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Research article

Integrating modeling, monitoring, and management to reduce critical uncertainties in water resource decision making

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ABSTRACT

Stream ecosystems provide multiple, valued services to society, including water supply, waste assimilation, recreation, and habitat for diverse and productive biological communities. Managers striving to sustain these services in the face of changing climate, land uses, and water demands need tools to assess the potential effectiveness of alternative management actions, and often, the resulting tradeoffs between competing objectives. Integrating predictive modeling with monitoring data in an adaptive management framework provides a process by which managers can reduce model uncertainties and thus improve the scientific bases for subsequent decisions. We demonstrate an integration of monitoring data with a dynamic, metapopulation model developed to assess effects of streamflow alteration on fish occupancy in a southeastern US stream system. Although not extensive (collected over three years at nine sites), the monitoring data allowed us to assess and update support for alternative population dynamic models using model probabilities and Bayes rule. We then use the updated model weights to estimate the effects of water withdrawal on stream fish communities and demonstrate how feedback in the form of monitoring data can be used to improve water resource decision making. We conclude that investment in more strategic monitoring, guided by *a priori* model predictions under alternative hypotheses and an adaptive sampling design, could substantially improve the information available to guide decision-making and management for ecosystem services from lotic systems.

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1. Introduction

Sustaining the ecological integrity of aquatic ecosystems while meeting human needs for water resources is one of the major challenges facing society today. In many regions, the growing demand for water supply and changing land use are altering hydrologic regimes in streams and rivers that society depends upon for ecosystem services. These services include: water supply for households, manufacturing, irrigation and aquaculture; production of fishes and other wildlife; flood control, pollution dilution, hydroelectric generation, transportation and recreation (Postel and Carpenter, 1997). Global climate change poses a further challenge to aquatic resource managers charged with conserving aquatic biodiversity and related ecosystem services. Rising water temperatures are expected to reduce habitat availability for coldwater-dependent species and may also create new habitat for warmwater species (Buisson et al., 2008; Chu et al., 2005; Jackson and Mandrake, 2002; Mohseni et al., 2003; Rosset et al., 2010; Steen et al., 2010). Changes in precipitation patterns also are anticipated to affect freshwater biota by altering flow regimes during critical life history periods (Jaeger et al., 1999; Peterson and Kwak, 1999; Wenger et al., 2011) and potentially reducing habitat volume (Xenopoulos et al., 2005). Thus, water resource managers are faced with difficult decisions on how to satisfy the needs of growing human populations while maintaining or restoring aquatic ecosystems in an ever shifting environment.

To aid in the decision-making process, water resource managers need tools for assessing the potential effectiveness of water resource conservation and restoration actions, assessing tradeoffs, and evaluating the relative influence of management assumptions on expected management effects. The development of effective tools is complicated by the existence of multiple interacting factors and the uncertainty associated with the response of ecological systems to management actions and natural variation. This uncertainty can be grouped into three general types as defined in Conroy and Peterson (2013): (1) environmental uncertainty, due to

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environmental and demographic variation, and having both spatial and temporal components; (2) statistical uncertainty, due to the use of sample data to estimate model parameters; and (3) structural uncertainty, due to an inability to determine the mechanisms driving the system dynamics. We emphasize the last of these because there often is profound uncertainty and disagreement about the primary physical and ecological processes driving the system dynamics and how they interact (Williams et al., 2002). Structural uncertainty can be incorporated in decision making tools through the use of alternative models each representing a hypothesis of ecological dynamics (Conroy and Peterson, 2013). To evaluate the relative effectiveness of alternative management actions, each model (hypothesis) can be assigned a plausibility or probability and these probabilities can be used to create a composite estimate of management effects. Alternatively, decision makers can choose to use one of the alternative models to predict management effects based on their relative belief in or evidence supporting each hypothesis. When management decisions are revisited through time or space, monitoring data can be used to update the relative belief in each hypothesis by comparing model-specific predictions to observed (actual) future conditions (Williams et al., 2002). This new information can then be used to improve knowledge of system dynamics and future decision making. The cyclical feedback that explicitly provides for learning to improve decision making through time has been defined as adaptive management (Walters, 1986). Thus, the most useful stream management tools would have the capacity to explicitly incorporate the effect of multiple sources of uncertainty on predictions of management outcomes and would provide an adaptive framework for learning through time to resolve key uncertainties and improve future decision making.

Stream resource managers have developed a variety of tools for evaluating the flow requirements of lotic ecosystems. These commonly used tools can be roughly categorized as habitat-based and flow regime approaches. Each approach has strengths and limitations that affect their utility as adaptive decision making tools. Habitat-based approaches are the most commonly used stream management tools that employ models to estimate changes in stream habitat availability and water quality as a function of streamflow (Tharme, 2003). The estimates from these models are then used to deduce the response of aquatic ecosystems to management actions (e.g., Bovee and Milhous, 1978; Bovee et al., 1998) and provide the basis for evaluating tradeoffs associated with human needs and aquatic ecosystem services. Habitat-based approaches do not explicitly incorporate ecosystem dynamics (e.g., population dynamics, birth, survival) and rely on managers to use model outputs to infer effects of management actions on ecosystem processes. As such, habitat-based approaches do not explicitly incorporate structural uncertainty but attempt to minimize its influence by employing what are believed to be conservative assumptions when evaluating management alternatives. For example, evaluations of management actions generally include extreme events, such as droughts or floods of record. Habitat-based approaches also are spatially explicit and require extensive measurement and modeling over relatively small spatial extents, which limits their use for managing over larger spatial extents (e.g., regions).

