to warrant a major change in behavior (i.e., relocating or inhibiting trap entry).

Shrimp abundance did dramatically decline when fish were added to in-stream cages, suggesting that the addition of mechanical and/or visual cues to chemical cues within the same pool did present imminent danger and cause shrimp to alter their behavior. A combination of predator cues generally elicits a greater behavioral response in prey than chemical cues alone (Crowl and Covich 1994, Scrimgeour et al. 1994, Shave et al. 1994, Dicke and Grostal 2001). In a laboratory experiment, adult *Atya lanipes* demonstrated a stronger response (i.e., increased shelter use and decreased movement) when exposed to the direct presence of a predatory shrimp (*Macrobrachium* spp.) than when exposed only to chemical cues (Crowl and Covich 1994). In a natural stream experiment, more *Atya* exited pools that contained free-ranging *Macrobrachium* than pools with *Macrobrachium* confined by a cage (Crowl and Covich 1994).

We have evidence that in most streams, but not all, emigration was a prevalent response to the addition of predatory fish among adult shrimp. Movement out of pool 0 nearly doubled with the addition of fish to in-stream cages (Fig. 3-5), but this change was not statistically significant. With 4 replicates, we had very low power to detect a
statistically significant response. In 3 of 4 streams, consistently more shrimp emigrated during the all-present period. Among these streams, 3-11 times more recaptured shrimp had left the manipulated pool during the all-present period than during the pre-manipulation and all-absent periods. In the 4th stream, none of the recaptured shrimp (n=6) left pool 0, nor did the abundance of shrimp decline following fish addition. For unknown reasons, shrimp abundance in this pool declined through time, with a low abundance of shrimp (4 per trap) prior to the fish addition. This reduced our ability to observe a change in shrimp abundance and movement patterns.

Although we believe emigration is primarily responsible for the decline in abundance observed in response to fish addition, there are at least 2 other plausible explanations. One is that shrimp reduced their activity levels within the manipulated pool and therefore, did not enter traps (Collins et al. 1983). Visual observations of shrimp densities at night would clarify whether our catch rates reflected relative abundance or activity levels of shrimp. Second, bigmouth sleepers possibly ate shrimp, which are vulnerable to predation at all sizes and small enough to swim through the mesh of the fish cage. Although 1 fish did eat an adult shrimp during the experiment, direct consumption could not have caused such a dramatic decline in shrimp abundance. Bigmouth sleepers fed ad libitum in aquaria prior to our fluvarium experiments ate <1 adult shrimp per day. Because fish were only in the stream cages for 5-6 days, they could have eaten 6 shrimp at most. To cause the declines in abundance observed following the fish additions, bigmouth sleepers had to eat at least an order of magnitude more than 6 shrimp. Although direct consumption may have occurred, emigration and reduced activity levels within the
manipulated pool are the most plausible explanations for the observed decline in shrimp abundance.

By using the same stream for each of the 5 treatments (pre-manipulation, chemical-present, chemical-absent, all-present, all-absent), we were better able to attribute changes in shrimp abundance to our manipulations. If each stream received only 1 treatment, underlying differences between streams and/or events (e.g., floods) that coincide with each manipulation could have confounded our results. For example, if the streams flooded during our experiment and were in fact responsible for changes in shrimp abundance, changes would be observed in all 4 streams rather than only the manipulated 2. Because shrimp abundance did not change during the chemical cue addition, there was likely no carryover effect during this period. However, the fish addition (all-present) was before the control period (all-absent) in 2 streams, potentially artificially lowering the abundance of shrimp during the latter period. This is unlikely in 1 stream because shrimp abundance increased during the time between treatments. In the 2nd stream, abundances declined over time and were low before and after the fish addition.

Alternative to our hypothesis that shrimp distributions result from behavioral avoidance of predatory fishes, adult shrimp distributions may be based on physical or chemical characteristics of streams, abundance of food resources, or avoidance of avian predators. *Atya lanipes* are very rare in 2 high-elevation tributaries with fish, but they are abundant in 2 tributaries with similar pool morphology that lie above fish barriers (Covich et al. 2009). Furthermore, there is little variation in water chemistry within and across watersheds in northeastern Puerto Rico (Ortiz-Zayas et al. 2005, Covich et al. 2009). Therefore, it is unlikely that physical or chemical attributes of streams influence
shrimp distributions at the watershed-scale. As filter feeders, *A. lanipes* may migrate to high-elevation reaches where food resources are most abundant (Greathouse et al. 2006). In Puerto Rico, more fine benthic organic matter is available in smaller order, high-elevation stream reaches (Greathouse et al. 2006). Counter to the resource availability hypothesis, postlarval *A. lanipes* showed no preference for the arm of a y-maze that contained leaf material (Kikkert et al. 2009). Further research balancing the relative roles of resource availability and predator-avoidance is necessary. Finally, avian predators, including egrets, herons, and kingfishers, are abundant along the main channel of the Espiritu Santo (personal observation) and could place significant predation pressure on shrimp. In mangroves on the southwestern corner of the island, Great Egrets (*Ardea alba*) and Snowy Egrets (*Egretta thula*) primarily eat freshwater shrimp (*Xiphocaris* spp., Miranda and Collazo 1997).

We believe that the biotic interaction between *Atya lanipes* and predatory fishes influences the migratory behavior of *A. lanipes* across entire watersheds, with postlarval shrimp migrating upstream until reaching refugia above waterfalls. More research on the cues shrimp use when navigating river networks is required to scale up from the predator-avoidance behavior we observed in artificial and natural stream experiments. Although others recognize that waterfalls may limit the distribution of predators and structure communities throughout entire watersheds (Poff 1997, Power and Dietrich 2002, Creed 2006), few discuss whether behavioral responses of prey operate at the scale of entire watersheds. For example, most predator-prey interactions have been studied at local spatial scales, but predators and prey often move across much greater areas (Lima 2002). In montane stream systems where the range of predators is limited by natural barriers, we
might find more examples of large-scale behavioral responses to predation, particularly by migratory fauna.

**Literature Cited**


Table 3-1. Frequency of times adult and postlarval *Atya lanipes* were observed in the unscented and scented arms of the fluvarium, G-test statistic, and p-values. Because adults did not favor one side during the control, the expected frequency for each adult G-test was 50% of all observations. Postlarvae did favor one side during the control period, and this bias (69% vs. 31%) was used to calculate expected frequencies for postlarval G-tests.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Unscented arm</th>
<th>Scented arm</th>
<th>G</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Adult <em>Atya</em></strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>bigmouth sleeper + <em>Atya</em></td>
<td>127</td>
<td>43</td>
<td>43.4</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>bigmouth sleeper</td>
<td>140</td>
<td>43</td>
<td>54.1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>mullet + <em>Atya</em></td>
<td>119</td>
<td>43</td>
<td>37.1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>mullet</td>
<td>116</td>
<td>40</td>
<td>38.7</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>eel + <em>Atya</em></td>
<td>106</td>
<td>51</td>
<td>19.7</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>eel</td>
<td>81</td>
<td>69</td>
<td>0.96</td>
<td>&lt; 0.5</td>
</tr>
<tr>
<td>control</td>
<td>74</td>
<td>77</td>
<td>0.06</td>
<td>&lt; 0.9</td>
</tr>
<tr>
<td><strong>Postlarval <em>Atya</em></strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>bigmouth sleeper + <em>Atya</em></td>
<td>101</td>
<td>30</td>
<td>4.6</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>crushed <em>Atya</em></td>
<td>119</td>
<td>23</td>
<td>17.1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>control</td>
<td>81</td>
<td>37</td>
<td>16.8</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
Table 3-2. Post-hoc estimates of the main effects (type of predator cue and fish presence/absence), the interaction, and individual comparisons between treatments during the field experiment. ‘Chemical’ refers to the addition of chemical cues only via streamside, flow-through tanks, whereas ‘all’ refers to the addition of chemical, mechanical, and visual cues by adding fish to in-stream cages.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Estimate</th>
<th>se</th>
<th>df</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cue (chemical – all)</td>
<td>4.6</td>
<td>1.4</td>
<td>12</td>
<td>3.24</td>
<td>0.007</td>
</tr>
<tr>
<td>Fish (absent – present)</td>
<td>3.8</td>
<td>1.4</td>
<td>12</td>
<td>2.69</td>
<td>0.02</td>
</tr>
<tr>
<td>Cue*fish</td>
<td>2.5</td>
<td>1.4</td>
<td>12</td>
<td>1.79</td>
<td>0.099</td>
</tr>
<tr>
<td>Chemical-absent – chemical-present</td>
<td>1.27</td>
<td>1.99</td>
<td>12</td>
<td>0.64</td>
<td>0.54</td>
</tr>
<tr>
<td>All-absent – all-present</td>
<td>6.31</td>
<td>1.99</td>
<td>12</td>
<td>3.17</td>
<td>0.008</td>
</tr>
<tr>
<td>Chemical-present – all-present</td>
<td>7.09</td>
<td>1.99</td>
<td>12</td>
<td>3.56</td>
<td>0.004</td>
</tr>
<tr>
<td>Pre-manipulation – chemical and all-absent</td>
<td>3.1</td>
<td>1.7</td>
<td>12</td>
<td>1.82</td>
<td>0.09</td>
</tr>
</tbody>
</table>
Figure 3-1. Schematic of the fluvarium, with 2 tanks (circles) providing source water for each arm of the fluvarium. Dimensions of the fluvarium are in cm. Arrows indicate the direction of flow.
Figure 3-2. Schematic of the 5 treatments during the field experiments conducted in 4 natural streams. Each circle represents a pool. Arrows indicate the direction of stream flow.
Figure 3-3. Proportion of total times adult and postlarval *Atya lanipes* were observed in each arm of the fluvarium, one with and one without fish and/or shrimp scent. Vertical lines indicate the proportion of visits to each arm during the control treatment. Asterisks indicate that the frequency of visits to each arm significantly differed (G-tests) from those of the control treatment. Although proportion of visits is shown, the frequency of visits was analyzed.
Figure 3-4. Relative average abundance (± 1 se) of *Atya lanipes* in 4 headwater streams prior to manipulation and during the chemical and all periods with fish absent or present. ‘Chemical’ indicates the addition of fish chemical cues by adding 2 *Gobiomorus dormitor* to a streamside flow-through tank. ‘All’ indicates the addition of fish chemical, mechanical, and visual cues by adding 1 *G. dormitor* to an in-stream cage.
Figure 3-5. Relative average abundance of *Atya lanipes* across 4 streams in 7 contiguous pools during the pre-manipulation, all-absent, and all-present treatments. Cages with 1 *Gobiomorus dormitor* were added to pool 0 (all-present treatment). Positive pools were upstream from pool 0 and negative pools were downstream from pool 0. The black portions of the bars indicate the abundances of recaptured *A. lanipes*. 
Average shrimp relative abundance

