A MIGRATORY SHRIMP'S PERSPECTIVE ON HABITAT FRAGMENTATION IN THE NEOTROPICS: EXTENDING OUR KNOWLEDGE FROM PUERTO RICO

BY

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ABSTRACT

Migratory freshwater fauna depend on longitudinal connectivity of rivers throughout their life cycles. Amphidromous shrimps spend their adult life in freshwater but their larvae develop into juveniles in salt water. River fragmentation resulting from pollution, land use change, damming and water withdrawals can impede dispersal and colonization of larval shrimps. Here we review current knowledge of river fragmentation effects on freshwater amphidromous shrimp in the Neotropics, with a focus on Puerto Rico and Costa Rica. In Puerto Rico, many studies have contributed to our knowledge of the natural history and ecological role of migratory neotropical shrimps, whereas in Costa Rica, studies of freshwater migratory shrimp have just begun. Here we examine research findings from Puerto Rico and the applicability of those findings to continental Costa Rica. Puerto Rico has a relatively large number of existing dams and water withdrawals, which have heavily fragmented rivers. The effects of fragmentation on migratory shrimps' distribution have been documented on the landscape-scale in Puerto Rico. Over the last decade, dams for hydropower production have been constructed on rivers throughout Costa Rica. In both countries, large dams restrict shrimps from riverine habitat in central highland regions; in Puerto Rico 27% of stream kilometers are upstream of large dams while in Costa Rica 10% of stream kilometers are upstream of dams. Research about amphidromy specific to non-island shrimps is increasingly important in light of decreasing hydrologic connectivity.

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INTRODUCTION

Migratory shrimps are an important component of the aquatic fauna in many regions of the new and old world tropics (Pringle et al., 1993; Crowl et al., 2001). Many migratory shrimp are amphidromous, living primarily in freshwater but dependent on saltwater for parts of their life cycle (Chace & Hobbs, 1969). Adult shrimp spawn in freshwaters, and then larval shrimp passively drift from upstream freshwater reaches to salt water where they develop into juveniles. They then migrate back upstream, where they spend the majority of their lifetime. Migratory shrimps play an important part in stream food webs and ecosystem function, particularly as organic matter processors (i.e., leaf "shredders" and algal consumers). In addition, they are conduits for movement of energy and matter between marine and freshwater systems.

Freshwater migratory shrimps can be negatively affected by river fragmentation, which occurs when rivers lose hydrological connectivity where dams, water withdrawals or water pollution create un-passable stream reaches for downstream drift of shrimp larvae or upstream juvenile migration (Holmquist et al., 1998; Pringle & Scatena, 1999b). Research on effects of fragmentation on migratory stream biota has been heavily concentrated in temperate regions and overwhelmingly biased towards fishes (Pringle et al., 2000; March et al., 2003). Nevertheless, tropical rivers are becoming increasingly fragmented, with losses in connectivity threatening the long-term persistence of migratory shrimps (Greathouse et al., 2006a). The relatively little knowledge of general shrimp ecology and limited information on the effects of river fragmentation in the tropics makes predicting shrimp response to river fragmentation more challenging. The exception to this case is Puerto Rico, where decades of research has examined the ecology of freshwater migratory shrimps and documented the impacts of fragmentation on their distribution and abundance (fig. 1; Pringle et al., 1993; Holmquist et al., 1998; Crowl et al., 2001).

We suggest that lessons from Puerto Rico may provide insights for other Neotropical regions inhabited by migratory shrimps that are under similar increasing pressure for river development. Here, we review what is known about the ecology and migratory behavior of shrimps in Puerto Rico and summarize effects of river fragmentation. We then use Costa Rica as a case study to test the broad applicability of this knowledge to other tropical countries.