Flow regime approaches for evaluating streamflow requirements recognize the dynamic nature of stream ecosystems and use models to estimate changes in aquatic ecosystem patterns as a function of changes in components of the flow regime, relative to a baseline condition (Arthington et al., 2006; Poff et al., 2010). These models then are used to evaluate the tradeoffs in perceived ecosystem function with the estimated societal benefits associated with alternative management actions. Flow regime approaches do not explicitly incorporate population processes but use models for estimating the relation between ecological patterns and flow regime patterns (e.g., relative number of drought tolerant species in a community vs. drought frequency). These models require assumptions of stationarity that are likely violated under climate change (Milly et al., 2008). Structural uncertainty can be incorporated in many flow regime approaches by identifying alternative models representing competing flow alteration-ecological response hypotheses (Poff et al., 2010). Flow regime approaches are primarily used to evaluate stream management policies over broad spatial and temporal extents and are not intended to predict the consequences of management actions at smaller spatial and temporal extents, such as the structure of the aquatic community in a stream reach during a specified year. This suggests that monitoring data need to be collected from multiple locations over several years to facilitate the evaluation of alternative hypotheses. Thus, flow regime approaches are likely difficult to implement in an adaptive management framework that assumes climate change and requires timely integration of monitoring data.

Recently, Freeman et al. (2013) proposed a dynamic, spatially-explicit modeling approach as an alternative to habitat and flow regime-based approaches for estimating how changes in flow regimes affect lotic ecosystems. The approach incorporated multiple uncertainties including structural uncertainty, which was incorporated using alternative models representing competing hypotheses of system dynamics. Freeman et al. (2013) demonstrated the general utility of the approach by evaluating a water extraction decision in a watershed in the southeastern United States and conducting sensitivity analyses. The sensitivity analysis indicated that estimates of the effects of varying amounts of water extraction on the resident fish community differed substantially among the alternative hypotheses of system dynamics. Here, we develop an adaptive framework for the dynamic approach of Freeman et al. (2013) that incorporates monitoring data to facilitate learning and improved water resource decision making. Our specific objectives were to (1) develop and integrate a monitoring design into the dynamic modeling approach, and (2) demonstrate how monitoring data are used to revise ideas of stream ecosystem dynamics and improve decision making.

2. Material and methods

2.1. Model overview

The processes used to develop the streamflow management decision models and framework are thoroughly detailed in Conroy and Peterson (2013) and are briefly described here. Multiple stakeholders from the Flint River basin, Georgia participated in several 2–3 day workshops in 2006–2007. The stakeholders included members from the Georgia Department of Natural Resources, US Fish and Wildlife Service, Farm Bureau, and two non-governmental organizations: the Nature Conservancy and the Instream Flow Council. During these meetings, the stakeholders identified their objectives and decision alternatives and developed prototype decision models. The stakeholder objectives included both ecological (e.g., native aquatic species conservation) and socioeconomic elements (e.g., water for human consumption, recreational opportunities). Most socioeconomic objectives, however, were discarded due to perceived scientific limitations. The alternative management actions identified by the stakeholders were limited to those within the authority of agency representatives and included water withdrawal and use permitting actions. To parameterize the prototype decision model, the stakeholders recruited an interdisciplinary team of technical experts. These experts modified the stakeholder prototype model to accommodate the integration

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of disciplinary-specific models. The final decision model simulates the local extinction, colonization, and reproduction of individual fish species in individual stream segments as a function of seasonal streamflows, water quality, and instream habitat. Stream segments are defined as stream sections bounded by tributary junctions. The model operates on an annual time step and colonization, extinction, and reproduction probabilities are estimated using empirical *meta*-demographic models that require streamflow and habitat inputs, described below.

2.2. Study area

We simulated stream fish dynamics and sampled fishes within the Potato Creek subbasin of the Flint River system in GA (Fig. 1). Potato Creek subbasin is located in the Piedmont physiographic province and represented warm-water stream systems valued for water supply, recreation and support of wildlife, including game fishes and fish species unique to the encompassing Apalachicola River basin (Freeman et al., 2013). We sampled fishes at sites on nine tributaries to the Potato Creek mainstem (Fig. 1). Sites were selected based on accessibility, landowner cooperation, and lack of large, local disturbances including discharges to the stream channel or riparian area. Drainage areas at the study sites ranged from approximately 8 to 47 km^2.

