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A method to assess longitudinal riverine connectivity in tropical streams dominated by migratory biota[†]

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ABSTRACT

1. One way in which dams affect ecosystem function is by altering the distribution and abundance of aquatic species.

2. Previous studies indicate that migratory shrimps have significant effects on ecosystem processes in Puerto Rican streams, but are vulnerable to impediments to upstream or downstream passage, such as dams and associated water intakes where stream water is withdrawn for human water supplies. Ecological effects of dams and water withdrawals from streams depend on spatial context and temporal variability of flow in relation to the amount of water withdrawn.

3. This paper presents a conceptual model for estimating the probability that an individual shrimp is able to migrate from a stream's headwaters to the estuary as a larva, and then return to the headwaters as a juvenile, given a set of dams and water withdrawals in the stream network. The model is applied to flow and withdrawal data for a set of dams and water withdrawals in the Caribbean National Forest (CNF) in Puerto Rico.

4. The index of longitudinal riverine connectivity (ILRC), is used to classify 17 water intakes in streams draining the CNF as having low, moderate, or high connectivity in terms of shrimp migration in both directions. An in-depth comparison of two streams showed that the stream characterized by higher water withdrawal had low connectivity, even during wet periods. Severity of effects is illustrated by a drought year, where the most downstream intake caused 100% larval shrimp mortality 78% of the year.

5. The ranking system provided by the index can be used as a tool for conservation ecologists and water resource managers to evaluate the relative vulnerability of migratory biota in streams, across different scales (reach-network), to seasonally low flows and extended drought. This information can be used to help evaluate the environmental tradeoffs of future water withdrawals.

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KEY WORDS: riverine connectivity; dams; water withdrawals; tropical streams; migratory biota; shrimps; Puerto Rico

INTRODUCTION

Longitudinal connectivity between upstream and downstream reaches (in both directions) plays a key role in structuring stream ecosystems. Dams and other hydrologic alterations disrupt this connectivity, affecting the transport of matter, energy and organisms (Dynesius and Nilsson, 1994; Ward and Stanford, 1995; Postel *et al*., 1996; Pringle, 1997[†]) and there is increasing concern that this is having negative influences on the biological integrity of riverine ecosystems and landscapes that they drain (Poff *et al*., 1997; Pringle, 2000, 2001; Pringle *et al*., 2000a; Rosenberg *et al*., 2000; Bunn and Arthington, 2002; Freeman *et al*., 2003; Greathouse *et al*., 2006a).

Methods for assessing hydrologic alteration have focused primarily on evaluating effects of altered discharge below a dam. For example, indicators of hydrologic alteration (e.g., IHA, Richter *et al*., 1996, 1998) focus on the downstream

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intra-annual changes in flow regime due to hydrologic perturbation. Other methods, such as the widely used Instream Flow Incremental Methodology (Stalknaker *et al*., 1995), translate hydrologic alteration into changes in habitat regimes in flow-regulated systems. These assessments of hydrologic alteration have evaluated effects of dams on flow variability and habitat quality downstream of dams; however, approaches that consider the cumulative effects of dams on connectivity (in both upstream and downstream directions) are less common (but see Kareiva *et al*., 2000). This is especially important for tropical streams dominated by migratory fauna that spend most of their lives in fresh water.

This paper presents an approach to evaluate both upstream and downstream effects of dams and water withdrawals on longitudinal connectivity in tropical streams dominated by shrimps. This paper focuses on a region of Puerto Rico (the Caribbean National Forest (CNF)) where long-term hydrological and climate data are available. The approach is tailored to reflect the physical and biological nature of these neotropical streams, which are characterized by minimal stream–groundwater and stream–floodplain interactions. Therefore, longitudinal (upstream–downstream) connectivity (as opposed to lateral (stream-floodplain) or vertical (stream-groundwater) connectivity, *cf* Ward, 1989) most greatly affects biological processes. An index of longitudinal riverine connectivity was developed that considers effects of dams and water withdrawals on transport of migratory biota in both upstream and downstream directions. Connectivity is defined here from an organismal perspective, using migratory shrimps as focal taxa (Lambeck, 1997). This paper builds on previous studies by combining long-term stream flow and water extraction data (Crook, 2005; Crook *et al*., 2007) with data on effects of water withdrawals on shrimp migration and mortality (Benstead *et al*., 1999, 2000). The application of this approach is illustrated by assessing the relative connectivity of two streams within the CNF.

This paper does not describe or predict biological responses to changes in longitudinal riverine connectivity. Rather, it illustrates an approach for comparing the relative vulnerability of streams across different scales (reach-network) to seasonal low flows and extended droughts that result in the mortality of migratory biota. This information can then be used by conservation ecologists and water resource managers to determine the environmental tradeoffs of future water withdrawals and to help direct the location, size, and design of future water intakes, especially in catchments that are already subject to large water withdrawals.