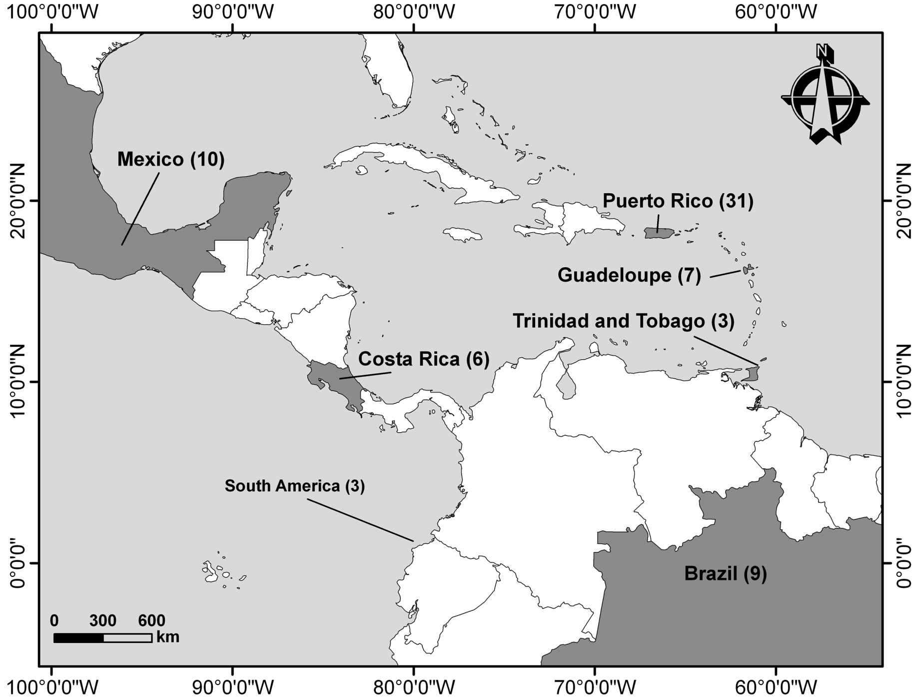

Fig. 1. Number of scientific publications on freshwater shrimp per region through 2009, found using the Web of Science search engine which did not include strictly regional journals.

HABITAT FRAGMENTATION AND SHRIMP: LESSONS FROM PUERTO RICO

Dams and water withdrawals have fragmented nearly all rivers in Puerto Rico. Contrary to most other tropical regions, over the period (1940-50) Puerto Rico exhibited an accelerated shift from an agricultural to an industrial based economy because of its association as a commonwealth of the United States (Grau et al., 2003). This rapid industrialization was accompanied by hydropower dam construction, which peaked in the 1950s (Pringle & Scatena, 1999a). Today, Puerto Rico has three times the number of large dams per unit land area as the continental United States and more dams than any other Caribbean island (Greathouse et al., 2006a). On the basis of a 1:100 000 scale stream network, we estimate that 27% of stream kilometers are upstream from large dams in Puerto Rico (fig. 2). Puerto Rico also has many small dams associated with water withdrawal for human consumption. For example the 11 269 hectare Caribbean National Forest (CNF), which is managed as a multi-usage area, contains 34 small dams and associated water withdrawal structures.

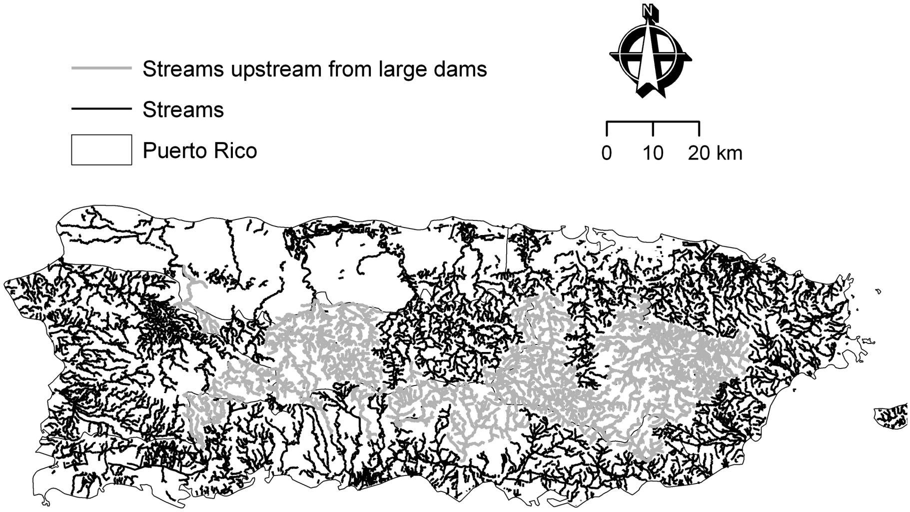

Fig. 2. Using 1:100 000 scale maps of rivers and streams from the United States National Atlas and a published map of large dams we calculate that 27% of stream kilometers are upstream of large dams (Greathouse, 2006a).