2.3. Fish sampling and occupancy estimation

Fishes were collected from the nine study sites in the Potato

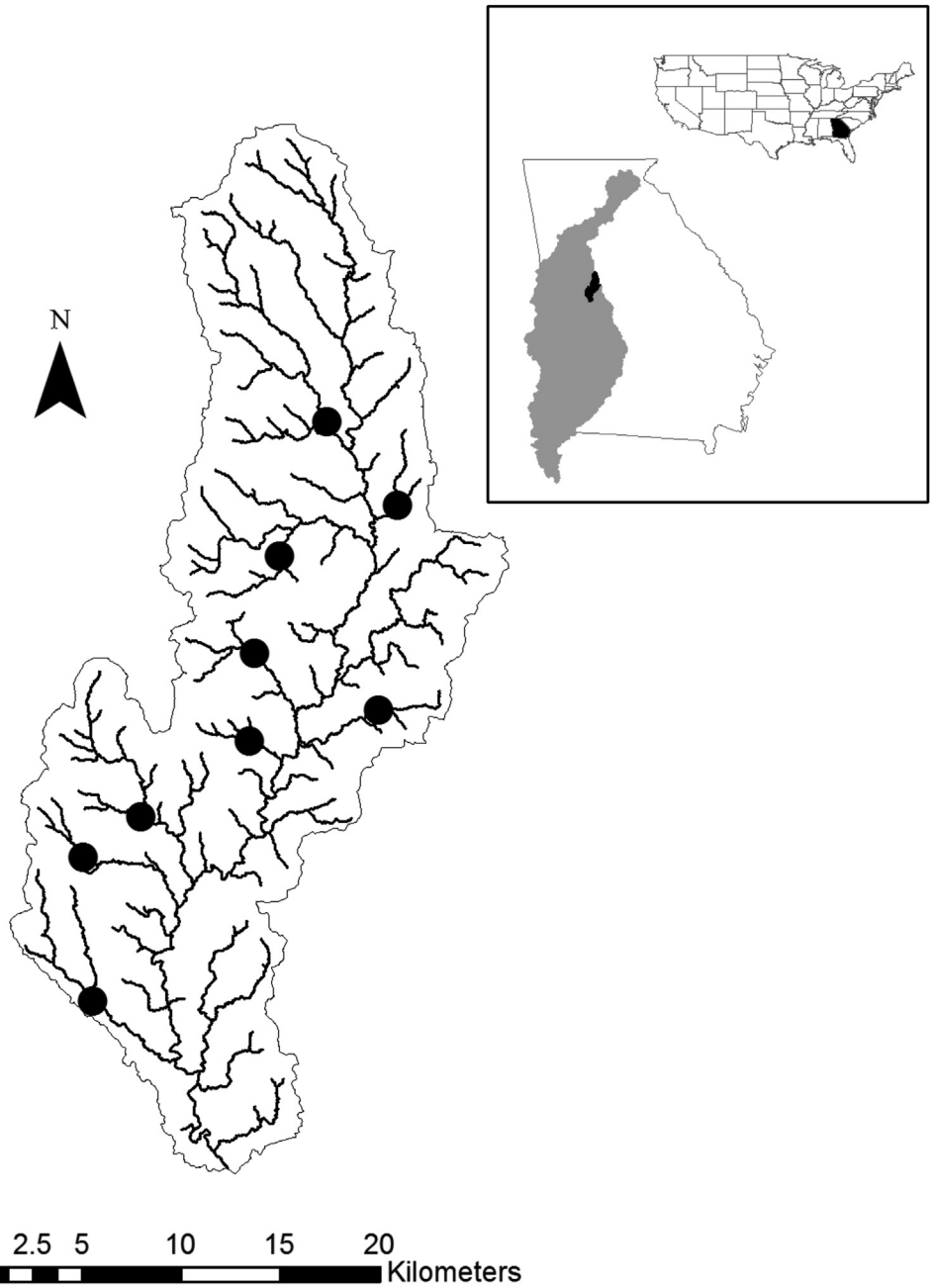


Fig. 1. Monitoring site locations within the Potato Creek, Georgia, subbasin of the Apalachicola-Chattahoochee-Flint basin (inset, in gray).

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Creek basin during late September 2011–2013 to correspond with our model estimates. We used a quadrat-based sample design at each site (Rabeni et al., 2009). On each sampling date at each study site, we placed block-nets at the upstream and downstream boundaries of two or three (depending on accessible stream length) reaches. Stream reaches ranged from 26 to 98 m in length, depending on the distance necessary to include the range of local stream channel variability. We sampled fishes in one pass through each block-netted reach using a seine (2.4 m × 1.8 m × 3 mm mesh) and a battery-powered backpack electrofisher. Captured fish were held in aerated, insulated containers until sampling was completed, and then identified, counted and released back to the stream.

Prior to or immediately following sampling, several habitat measures were collected in each sample site. Stream temperature was measured in the middle of the site using a hand held thermometer and recorded to the nearest 0.1 °C. The reach length and wetted stream width (to the nearest 0.1 m) was measured perpendicular to flow. Average depth was estimated from measurements made with a wading rod at three points along transects positioned perpendicular to flow and spaced at 10 m intervals along the length of the reach. Crews also estimated wood density in the channel as the total area of woody debris divided by the wetted area of the study site.

Not all species are detected when sampling, so to account for the possibility of false absences in the monitoring data we fit occupancy models (MacKenzie et al., 2006) using the single season occupancy estimator and the R statistical software package "rjags" (Plummer, 2003). Candidate occupancy models were fit separately for each species and accounted for incomplete detection (i.e., failure to detect a species when present). We were primarily interested in obtaining the best predicting occupancy model so we evaluated the relative fit of models containing all possible combinations of the detection probability predictors (sample unit average depth, width, length, and water temperature) and occupancy probability predictors: average stream width and depth, year, and a random effect corresponding to site to account for potential unexplained among site variance. All models were fit using 100,000 iterations with 5000 burn in iterations and diffuse priors. The best approximating models were selected using Bayesian Information Criteria (Link and Barker, 2010) and were used to predict the probability of species presence when a species was not detected. Species were considered present at a sample site when they were detected or occupancy probabilities $\geq$0.5, otherwise they were assumed absent. For each species, we estimated the local extinction events as number of segments where a species was estimated to be present in year t but was absent in year t+1. Colonization events were similarly calculated as the number of segments where a species was estimated to be absent in year t and was present in year t+1. The relative frequency of estimated local extinction and colonization events for 2011–2013 (the monitoring period) was estimated as the proportion of monitored segments in Potato Creek subbasin.

2.4. Stream network

A fine-resolution stream network for the Potato Creek system was generated from a 1 arc-second or an approximately 30-m scale National Elevation Dataset (Gesch, 2007; Gesch et al., 2002) Digital Elevation Model (DEM) for the Apalachicola-Chattahoochee-Flint (ACF) basin (Elliott et al., 2014). The network, generated using programs Bldgrds and Netrace (Benda et al., 2007), had a similar drainage density and structure to the medium-resolution (1:100,000) National Hydrography Dataset (NHD) stream network. Every stream reach (delineated by changes in stream gradient or valley width) in the network was populated with individual geomorphic attributes. Attributes at the reach scale included upstream drainage basin area, gradient, channel width, valley width, Strahler and Shreve stream order, stream power, and measures of stream confinement. Channel width was modeled as a function of drainage basin area using regional stream channel geometry relationships. Valley width was modeled as a function of drainage basin area from regional channel geometry relationships of bankfull width and depth intersected with valley walls in the 30-m DEM. Stream channels less than 10 m wide or with a ratio of valley width to bankfull width less than 4 were designated as confined channels. The fine network data were summarized at the segment scale (tributary junction to tributary junction). Segments were additionally identified as isolated if they were located upstream of a dam or impoundment within each basin, identified from the National Inventory of Dams or from National Aerial Inventory Program (NAIP) aerial photography from 2009 to 2010 (Elliott et al., 2014).