Study site

The Caribbean National Forest (CNF; 11 269 ha) is located in north-eastern Puerto Rico, and provides an ideal opportunity to evaluate effects of water intakes on longitudinal connectivity in neo-tropical streams because of the availability of long-term hydrologic and climate data for streams dominated by migratory biota. Nine streams drain the CNF within seven major catchments. These catchments are physically characteristic of montane streams in the Caribbean. Physical habitat of headwater streams is characterized by steep gradients, large boulders with coarse interstitial sediment, and alternating pools and cascades (Ahmad *et al*., 1993). Precipitation is orographic in origin and varies both throughout the year and inter-annually. Rainfall and stream discharge generally peak in May and November, and March has the least rainfall and lowest stream discharge. Flood flows are common, with discharge increases up to 10-fold in less than an hour (Covich and McDowell, 1996). Headwater streams are forested, whereas low-elevation streams are surrounded by urban, suburban, industrial and agricultural land (Pringle *et al*., 2000b). There are at least 34 water intakes on streams draining the CNF (Figure 1), to provide municipal water supplies for the surrounding area. These intakes directly affect in-stream biota by reducing usable habitat (Scatena and Johnson, 2001), blocking access to usable habitat (Benstead *et al*., 1999) and causing direct and indirect mortality (March *et al*., 1998; Benstead *et al*., 1999). On a typical day these intakes collectively divert 70% of the flow generated within the CNF before it reaches the ocean, or approximately 66.4 million gallons per day (Crook *et al*., 2007).

Streams in the CNF have six species of fish, two native species of grazing neritinid gastropods (i.e. snails), more than 60 species of aquatic insects, and 11 species of decapod crustaceans (Covich and McDowell, 1996). The grazing goby (*Sicydium plumieri*), shrimps and crabs are found above major waterfalls (Scatena and Johnson, 2001). The shrimp families, Atyidae and Xiphocarididae, are key facilitators of in-stream ecological processes in mid- and high-elevation streams. They are important for organic matter processing and determining benthic insect and algal community composition (Pringle *et al*., 1993, 1999; Pringle and Blake, 1994; Pringle, 1996; Crowl *et al*., 2001; March *et al*., 2001, 2002). Three genera of shrimps exhibit highest abundance: *Macrobrachium*, *Atya*, and *Xiphocaris* (Scatena and Johnson, 2001). These shrimps are amphidromous: they spend most of their lives in fresh water, but spend larval stages in estuaries and/or coastal waters (Chace and Hobbs, 1969; Hunte, 1978; March *et al*., 1998).

METHODS

Rationale

This index is focused on migratory shrimps because: (1) they dominate faunal biomass in streams (Covich, 1988; Covich *et al*., 1991); (2) their migratory range encompasses the stream network from estuaries to upper reaches (March *et al*., 1998); and (3) they play an important role in regulating ecosystem processes such as algal standing crop accrual, decomposition, and nutrient cycling (Pringle, 1996; Pringle *et al*., 1999; Crowl *et al*., 2001; March *et al*., 2001, 2002; Greathouse *et al*., 2006a,b).

Effects of water withdrawal were evaluated individually for different stages of the shrimp life-cycle because water withdrawal affects larval and juvenile shrimps differently. However, it is the combination of effects on different life stages that determines overall effects of water withdrawal on shrimps. Cumulative effects of multiple dams on a stream reach may also differentially affect stages in the shrimp life-cycle and shrimps overall. Therefore, it is the combination of these factors that determines the overall effect of water withdrawal on longitudinal riverine connectivity.

Larvae are released in headwater streams and drift passively to the estuary where they remain for approximately 50–100 days (Chace and Hobbs, 1969; Hunte, 1978). Temporal

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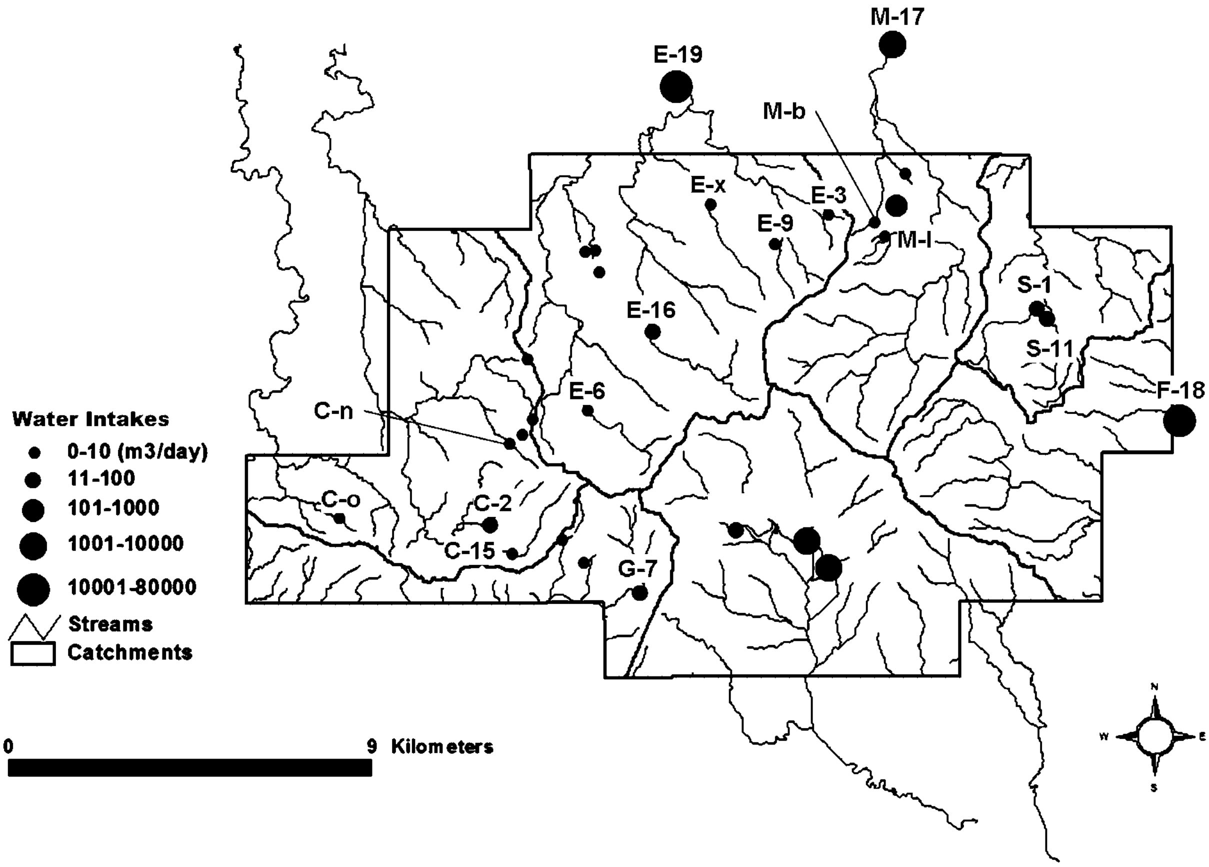