Pre-manipulation

All-absent

All-present

Pool

Marked

Unmarked

-3 -2 -1 0 1 2 3
CHAPTER 4

MODELING SHRIMP (*ATYA LANIPES*) MIGRATION THROUGH TROPICAL
ISLAND RIVER NETWORKS

Abstract

The dendritic structure of rivers has been investigated in terms of stream geomorphology and patterns in species diversity, but less is known regarding how migratory organisms navigate river networks. We developed a series of nested models to examine how upstream migration and recruitment of postlarval, amphidromous shrimp (*Atya lanipes*) influences adult shrimp distributions across a river network on the island of Puerto Rico. We used a maximum likelihood approach to parameterize our models based on observed abundances of adult shrimp in tributary headwaters. We modeled a variety of migration scenarios based on hypotheses regarding how shrimp navigate river networks, including which branch they choose at a fork in the river and how far they migrate upstream, which depends on mortality and settlement. Our models showed that if postlarval migration does influence adult shrimp distributions, postlarvae must cue on unknown characteristics of tributaries as they migrate upstream, causing them to have a greater affinity for some tributaries than others. Alternatively, adult shrimp distributions may reflect local processes, such as habitat stability and avoidance of predatory shrimp. Because *Atya spp.* have a long life span and long biomass replacement times, low recruitment rates likely maintain these populations with little effect of postlarval migration on adult populations. We were unable to accurately model the decline of migrants with distance upstream, with mortality and settling rates often parameterized to

3 Coauthored by Catherine L. Hein, James A. Powell, and Todd A. Crowl
equal zero. Further investigation of actual migration rates throughout the river network is necessary to improve our models. By applying our approach of modeling migration within a particular river network to a variety of taxa and systems, we might improve our understanding of how migratory behaviors scale up to patterns in species distributions across entire watersheds.

**Introduction**

Spatial ecologists have recently applied network theory to metapopulation dynamics, gaining insights into the connectance of habitats and stability of populations (Urban and Keitt 2001, Fortuna et al. 2006). Network or graph theory, a statistical approach that describes the properties of networks, has been applied to a variety of biological systems and describes the structure and function of interacting genes, proteins, organisms, and species (Proulx et al. 2005). In the case of metapopulations, each node represents a population of individuals in a habitat patch and each link or edge represents a movement corridor between habitat patches (Urban and Keitt 2001, Fortuna et al. 2006). Most examples of spatial applications to network theory are represented by lattice networks (2-dimensional, non-directional), but many natural systems are best described by dendritic or fractal-like networks (e.g., branched vegetation, rivers, and caves; Campbell Grant et al. 2007). Unlike lattice representations of landscapes, both links and nodes of dendritic networks serve as habitat, nodes act as transfer points between branches, and movement is restricted to the extent of dendritic networks (Campbell Grant et al. 2007). Dendritic network geometry itself may structure ecological processes,
resulting in unique patterns that may not be understood by studying each piece of a network individually (Campbell Grant et al. 2007).

Although the dendritic nature of river networks has long been recognized, the majority of work in stream systems has focused on the linear nature of streams (Fisher 1997). For example, the river continuum concept (Vannote et al. 1980) and nutrient spiraling theory (Newbold et al. 1982) provide frameworks for understanding processes that occur longitudinally, but do not explicitly account for changes that might occur at river branches (Fisher 1997). Recently, Benda and others (2004) offered the Network Dynamics Hypothesis that predicts how the spatial structures of river networks can influence the physical and biological properties of streams across the landscape. By adding water and sediment to the main stem, tributary junctions can modify river geomorphology from what would be expected given traditional hydraulic geometry relations (Rhoads 1987, Rice et al. 2001). Perhaps due to higher habitat heterogeneity and/or food resources at river nodes, species diversity of aquatic invertebrates (Rice et al. 2001) and some fishes (Fernandes et al. 2004) can be higher downstream from river confluences.

Although migratory behavior of diadromous salmonids and a few other fishes has been widely studied (Hasler et al. 1978, Keefer et al. 2006), surprisingly little is known about how other diadromous species navigate entire river networks. Chemical compounds from local geology impart information to adult salmonids, which use olfaction to return to their natal streams for spawning (Hasler et al. 1978). Pheromones released from juvenile sea lampreys (Petromyzon marinus) and then from spermiating males guide adults upstream to spawning areas (Binder and McDonald 2007).
Amphidromy and catadromy, two forms of diadromy where the adult life stage occurs in freshwater and the larval life stage occurs in saltwater, are widespread life history strategies found among fishes, shrimps, and snails in tropical regions (McDowall 2004). Very little is known about the migration of amphidromous and catadromous species in tropical regions. More work at the scale of entire river networks is necessary to understand how olfaction and other potential migratory cues might lead to landscape-level patterns in species distributions and population dynamics (Keefer et al. 2006).

The ecology of an amphidromous shrimp, *Atya lanipes*, has been well-studied (Covich and McDowell 1996, Covich et al. 2003, Covich et al. 2009), and recent work has elucidated information on this species’ migratory behavior (Benstead et al. 2000, Kikkert et al. 2009). *Atya lanipes* live and breed in headwater streams, their eggs wash downstream to the ocean where larvae develop, and postlarvae then migrate upstream (Covich and McDowell 1996, Kikkert et al. 2009). Migration occurs at night during the wet and dry seasons, but migration rates decrease during flood events and during the full moon phase (Kikkert et al. 2009). Because shrimp populations across the island of Puerto Rico are not genetically distinct (Cook et al. 2008), it is unlikely that postlarvae return to the stream where their parents bred. Natural barriers to predatory fishes could be important for understanding shrimp migration. Adult *Atya lanipes* are rarely found in stream reaches that contain predatory fishes (Covich et al. 2009, Chapter 2), and both adults and postlarvae avoid fish scented water in lab experiments (Kikkert et al. 2009, Chapter 3). Thus, postlarval shrimp may continue migrating upstream until they surpass waterfalls, thereby attaining refuge from fish predation (Chapters 2 and 3).
We developed mathematical models specific to a particular river network on the island of Puerto Rico to test whether postlarval colonization (i.e., upstream migration and recruitment) influences the distributions of adult *Atya lanipes*. We both (1) generated insight and hypotheses about shrimp migration across riverescapes, and (2) developed an analytical approach that could be used to understand the mechanisms at play when diadromous species navigate river networks. As diadromous species migrate upstream, they are faced with many decision points in terms of choosing among habitats and choosing among forks in a bifurcating river network. We included both components in our mathematical models and used a maximum likelihood approach (Hilborn and Mangel 1997) to parameterize alternative models of shrimp migration based on observed abundances of adult shrimp in tributaries of the Espíritu Santo River. We modeled and compared empirical data to four hypotheses regarding branch choice: (1) shrimp have the same probability of entering a branch at every node, (2) shrimp have a greater probability of detecting and entering the larger branch at each bifurcation (drainage area), (3) shrimp have a greater probability of choosing the branch with more upstream habitat (pool area), and (4) branch choice is based on unmeasured or more complex factors and results in unique turning probabilities at each node not predictable based on the prior hypotheses (Table 4-1).

The upstream extent of adult shrimp distributions ultimately depends on the mortality and settling rates (hereafter, ‘mortality/settling rate’) of migrating individuals. We expected that the number of migrants should decrease with increasing distance upstream as individuals stop migrating or die. Mortality could be due to energetic costs, predation by fish, large shrimp (*Macrobrachium* spp.), and birds, and anthropogenic
alterations (e.g., dams). We developed five alternative models for migrant decline with distance upstream: (1) all shrimp migrate to the headwaters, (2) there is a constant decline in the number of migrants with distance upstream, (3) fish predation below barriers is solely responsible for loss of migrants, (4) shrimp that stop migrating above fish barriers determine the mortality/settling rate, and (5) a combination of factors is responsible for loss of migrants upstream, with different mortality/settling rates up and downstream from barriers (Table 4-1). We used Akaike’s Information Criterion (Burnham and Anderson 2002) to compare alternative models based on each combination of branch choice and mortality/settling rate.