Both large and small dams in Puerto Rico affect distribution and abundance of shrimps, with 15 known species (table I; Holmquist et al., 1998). Dams impede upstream migration of shrimp juveniles and downstream drift of shrimp larvae to the estuary (Holmquist et al., 1998; Benstead et al., 1999; Greathouse et al., 2006a). They can also decrease successful recruitment of post-larval shrimp that rely on the signature of freshwater for migratory clues (March et al., 2003). Holmquist et al. (1998) found that dams >15 m tall, without spillway discharge (a structure which allows a limited quantity of water to flow over the dam), completely impeded upstream migration by juvenile shrimp, effectively extirpating shrimp populations above the dam. In contrast, dams >15 m tall, with intermittent spillway discharge, still allowed some shrimp to persist upstream from the dam (Greathouse et al., 2006a).

Dams <15 m tall directly affect in-stream biota by reducing suitable habitat, blocking access to suitable habitat, and causing direct and indirect mortality (March et al., 2003). Smaller dams are typically formed by a concrete wall (low-head dam) that creates a reservoir from which water is directly removed. The other less common structure is an "in-channel" water withdrawal system which pumps water out through risers and alters the physical environment much less than the typical low-head dam (March et al., 2003). Small low-head dams can impede upstream migration of juvenile shrimp when there is no spillway discharge, whereas in-channel intakes are less likely to cause

TABLE I
The decapod species of Puerto Rico (Holmquist 1998)

Decapod species
Macrobrachium faustinum
Micratya poeyi
Atya lanipes
Atya scabra
Xiphocaris elongata
Macrobrachium heterochirus
Potimirim mexicana
Atya innocuous
Potimirim americana
Epilobocera sinuatifrons
Macrobrachium acanthurus
Macrobrachium carcinus
Potimirim glabra
Macrobrachium crenulatum
Palaemon pandaliformis

mortality (March et al., 2003). According to a hydrological budget created for the CNF, on a typical day, water intakes collectively divert 70% of the mean flow generated within the CNF before it reaches the ocean (Crook et al., 2007). These water intakes reduce suitable habitat and many streams are dry during part of the year. In some cases, wastewater discharged below the water intakes is the only flowing water in streams during dry periods (Hunter & Arbona, 1995; Pringle & Scatena, 1999a).

Cumulative effects of dams in highly fragmented systems can impede the migration of shrimp to varying degrees. Approaches that consider cumulative effects of multiple barriers on connectivity at the river scale are rare but important for management of migratory fauna that spend most of their lives in freshwater. One example is the Index of Longitudinal Riverine Connectivity (ILRC) which was created to evaluate the relative level of connectivity or alteration of the streams in the Caribbean National Forest of Puerto Rico, through estimation of the probability that an individual shrimp will be able to migrate downstream to the estuary and return to the reach where it was released as a larvae (Crook et al., 2009). The CNF includes nine watersheds and at least thirty-four water intakes. The ILRC characterized nine of the streams as "low" connectivity, three of the streams as "moderate" connectivity and five streams as "high" connectivity. During drought years, some CNF streams are dry for most of the year and are more likely to become impermeable barriers to shrimp migration. When there is no water flowing over the dam, mortality of juvenile shrimps migrating upstream is 100%. If some minimum flow is maintained, the probability of upstream migration increases from "zero" to some probability. The ILRC illustrated that the maintenance of some minimum flow is the most important factor to ensure shrimp passage. Other studies have gone into further detail about ways to mitigate the impact of dams on shrimp migration by maintaining fish ladders, reducing abstraction during peak migration times and altering dam structures (Benstead et al., 1999; March et al., 2003).