Figure 1. Intakes on streams draining the CNF. Intakes labelled are evaluated using the ILRC. Catchments are delineated in black and intakes are depicted with solid circles. Circle size corresponds with estimated water withdrawal capacity. Catchments, from left, are: Canovanas/Loiza, Espiritu Santo, Mameyes, Sabana, Fajardo, Blanco, Gurabo.

variation in release of larvae is not well understood; however, it is known that larvae reach peak drift densities at night (March *et al*., 1998). It has also been hypothesized that larvae are released year-round, with a greater number of larvae released during wetter months (Scatena and Johnson, 2001). Because larvae drift passively and are presumably uniformly mixed in the water column, it was assumed that the proportion of larval mortality, due to water withdrawal, reflects the proportion of water withdrawn. In accordance with this assumption, the measure of the effect of water withdrawal on larval shrimps is based on the proportion of the Q50 (amount of flow equalled or exceeded 50% of the time, or the median flow) withdrawn, based on long-term data.

After larvae reside in the estuary, they moult and return to fresh water as juveniles. Juveniles are able to scale large waterfalls to reach headwater streams, and accordingly can climb over impoundments such as low-head dams as long as there is some amount of flow over the impoundment (Benstead *et al*., 2000). Juveniles appear to receive a migration cue from flowing water, and a lack of flow over an impoundment constitutes a complete barrier to migration (Hamano and Hayashi, 1992; Holmquist *et al*., 1998; Benstead *et al*., 1999). When juveniles are unable to migrate beyond an impoundment in low-elevation reaches, they are vulnerable to predatory fish and birds, resulting in juvenile shrimp mortality that is directly related to water withdrawals (Benstead *et al*., 1999). Therefore, the measure of the effect of water withdrawal on juvenile shrimps is based on the proportion of days with discharge over an intake.

Overall, this index aims to estimate the probability that an individual 'average' shrimp will be able to migrate downstream to the estuary and return to the reach where it was released as a larva. Therefore, the percentage of the Q50 remaining in the stream after a withdrawal is used to estimate the probability that the average larva will pass downstream because this estimates the flow remaining in streams on a typical day. The percentage of days with flow over an impoundment is used to estimate the probability that the average juvenile shrimp will be able to migrate upstream. If a shrimp arrives at a dam ready to migrate upstream, the probability that it will be able to do so is equal to the probability that there will be flow over the dam, or the percentage of days with flow over the dam.

Calculations

Percentage exceedance (Pex) was calculated using daily runoff data for the period of record for seven USGS stream gauges. USGS gauges used were: 50075000 (Blanco), 50065500 (Mameyes), 50071000 (Fajardo), 50063800 (Espíritu Santo), 50057000 (Gurabo), 50067000 (Sabana), and 50061800 (Grande de Loiza/Canovanas). Percentage exceedance is the percentage of time that a certain flow is equalled or exceeded (Dunne and Leopold, 1978). In order to calculate *Pex*, average daily flow events for the period of record were ranked in order

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from greatest to least, and applied to the following equation:

$$Pex = m/(N+1) \tag{1}$$

where N = number of events and m = rank.

$Q50$ is the flow equalled or exceeded 50% of the time, or the median flow. To adjust $Q50$ to the area draining into a particular dam, flow (Q) was divided by the area draining into the stream gauge. This number was multiplied by the area draining into the intake (determined using the X-tools extension in ArcView 3.2a™) to obtain $Q50$ draining into the intake in cubic metres per day ($m^3\ day^{-1}$). Water removed via an upstream intake reduces the amount of water flowing into the next intake. Therefore, estimated water withdrawal (in $m^3\ day^{-1}$) for a given intake and all upstream intakes was subtracted from $Q50$ to determine the proportion of water remaining in a given stream after water withdrawal. The proportion of $Q50$ remaining corresponds with larval survival on a typical day.

$$\Pr D_k = \left[Q50_k - \sum_{i=1}^{x}(X_i)\right] \Big/ Q50_k \tag{2}$$

where $\Pr D_k$ = probability of downstream larval passage of intake k, X_i = water withdrawal ($m^3\ day^{-1}$) at intake i, and x = number of dams upstream from and including k.