Methods

Study Area

The Espíritu Santo River drains the steep terrain of the Luquillo Experimental Forest (18°18’N, 65°47’W) in northeastern Puerto Rico. Abundant waterfalls and cascades characterize the streams in this watershed as they drop from peaks greater than 1000 m above sea level (a.s.l.) over a 19 km distance to the Atlantic Ocean (Pike 2007). Stream flow is highly variable and responds rapidly to heavy rainfall events; the discharge can increase 10-fold within one hour (Covich and McDowell 1996). The mean annual discharge (from 1994-2002) and peak discharge recorded (from 1966-2004) are 1.7 m$^3$s$^{-1}$ and 600 m$^3$s$^{-1}$ at a site downstream from the catchment we studied (U.S. Geological Survey (USGS) station number 50063800, gauged drainage area 22.3 km$^2$; http://nwis.waterdata.usgs.gov/nwis).
We studied a major portion of the Espíritu Santo watershed that spans the headwaters to a point midway upstream from the ocean (11.7 km) at approximately 240 m a.s.l. (Fig. 4-1). This catchment contains eight nodes, which represent a variety of confluence types: small tributaries entering the Espíritu Santo River (nodes 1, 2, and 3), two small tributaries merging (node 4), and a large stream, the Sonadora, entering the Espíritu Santo (node 5). The size ratio of tributary to main stem drainage areas ranged from 0.04 (node 3) to 0.91 (node 8). The drainage area of the entire catchment was 15.2 km² and that of the smallest tributary within the catchment was 0.11 km² (tributary C). Half of the confluences in this network were below natural barriers to predatory fishes (nodes 1, 2, 3, and 5).

**Field Data**

We sampled the relative abundances of adult *Atya lanipes* in the headwaters of seven tributaries flowing into the Espíritu Santo River (Fig. 4-1). To standardize the general location of the sample reach within each tributary, we selected the highest elevation pool large enough to sample (at least 1 m² and 0.5 m deep) and then sampled 6-15 contiguous pools downstream. We also included data collected on the lower portions of two tributaries (C and D) as part of another study (Chapter 3) and data collected on the Toronja (tributary D) and Prieta (tributary E) as part of the Long-Term Ecological Research monitoring program (Covich and McDowell 1996, Covich et al. 1996, Covich et al. 2003, Covich et al. 2009). In total, 77 pools were sampled between February and July of 2007. We measured the length, three widths, and five depths of each pool sampled, and used a tape measure to determine distances between pools. Although most
distances throughout the river network were determined using ArcGIS 9.1 (ESRI 2005; Appendix 1), we used a tape measure to determine the entire length of tributaries A and B and portions of tributaries C, D, and E.

We used cylindrical, wire-mesh, Gee-minnow traps (Cuba Specialty Mfg. Co., Inc. Fillmore, New York) with a 3-cm diameter opening to sample shrimp in each pool. Traps were baited with 22-g of dry cat food and set overnight (approximately 12 hours) at a density of 0.5 traps m$^{-2}$ of pool surface area. The relative abundance of shrimp was calculated as the total number of shrimp caught in a pool divided by the number of traps set in the pool.

**Mathematical Models**

We modeled shrimp migration through river networks in terms of branch choice at nodes and the mortality/settling rate over distance traveled. We tested a number of alternative hypotheses regarding which factors influence shrimp branch choice and mortality/settling rate, resulting in a set of 20 models (Table 4-1). We present the most complex model below:

\[ n_{pred} = NP_j z_b z_a \]  \hspace{1cm} (1)

where \( n_{pred} \) is the predicted abundance of adult shrimp in each headwater pool sampled, \( N \) is the total number of shrimp that start at node 1, \( P_j \) is the net probability of turning left (as the shrimp migrates upstream) at node \( j \), \( z_b \) is the proportion of shrimp that continue migrating upstream below fish barriers (hereafter, ‘observed arrival fraction’), and \( z_a \) is the observed arrival fraction of migrants above barriers. The net turn probability \( (P_j) \) is the product of turn probabilities at each node downstream \( (p_j) \). For example, the
proportion of shrimp that turn into tributary B depends on the net probability of turning left at node 2 ($P_2$), which is the proportion of shrimp that turned right at node 1 and then turned left at node 2 ($1-p_1p_2$). Our models did not account for local habitat heterogeneity at tributary junctions and assumed that all migrants in the main stem could detect and migrate up tributaries. We tested four alternative branch choice models: (1) branch choice is random, with a single probability of turning left at all nodes in the river network, (2) the turning probability is proportional to relative upstream drainage area, (3) the turning probability is proportional to upstream pool area, and (4) the turning probabilities are unique (no simple hypotheses) at each node (Table 4-1). The relative drainage area was calculated as the upstream drainage area of the left branch divided by the entire drainage area upstream from the node, and the relative pool area was calculated as the sum of pool areas sampled in the left branch divided by the sum of pool areas sampled in the entire catchment upstream from the node. The probabilities of turning left ($p_j$) for models using relative drainage or pool area were fitted as:

$$p_j = c_0 + c_1 r_j^{da} \quad \text{or} \quad p_j = c_0 + c_1 r_j^{pa}$$

(2)

where $c_0$ and $c_1$ are fitted constants and $r_j$ denotes the observed relative drainage ($da$) or pool area ($pa$) at each node $j$. Because we only sampled one of two branches upstream from nodes 7 and 8, we defined the left turn probability at node 7 ($p_7$) to equal 1.0 and the left turn probability at node 8 ($p_8$) to equal 0.0 (Fig. 4-1). Initially, we parameterized turn probabilities at nodes 7 and 8, but the lack of shrimp abundance information in two tributaries allowed the model to perfectly fit all tributaries for which there was data and then assign unrealistically high densities of shrimp to the two unknown tributaries.
We assumed that the observed arrival fraction of migrants ($z$) results from a combination of mortality and settlement that operates at a constant rate per distance:

$$z_b = e^{-\lambda L_b} \quad z_a = e^{-\lambda L_a}$$

(3)

where $\lambda$ is the mortality/settling rate, $L$ is the distance traveled, and the subscripts $b$ and $a$ denote portions of the river network below and above natural barriers to predatory fishes, respectively. An upstream decline in the number of migrating shrimp could result from shrimp stopping at pools lower in the network and from mortality related to energetic costs, predation, and anthropogenic disturbances. We tested five alternative hypotheses related to the upstream decline of migrating shrimp: (1) the mortality/settling rate is zero throughout the river network, (2) there is one constant mortality/settling rate throughout the network, (3) the mortality/settling rate is constant below and zero above barriers, (4) the mortality/settling rate is constant above and zero below barriers, and (5) there are different mortality/settling rates below and above barriers (Table 4-1).

We combined each of our hypotheses on branch choice with each of our hypotheses on mortality and settling rates for a total of 20 models. The prediction of shrimp abundance in any of the seven tributaries sampled (A-G, Fig. 4-1), is thus a combination of each turning probability and mortality/settling rate above and below barriers. For example, the predicted abundance of shrimp in tributary B is the proportion of shrimp that turned right at node 1 and then turned left at node 2 ($(1-p_1)p_2$). If we assume different mortality/settling rates above and below barriers, the abundance of shrimp in tributary B is lowered by the mortality/settling rate over the distance traveled from node 1 to the barrier in tributary B and the mortality/settling rate over the distance traveled above the barrier in tributary B (Fig. 4-1).
We assumed that there is a multiplicative error ($\varepsilon$) relating observed adult shrimp abundances ($n_{obs}$) to predicted abundances ($n_{pred}$):

$$n_{obs} = \varepsilon n_{pred}. \quad (4)$$

We take the distribution of $\varepsilon$ to be log-normal $\log(\varepsilon) \sim \mathcal{N}(0, \sigma^2)$. To correct the mean of $\varepsilon$ to equal 1,

$$\varepsilon = \varepsilon e^{-\frac{\sigma^2}{2}}. \quad (5)$$

Thus, the probability density function of $\varepsilon$ is:

$$f(\varepsilon) = \frac{1}{\sqrt{2\pi} \sigma n_{obs}} e^{-\frac{(\log(n_{obs}) - \log(\varepsilon)^2)}{2\sigma^2}}. \quad (6)$$

We assume that mortality/settling rates ($\lambda$) are sampled from a normal distribution. Because we did not directly measure the mortality/settling rates of shrimp migrating upstream, we use $\lambda$ to denote the true mortality/settling rate and $s$ to denote a multiplier adjusting mortality/settling rate with a normal distribution, $s \sim \mathcal{N}(1, \nu^2)$. The observed arrival fraction ($\zeta$) is then,

$$\zeta = e^{-\lambda s}. \quad (7)$$

and

$$s = -\frac{\ln(\zeta)}{\lambda L}. \quad (8)$$

Because $s$ is normally distributed, $\zeta$ has a log-normal distribution. The cumulative distribution function of $\zeta$ is:
\[ F(\hat{z}) = P(0 < \zeta < \hat{z}) = \int_0^\infty pdf(\zeta) d\zeta = \int_0^\infty \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(x-\mu)^2}{2\sigma^2}} ds \] 

and the probability density function of \( \hat{z} \) is:

\[ f(\hat{z}) = \frac{1}{\sqrt{2\pi\nu^2\lambda^2 L^2}} e^{-\frac{(\ln(\hat{z})+\lambda L)^2}{2\nu^2\lambda^2 L^2}}. \] 

Just as we corrected the error term (\( \hat{e} \)) to have mean 1 (Eq. 5), we standardize the observed arrival fraction of shrimp \( z \) to be

\[ \hat{z} = z e^{-\frac{1}{2} \lambda^2 L^2}, \] 

so that the expected value of \( z \) is \( e^{-\lambda L} \).