The stream network was created in the context of a scalable geomorphic network for the entire ACF basin (Elliott et al., 2014), resulting in a coarser stream resolution than the resolution of the network used to parameterize metapopulation models (Peterson and Shea, 2015). Whereas the ACF-wide resolution approximated a medium resolution (1:100,000) NHD network, estimates of stream-size effect on metapopulation dynamics had been derived using a data set in which link-magnitude was measured from a higher resolution (ca.1:24,000) NHD. Therefore, to attribute segments in the basin network with link-magnitude values comparable to those used in the metapopulation models, we adjusted the Shreve value (number of upstream first-order streams) for each segment using a regression ($r^2 = 0.997$) of Shreve values from a high-resolution NHD network and values from the ACF-wide resolution for 30 randomly selected points in the basin.

2.5. Hydrologic model

Daily streamflows were simulated for the period 1961 to 2013 in each segment in the Potato Creek Basin using the USGS Precipitation Runoff Modeling System (LaFontaine et al., 2013 and unpublished). PRMS, a spatially distributed, deterministic, physically based hydrologic model (Leavesley and Stannard, 1995), used daily precipitation and temperature values to simulate stream runoff. Other inputs to the PRMS model included soil maps (State Soil Geographic database, STATSGO, summarized at a 1 km grid) and the National Land Cover Database (30 m grid resolution) for 2001 to parameterize relative subsurface, land cover and vegetation characteristics for each hydrologic response unit (HRU; Viger et al., 2010; LaFontaine et al., 2013 and unpublished). PRMS simulated daily flow in each segment of the study basin by combining flow from the upstream segments with surface, subsurface and groundwater fluxes from each segment's contributing HRU. The PRMS model was calibrated using a multi-objective, stepwise calibration tool (Hay and Umemoto, 2006; Hay et al., 2006) that adjusted values of selected parameters using the Shuffled Complex Evolution algorithm (Duan et al., 1993) until the difference between simulated and measured streamflow statistics at a USGS gage within the basin was minimized.

2.6. Fish metapopulation model

Stream fish responses were simulated using a spatially-explicit metapopulation model for 28 species (Table 1) common to streams in the Potato Creek basin and that were detected at least once during fish sampling. Simulations were initiated using species-specific probabilities of occurrence estimated in relation to stream size (link magnitude), juxtaposition (link magnitude of the next downstream segment) and land use characteristics (Ruiz and

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Table 1
Proportion of segments where local extinction and colonization (in parentheses) was estimated to occur based on occupancy estimation at the monitored sites ("Estimated occupancy"), and on the dynamic metapopulation approach (results shown for monitored segments and all segments). Estimates from the dynamic models were averaged across alternative models of system dynamics.

Species	Estimated occupancy	Monitored segments	All segments
Ameiurus brunneus	0.06 (0.06)	0.04 (0.1)	0.02 (0.11)
Ameiurus natalis	0.06 (0.00)	0.00 (0.29)	0.03 (0.24)
Ameiurus nebulosus	0.00 (0.00)	0.01 (0.24)	0.03 (0.25)
Cyprinella venusta	0.11 (0.06)	0.03 (0.31)	0.04 (0.12)
Ericymba amplamala	0.06 (0.17)	0.02 (0.27)	0.04 (0.13)
Esox americanus	0.06 (0.11)	0.05 (0.33)	0.05 (0.26)
Gambusia sp.	0.06 (0.28)	0.04 (0.06)	0.06 (0.26)
Hybopsis sp. cf. *H. winchelli*	0.11 (0.17)	0.04 (0.05)	0.04 (0.13)
Lepomis auritus	0.06 (0.11)	0.02 (0.08)	0.02 (0.12)
Lepomis cyanellus	0.06 (0.11)	0.00 (0.24)	0.03 (0.26)
Lepomis gulosus	0.17 (0.06)	0.00 (0.29)	0.03 (0.23)
Lepomis macrochirus	0.17 (0.11)	0.00 (0.25)	0.03 (0.25)
Lepomis microlophus	0.11 (0.11)	0.01 (0.26)	0.03 (0.24)
Micropterus salmoides	0.06 (0.17)	0.00 (0.29)	0.03 (0.21)
Minytrema melanops	0.00 (0.00)	0.01 (0.27)	0.04 (0.12)
Moxostoma lachneri	0.06 (0.11)	0.01 (0.24)	0.03 (0.11)
Moxostoma rupiscartes	0.11 (0.06)	0.01 (0.24)	0.03 (0.11)
Nocomis leptocephalus	0.06 (0.11)	0.04 (0.29)	0.05 (0.27)
Notemigonus crysoleucas	0.06 (0.06)	0.04 (0.29)	0.05 (0.27)
Notropis cummingsae	0.06 (0.00)	0.04 (0.08)	0.04 (0.14)
Notropis hudsonius	0.06 (0.00)	0.03 (0.31)	0.04 (0.12)
Notropis longirostris	0.00 (0.00)	0.02 (0.26)	0.04 (0.13)
Notropis lutipinnis	0.11 (0.11)	0.03 (0.31)	0.04 (0.13)
Notropis texanus	0.06 (0.17)	0.02 (0.03)	0.04 (0.13)
Noturus leptacanthus	0.11 (0.11)	0.00 (0.00)	0.03 (0.12)
Percina nigrofasciata	0.06 (0.11)	0.01 (0.19)	0.03 (0.13)
Pomoxis nigromaculatus	0.11 (0.17)	0.00 (0.25)	0.03 (0.25)
Semotilus thoreauianus	0.11 (0.17)	0.04 (0.29)	0.05 (0.27)

Peterson, 2007) for each segment in the network. At each subsequent time step (corresponding to spring, March–June, and summer, July–September, of each year), the model simulated species-specific state transitions (i.e., *meta*-demographic rates: local extinction, colonization, reproduction) as functions of streamflow statistics, stream channel geomorphology and size, and species-specific traits (Peterson and Shea, 2015). The flow statistics were calculated from the PRMS output of segment-specific daily flows for spring and summer, and represented four aspects of flow regimes: average flow (median daily flow); low-flow magnitude (minimum 10-day moving-average of daily flow); high-flow magnitude (maximum 10-day moving-average of daily flow); and flow variability (standard deviation of daily flows). Flow statistic values for each year and stream segment were normalized to the segment-specific, long-term (1961–1999) seasonal median flow.