Thus far we have only considered connectivity within the freshwater part of the shrimp life cycle. By having larvae that are dispersed through the marine system, shrimp have the ability to reach wider distributional ranges, and to recolonize freshwater streams following disturbance events (McDowall, 2004; Covich, 2006). Genetic analysis of mitochondrial DNA of seven amphidromous shrimp species (*Atya lanipes*, *Atya scabra*, *Atya innocous*, *Micratya poeyi*, *Micratya* sp., *Xiphocaris elongata*, and *Macrobrachium faustinum*) showed high gene flow in shrimp within and between drainages, highlighting the role of marine dispersal (Cook et al., 2009). Marine dispersal may be the determining component in the genetic structure and connectivity of shrimp species island-wide and underscores the advantages of obligate amphidromy. The majority of river fragments upstream from large dams are concentrated in the central highland region of Puerto Rico (fig. 2); if flow were restored, shrimps would have the potential to recolonize streams where they had been extirpated because of habitat fragmentation.

Understanding impacts of fragmentation on shrimps, beyond just impeding movement and hindering migration, requires an appreciation of the important ecological role played by shrimps. In Puerto Rico, shrimps are highly abundant, regulate stream ecosystem processes, and structure the stream food web (Covich et al., 1999; Pringle et al., 1999; Crowl et al., 2001; March et al., 2001). For example, Pringle (1996) found that atyid shrimps both significantly reduced the algal standing crop and altered the species composition of algae. Atyid and xiphocarid shrimps have also been found to reduce the fine particulate organic matter and increase the nutrient quality of the epilithon (Pringle et al., 1999). Shrimps in Puerto Rican streams have also been shown to increase leaf decomposition rates (Crowl et al., 2001; March et al., 2001). Shrimps not only directly affect primary production and decomposition, they also affect the macroinvertebrate community by depressing populations of several taxa including chironomids (Pringle et al., 1993). In high densities shrimp can be a key component in maintaining stability of stream ecosystem processes (Pringle et al., 1999; Crowl et al., 2001). In areas where shrimp have been extirpated (i.e., upstream from dams >15 m with no spillway discharge), instream ecosystem processes change significantly. The consequences of shrimp extirpation include greater algal standing crop, and more fine benthic organic and inorganic matter of a lesser quality (Greathouse et al., 2006a).

COSTA RICA CASE STUDY

In this section we examine whether insights that we have gained from Puerto Rico about the ecology of migratory shrimps and the effects of river fragmentation are applicable to other Neotropical shrimp populations. Freshwater migratory shrimps in other Neotropical countries are increasingly facing some of the same threats to their long-term viability as the shrimp fauna in Puerto Rico (Greathouse et al., 2006a). Costa Rica provides a case study on the basis of the fact that (1) there is good general knowledge of ecology of Costa Rican rivers and (2) the country is in the midst of a wave of hydropower development that has fragmented rivers that harbor migratory shrimps.

Local environmental differences can alter the life history of shrimp species and pose different conservation concerns. Two differences in the natural history and ecology of shrimps between Puerto Rico and Costa Rica are noteworthy. First, the Costa Rican shrimp fauna is composed of 17 shrimp species, the distribution of which relates to the country's central volcanic mountain range (table II). All shrimp species in both Puerto Rico and Costa Rica are known to be amphidromous (Chace & Hobbs, 1969). Of the 15 shrimp species found in Puerto Rico, six also occur in Costa Rica. Four of these (*M. acanthurus*, *M. heterochirus*, *M. crenulatum*, and *M. carcinus*) have only been found on the Caribbean slopes. The other two (*Atya scabra* and *A. innocuous*) have a more universal distribution and occur on both the Pacific and Caribbean slopes.

Second, in Puerto Rican streams, shrimps reach such high densities as to be considered the dominant macrofauna, whereas in Costa Rican streams, shrimps occur at a lower density and fish are considered to be dominant. The occurrence and density of shrimp fauna in Puerto Rico and Costa Rica is variable, depending on the size of the stream, the distance to the estuary and other factors such as density of predators. In Puerto Rico, in predator-free stream reaches upstream of waterfalls (which serve as barriers to predatory fish but not shrimp), the density of *Xiphocaris* shrimp can reach $10/m^2$ and *Atya* shrimp $16/m^2$; below waterfalls (in predator-rich reaches) the mean density of shrimps has been estimated at $0.2/m^2$ for *Xiphocaris* and $0.3/m^2$ for *Atya*