We used maximum likelihood (Hilborn and Mangel 1997) to parameterize our models based on the observed shrimp abundances in seven tributaries throughout the river network. The probability density function of a single observation based on our most complex model (i.e., unique turning probabilities and two mortality/settling parameters) is:

\[ P(x = n_{obs}, z_a, z_b / N, \sigma, \lambda_a, \nu_a, L_a, \nu_b, \lambda_b, L_b, P_j) \]

\[ = \frac{e^{-\frac{x^2}{2}\frac{\sigma^2 \lambda_a \nu_a L_a^2}{\sigma^2 \lambda_b \nu_b L_b^2}} \frac{(\ln(z_a)+\lambda_a L_a)^2}{2\lambda_a \nu_a L_a^2} \frac{(\ln(z_b)+\lambda_b L_b)^2}{2\lambda_b \nu_b L_b^2} \frac{\sigma^2 \nu_a L_a}{\sigma^2 \nu_b L_b}}{\sqrt{(2\pi)^4 \sigma^4 \lambda_a \nu_a L_a^2 \lambda_b \nu_b L_b^2 x^{2} z_a^{2} z_b^{2}}}. \] 

Because the observed arrival fraction of migrants (\( z \)) was not directly observed, we constructed the likelihood from the expectation of the observations based on mortality/settling rates. Thus, the likelihood of an observation, \( x \), is
\[
\mathcal{L}[x / \sigma, \lambda_a, \nu_a, L_a, \lambda_b, \nu_b, L_b, P_j] = \int_0^\infty \int_0^\infty P(x, z_a, z_b / N, \sigma, \lambda_a, \nu_a, L_a, \lambda_b, \nu_b, L_b, P_j) dz_a dz_b .
\]

(13)

The latter integration was performed by applying the method of steepest descents (Marsden and Hoffman 1987). Parameters were chosen for each model by minimizing the negative log of the product of the likelihoods:

\[
L = -\log \left[ \prod_{\text{data}} \mathcal{L}(x / N, \sigma, \lambda_a, \nu_a, L_a, \lambda_b, \nu_b, L_b, P_j) \right] .
\]

(14)

Due to the complexity of the objective function, minima were found using the Nelder-Mead simplex method implemented by \texttt{fminsearch} in MATLAB (Mathworks, Natick, Massachusetts, USA).

We repeated the maximum likelihood process with 10,000 bootstrap samples of the data. We used these bootstrap iterations to calculate confidence intervals for the parameters of each model. We used Akaike’s Information Criterion (AIC = \( L + 2m \), where \( m \) is the number of free parameters used in the model) to determine which of the 20 models fit the shrimp distribution data best (Burnham and Anderson 2002). This metric calculates the likelihood of the data given each model, but chooses the most parsimonious model by penalizing each additional parameter with an added constant (Burnham and Anderson 2002). Thus, the best of many competing models minimizes the AIC. We calculated the AIC for each of the 200,000 models created by the bootstrap iterations and then calculated the proportion of times each of the models had lower AIC values than each of the competing models. This allowed us to determine how consistently a particular model performed well.
Results

Our models indicate that branch choice could be one critical component of shrimp colonization processes in river networks. Models that used the same turning probability at every node or scaled the turning probability with relative drainage area performed very poorly, whereas models that parameterized unique turning probabilities at every node or scaled the turning probability with pool area predicted the average adult shrimp abundances throughout the river network well (Table 4-2, Fig. 4-2). To fit the observed patterns in shrimp abundances, our models had to route most shrimp to tributary E and large numbers of shrimp to tributaries B, C, and D (Fig. 4-3). All five models using the same turning probability were among the models with highest AIC scores and poorest fit (Table 4-2). Because the probability of turning left among these models was 0.38 on average (Table A-2), shrimp abundance was over-predicted in tributaries low in the river network (A and B) and under-predicted in several higher elevation tributaries that branched to the left (C-E, Figs. 4-2 and 4-3). Shrimp abundance was over-predicted in tributary G because it was accessed by making four right turns, each with probability 0.62 (Figs. 4-2 and 4-3). Drainage area also performed poorly, with the next set of highest AIC scores (Table 4-2). Like models with the same turn probabilities, those based on drainage area over-predicted shrimp abundance in tributaries A and B and under-predicted abundance in tributaries C, D, and E (Fig. 4-2).

Only models with unique (tributary specific) turn probabilities predicted high shrimp abundances in tributary E (Fig. 4-2). One of the best models (that with unique turn probabilities and two mortality/settling rates, hereafter ‘unique-two’) had much higher turn probabilities at nodes 5 and 6 than would be expected given the relative
drainage areas at these nodes (Table 4-3, Fig. 4-3). If most shrimp migrate up the
largest branch at each node, one would expect very high shrimp abundances in tributaries
G and F (Fig. 4-3). However, these tributaries had low abundances, with a mean of 4.4
and 6 adult shrimp per trap in tributaries F and G, respectively (Fig. 4-2). Models that
based turn probabilities on relative pool area or unique parameters assigned higher left
turn probabilities at nodes 5 and 6 (Table 4-3, Table A-2). Thus, the major “shrimp
highway” ran along the main stem and then turned left at nodes 5 and 6, with tributary E
receiving most shrimp (Fig. 4-3). This sharply contrasts the depiction of the river network
in terms of actual discharge, with most water flowing from G and F into the main stem of
the Espíritu Santo (Fig. 4-3). Similarly, tributaries C and D are more prominent in terms
of shrimp migration than would be expected given relative drainage areas (Fig. 4-3).

We were unable to accurately model the decline of migrants with distance
upstream, with 9 of 20 parameterized mortality/settling rates equal to zero (Table A-2).
No single hypothesis about declining number of migrants with distance upstream
consistently outperformed the others, with ‘zero’, ‘zero below’, and ‘two rates’
represented among the top 3 of 20 models (Table 4-2). Furthermore, a few of the more
complex models (i.e., ‘zero above’, ‘two rates’) collapsed into simpler models. The fitted
mortality/settling rate below barriers ($\lambda_b$) was zero in all models that assumed fish
predation below barriers and in 3 of 4 models that parameterized two mortality/settling
rates (Table 4-2, A-2). Thus, we were unable to test the hypotheses that fish predation
below barriers causes declines in the number of migrating shrimp (‘zero above’) or that
ergetic costs, predation, and settlement cause different mortality/settling rates above
and below barriers (Table A-2).
Models that collapsed into the same mortality/settling type did not necessarily perform equally well. For example, three models with unique turn probabilities were fitted to have a mortality/settling rate of zero throughout the river network, but the AIC values ranged from 136.9-209.8 (Table 4-2, A-2). Although the best model (‘unique-zero below’) parameterized the mortality/settling rate above barriers to equal 0 and was penalized for fitting two extra parameters to do so, its AIC value was still 30 units lower than the model that assumed a mortality/settling rate of zero throughout (Table 4-3). The parameters fit to branch choice at each node were very different in these two models, with higher left turn probabilities at nodes 1-3 and slightly lower values at nodes 5 and 6 in the best model (Table A-2). Conversely, the turn probabilities fit by the two best models were very similar to one another, but the mortality/settling rates were very different (Table 4-2, A-3). One model fit a mortality/settling rate of zero throughout the river network and the other model fit a mortality/settling rate of 0.76 below and 0.0 above barriers (Table 4-2, 4-3, A-2). This indicated that parameterizing branch choice had a much larger effect on model performance than parameterizing mortality/settling rate.

Although we did not model the high variability of shrimp abundance among pools within tributaries, our best models accurately predicted the average shrimp abundance in each tributary, which ranged from 4.4 to 49.7 shrimp per trap (Fig. 4-2). Furthermore, the ranking of models remained relatively consistent when we modeled 10,000 bootstrap samples of the data, with the same top three models as those based on the original data (Table 4-2, A-3). Compared to each model derived from the original data set, the ‘unique-two’ model always had the highest proportion of bootstrap samples with a lower AIC value (Table A-3). For example, 67.8% of the bootstrap samples of the ‘unique-two’
model had lower AIC values than the ‘pool area-zero’ model based on original data (Table A-3). From comparisons of AIC values based on the original and bootstrapped data, we learned that the ‘pool area-zero’ model consistently performed second best, and the ‘unique-zero below’ model usually performed third best (Table A-3).

In two of the three best models, ‘unique-two’ and ‘pool area-zero’, the bootstrap estimates of turn probabilities were tightly distributed with median values near those parameterized using the original data set. In both models, the turn probabilities shared similar ranges at nodes 1 and 2, were different at nodes 3 and 4, and shared very high left turn probabilities at nodes 5 and 6 (Table 4-3). However, the parameterized values based on the original data of the ‘unique-zero below’ model were much higher than the medians from the bootstrap samples and often exceeded the 90% confidence intervals (Table 4-3). In addition, the confidence intervals of these parameter values were very wide, indicating that the ‘unique-zero below’ model was not stable even though it had the lowest AIC score when parameterized with the original data set.

Discussion

Our models suggested that variation in adult shrimp abundances between tributaries either results from differential postlarval recruitment into tributaries that possess particular attributes or from variations in within-tributary processes that influence adult survivorship. Because *Atya spp.* have a long life span and long biomass replacement times (Cross et al. 2008), low recruitment rates likely maintain these populations with little effect of postlarval migration on adult populations. We were unable to accurately model the observed decline of migrants with distance upstream (D. A. Kikkert, *personal*
Further investigation of actual migration rates throughout the river network is necessary. Our models indicate that branch choice by postlarvae as they migrate upstream could be important for predicting adult shrimp distributions, with relative pool areas signifying upstream habitat or unique turn probabilities at each node reflecting unknown cues. The probability of a left turn at nodes 5 and 6 had to be very high to accurately predict adult shrimp abundances in tributary E (Table 4-3, Figs. 4-2 and 4-3). Shrimp may be using a variety of untested cues to navigate the river network, including water temperature, water chemistry, turbidity, food resources, and pheromones (Leggett 1977, Kikkert et al. 2009, Binder and McDonald 2007). In a variety of y-maze experiments, postlarval *Atya* show no preference for the arm with leaf material, they are attracted to the arm with higher flow, they avoid the arm with high turbidity, and they avoid the arm with fish scent (Kikkert et al. 2009, Chapter 3). More experimental work coupled with field observations of migration rates above each confluence are necessary to determine whether migration rates into particular tributaries are higher and what factors might cause an affinity for particular tributaries.