The percentage exceedance curve was used to find the Pex value that equals the volume of water withdrawal. This indicates the flow that is counteracted by water withdrawal, such that there is no water flow below the intake. This Pex equals the percentage of days with flow remaining below an intake.

$$\Pr U_k = Pex_{k=x} \tag{3}$$

where $\Pr U_k$ = probability of upstream juvenile passage at intake k, and $Pex_{k=x}$ = percentage of time that flow exceeds water withdrawal x at intake k.

Exception: water intakes that provide minimum flows are assumed to have zero effect on the upstream migration of juvenile shrimps. Therefore, such intakes are assigned a $\Pr U_k$ value of 1.

Calculating cumulative effects of water withdrawals in linear succession

In order to account for cumulative effects of water withdrawal from multiple intakes in linear succession, $\Pr D_k$ and $\Pr U_k$ for individual intakes were used to account for upstream and downstream effects of other intakes.

The probability of larval passage to the estuary is influenced by individual water intakes in addition to all downstream intakes. For example, if a larval shrimp were released above a series of three intakes, it would have to pass three intakes successfully to reach the estuary. Therefore, the probability that larvae will reach the estuary is the product of the probabilities of larval passage at each intake in linear succession.

$$\Pr DC_k = \prod_{k=1}^{y} \Pr D_k \tag{4}$$

where $\Pr DC_k$ = probability that larvae reach the estuary from above a given point (cumulative downstream passage), and y = number of intakes downstream from a given point.

The effect of water withdrawal on juvenile shrimps is influenced by individual intakes in addition to all downstream intakes. Where there are intakes in linear succession, juvenile shrimps may have to climb past all intakes in order to reach their ultimate habitat. In order to account for the lower probability that an individual juvenile shrimp will successfully scale multiple intakes, the proportion of days with flow for any downstream intake is multiplied by the proportion of days with flow for any upstream intake.

$$\Pr UC_k = \prod_{k=1}^{y} (\Pr U_k) \tag{5}$$

where $\Pr UC_k$ = probability that juveniles migrate past multiple intakes to a given point (cumulative upstream passage), and y = number of intakes downstream from a given point.

Calculating an index of longitudinal riverine connectivity (ILRC)

The effect of a particular water withdrawal on longitudinal riverine connectivity can be evaluated by combining effects of water withdrawal on larval and juvenile shrimps. Larvae require downstream transport to the estuary for advancement to the next life cycle, and juveniles similarly require access to freshwater reaches. Therefore, these two life-stages represent the longitudinal connectivity of streams from headwaters to estuaries. It is reasonable to assume that if either larvae or juveniles are blocked from required downstream or upstream movement, transport and movement of other important matter and/or organisms are also inhibited, therefore reducing longitudinal riverine connectivity.

The cumulative effect of individual water intakes on longitudinal riverine connectivity is quantified through an index of longitudinal riverine connectivity (ILRC). The index is calculated at each water intake (k):

$$ILRC = \Pr DC_k * \Pr UC_k \tag{6}$$

Establishing index classification

Previous studies of dam effects on shrimp abundance in Puerto Rico were evaluated in an effort to calibrate the ILRC. Holmquist *et al.* (1998) found that large dams (height >15 m) without spillway discharge are a complete barrier to shrimps. A small number of shrimps were found above dams with spillway discharge. Studies by Greathouse *et al.* (2006a) confirmed these findings.

N. Hemphill and E. García (formerly USDA Forest Service; unpublished data) found that dams significantly decreased species richness, diversity and density for migratory shrimps in both high- and low-elevation streams draining the CNF. All three of the above community variables were significantly higher in streams lacking dams than in those without dams within a given catchment. Furthermore, Hemphill and García (unpublished data) found that only three shrimp species persisted in catchments with three dams, and that the presence of a large dam at low elevation resulted in the loss of 72% of species.

There are many factors influencing the effect of water withdrawal on migratory shrimps, including intake size, location within a catchment, and number of intakes within a catchment. Information from previous studies is useful for general trends — for instance, large dams without spillway discharge are complete barriers to migration, and catchments with multiple dams have compromised community structure. However, the CNF lacks large dams, and all catchments draining the CNF (with the exception of Rio Fajardo) have three or more low-head dams. Therefore, it was most appropriate to arbitrarily assign qualitative classes of connectivity until more specific biological data are obtained.

Qualitative classes of high, moderate and low connectivity were assigned by dividing the ILRC score range into three groups: 0–0.33, 0.34–0.66, and 0.67–1. Therefore, 0–0.33 corresponds with low, 0.34–0.66 with moderate, and 0.67–1 corresponds with high connectivity. Similarly, Richter *et al.* (1998) suggested that arbitrary classes of hydrologic alteration adequately describe relative hydrologic alterations at the river network scale, especially in the absence of compelling ecological justification otherwise. The utility of this classification system lies in the relative comparison of intake effects.

Assumptions

An assumption is that the ILRC is related to biotic response to dams and water withdrawals. It is known, for example, that water withdrawals cause direct larval mortality and that longitudinal connectivity in both directions is eliminated above dams with no spillway discharge (Holmquist *et al.*, 1998; Greathouse *et al.*, 2006a). However, we do not know the threshold of connectivity at which the index would reflect negative effects on long-term shrimp abundance, diversity and distribution. The index proposed here is a first step towards an empirically tested and biologically calibrated index of longitudinal riverine connectivity.