Effects of flow characteristics on species-specific *meta*-demographic rates were estimated using an empirical dataset of fish species and life stage occurrences observed seasonally over four years in 23 stream reaches located in the lower Flint River basin (Peterson and Shea, 2015). Analyses of the empirical data, however, indicated support for alternative flow effects on *meta*-demographic rates and this source of uncertainty was incorporated by including alternative models. Alternative extinction models included the effects of season-long flows as indexed by median seasonal flows (henceforth, chronic flows) and short-term low flows as indexed by minimum 10-day moving-average flows (henceforth, acute flows). Two alternative models of the effects of flows on reproduction included high flows during the spring as indexed by maximum 10-day moving-average of daily flow and flow variability during the summer rearing period as measured by the standard deviation of daily flows. Reach specific colonization probabilities were only modeled as a function of seasonal maximum 10-day moving-average of daily flow. Multiple local extinction and colonization events were observed in the empirical dataset but the source of colonists could not be determined (Peterson and Shea, 2015). Thus we hypothesized two colonization sources based on metapopulation theory. In the "mainstem-tributary" model (analogous to 'mainland-island dispersal'; Hanski and Gilpin, 1991), fish were allowed to colonize segments provided the species was present in the mainstem of Potato Creek, and the segment was not isolated by an impoundment. In the more restrictive model, analogous to classic metapopulation dispersal (Levins, 1969), colonization could only occur from adjacent occupied segments within a distance of 7 km ("tributary dispersal"). Thus, we used a total of eight alternative models (i.e., 2 extinction $\times$ 2 reproduction $\times$ 2 dispersal) to simulate the dynamics of fish populations in Potato Creek.

Simulations of the dynamics of fish populations were conducted for the period 2000–2013 using modeled streamflow in each reach. Simulations were conducted using the 8 alternative models, described above, run for 2500 iterations using MetaPop software (Peterson and Key, 2011), in which initial occupancy status and subsequent state transitions were modeled as draws from a Bernoulli distribution with the corresponding estimated probabilities. For example, if a species was absent from a stream segment in time t, presence at time $t+1$ was simulated using a Bernoulli distribution with a probability of success equal to the estimated colonization probability. For each species, stream segment, year, and alternative model, the probability of species occupancy in the summer was estimated as the averaged simulated occupancy from the 2500 iterations. The estimated occupancy probabilities were then used to evaluate the relative support for the alternative models, as described below. To estimate the prevalence of local extinction and colonization events, we assumed that a species was present in a segment within a year when the estimated summer occupancy probability $\geq$0.5, otherwise they were assumed absent. We also estimated the relative frequency of colonization and extinction events as described above, using the simulated occupancy for each alternative model. The relative frequency of

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simulated local extinction and colonization events for 2011–2013 (the monitoring period) was estimated as the proportion of monitored segments and all segments in Potato Creek subbasin.

2.7. Analysis of alternative fish population dynamic models

We used Bayes' rule to assess the relative support for the alternative extinction, reproduction, and dispersal models as:

$$P(m_i|\boldsymbol{D}) = \frac{P(m_i)P(\boldsymbol{D}|m_i)}{\sum_{i=1}^{8} P(m_i)P(\boldsymbol{D}|m_i)}, \quad (1)$$

where $P(m_i|\boldsymbol{D})$ is the posterior probability, $P(m_i)$ is the prior probability, and $P(\boldsymbol{D}|m_i)$ is the conditional likelihood of observing the annual monitoring data $\boldsymbol{D}$, given the predictions for model i. Freeman et al. (2013) assumed equal probabilities for the 8 alternative models, so the model probabilities at the beginning of our evaluation were 0.125 each (i.e., 0.5^3). The likelihood was calculated assuming a binomial distribution with probability of success equal to the (metapopulation model) simulated occupancy probability and the observed species presence (via monitoring) at each study site. Using the 2011–2013 monitoring data, we updated the probabilities sequentially. That is, the posterior probabilities calculated using the 2011 simulations and monitoring data were used as priors for the 2012 simulated output and monitoring data.

Using the final 2013 posterior model probabilities, we simulated the water withdraw scenario described in Freeman et al. (2013) for the mainstem Potato Creek and estimated the relation between the amount of water withdrawal and fish species richness (total number) in the downstream segments. The water withdrawal simulation is thoroughly described in detail in Freeman et al. (2013). Briefly, we simulated monthly water withdrawal for the city of Thomaston, Georgia USA during 1980–2000 at no (zero) water use and four levels: 1.9, 3.8, 7.6, or 15 million liters per day. Water withdrawal ceased when streamflows above the withdrawal point fell at or below the 7Q10 flow statistic, per Georgia state regulations. The metapopulation dynamics then were simulated for 2500 iterations using the 8 alternative models. Models for individual species were averaged using the original 0.5 probabilities and the 2013 posterior probabilities as weights. Species were assumed present when the averaged probability of presence >0.5. We estimated the change in estimated total number of fish species in the downstream segment relative to the no water use scenario and expressed as a percentage of the number of species under no water use.

3. Results

Streamflow varied considerably during the three monitoring years. The region experienced severe drought in 2011–2012 and as a result, flows throughout the region were substantially lower than long-term averages. This pattern is illustrated at a long-term USGS gage located immediately downstream from Potato Creek (Fig 2). Streamflows, however, were much higher during the spring and summer in 2013, with the region experiencing several high flow events during this period (Fig. 2).