Although half of our models parameterized mortality/settling rates to be zero, we do not believe that the majority of postlarval shrimp reach headwater streams as they migrate upstream from the ocean. In fact, the number of migrants rapidly declines from an average of 200 shrimp per hour at a site on the Espíritu Santo River downstream from node 1 (approximately 11.4 km from the ocean, Kikkert et al. 2009) to 15-30 shrimp per hour between confluences 5 and 6, to 2-4 shrimp per hour upstream from confluence 6 in tributary E (Kikkert, personal communication). These preliminary field observations
suggest that the number of migrants does decay with distance upstream and that more postlarvae may migrate up the larger of two branches at each confluence. By bounding mortality/settling rate values with estimates from field observations, our models might better simulate this aspect of shrimp migration.

Rather than represent network navigation by migrating postlarvae, our models that used relative pool areas or unique turn probabilities to predict adult distributions may reflect localized processes within stream reaches that control adult abundances, such as habitat stability and productivity. *Atya lanipes* have a relatively long life span (~minimum 8 years), very slow growth rates (-0.001-0.005 mg mg\(^{-1}\) day\(^{-1}\)), and high fecundity during most of the year (Johnson et al. 1995, Cross et al. 2008). Some individuals that were marked in 1991 are still recaptured (Cross et al. 2008), suggesting that adult shrimp have high survivorship once they reach headwater streams. The production to biomass ratio of *Atya spp.* in Prieta (tributary E) is also low (mean 0.15-0.2) with biomass replacement times of 5-10 years (Cross et al. 2008). Thus, a small recruitment rate should sustain adult populations in headwater streams, with little effect of postlarval migration on adult populations. The high left turning probabilities at nodes 5 and 6 parameterized by our best models likely reflect a characteristic that allows tributary E to support large shrimp populations rather than a cue attracting most migrating shrimp.

Disturbances in the form of hurricanes and droughts influence adult *Atya* distributions in headwater streams (Covich et al. 1996, 2003). Eight months after Hurricane Hugo, shrimp abundances in the Prieta (tributary E) declined in the highest elevation pools, presumably because shrimp moved downstream, but abundances increased throughout the study reach during the four years after the hurricane (Covich et
During a 1994 drought, shrimp densities increased in the remaining, shrinking pools as small pools dried up (Covich et al. 1996, 2003). In addition, adult shrimp move to other pools when free-ranging, predatory shrimp (*Macrobrachium* spp.) enter a pool (Crowl and Covich 1994). Finally, the relative abundance of shrimp increases with pool size in the Prieta; these relations explain 44-91% of the variance in adult *Atya* abundance (Covich et al. 1996, Pyron et al. 1999, Scatena and Johnson 2001). Local pool permanence, stability, habitat, and predator-prey interactions may therefore have the greatest effect on adult shrimp abundances.

However, network position is very important for understanding adult *Atya* distributions across entire watersheds, with very few *Atya* in headwater streams that are accessible to predatory fishes (Pyron et al. 1999, Scatena and Johnson 2001, Covich et al. 2009, Chapter 2). When pools from a variety of streams are included, regression models predicting *Atya* abundance based on pool habitat often explain little of the variation in abundance (Pyron et al. 1999, Scatena and Johnson 2001, Covich et al. 2009), whereas the location of stream pools relative to fish barriers best predict *A. lanipes* abundance and presence/absence (Covich et al. 2009, Pike 2007, Chapter 2). All of the tributaries we sampled, except tributary A, were above barriers to predatory fishes, but shrimp abundance was variable among tributaries (Fig. 4-2). We observed the highest abundances in tributary E and abundances in tributaries B-D were on average two times higher than those in tributaries A, F, and G. Because tributaries B-E are above barriers, but are a much shorter distance upstream than tributaries F and G, migrating shrimp may have a greater likelihood of colonizing these tributaries. The majority of the distance traveled to tributaries F and G from their confluence (node 5) is above barriers to
predatory fishes. Although we did not observe any adult Atya in the Espíritu Santo or Sonadora Rivers below barriers to predatory fishes, we did observe intermediate abundances of adult shrimp in large pools along these rivers above barriers (unreported data). Thus, shrimp may stop migrating once they surpass fish barriers, resulting in lower adult shrimp abundances in the headwaters of tributaries F and G as shrimp occupy habitat downstream.

To understand the relative roles of colonization and local processes on adult Atya distributions, we need to conduct field surveys investigating postlarval shrimp migration throughout the river network. By estimating migration rates in both branches above each confluence in the river network, we could directly parameterize turn probabilities and mortality/settling rates above and below fish barriers. If the parameterized values from our best model strongly contrast those estimated in the field, it is likely that the unique turn probabilities parameterized by our models represented localized processes within stream reaches, such as pool habitat and stability. By incorporating a population model based on the estimated turnover time of Atya populations in headwater streams (Cross et al. 2008), we could estimate the recruitment rate to each tributary necessary to maintain the observed shrimp abundances over time. The latter approach would be more realistic than our current model, which essentially populates empty streams, and would probably result in much higher mortality/settling rates.

Our modeling effort represents the first attempt to formalize alternative hypotheses regarding the influence of postlarval shrimp migration through river networks on adult distributions across the landscape. This approach is useful for directing future research on shrimp migration and is similar to many other initial attempts at
understanding the behavior of migratory species (Leggett 1977). The migrations of winter flounder (*Pseudopleuronectes americanus*), Pacific salmon (*Oncorhynchus spp.*), and eels (*Anguilla anguilla* and *A. rostrata*) have all been simulated fairly well by specifying a random walk within the confines of basic known behaviors (e.g., preferring depths < 20 fathoms, diel vertical migration, preferred temperature, etc.) and the physical environment (e.g., ocean currents, tidal influences in estuaries, etc.; Salla 1961, Leggett 1977, Dingle 1996). Over the past 40 years, much more information has been learned regarding the behavior of migratory fauna (Dingle 1996), including the use of olfaction by salmon to home to natal streams (Hasler et al. 1978, Keefer et al. 2006). As more studies are conducted in this area, we hope to see similar gains made in our understanding of amphidromous shrimp migration.

We highlight our approach of modeling shrimp migration within a particular river network and encourage its application to other migratory fauna and river systems. Recently, others have shown that the dendritic structure of river networks and vegetation affects rates and patterns of dispersal and predator-prey interactions and may also have implications for understanding exotic species invasions, gene flow, and patterns of extinction (Johnson et al. 1995, Cuddington and Yodzis 2002, Campbell Grant et al. 2007). Although long-distance migration has been studied across a wide variety of taxa and systems (Dingle 1996), few have explicitly studied how migratory behaviors of tropical, freshwater fauna observed in the laboratory or in reaches of natural streams scale up to patterns observed in large river networks across the landscape. Models based on dendritic network structure rapidly become complex as processes occurring upstream depend on a sequence of events occurring lower in the network, but today’s high
computing power should not inhibit such endeavors. By explicitly using river network structure to model migration, we might improve our understanding of both migratory species and the systems they connect.

Literature Cited


Table 4-1. Summary of each model type with associated equations and hypotheses.

Mortality/settling rate refers to the decreasing number of migrants with distance upstream.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>Hypothesis</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Branch Choice</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>same at each node</td>
<td>$p$</td>
<td>branch choice is the same throughout the network</td>
</tr>
<tr>
<td>relative drainage area</td>
<td>$p_j = c_0 + c_1 r_j^{da}$</td>
<td>shrimp are more likely to go up larger branches, which offer more upstream habitat and are easier to detect</td>
</tr>
<tr>
<td>relative pool area</td>
<td>$p_j = c_0 + c_1 r_j^{pa}$</td>
<td>branches with greater upstream pool area offer more habitat</td>
</tr>
<tr>
<td>unique at each node</td>
<td>$p_j$</td>
<td>unmeasured variables influence branch choice</td>
</tr>
<tr>
<td><strong>Mortality/Settling Rate</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>zero</td>
<td>$z_b = z_a = 1$</td>
<td>postlarvae have high survivorship and propensity to continue migrating</td>
</tr>
<tr>
<td></td>
<td>$\lambda_a = \lambda_b = 0$</td>
<td></td>
</tr>
<tr>
<td>one rate</td>
<td>$z_b = z_a = e^{-\lambda L}$</td>
<td>energetic costs, predation, shrimp stop migrating</td>
</tr>
<tr>
<td></td>
<td>$\lambda_a = \lambda_b$</td>
<td></td>
</tr>
<tr>
<td>zero above barriers</td>
<td>$z_b = e^{-\lambda L_o}$</td>
<td>fish predation below barriers</td>
</tr>
<tr>
<td></td>
<td>$z_a = 1$, $\lambda_a = 0$</td>
<td></td>
</tr>
<tr>
<td>zero below barriers</td>
<td>$z_a = e^{-\lambda L_u}$</td>
<td>shrimp stop migrating above barriers</td>
</tr>
<tr>
<td></td>
<td>$z_b = 1$, $\lambda_b = 0$</td>
<td></td>
</tr>
<tr>
<td>two rates</td>
<td>$z_b^*z_a$</td>
<td>energetic costs, fish predation below barriers, shrimp stop migrating</td>
</tr>
</tbody>
</table>
Table 4-2. AIC scores for each of 20 models. ‘Mortality/settling rate’ gives the specified model type and ‘parameterized mortality/settling rate’ lists the resulting model after mortality/settling rates above ($\lambda_a$) and below ($\lambda_b$) barriers were parameterized. Delta is the difference in AIC values between each model and the model with the lowest AIC value.