In this study, larvae are assumed to be uniformly mixed throughout the water column. This is a reasonable assumption based on the work of March *et al.* (1998, 2003) and Benstead *et al.* (1999). However, larval density may vary with flow volume: some evidence suggests that adult shrimps may release more larvae during storm flows and/or in accordance with the lunar cycle (Scatena and Johnson, 2001). Females may also migrate to lower reaches to release larvae, so upper reaches may not be as affected by dams. The assumption of temporal uniformity in the release of shrimps is tempered by the fact that the index evaluates the percentage of the median flow diverted: if shrimp larvae density varies with flow volume, at least the index consistently compares the effect of water withdrawal at one flow volume.

This study also assumes no decrease in juvenile survival and migration regardless of flow volume. Evidence suggests that increased juvenile migration may coincide with storm flows (Scatena and Johnson, 2001). Also, very low flow over a dam may cause a 'bottleneck' of juveniles below the dam (Benstead *et al.*, 1999). As juveniles wait to scale the dam, they may be subject to a high rate of mortality due to predation. Low water quality may also act as a barrier to migrating juveniles; however, this index only considers the effects of dams and water withdrawal on shrimps. The index also assumes that reservoirs above dams impose no mortality or effects on juveniles. This index is designed for small water intakes; as the reservoirs behind these impoundments are small, they probably do not affect the upstream movement of juvenile shrimps. It is also assumed that freshwater withdrawals do not alter estuarine conditions required by larvae during their obligate estuarine stage.

CASE STUDY APPLICATION

The index was applied to water intakes on streams draining the CNF to illustrate the application of the ILRC. Although the ILRC was developed specifically for the streams of the CNF, this index is applicable to other systems. ILRC results for the CNF are given in Table 1 and illustrated in Figure 2. Of the 17 intakes evaluated in and around the CNF, five resulted in high, three in moderate, and nine in low longitudinal connectivity according to the ILRC (Figure 2). In general, very small

Table 1. Characteristics of 17 intakes draining the CNF and results of ILRC.

Intake	Stream	Withdrawal ($m^3\ d^{-1}$)	*DA* (ha)	*Q*50 ($m^3\ d^{-1}$)	Pr D_k	Pr U_k	Pr DC_k	Pr UC_k	ILRC
C-15	Cubuy	727	188	2178	0.66	0.95	0.66	0.95	0.63
C-2	Los Santos	2502	186	2153	0.00	0.42	0.00	0.42	0.00
C-n	La Motilla	2	38	440	1.00	1.00	1.00	1.00	1.00
C-o	spring	7	40	465	0.98	1.00	0.98	1.00	0.98
E-16	Espiritu Santo	3598	533	15758	0.77	0.99	0.10	0.58	0.06
E-19	Espiritu Santo	78680	3272	97482	0.13	0.59	0.13	0.59	0.08
E-3	Jimenez	709	33	979	0.27	0.64	0.04	0.38	0.01
E-6	Grande	56594	455	13458	0.00	0.11	0.00	0.11	0.00
E-9	Jimenez	946	103	3034	0.69	0.95	0.09	0.56	0.05
E-x	Grande	1001	183	5408	0.82	0.99	0.10	0.58	0.06
F-18	Fajardo	45452	3142	65600	0.31	1.00	0.31	1.00	0.31
G-7	Gurabo	4703	290	2129	0.00	0.22	0.00	0.22	0.00
M-17	Mameyes	18938	3724	173800	0.89	1.00	0.89	1.00	0.89
M-b	Tabonuco	0.5	33	1542	1.00	1.00	0.89	1.00	0.89
M-l	Linguete	68	16	759	0.91	1.00	0.81	1.00	0.81
S-1	Cristal	3002	283	6142	0.51	0.78	0.51	0.78	0.40
S-11	Sabana	3002	261	5677	0.47	0.75	0.47	0.75	0.35

The first letter of each intake indicates the catchment within which it is located: C = Grande de Loiza/Canovanas, E = Espíritu Santo, F = Fajardo, G = Gurabo, M = Mameyes and S = Sabana. DA is the catchment area draining to the intake (determined using the X-tools extension in ArcView 3.2a). *Q*50 = median flow. Pr D_k = probability that larvae pass an intake going downstream. Pr U_k = probability that juveniles pass intake going upstream. Pr DC_k = probability that larvae pass multiple intakes in linear succession going downstream. Pr UC_k = probability that juveniles pass multiple intakes in linear succession going upstream. *ILRC* = index of longitudinal riverine connectivity.