Crews collected 28 fish species from at least two of the sample sites on two or more occasions. Four of these species *Lepomis macrochirus*, *Notropis lutipinnis*, *Percina nigrofasciata*, and *Lepomis auritus* were detected at 75% or more of sample sites, whereas five species *Ameiurus nebulosus*, *Cyprinella venusta*, *Ericymba amplamala*, *Esox americanus* and *Lepomis microlophus* were collected from less than 25% of the sample sites. The frequency of local extinction and colonization events varied substantially among species. Estimated extinction and colonization based on the occupancy model estimates indicated that larger bodied taxa, such as *Lepomis gulosus* and *L. macrochirus*, had relatively high numbers of local extinction events (17%) compared to the remaining taxa (Table 1), whereas estimated colonization events were greatest for *Gambusia* sp. The estimated frequency of local extinction events was greatest when estimated from occupancy models using the monitoring data, averaging 7% across species compared to averaged estimates of 2% (monitored segments) and 3% (all segments of Potato Creek) based on the dynamic metapopulation simulations. However, proportion of colonization events was greatest based on estimated metapopulation dynamics, averaging 22% and 17% for the monitored segments and all segments, respectively.

The relative frequency of estimated local extinction and colonization events varied substantially among alternative models. Local colonization was greatest under the mainstem-dispersal hypotheses, particularly when all segments were considered (Table 2). Local extinctions due to non-reproduction were greatest under the flow variability hypothesis. Local extinctions also varied between the extinction hypotheses, however, there appeared to be an interaction between dispersal and local extinction that resulted in a more complicated pattern that differed substantially between monitored segments and all segments (Table 2).

The posterior probabilities for the alternative hypotheses explaining local extinction, reproduction, and dispersal changed monotonically through time for most species (Fig. 3). However, the direction of change varied substantially among species. Support for the effect of acute low flows increased for 11 species and decreased for 11 species through time. Similarly, support for flow variability effects on reproduction decreased for 11 species and increased for 12. In contrast, the relative support for tributary dispersal increased for 8 species and decreased for 14 species (Fig 3). The change in relative support for the alternative models also affected the estimated effect of water withdrawal on estimated species richness with the greatest difference occurring at high water withdrawal levels (Fig. 4).

4. Discussion

Successful implementation of adaptive management requires the formal integration of management (decision-making), modeling (research), and monitoring (Conroy and Peterson, 2009). Our dynamic occupancy approach integrates monitoring and modeling by making spatially-explicit predictions of species occupancy under alternative hypotheses that facilitate comparisons with 'actual' occupancy as estimated using an occupancy-based monitoring protocol. We demonstrated that the approach can be used to evaluate alternative management decisions (in this case, permitted water withdrawal) in the context of tradeoffs between two objectives: fish community integrity and water yield for human use. The approach was developed to provide decision-makers with the tools needed to identity optimal water development and conservation strategies in the face of climate and land use change and stream fragmentation in a rapidly developing region. However, a current regulatory focus on minimum flows to protect stream ecosystem services (Caldwell, 2005) has precluded incorporating effects of changes in other flow components (such as high flows that influence colonization rates) or stream system fragmentation into water planning processes. An additional impediment is the lack of formal monitoring to track ecosystem responses to management actions. Adaptive management generally relies on management actions altering the system state(s) of interest (here, occupancy) and subsequent comparison of those changes to predictions to facilitate learning and improved decision making (Walters, 1986). In many instances, natural variation in system drivers also facilitates learning, provided there is an integrated

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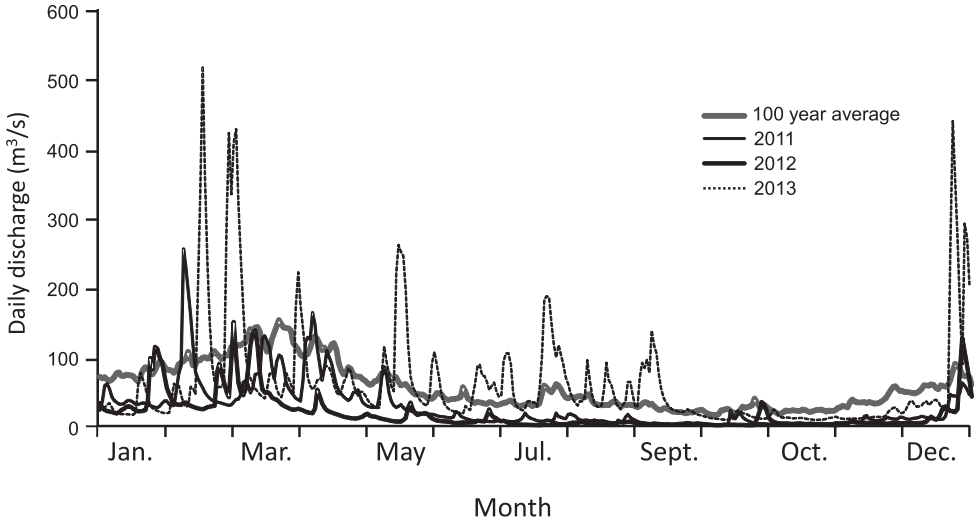


Fig. 2. Daily discharge for the Flint River below Potato Creek, Georgia, at US Geological Survey gage number 2347500 for each year of the study in comparison to mean estimated daily discharge based on 100 years of data.

Table 2
Proportion of segments where local extinction and colonization (in parentheses) was estimated to occur in the monitored segments and all segments in Potato Creek as estimated using the dynamic metapopulation approach for the combinations of alternative hypotheses.