<table>
<thead>
<tr>
<th>Branch choice</th>
<th>Mortality/settling rate</th>
<th>Parameterized mortality/settling rate</th>
<th>AIC</th>
<th>delta</th>
</tr>
</thead>
<tbody>
<tr>
<td>unique</td>
<td>zero below</td>
<td>zero</td>
<td>136.9</td>
<td>0.00</td>
</tr>
<tr>
<td>unique</td>
<td>two rates</td>
<td>zero above</td>
<td>138.0</td>
<td>1.1</td>
</tr>
<tr>
<td>pool area</td>
<td>zero</td>
<td>zero</td>
<td>138.5</td>
<td>1.6</td>
</tr>
<tr>
<td>pool area</td>
<td>zero below</td>
<td>zero below</td>
<td>141.5</td>
<td>4.5</td>
</tr>
<tr>
<td>pool area</td>
<td>one rate</td>
<td>one rate</td>
<td>141.8</td>
<td>4.9</td>
</tr>
<tr>
<td>pool area</td>
<td>zero above</td>
<td>zero</td>
<td>142.5</td>
<td>5.6</td>
</tr>
<tr>
<td>pool area</td>
<td>two rates</td>
<td>zero below</td>
<td>147.9</td>
<td>11.0</td>
</tr>
<tr>
<td>unique</td>
<td>one rate</td>
<td>one rate</td>
<td>154.9</td>
<td>18.0</td>
</tr>
<tr>
<td>unique</td>
<td>zero</td>
<td>zero</td>
<td>167.0</td>
<td>30.0</td>
</tr>
<tr>
<td>drainage</td>
<td>zero below</td>
<td>zero below</td>
<td>188.4</td>
<td>51.5</td>
</tr>
<tr>
<td>----------------</td>
<td>------------</td>
<td>------------</td>
<td>-------</td>
<td>------</td>
</tr>
<tr>
<td>area</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>drainage</td>
<td>zero</td>
<td>zero</td>
<td>189.6</td>
<td>52.7</td>
</tr>
<tr>
<td>area</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>drainage</td>
<td>two rates</td>
<td>zero below</td>
<td>193.2</td>
<td>56.3</td>
</tr>
<tr>
<td>area</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>drainage</td>
<td>one rate</td>
<td>one rate</td>
<td>193.2</td>
<td>56.3</td>
</tr>
<tr>
<td>area</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>drainage</td>
<td>zero above</td>
<td>zero</td>
<td>195.1</td>
<td>58.2</td>
</tr>
<tr>
<td>area</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>same</td>
<td>zero</td>
<td>zero</td>
<td>202.9</td>
<td>66.0</td>
</tr>
<tr>
<td>same</td>
<td>zero below</td>
<td>zero below</td>
<td>206.4</td>
<td>69.5</td>
</tr>
<tr>
<td>same</td>
<td>zero above</td>
<td>zero</td>
<td>206.9</td>
<td>70.0</td>
</tr>
<tr>
<td>same</td>
<td>one rate</td>
<td>zero</td>
<td>206.9</td>
<td>70.0</td>
</tr>
<tr>
<td>unique</td>
<td>zero above</td>
<td>zero</td>
<td>209.8</td>
<td>72.9</td>
</tr>
<tr>
<td>same</td>
<td>two rates</td>
<td>zero below</td>
<td>210.5</td>
<td>73.6</td>
</tr>
</tbody>
</table>
Table 4-3. Net left turn probabilities ($P_i$) of nodes 1-6 for the three best models (unique turn probabilities and zero mortality/settlement below barriers, unique turn probabilities and two mortality/settling rates, turn probabilities scaled to pool area and zero mortality/settlement). 90% confidence intervals (CI; lower bound, median, upper bound) for each parameter value are based on 10,000 bootstrap iterations. The relative drainage areas (drainage area of left branch divided by total drainage area upstream from node) are also included for comparison. Ø denotes the empty set.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Unique-zero below</th>
<th>Unique-two rates</th>
<th>Pool area-zero</th>
<th>Drainage area</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Value</td>
<td>CI</td>
<td>Value</td>
<td>CI</td>
</tr>
<tr>
<td>$P_1$</td>
<td>0.07</td>
<td>Ø, 0.02, 0.11</td>
<td>0.03</td>
<td>0.02, 0.04, 0.09</td>
</tr>
<tr>
<td>$P_2$</td>
<td>0.10</td>
<td>Ø, 0.02, 0.11</td>
<td>0.04</td>
<td>0.02, 0.05, 0.12</td>
</tr>
<tr>
<td>$P_3$</td>
<td>0.22</td>
<td>0.04, 0.08, 0.28</td>
<td>0.25</td>
<td>0.19, 0.25, 0.34</td>
</tr>
<tr>
<td>$P_4$</td>
<td>0.49</td>
<td>0.04, 0.08, 0.28</td>
<td>0.49</td>
<td>0.39, 0.49, 0.60</td>
</tr>
<tr>
<td>$P_5$</td>
<td>0.93</td>
<td>0.22, 0.44, 0.97</td>
<td>0.84</td>
<td>0.75, 0.86, 0.93</td>
</tr>
<tr>
<td>$P_6$</td>
<td>0.94</td>
<td>0.50, 0.69, 0.88</td>
<td>0.92</td>
<td>0.84, 0.92, 0.96</td>
</tr>
</tbody>
</table>
Figure 4-1. Map of the study catchment within the Espíritu Santo watershed in northeastern Puerto Rico. Bold portions of the river network indicate reaches where adult shrimp abundances were estimated by trapping. Letters identify each sampled tributary and numbers denote each node in the river network. Natural barriers (i.e., waterfalls) to predatory fishes are denoted with a line perpendicular to the stream.
Figure 4-2. Stylized diagram of the river network in the Espíritu Santo watershed including the observed and predicted adult shrimp abundances per pool of seven tributaries (A-G). Each plot depicts relative shrimp abundance (average number per trap) vs. distance upstream from node 1. Mean ± SD of relative shrimp abundance in each tributary is reported in the upper right portion of each plot. Predicted values of four representative models are shown: 1) same turn probability and zero mortality/settlement, 2) drainage area and zero mortality/settlement, 3) pool area and zero mortality/settlement, and 4) unique turn probabilities and two mortality/settling rates. Natural barriers (i.e., waterfalls) to predatory fishes are denoted with a line perpendicular to the stream.
Figure 4-3. Stylized diagram of the river network with stream width proportional to the net turn probabilities estimated according to the ‘same-zero’ model, direct drainage area proportions (see Table 4-3), the ‘pool area-zero’ model, and the ‘unique-two rates’ model. The size of each circle scales with the observed, relative abundance of adult shrimp in each tributary (denoted with a letter).
A landscape perspective was critical for understanding community structure on the island of Puerto Rico, especially because these tropical streams tend to have a steep gradient and are dominated by migratory fauna. Anthropogenic changes to the landscape had little effect on fish and shrimp species distributions, which were primarily affected by natural barriers (Chapter 2). The upstream extent of all predatory fishes was limited by the location of waterfalls, but shrimp and herbivorous gobies could access stream reaches upstream from fish barriers (Chapter 2). Thus, predator-prey interactions between fishes and shrimps were mediated by the steep terrain of these watersheds, with shrimp likely avoiding predation by migrating above fish barriers as postlarvae. Lab and field experiments (Chapter 3) combined with a mathematical model of shrimp migration (Chapter 4) provided the first mechanistic evidence for watershed-level, predator-avoidance behavior by a diadromous shrimp (*Atya lanipes*).

The high stream power of streams in northeastern Puerto Rico combined with the spatial configuration of anthropogenic alterations to the landscape makes these stream ecosystems fairly resistant to human disturbances. Most stream reaches above natural barriers to fishes were protected from urban and agricultural development, logging, and fishing by the Luquillo Experimental Forest. The lack of high-head dams allowed shrimp to access headwater reaches, which provide refugia from fish predation. Furthermore, most culverts that could pose barriers to fishes were located above waterfalls and had no effect on species distributions. Although levels of agricultural and urban development in
the lower part of the watersheds were comparable to other areas impacted by land use change (Paul and Meyer 2001, Riley et al. 2005), fish and shrimp species distributions did not appear to be impacted. High stream power may dilute pollutants and wash out fine sediment deposits, and the migratory life history strategy of the organisms allows rapid recovery from pulsed disturbances (Greathouse et al. 2005). However, tropical, montane systems are still susceptible to anthropogenic alterations. For example, exotic fishes in Hawaii have excluded native fishes from sites low in the river drainage (Brasher et al. 2006). Perhaps the largest current threat to diadromous fauna in Puerto Rico is water withdrawal. Currently, 70% of water draining the Luquillo Experimental Forest is diverted into municipal water supplies before reaching the ocean, and water demands are expected to increase (Crook et al. 2007). Continued water withdrawal may reduce and disconnect upstream habitats that harbor the highest shrimp densities in the watershed (Covich et al. 2003).