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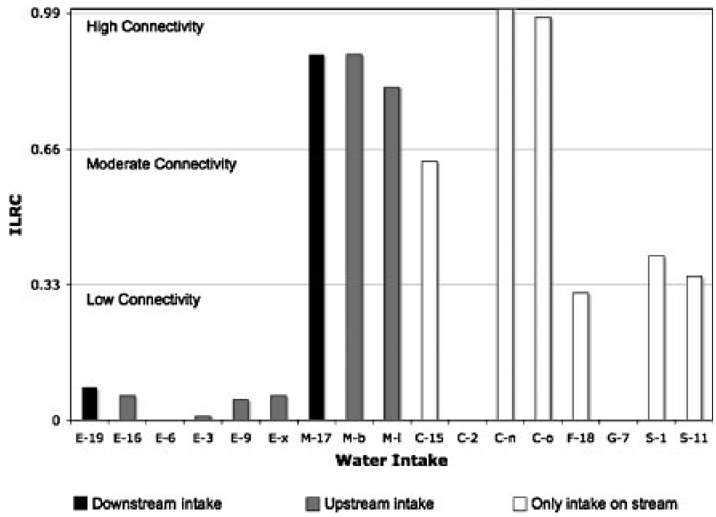

Figure 2. Results of ILRC for 17 water intakes on streams draining the CNF. Equation 6 is used to calculate ILRC; therefore, cumulative effects of intakes in linear succession are considered. Qualitative classifications of high, moderate and low longitudinal riverine connectivity are shown. Water intakes are labelled according to catchment: C = Canovanas/Loiza, E = Espíritu Santo, F = Fajardo, G = Gurabo, M = Mameyes, S = Sabana.

'within-forest' intakes had a small effect on shrimps; however, some intakes (especially those located upstream or downstream of another intake) had a strong effect on longitudinal connectivity. Larger intakes outside the CNF generally had a stronger effect on larval and juvenile shrimp migration. However, larger intakes with alternative withdrawal designs (M-17, F-18) had reduced impact on longitudinal connectivity. All intakes with little effect on connectivity had flow over their impoundment 100% of the time. Intakes resulting in moderate connectivity had flow over their respective impoundments 75–95% of the time. Intakes resulting in low connectivity had flow over their respective impoundments 11–99% of the time, and three of these diverted more than the median flow (Table 1).

An in-depth look at the Rio Mameyes and Rio Espíritu Santo catchments is given to demonstrate application of the ILRC and to compare a catchment with low water withdrawal (Rio Mameyes) to a catchment with high water withdrawal (Rio Espíritu Santo). The ILRC is also calculated for a drought, average, and wet year for each catchment to demonstrate inter-annual variations in vulnerability of shrimps to the effects of water withdrawal.

Average year calculations are based on the period of record at each gauge: 26 years for the Rio Mameyes stream gauge and 44 years for the Rio Espíritu Santo stream gauge. ILRC results for intakes on the Rio Mameyes range from 0.81 to 0.89 (high connectivity). ILRC results for intakes on the Rio Espiritu Santo range from 0 to 0.08 (low connectivity) (Table 2).

The ILRC was calculated for a wet year (1971) and a dry year (1994 — drought year that caused Puerto Rico to be declared an agricultural disaster area by the federal government) for comparison with the average year (Table 2). The ILRC was also calculated for the wettest (November) and driest (March) months within these years (Table 2). According to the index, larval density and juvenile shrimps are much more vulnerable to effects of water withdrawal within the Rio Espíritu Santo catchment than the Rio Mameyes catchment. All three intakes within the Rio Mameyes catchment fall into the category of high connectivity for both the wet and dry year. In addition, two Mameyes intakes have high connectivity during the driest month during a drought year, and the third intake is on the high end of moderate connectivity. In comparison, all of the Espíritu Santo intakes fall into the category of low connectivity for the driest month of a drought year (ILRC = 0 for all intakes). To illustrate the variation between wet months within wet years and dry months in dry years in the Espíritu Santo catchment, results for the E-19 intake (located at the base of the Espíritu Santo catchment) range from 0.69 (wet month of wet year) to 0 (dry month of dry year). Because this intake is located at the base of the catchment, it affects the connectivity of the entire catchment. Except during months with very high stream flow (e.g. November of 1971), this intake dramatically reduces connectivity in an upstream direction (with respect to juvenile shrimp migration) of the Rio Espíritu Santo. To compare the two intakes further, the only time that any Mameyes intake results in less than high connectivity is during the driest month of a drought year. In contrast, the only time that any Espíritu Santo intake results in more than low connectivity is during the wettest month of a wet year.

DISCUSSION

This case study application of the ILRC suggests that it may be useful in assessing relative impacts of dams and water withdrawal operations in tropical streams dominated by migratory biota, such as shrimps. The ILRC allows assessment of cumulative effects of multiple dams (in addition to individual dams) and intake design on riverine connectivity. Furthermore, it enables evaluation of connectivity in relation to months of seasonally low discharge and drought (in addition to using long-term averages) through use of discharge data from drought years.

It is important to note, however, that it is hard to isolate the effects of an individual dam when it is upstream or downstream of another dam. In reality, it is the cumulative effects of all dams in linear succession that affect shrimp

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Table 2. In-depth look at the ILRC and the probability that larvae and juveniles will pass intakes (see Table 1 for abbreviations) for the Mameyes (M) and Espíritu Santo (E) catchments during wet and dry seasons and years: (a) results of the ILRC for wet, dry and average years; (b) results of ILRC for wet and dry months for a wet year; (c) results of the ILRC for wet and dry months for a dry year