Dispersal	Extinction	Reproduction	Monitored segments	All segments
Tributary	Acute low flows	Flow variability	0.03 (0.20)	0.06 (0.17)
	Acute low flows	High flows	0.01 (0.18)	0.03 (0.12)
	Chronic low flows	Flow variability	0.02 (0.19)	0.04 (0.16)
	Chronic low flows	High flows	0.05 (0.25)	0.01 (0.11)
Mainstem	Acute low flows	Flow variability	0.01 (0.23)	0.08 (0.26)
	Acute low flows	High flows	0.04 (0.27)	0.01 (0.18)
	Chronic low flows	Flow variability	0.00 (0.23)	0.08 (0.27)
	Chronic low flows	High flows	0.01 (0.18)	0.01 (0.19)

monitoring system in place (Alexander et al., 2006). The drought of record in the region that occurred in the first two monitoring years followed by an average to high flow year during the last year of monitoring has provided one such opportunity to begin to reduce some critical uncertainties about the dynamics of stream fish populations at landscape scales. Interestingly, the *meta*-demographic models were parameterized using data that were collected, in part, during the previous drought of record in the region (Peterson and Shea, 2015). Thus, we expect similar opportunities to occur in the future, provided there is support for continued monitoring in the basin. Monitoring could also provide observations of streamflow dynamics (such as unexpected stream drying, or conversely, local groundwater maintenance of streamflow during drought) to improve accuracy of hydrologic simulations.

Although we were able to learn from our monitoring data, in hindsight we think that our monitoring could have benefitted from a more strategic selection of sample locations. Learning, in this sense, occurs when a 'true' (or measurable) local extinction or colonization event occurs in locations where two or more models disagree on whether the event occurred. A comparison of species-specific local colonization and extinction rates estimated with the metapopulation dynamics model suggested that the estimated rates differed between the monitored segments and all segments in Potato Creek. In fact, these rates were often much lower in the monitored segments, particularly for extinction. Monitored sites were also larger than the majority of segments composing the entire network and were on average better connected to the mainstem, so lower extinction rates would be expected. To maximize learning opportunities, we believe that the potential monitoring area should have been stratified *a priori* based on the level of disagreement among models. For example, occupancy could be estimated by simulated metapopulation dynamics under future conditions and the stream segments stratified using the variance in estimated occupancy among alternative models. Greater cost efficiency also could be gained by concentrating monitoring during times of greatest potential learning, such as floods and droughts and for critical periods following implementation of future water and land management actions. We envision a system where a low level of baseline monitoring is conducted annually at a set of sites using the stratum (as described above) and greater sampling effort occurs when learning opportunities occur. The definition of learning opportunities could be based on *a priori* simulation results or the intuition of researchers and managers. Ideally, the monitoring protocol would incorporate a probabilistic design such as used for adaptive sampling (Thompson and Seber, 1996). In an era of decreasing management resources, there is need to develop such an approach.

The *meta*-demographic rate with the greatest disagreement between the monitoring estimates and the simulated dynamic occupancy estimates was local extinction. The local extinction rate estimated using the monitoring data was much higher than the estimates based on the simulations. We believe that this was due in part to our use of an arbitrary cutoff (0.5) to estimate 'observed' presence when a species was not detected at a monitoring site. A species could have been truly present at a site for an 'observed' absence, but was missed during sampling and the estimated occupancy probability was not sufficient to assume presence. Thus, our approach to updating the model probabilities did not take into

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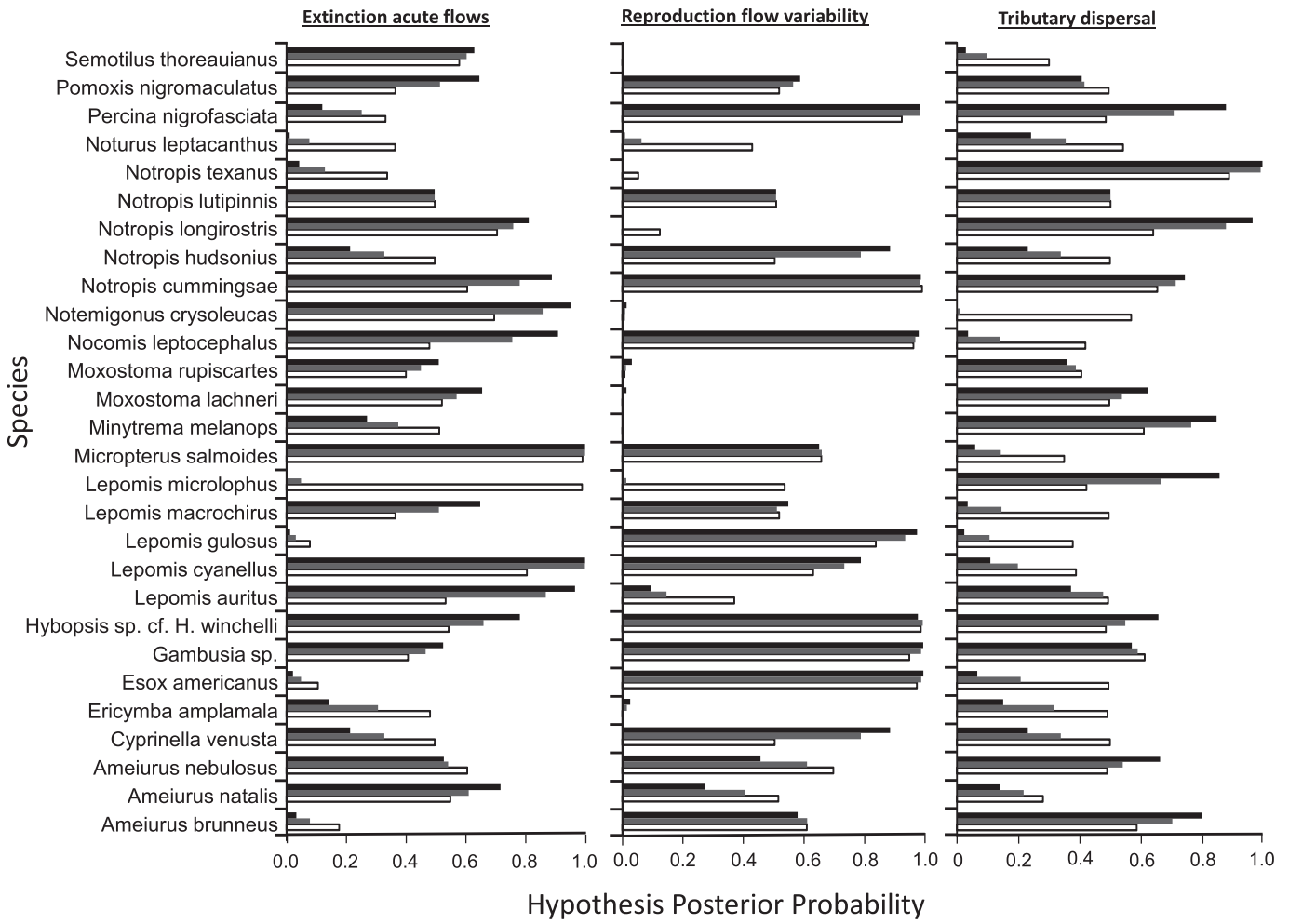