TABLE II

The freshwater shrimp species that occur on the Atlantic, Pacific or both slopes of Costa Rica (Obregon, 1986). * Indicate species that also occur in Puerto Rico

Atlantic	Pacific	Both
*Macrobrachium acanthurus**	*Macrobrachium tenellum*	*Atya scabra**
*Macrobrachium heterochirus**	*Macrobrachium occidentale*	*Atya crassa*
Macrobrachium olfersi	*Macrobrachium digueti*	*Atya innocous**
*Macrobrachium carcinus**	*Macrobrachium hancocki*	
Macrobrachium amazonicum	*Macrobrachium americanum*	
*Macrobrachium crenulatum**	*Macrobrachium Panamense*	
	Atya margaritacea	
	Palaemon gracilis	

(Covich et al., 2009). *Macrobrachium* spp. can vary in density from 1-5 per pool, with mean pool area being 75.7 m^2 (Covich et al., 2006). These lower densities are comparable to estimates of *Macrobrachium* spp. populations (0.2/m^2) from lowland stream reaches in Costa Rica (Snyder, unpub. data).

Rivers in Costa Rica, as well as other Central and South American countries, are being targeted for new dam construction (Anderson et al., 2006a). Since 1990, $>$30 small to medium sized hydropower plants have been built in Costa Rica (Anderson et al., 2006b). Many hydropower plants operate as water diversion dams, where water is diverted from the river to an off-channel reservoir and then through a turbine house, before it is discharged again into the stream (Anderson et al., 2006a). Operation leaves a reach with highly reduced flow downstream from the diversion dam. The size of the dam and geographic relief of the landscape are factors that affect the length of the reach, but the dewatered reach in general ranges from 1-7 km for many Costa Rican diversion dams (Anderson et al., 2006b).

APPLICABILITY OF LESSONS LEARNED FROM PUERTO RICO

Lesson 1. — On the basis of studies from Puerto Rico, whether water passes over a dam and how frequently it does is important to connectivity from a shrimp's perspective. Large dams without spillway discharge are making streams impassable to migratory shrimp. Maintaining some minimum flow is the most important variable for maintaining connectivity in shrimp populations in Puerto Rico. A few studies suggest this lesson may be true for shrimp in Costa Rica as well. In the Sarapiquí River drainage on the northern Atlantic slope, Costa Rica, shrimp populations were quantified with shocking and snorkel surveys near two small dams in 2001 during the wet and dry seasons (E.P.A., unpublished data; Anderson et al., 2006a). One dam, on the Puerto Viejo River, is 8 m tall and has a 4 km dewatered reach directly downstream of the dam which is maintained with a minimum flow of ∼10% of the average annual river discharge. The other dam is ∼3 m and is located on a tributary to the Puerto Viejo River, with a dewatered reach of 2 km. The mean annual discharge of the Puerto Viejo River and Quebradon stream at the site of the dam was 8.5 m^3/s and 1 m^3/s respectively, based on historical records over the period 1960-1990 (Anderson et al., 2006a). Both of these dams get overtopped during periods of high discharge during frequent storm events; this happens more frequently at the smaller dam. At the smaller dam (3 m), there was no difference in shrimp abundance above or below the dam, whereas at the taller dam (8 m) far fewer shrimp were found upstream from the dam than below the dam (fig. 3). The downstream end of the dewatered reach contained an order of magnitude more shrimp than other reaches of the stream.