In montane landscapes, few have been able to differentiate between anthropogenic and natural effects on species assemblages because agricultural and urban areas generally lie in valleys, thereby confounding anthropogenic and natural gradients (Van Sickle 2003, Allan 2004). Because *A. lanipes* were only present in forested reaches above waterfalls, we could not determine whether anthropogenic disturbances or biotic interactions affected their distribution. However, we were still able to draw conclusions regarding anthropogenic effects on freshwater communities strongly influenced by the steep gradient in Puerto Rico. The fact that the fishes *A. monticola*, *A. rostrata*, and *G. dormitor* were generally only present at sites downstream from urban and agricultural land eliminated the possibility of current human activities extirpating these species.
The disparate distributions of predatory fishes (*A. monticola*, *A. rostrata*, and *G. dormitor*) and a prey shrimp (*A. lanipes*) led us to believe that postlarval shrimp continue migrating upstream until they surpass fish barriers. Others have arrived at the same hypothesis based on similar observations (Covich and McDowell 1996, Greathouse et al. 2006, Covich et al. 2009), but we were the first to test these ideas through a series of mechanistic experiments and a model that incorporated an entire river network. Both postlarval and adult *A. lanipes* avoided fish scent in a y-maze fluvarium. Adults responded to kairomones of *A. monticola* and *G. dormitor*, but appeared to only avoid *A. rostrata* when exposed to kairomones and alarm cues (i.e., eels fed shrimp). Avoidance of fish scent by adult shrimp in the artificial environment did not scale up to experiments conducted in natural streams; the abundance of adult *Atya* did not change in response to the addition of bigmouth sleeper chemical cues in four natural, headwater streams (Chapter 3). Behaviors observed in an artificial setting do not necessarily scale up to the natural environment (Carpenter 1996, Cooper et al. 1998). Indeed, Peckarsky et al. (1997) found that while individual macroinvertebrate behaviors could scale up to expected community-level patterns, a complex array of factors often drown out these signals. Alternatively, the concentration of chemical cues added to natural streams may have been too low for detection. We did observe a decline in adult shrimp abundance when bigmouth sleeper were added directly to in-stream cages, indicating that predator-avoidance behavior can be manipulated in the natural environment (Chapter 3).

Although we conducted experiments in the natural environment to examine how shrimp behaviorally respond to predatory fishes, the temporal and spatial scales of our experiments (i.e., weeks and tens of meters) was still much smaller than that of the
migratory process we hypothesized (i.e., years and kilometers). Ideally, we would have tested whether postlarval migration changes if we added fish above barriers and removed fish below, but the logistics of performing such experiments were infeasible. Our field experiments were a brave attempt at manipulating the predator environment in a flashy system not conducive to traditional field experimentation, which often uses fences, cages, and other materials to manipulate the system.

To integrate our ideas about how migratory and fish avoidance behavior by postlarval shrimp scale up to observed adult shrimp (A. lanipes) distributions across the landscape, we developed a set of nested models specific to a particular river network (Chapter 4). These models tested a variety of migration scenarios based on hypotheses regarding how shrimp navigate river networks, including which branch they choose at a fork in the river and how far they migrate upstream, which depends on mortality and settling rates. Our models suggested that either 1) postlarval shrimp cue on unknown characteristics of tributaries as they migrate upstream, causing them to have a greater affinity for some tributaries than others, or 2) adult distributions reflect local processes, such as habitat stability and avoidance of predatory shrimp, rather than postlarval migration and recruitment. To accurately predict average adult abundances in each tributary, branch choice at each node either scaled with upstream pool area or was uniquely parameterized at each tributary junction. When branch choice scaled with upstream drainage area or was parameterized to be the same at all tributaries, our models performed poorly. We were unable to accurately model the observed decline of migrants with distance upstream (D. A. Kikkert, personal communication), with mortality and settling rates often parameterized to equal zero. By bounding mortality/settling rate
values with estimates from field observations, our models might better simulate this aspect of shrimp migration. Because *Atya* spp. have a long life span and long biomass replacement times, low recruitment rates likely maintain these populations with little effect of postlarval migration on adult populations. Both mortality due to fish predation below barriers and settling in pools above barriers should be important processes for understanding how colonization influences adult distributions. Further investigation of actual migration rates throughout the river network is necessary to distinguish these alternative hypotheses.

We highlight our approach of modeling migration through a particular river network and encourage its application to other migratory fauna and river systems. Although long-distance migration has been studied across a wide variety of taxa and systems (Dingle 1996, Alerstam 2006), few have explicitly studied how migratory behaviors of tropical, freshwater fauna observed in the laboratory or in reaches of natural streams scale up to patterns observed in large river networks across the landscape. By applying our approach of modeling migration within a particular river network to a variety of taxa and systems, we might improve our understanding of how migratory behaviors scale up to landscape-level patterns in species distributions.

In conclusion, we found that river network structure was important for understanding stream communities of diadromous species on the island of Puerto Rico. Not only was the location of anthropogenic features in relation to natural barriers important for determining anthropogenic impacts on stream fauna, but the position of fish barriers also mediated predator-prey interactions and may result in watershed-level predator-avoidance behavior by migrating shrimp. In montane river systems with
migratory fauna, scientists would benefit by creatively designing new experiments and models that incorporate river network structure, as this is the template upon which all processes occur.

LITERATURE CITED


Appendix 1. Methods using ArcGIS 9.1 to derive distances throughout the river network and drainage areas upstream from each confluence.

We describe methods to (1) create a map and 10 m digital elevation model (DEM) that correctly depicts the river network, (2) calculate stream lengths in the river network, and (3) calculate upstream drainage areas. Because most tributaries (i.e., A, C, D, and E) were not shown on the 1:25,000 scale map, we used a 10 m DEM (Pike et al. 2007) and the flow accumulation tool in ArcGIS 9.1 (ESRI 2005) to predict the flow path of tributaries A and C. We defined these tributaries to occur after 100 cells flow into a single downstream cell. We used a GIS layer from the Luquillo LTER website (http://www.ites.upr.edu/thomlinson/spatialdata/elverde.html) to depict the correct flow paths of tributaries D and E. We used the editing tools in ArcGIS 9.1 to add these four tributaries to the hydrography layer of streams in northeastern Puerto Rico (from U.S. Geological Survey Digital Line Graphs and posted on http://biocomplexity.warnercnr.colostate.edu/data.htm). After creating a vector shapefile that correctly depicts the river network of interest and splitting stream vectors at each node and natural barrier, we calculated 2-D stream lengths using script code with Visual Basic (VBA). We used the ‘surface length’ tool in 3-D Analyst Tools to account for elevational changes in our stream length calculations. This tool uses a DEM and Pythagorean’s Theorem to improve the calculation of length in environments with steep terrain ( ). To calculate upstream drainage areas, we used the 10 m DEM (Pike 2007) and the Hydrology Tools in ArcGIS 9.1. Because the 10 m DEM did not correctly predict some of the small tributaries, we used our corrected stream shapefile to burn these
flowpaths into the DEM. This process decreases the elevation of raster cells in the flow path by 10 m and then smoothes the elevations of buffering raster cells to gradually reach the elevation outside a 30 m wide buffer. We then created a flow direction raster based on the corrected DEM and used the Watershed tool to delineate watersheds for each branch of each confluence.
Table A-2. Parameter values for each of 20 models. Values followed by * were pre-defined by each model type. Individual turn probabilities for the drainage area and pool area models were calculated based on the parameter values of $c_0$ and $c_1$.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Same</th>
<th>Drainage area</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>zero</td>
<td>zero</td>
</tr>
<tr>
<td></td>
<td>above</td>
<td>below</td>
</tr>
<tr>
<td>$\lambda_b$</td>
<td>0.0* 0.0 0.0* 0.0</td>
<td>0.0 0.0* 0.08 0.0*</td>
</tr>
<tr>
<td>$\nu_b$</td>
<td>0.1* 0.36 0.1* 0.39</td>
<td>0.05 0.1* 0.18 0.01</td>
</tr>
<tr>
<td>$\lambda_a$</td>
<td>0.0* 0.0* 0.09 0.0</td>
<td>0.08 0.0* 0.35 0.08</td>
</tr>
<tr>
<td>$\nu_a$</td>
<td>0.1* 0.1* 0.07 0.39</td>
<td>0.30 0.1* 0.18 0.29</td>
</tr>
<tr>
<td>$c_0$</td>
<td>0.0* 0.0* 0.0* 0.0*</td>
<td>0.0* 0.22 0.15 0.08</td>
</tr>
<tr>
<td>$c_1$</td>
<td>1.0* 1.0* 1.0* 1.0*</td>
<td>1.61 20.4 1.77 1.65</td>
</tr>
<tr>
<td>$P_1$</td>
<td>0.39 0.39 0.36 0.39</td>
<td>0.36 0.30 0.25 0.17</td>
</tr>
<tr>
<td>$P_2$</td>
<td>0.39 0.39 0.36 0.39</td>
<td>0.29 0.25 0.17 0.26</td>
</tr>
<tr>
<td>$P_3$</td>
<td>0.39 0.39 0.36 0.39</td>
<td>0.28 0.23 0.16 0.24</td>
</tr>
<tr>
<td>$P_4$</td>
<td>0.39 0.39 0.36 0.39</td>
<td>0.61 0.64 0.51 0.58</td>
</tr>
<tr>
<td>$P_5$</td>
<td>0.39 0.39 0.36 0.39</td>
<td>0.72 0.78 0.63 0.69</td>
</tr>
<tr>
<td>$P_6$</td>
<td>0.39 0.39 0.36 0.39</td>
<td>0.35 0.32 0.23 0.32</td>
</tr>
<tr>
<td>$N$</td>
<td>0.08 0.08 0.09 0.08</td>
<td>0.09 0.07 0.07 0.12</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>1.00 1.00 1.00</td>
<td>1.00 0.93 0.94 0.91</td>
</tr>
<tr>
<td></td>
<td>Pool area</td>
<td>Unique</td>
</tr>
<tr>
<td>---------</td>
<td>-----------</td>
<td>--------</td>
</tr>
<tr>
<td></td>
<td>zero</td>
<td>zero</td>
</tr>
<tr>
<td></td>
<td>above</td>
<td>below</td>
</tr>
<tr>
<td>$\lambda_b$</td>
<td>0.0*</td>
<td>0.0</td>
</tr>
<tr>
<td>$\nu_b$</td>
<td>0.1*</td>
<td>0.47</td>
</tr>
<tr>
<td>$\lambda_a$</td>
<td>0.0*</td>
<td>0.0*</td>
</tr>
<tr>
<td>$\nu_a$</td>
<td>0.1*</td>
<td>0.1*</td>
</tr>
<tr>
<td>$c_0$</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>$c_1$</td>
<td>1.11</td>
<td>1.11</td>
</tr>
<tr>
<td>$P_1$</td>
<td>0.11</td>
<td>0.11</td>
</tr>
<tr>
<td>$P_2$</td>
<td>0.09</td>
<td>0.09</td>
</tr>
<tr>
<td>$P_3$</td>
<td>0.44</td>
<td>0.44</td>
</tr>
<tr>
<td>$P_4$</td>
<td>0.62</td>
<td>0.62</td>
</tr>
<tr>
<td>$P_5$</td>
<td>0.86</td>
<td>0.86</td>
</tr>
<tr>
<td>$P_6$</td>
<td>0.69</td>
<td>0.69</td>
</tr>
<tr>
<td>$N$</td>
<td>0.06</td>
<td>0.06</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>0.69</td>
<td>0.69</td>
</tr>
</tbody>
</table>
Table A-3. Proportion of times that each model based on 10,000 bootstrap samples of the data (left-most column) had lower AIC values than models parameterized using the original data set (top two rows). Values in bold show the proportion of times that the model based on the bootstrap samples had a lower AIC value than the same model based on the original data set.