(a)	Wet year (1971)					Dry year (1994)					Average year
Intake	Pr U_k	Pr UC_k	Pr D_k	Pr DC_k	ILRC	Pr U_k	Pr UC_k	Pr D_k	Pr DC_k	ILRC	ILRC
M-b	1.00	0.90	1.00	1.00	0.90	1.00	0.84	1.00	1.00	0.84	0.89
M-l	0.91	0.82	1.00	1.00	0.82	0.86	0.72	1.00	1.00	0.72	0.81
M-17	0.90	0.90	1.00	1.00	0.90	0.84	0.84	1.00	1.00	0.84	0.89
E-3	0.34	0.09	0.50	0.31	0.03	0.00	0.00	0.28	0.06	0.00	0.01
E-6	0.00	0.00	0.13	0.13	0.00	0.00	0.00	0.02	0.02	0.00	0.00
E-9	0.71	0.18	0.98	0.61	0.11	0.30	0.00	0.70	0.15	0.00	0.05
E-16	0.79	0.20	1.00	0.62	0.12	0.49	0.00	0.92	0.20	0.00	0.06
E-19	0.25	0.25	0.62	0.62	0.16	0.00	0.00	0.22	0.22	0.00	0.08
E-x	0.86	0.22	1.00	0.62	0.13	0.59	0.00	1.00	0.22	0.00	0.06

	Wet year (1971)										
(b)	Wet month (November)					Dry month (March)					Year
M-b	1.00	0.96	1.00	1.00	0.96	1.00	0.83	1.00	1.00	0.83	0.90
M-l	0.97	0.93	1.00	1.00	0.93	0.85	0.71	1.00	1.00	0.71	0.82
M-17	0.96	0.96	1.00	1.00	0.96	0.83	0.83	1.00	1.00	0.83	0.90
E-3	0.73	0.50	1.00	1.00	0.50	0.00	0.00	0.48	0.42	0.00	0.03
E-6	0.00	0.00	0.30	0.30	0.00	0.00	0.00	0.07	0.07	0.00	0.00
E-9	0.88	0.61	1.00	1.00	0.61	0.54	0.00	1.00	0.42	0.00	0.11
E-16	0.91	0.63	1.00	1.00	0.63	0.66	0.00	1.00	0.42	0.00	0.12
E-19	0.69	0.69	1.00	1.00	0.69	0.00	0.00	0.42	0.42	0.00	0.16
E-x	0.93	0.64	1.00	1.00	0.64	0.72	0.00	1.00	0.42	0.00	0.13

	Dry year (1994)										
(c)	Wet month (November)					Dry month (March)					Year
M-b	1.00	0.91	1.00	1.00	0.91	1.00	0.80	1.00	1.00	0.80	0.84
M-l	0.92	0.84	1.00	1.00	0.84	0.83	0.66	1.00	1.00	0.66	0.72
M-17	0.91	0.91	1.00	1.00	0.91	0.80	0.80	1.00	1.00	0.80	0.84
E-3	0.19	0.02	0.63	0.36	0.01	0.00	0.00	0.10	0.01	0.00	0.00
E-6	0.00	0.00	0.14	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E-9	0.65	0.07	0.75	0.43	0.03	0.00	0.00	0.48	0.04	0.00	0.00
E-16	0.74	0.07	0.80	0.46	0.03	0.23	0.00	0.90	0.01	0.00	0.00
E-19	0.10	0.10	0.57	0.57	0.06	0.00	0.00	0.08	0.08	0.00	0.00
E-x	0.80	0.08	1.00	0.57	0.05	0.38	0.00	1.00	0.08	0.00	0.00

migration. Therefore, with regard to individual dams, the index is looking at the ability of an average shrimp to migrate past that dam. For instance, if a dam has low connectivity, it means that there is a low probability that a larva can migrate downstream to the estuary and migrate back upstream past that intake as a juvenile. The intake of interest may not divert a high proportion of stream flow, but a dam downstream may, causing the dam of interest to have a low score.

Effects of multiple dams

Upstream and downstream effects of multiple dams in linear succession can dramatically decrease the probability of downstream passage of larvae and upstream passage of juveniles beyond water intakes. In the Rio Espíritu Santo catchment, some individual intakes (e.g. E-16, E-9 and E-x) do not greatly affect connectivity (i.e. from the perspective of shrimp larvae drifting downstream and juveniles moving upstream). However, when these intakes are evaluated in relation to downstream intake E-19, each intake results in low connectivity. In comparison, all intakes within the Rio Mameyes catchment result in high connectivity. This indicates the power of conserving minimum flows for maintaining in-stream connectivity. It is arguable whether it is better to have a few large intakes or many small intakes. In the CNF, the answer may lie in the relative volume of water diverted in comparison with flow volume. Intakes that divert a large proportion of flow on the main stem of a river dramatically decrease connectivity throughout the catchment, in terms of juvenile shrimp migration in an upstream direction. Main-stem intakes also reduce the probability that larvae originating above the intake will reach the estuary. In contrast, small intakes higher in a catchment may cause local habitat fragmentation if the proportion of flow diverted is high, but may not have a dramatic effect throughout the catchment. Intakes that divert a small proportion of flow may cause little or no habitat fragmentation, in either case.

When considering the cumulative effects of water withdrawals in linear succession, the important spatial units to consider are the lengths of streams affected by water withdrawal within a catchment. Longitudinal connectivity can be evaluated at the individual water intake level (as the effect of that intake on connectivity), but the cumulative effects of water withdrawal cannot be evaluated accurately without considering all water intakes in linear succession. As such, it is important to note that there is a large dam (La Loiza dam) on the Rio Grande de Loiza that is not considered in this study. Only a small portion of this drainage is located within the CNF, and given that the ILRC is designed for small impoundments, the effect of the Loiza dam on connectivity is outside the scope of this study. In addition, several small intakes within the CNF were left out of analyses given that the area draining to each could not be determined, because the areas were very small and topographic maps available did not support such fine-scale measurements.