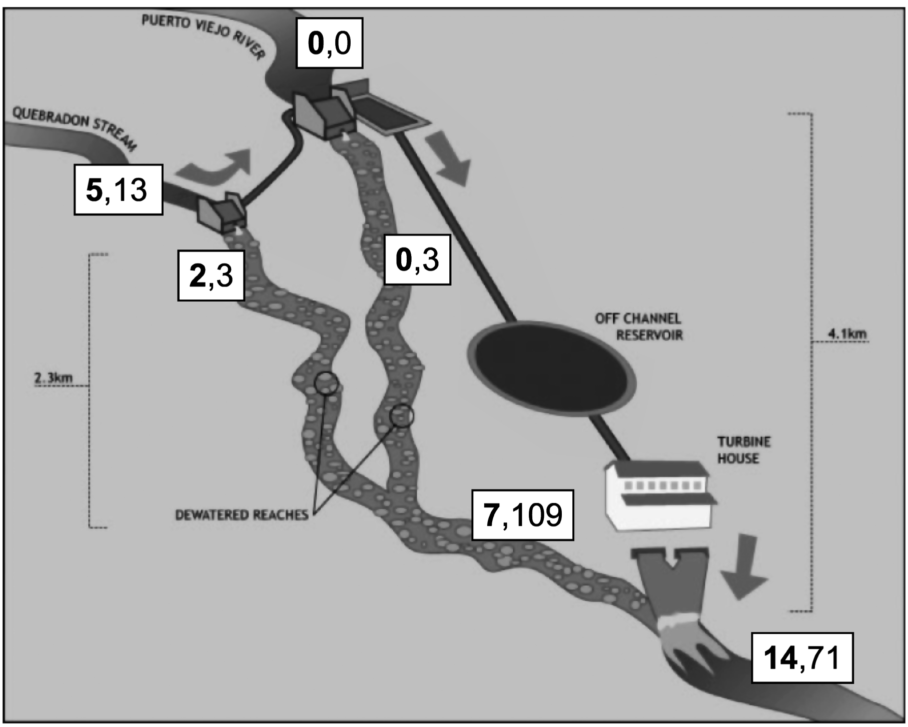

Fig. 3. Density of *Atya* and *Macrobrachium* shrimps collected by snorkeling and electrofishing surveys above and below the Quebradon (3 m) and Dona Julia (8 m) dams on the Quebradon stream and Puerto Viejo River in Sarapiqui, Costa Rica. Black boxes represent *Macrobrachium* spp. and grey boxes indicate *Atya* spp.

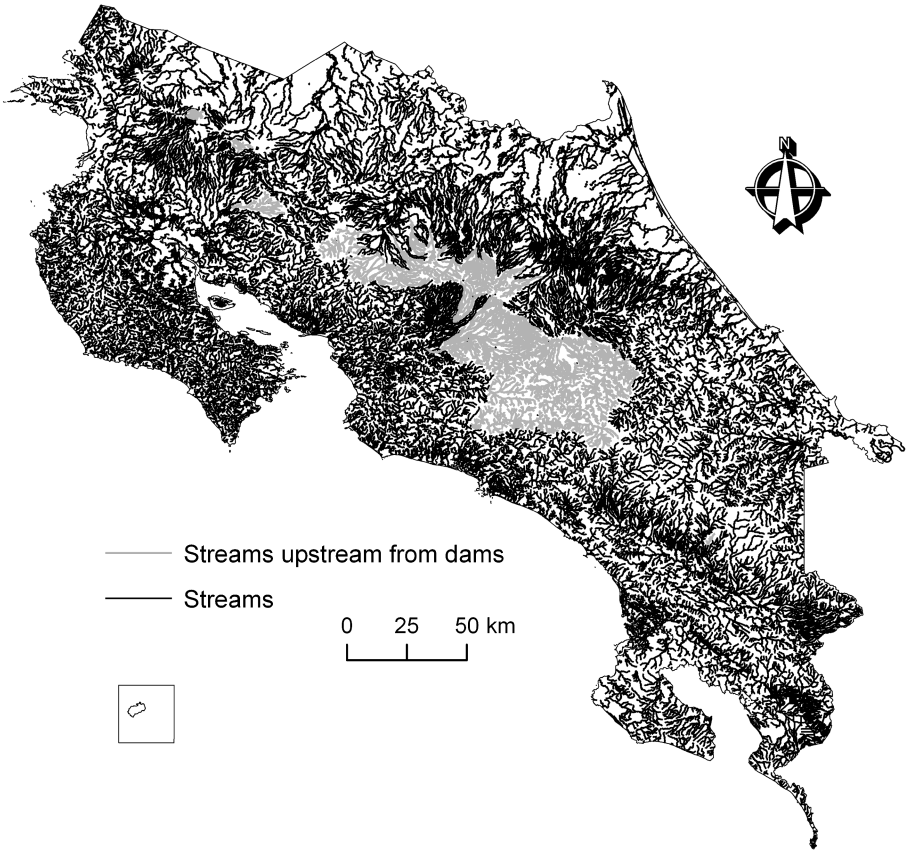

Fig. 4. Using 1:50 000 scale maps of rivers and streams from the Atlas Costa Rica we calculate that 10% of stream kilometers are upstream of large dams.