<table>
<thead>
<tr>
<th></th>
<th>Pool area</th>
<th>Unique</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>zero</td>
<td>zero</td>
</tr>
<tr>
<td></td>
<td>above</td>
<td>below</td>
</tr>
<tr>
<td><strong>Pool area</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>zero</td>
<td>0.58</td>
<td>0.71</td>
</tr>
<tr>
<td>zero above</td>
<td>0.42</td>
<td>0.56</td>
</tr>
<tr>
<td>zero below</td>
<td>0.51</td>
<td>0.65</td>
</tr>
<tr>
<td>one rate</td>
<td>0.47</td>
<td>0.62</td>
</tr>
<tr>
<td>two rates</td>
<td>0.32</td>
<td>0.44</td>
</tr>
<tr>
<td><strong>Unique</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>zero</td>
<td>0.38</td>
<td>0.44</td>
</tr>
<tr>
<td>zero above</td>
<td>0.05</td>
<td>0.06</td>
</tr>
<tr>
<td>zero below</td>
<td>0.55</td>
<td>0.67</td>
</tr>
<tr>
<td>one rate</td>
<td>0.18</td>
<td>0.24</td>
</tr>
<tr>
<td>two rates</td>
<td>0.68</td>
<td>0.81</td>
</tr>
</tbody>
</table>
CURRICULUM VITAE

Catherine L. Hein

Work Address
Utah State University
Department of Watershed Sciences and The Ecology Center
UMC 5210
Old Main Hill
Logan, UT 84322-5210

Contact Information
435-797-2498
clhein@gmail.com

EDUCATION

2009 Ph.D. in Ecology, Watershed Sciences, Ecology Center, Utah State University. Advisor: Dr. Todd Crowl

2004 M.S. in Limnology and Marine Science, Center for Limnology, University of Wisconsin-Madison. Advisor: Dr. Jake Vander Zanden,

2002 B.S. in Zoology and Biological Aspects of Conservation with honors in the major and in the liberal arts, University of Wisconsin-Madison.

RESEARCH EXPERIENCE

2004-8 Watershed Sciences, Utah State University
As a research assistant for an NSF Biocomplexity grant, I examined the influence of natural and anthropogenic factors on fish and decapod community structure in tropical island streams at the Luquillo Long-Term Ecological Research (LTER) site in Puerto Rico.

2004-8 Luquillo LTER, University of Puerto Rico
I assisted with data collection for the long-term monitoring of shrimp populations in the Luquillo mountains, mentored undergraduate research projects, and attended annual meetings.

2002-4 Center for Limnology, University of Wisconsin-Madison
As a research assistant at the North Temperate Lakes LTER site, I assessed the efficacy of trapping to control an exotic rusty crayfish population and monitored for a community-level response to the removal.

2001 Center for Limnology, University of Wisconsin-Madison
For my senior honor’s thesis, I designed and implemented the removal of exotic rusty crayfish from Sparkling Lake, WI as part of the North Temperate Lakes Biocomplexity project. Mentor: Dr. John Magnuson

2000 Biological Station, Monteverde, Costa Rica
As an undergraduate, I studied the effects of morphological characteristics of flowers in the family Gesneriaceae on susceptibility to nectar robbery by hummingbirds. Mentor: Dr. Karen Masters

2000 Center for Limnology, University of Wisconsin-Madison
As an undergraduate, I studied the effects of substrate types on macroinvertebrate assemblages in Big Spring and Pickford Spring in Madison, WI. Mentor: Dr. John Magnuson
TEACHING AND MENTORING EXPERIENCE

2007 Instructor of record, Ecology for Majors, Utah State University Ecology 2220. This is the general ecology course required for all students that have a major in the biological sciences. I designed the syllabus, prepared and gave lectures to 77 students, wrote assignments and exams, graded with the help of a teaching assistant, and assigned final grades.

2007 Mentor of Research Experience for Undergraduates recipient, University or Puerto Rico. Valerie Shoepfer conducted experiments to test the identity and quantity of elements that leach out of fresh and senesced tree leaves after they fall into a stream.

2007 Watershed Analysis teaching assistant, Utah State University WATS 4950/6900. I was responsible for preparing, teaching and grading laboratory exercises that would introduce students to ArcGIS. The lessons that I prepared taught students to find GIS data sets and develop skills pertinent to watershed analysis (e.g. delineate a watershed and calculate stream lengths, slope, road densities, percentages of land cover, etc.).

2006 Mentor of Research Experience for Undergraduates recipient, Colorado State University. Sarah Redd studied the population of a large freshwater shrimp (*Macrobrachium carcinus*) in a Puerto Rican stream. She tested a variety of capture and marking methods and obtained population estimates and movement data.

2006 Mentor of Research Experience for Undergraduates recipient, University of Puerto Rico. Maria Ocasio Torres compared decapod assemblages in streams with and without predatory fishes.

2003 Head Limnology Lab teaching assistant, University of Wisconsin-Madison Zoology 316. The lab focused on limnological processes, collecting and analyzing water samples, experimental design, and scientific writing and presentations.


2002-3 Manager of three student hourlies for a rigorous field-based project examining part of North Temperate Lakes LTER and Biocomplexity.

2002 Limnology Lab teaching assistant, University of Wisconsin-Madison Zooology 316.

PUBLICATIONS


In Review


In Preparation


CONFERENCE PRESENTATIONS


Hein, C.L., B.M. Roth, M.J. Vander Zanden, and J.M. Magnuson. 2003. The removal of the rusty crayfish from Sparkling Lake, WI. Ecological Society of America, Savannah, GA.

INVITED PRESENTATIONS

2008 The role of natural and anthropogenic factors in structuring diadromous communities in tropical island streams. Seminar at Harvard University


2004 Is your lake a little rusty? Rusty crayfish in WI. WI Lakes Convention.

2003 Management options for rusty crayfish (Orconectes rusticus) in WI. WI DNR Lakes Quarterly Meeting.

2003 Progress report on the rusty crayfish removal in Sparkling Lake. Plum Lake Association Meeting, Vilas County, WI.

2002 Rusty crayfish recommendations. Plum Lake Association Meeting, Vilas County, WI.


2002 The history of limnology at UW-Madison and ongoing research. Wisconsin Idea Radio Program, WSUM 91.7 Student Radio.

AWARDS

2008 Graduate Student Senate Travel Award, Utah State University

2007 Ecology Center Research Award, Utah State University

2006 Graduate Student Senate Travel Award, Utah State University

2004 Research Vice President Fellowship, Utah State University

2003 John Jefferson Davis Travel Award, University of Wisconsin-Madison
2003  Anna Grant-Birge Memorial Award, University of Wisconsin-Madison
2003  NIH Grant for a short course at the University of Tennessee titled Introduction to the Mathematics of Biological Complexity
2001  Research Experience for Undergraduates Fellowship, University of Wisconsin-Madison

SERVICES
2006 – 2008 selected and hosted guest speakers as a graduate student on the Ecology Center Committee

REVIEWER FOR
Aquatic Living Resources
Biological Conservation
Biological Invasions

SOCIETY MEMBERSHIP
Association for Tropical Biology
American Fisheries Society
Ecological Society of America
North American Benthological Society

REFERENCES
Todd A. Crowl, facrowl@gmail.com, 435-760-1335
Alan P. Covich, a.covich@gmail.com, 706-542-6006
M. Jake Vander Zanden, mjvanderzand@wisc.edu, 608-262-9464
John J. Magnuson, jjmagnus@wisc.edu, 608-262-3010