Fig. 3. Posterior probabilities for alternative hypotheses of the factors affecting local extinction (acute vs. chronic low flows), reproduction (high flows vs. flow variability), and stream network dispersal (tributary dispersal vs. mainstem dispersal). Initial probabilities were set at 0.5 and bars represent posterior probabilities after updating with monitoring data collected in 2011 (white), 2012 (gray) and 2013 (black).

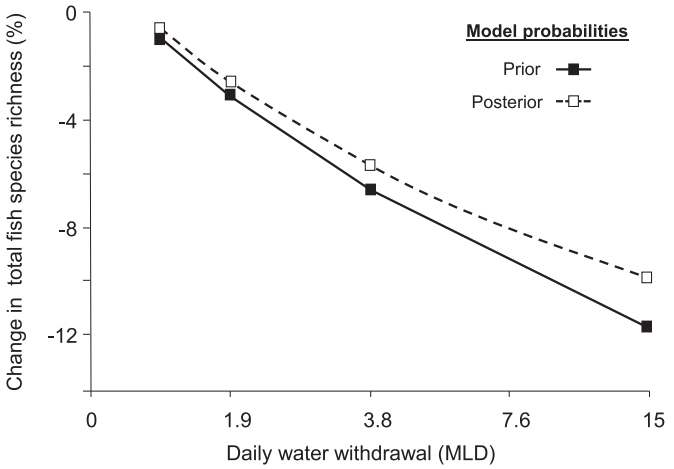


Fig. 4. Simulated outcomes of increasing levels of water withdrawal from Potato Creek mainstem on changes in fish species richness, averaged across downstream segments, for a 54-year simulation. Species richness estimated assuming equal probabilities for the alternative models (prior) and posterior probabilities calculated using occupancy monitoring data.

account the uncertainty regarding 'true' species presence when it was not detected. To incorporate this uncertainty, we plan to integrate the process of model updating with the single season occupancy estimation procedure used to estimate the probability of occupancy for sites where a species was not collected.

As we illustrated above, it is essential to formally integrate monitoring and modeling in an adaptive management framework. That is, the models must make predictions that can be measured so that predictions under alternative models can be compared to monitoring data. The occupancy and metapopulation approaches used here were well-suited to this task. However there are other equally important considerations when developing an adaptive management framework. Chief among these is the tractability of the modeling framework. The stakeholders that provided essential input to the model development desired spatially explicit estimates, for multiple species, over landscape scales that are meaningful to managers (detailed in Conroy and Peterson, 2013). Modeling species abundance in hundreds of segments over relatively long time frames (decades) would have greatly increased the dimensionality of the model to the point of intractability, even if the necessary demographic rates were available (they were not). Similarly, monitoring abundance of multiple species in stream segments would likely require much more effort than estimating occupancy. We found that representing the estimated and monitored population status with a few population states (e.g., present

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and absent) allowed us to create a feasible and useful adaptive management framework. We recognize that such a simplification may not be as useful for all species, particularly long-lived species with dynamics that respond more slowly to changes to the environment. Thus, we have encouraged the development of dynamic metapopulation models for freshwater mussels that incorporate multiple population states based on mussel abundance (e.g., absent, rare, common; Shea, 2011) and are incorporating these into a revised decision model that will include both fish and mussels. Such an approach should also be useful for taxa with similar life histories.

The approach we presented here includes two objectives identified by the stakeholders during model development: aquatic community integrity and water yield for human use. However during several workshops, stakeholders also identified additional, valued ecosystem services provided by lotic systems: water exported to downstream areas; non-consumptive activities such as boating and kayaking; and the aesthetic value of naturally flowing streams. Decision makers prohibited the inclusion of these values into the framework that we presented here under the mistaken assumption that incorporating these social values was unsupported by science. The science of human dimensions, however, is rapidly advancing, particularly as related to natural resource management, and the involvement of stakeholder values is often essential for managing trust resources (Manfredo et al., 2009). In the future, we hope to incorporate these additional values and encourage others to consider societal values when developing approaches to managing similar trust resources.

5. Conclusions

In this paper, we have described an adaptive management framework for managing lotic resources with multiple objectives. The approach is both cost effective, allowing managers to monitor populations with minimal effort, and computationally feasible. Although not shown here, the reduced dimensionality of our spatially-explicit models allows them to be dynamically solved using simulation optimization approaches when needed, such as genetic algorithms. This will allow decision makers to evaluate the tradeoffs involved in sequential decisions and identify optimal policies. We also found that our monitoring efforts, while useful, could have been apportioned to facilitate faster learning through time and improved decision making and we recommend the development of an adaptive sampling design aimed at focusing sampling efforts at places and times where the greatest learning can occur for a minimal amount of effort.

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