Effect of dry seasons and drought

Results of the application of the ILRC to intakes within the Rio Mameyes and Rio Espíritu Santo catchments (Table 2) suggest that shrimps are exceptionally vulnerable to the effects of water withdrawal during times of low stream flow, especially in catchments with many dams. During an average year, all intakes result in low connectivity within the Rio Espíritu Santo catchment. Within the same catchment, all intakes result in zero connectivity during a drought year. Even during a wet year, all of these intakes result in low connectivity, and only during the wettest month do any intakes result in moderate connectivity.

During the drought year of 1994, all Mameyes intakes resulted in high connectivity and all Espíritu Santo intakes resulted in low connectivity. This suggests that shrimp larvae and juveniles were severely limited in their ability to move throughout the Espíritu Santo catchment in order to advance to the next life-stage. During this drought year, water flowed over intake E-19 (lowest elevation, main-stem dam) only 22% of the time. Therefore, juvenile shrimps probably formed a migration 'bottleneck' below this dam, increasing the rate of predation-related mortality of juveniles (Benstead *et al.*, 1999, 2000). In addition, all of the Q50 was diverted at intake E-19 during this time, suggesting that most larval shrimps were entrained in the intake structure, resulting in direct mortality. In contrast, shrimp recruitment was relatively undisturbed even during the drought year in the Rio Mameyes.

Evaluation of effects of water withdrawal during dry seasons and drought are useful in thinking about the long-term effects of water withdrawal on a stream. Short dry seasons may not greatly affect overall shrimp recruitment, but longer droughts may. In any case, consideration should be given to the potential effects of proposed water intakes on low flow events, especially for streams with water intake(s) on the main stem.

Effect of intake design

According to this index, the effect of individual withdrawal points on shrimps indicates that withdrawal points with minimum-flow requirements or alterative designs (M-17: French drain, minimum flow > Q99; F-18: impoundment with off-stream reservoir, minimum flow equals Q99) result in higher connectivity and biotic integrity than do traditional intakes without minimum flows. Higher connectivity is due to maintenance of in-stream flow and limited water withdrawal. The largest intake on the Rio Espíritu Santo (E-19: impoundment, no minimum flow requirement) causes significant reductions in stream discharge (82% of median flow). It probably dramatically decreases upstream migration of juveniles, potentially affecting the community composition of headwater streams. Because this dam is located low in the drainage, alteration of this water intake to accommodate a minimum flow requirement would increase longitudinal riverine connectivity of the entire catchment.

Using the index of longitudinal riverine connectivity

The ILRC was designed for streams draining the CNF in Puerto Rico; specifically, streams influenced by small dams (<3 m in height) or other water intakes. However, this index may be applicable to other streams influenced by small water intakes throughout the Caribbean and shrimp-dominated streams in other tropical regions of the world. At least one stream gauge with long-term discharge data, in combination with estimated or actual water withdrawal volume data, are necessary to calculate the index for streams within a catchment. It is important to keep in mind that this index has not been empirically tested but is based on best available knowledge of shrimp distribution patterns in Puerto Rico (Holmquist *et al.*, 1998; Greathouse *et al.*, 2006a,b). Future research could compare index values to shrimp abundance data upstream and downstream of each dam within multiple catchments to ascertain the usefulness of this index in evaluating the impacts of water withdrawal on migratory shrimps.

This approach could also be used to evaluate potential benefits of restructuring the way a dam operates and/or reducing the impact of future water intakes. For example, by providing a minimum flow over a dam where all flow is currently entrained by an associated water intake, the probability of upstream migration of juveniles would go from 0 to 1. Likewise, one could evaluate hypothetically the impacts of adding an additional water intake in a given location. This information may be helpful for water managers and policy makers in their efforts to balance in-stream flow with demands of current and future municipal water supplies.

CONCLUSIONS

The method to assess longitudinal riverine connectivity presented here provides a conceptual framework to examine relative effects of water withdrawals on potential movement and transport of migratory biota by using shrimps as focal taxa. The ILRC was developed because long-term, large-scale ecological data on shrimps are limited for the CNF, making it difficult to decipher the relationship between water withdrawal and ecological functioning. Also, it would be nearly impossible to gather all of the data necessary to understand fully the relative differences in the effects of dams on shrimp migration, especially when exacerbated by drought. Combining the results of published studies with long-term discharge data into an ILRC allows one to gain a better understanding of the relative effects of dams on migratory shrimps, which play an important role in structuring stream ecosystems. The index can be used to guide future research to gather the data necessary to address more in-depth questions regarding the effects of dams on hydrologic connectivity and ecosystem function. For instance: What is the biological threshold of water withdrawal for shrimp populations? At what point does shrimp mortality due to decreased longitudinal connectivity lead to a reduction in overall shrimp populations? To what extent does decreased longitudinal connectivity affect stream ecosystem function? Do water withdrawals affect some shrimp species more than others? What is the impact of water withdrawals on other migratory species, such as fish?

As more water is demanded by growing populations in developing tropical regions, informed water planning is essential to maintain the structure and functioning of stream ecosystems. Our hope is that this ILRC will be useful in evaluating environmental effects of dams and associated water withdrawals and in aiding resource managers in decisions regarding the location, size and design of future intakes for water withdrawals.

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