Lesson 2. — Much like Puerto Rico (7% in protected areas), very few rivers in Costa Rica are protected from the estuary to the headwaters. To characterize the length of streams potentially off-limits to migratory shrimp as a result of hydropower development in Costa Rica, we used a geographic information system to measure the number of stream kilometers upstream and downstream of dams nationwide at the 1:50 000 scale. Approximately 10% of total Costa Rican stream kilometer length is presently upstream from dams (fig. 4). This is a smaller proportion of the total stream length than in Puerto Rico (27%), but in both areas the spatial location of the fragmented stream reaches upstream of large dams is in the central highlands. To further examine river fragmentation in Costa Rica, we quantified the number of stream kilometers within national parks that are protected from hydropower development. Twenty-seven percent of Costa Rican land is located in protected areas but most of this land is

TABLE III
The percentage of stream kilometers in national parks in seven elevational bands in Costa Rica

Elevation (m)	% in park	% of total stream length
0-500	19	44.57561937
501-1000	42	24.95530437
1001-1500	49	15.52169264
1501-2000	64	9.103736272
2001-2500	82	5.205147832
2501-3000	0	0.217288801
3001-3700	81	0.421210713

at higher elevations which leaves lowland rivers and streams relatively more vulnerable to fragmentation than those at higher elevations (table III).

The relationship between marine dispersal and population connectivity between watersheds has yet to be examined in Costa Rica. Compared to Puerto Rico's almost uniformity of short, steep streams, Costa Rica has a high diversity of river types, including steep mountain streams and meandering lowland rivers. On average, the migratory distances a shrimp would need to travel upstream to reach a fish-barrier waterfall is much longer in Costa Rica than in Puerto Rico (∼14 km in Puerto Rico vs. >60 km in Costa Rica). Continental estuaries are larger than those of Caribbean islands, which might influence the estuary retention time and create longer travel distances of amphidromous species. The levels of hydrologic connectivity at which viable shrimp populations can be maintained are likely to be different among species and between island and mainland populations. In Costa Rica, maintaining the same level of integrity of shrimp populations could require more free-flowing protected rivers than in Puerto Rico.

Lesson 3. — Shrimps in Puerto Rico are key components of ecosystems, and ecosystem processes are altered in areas upstream of dams where shrimp no longer persist (Pringle et al., 1993; Covich et al., 1999; Greathouse et al., 2006b). In Costa Rica, the impact of shrimps' absence on general ecosystem processes may be less severe than in Puerto Rico. Although shrimps in Costa Rica have been shown to reduce inorganic sediment mass, organic ash free dry mass, and densities of macroinvertebrate insects (Pringle & Hamazaki, 1998), they are less abundant than shrimps in Puerto Rico and part of a much more diverse freshwater fauna. Including introduced species, 174 fishes have been reported from Costa Rican freshwater ecosystems (Froese & Pauly, 2009). While the native fish fauna of Puerto Rican ($n = 70$) is composed of all migratory fish, the Costa Rican fish fauna contains many non-migratory species and potentially predatory species (Greathouse et al., 2006b).

FUTURE RESEARCH DIRECTIONS

We propose four potential future research directions that could significantly increase our understanding of shrimp populations and their viability in the face of increasing river fragmentation. First, what are the biological factors that affect the seasonal and daily migration patterns of upstream and downstream migration of different species? Second, how do other sources of river fragmentation such as harvesting and decreased water quality from wastewater or agricultural run-off affect shrimp populations? Third, there is a need for greater understanding of cumulative effects of river fragmentation on shrimp populations. Fourth, we recommend use of population genetic techniques to examine the extent that marine dispersal is determining the genetic make-up of continental fauna and the connectivity of shrimp populations across watersheds.

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