Forecasting Fish Communities in River Networks

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Fish communities in river networks provide significant ecosystem services that will likely decline under future land use and climate change. We developed a model that simulates the consequences to multiple populations of one or more fish species-a meta-community-from multiple stressors across a river network. The model is spatially-explicit and age-structured, with three components: habitat suitability; population dynamics, including species interactions; and movement across a spatial network. Although this model is simple, it can form the basis of fisheries assessments and may be incorporated into an integrated modeling system for watershed management and prediction.

Key words : river networks, fish species, habitat, integrated modeling

INTRODUCTION

Fish in river systems are important providers of ecosystem services, including food production, and recreation, and ecosystem regulation (Holmlund and Hammer, 1999). The are also important indicators of overall health of the aquatic ecosystem. The Millennium Ecosystem Assessment (2005) concluded that future habitat change and pollution worldwide will have a high impact on rivers; this will affect the sustainability of services provided by fish. Science-based models relating environmental factors to the long-term dynamics of fish communities can support river basin management.

Environmental factors have often been linked to parameters in fish population models (e.g., Jessup, 1998; Barber, 2008). These models typically represent multiple age classes with a population projection matrix approach (Caswell, 2000; Ackakaya, 2002). More complex fish population models include spatial dynamics and movement (Railsback *et al.*, 1999). Movement can be represented with a simple distance-based approach (Akcakaya, 2002; Muneepeerakul *et al.*, 2008), or a more detailed approach, such as optimization based on optimal foraging theory, life history theory, and ideal free distribution (Giske *et al.*, 1998).

We developed a model for projecting changes in riverine fish communities in response to multiple environmental stressors across entire river net-

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works within watersheds. Our approach is of intermediate complexity but also iterative, starting simple and building in complexity as appropriate. We are linking this model with watershed/waterbody models in an integrated modeling framework, so that multiple watershed services may be assessed.

MODEL STRUCTURE

We developed an age-structured model simulating one or more fish species over multiple timesteps. Species' populations occur in segments of a river network, which are typically 100s of meters long. Each segment has one or more environmental attributes. The model includes three parts-habitat suitability, population dynamics, and species movement-described below (model parameters are summarized in Table 1). Initial fish distributions and number of timesteps are specified by the user. Output includes each species' population size in each segment through time; it can be summarized across segments, across species, and for

the metacommunity (all species and segments). For runs with multiple species, we calculate species richness per segment as the number of species with population numbers above some threshold. Monte Carlo simulations can be used to determine uncertainty bounds for the results.

1. Habitat suitability

A habitat suitability approach represents habitat in a river segment i (h_i) as a value between 0 (least suitable) to 1 (most suitable). Early habitat suitability indices (U.S. Fish and Wildlife Service, 1981) created a suitability score for each environmental factor affecting habitat, and combined them through a mean or minimum. Currently, multiple regression, neural network, and Bayesian models are popular tools for predicting fish habitat because they account for the interdependence of factors (Guisan and Zimmermann, 2000). Habitat suitability is calculated here with logistic regression, assuming that the categorical response variable of species presence indicates suitability. Model input

Table 1. Parameters used in the model.

Parameter	Definition (units)	Source For Hyco Creek example
A	Number of age classes or stages (years)	Barber, 2008
$a_{m,s}$	Age/stage of maturity of species s (years)	Barber, 2008
α_{ij}	Interaction of species s on species j	Assumed 0.05 for species within same family, else zero
β	Compensation factor	Hassell 1975, default=1
b_s	Self-thinning exponent for species s, used in calculation for survival, b_{min} and, b_{max} are the minimum and maximum values for the species	Barber, 2008; Eq. 4; Table 2
C	Coefficients for habitat suitability factors	Table 2
D	Fraction of individuals that move, as opposed to die	Assumed 0.66 for all species
E	Environmental factors for habitat suitability (Various units)	NHDPlus (www.horizon-systems.com/nhdplus/)
$f_{a,s}$	Fecundity rate for age class a of species s (1/year)	Barber, 2008; Table 2
$\gamma_{a,s}$	Growth rate of age class a for species s, used in calculation of survival (1/year)	Barber, 2008; Table 2
$h_{s,i}$	Habitat suitability (0-1) for species s in segment i	Eq. 1
I	Immigration from outside (1/year)	Not used
K_s	Carrying capacity for species s (Number of individuals)	Set equal to 2X Individ/ha in Table 2
L	Links among segments - represented as an RxR matrix	NHDPlus
m_{ij}	Movement between segments i and j (Number of individuals)	Eq. 5
$\mu_{s,a}$	Maximum adult movement distance for species s, a (m or #segments)	Assumed 1 segment
$N_{s,r}$	Number of individuals of age class a of species s in segment r,	Eq. 2
R	Number of river segments in the system	NHDPlus
S	Number of fish species in the system	6, Barber and Cyterski, unpublished data
σ	Survival rate (1/year)	Eqs. 3, 4

includes environmental factors (E_1, E_2, E_3, $\cdots$) for each river segment, which can vary through time. The logistic regression equation is

$$h(t)=1/(1+exp-[c_0+c_{e1}E_1(t)+c_{e2}E_2(t)+c_{e2}E_2(t)+\cdots]) \quad (1)$$

where c_0 is the regression intercept and (c_{e1}, c_{e2}, c_{e3}, $\cdots$) are coefficients for the environmental factors. Coefficients are determined in a separate analysis, based on available fish data for the watershed. We assume that habitat suitability varies by species but not by age class and is homogeneous within a river segment but may vary across segments. We recognize that habitat suitability may also vary by age class, which could be represented in the model with additional complexity. Habitat suitability affects population survival in the model.

2. Population dynamics

Population numbers are updated in each age class through time using a Leslie matrix approach. For example, in a three-age class population for a species in a particular river segment, the number of individuals in all age classes ($\overline{N}$) is updated in time as

$$\overline{N}_s(t+1)=\begin{bmatrix} f_{1,s}\sigma_0 & f_{2,s}\sigma_0 & f_{3,s}\sigma_0 \\ \sigma_{1,s} & 0 & 0 \\ 0 & \sigma_{2,s} & 0 \end{bmatrix}\overline{N}_s(t), \quad (2)$$

Where $f_{a,s}$ and $\sigma_{a,s}$ are fecundity and survival rates for age class a of species s, and all elements are non-negative. Only mature fish reproduce, so $f_{a,s}=0$ for all $a>a_m$, the age of maturity. Fish older than maximum age are assumed to die off.

Survival within a segment can be modeled straightforwardly using the well known empirical self thinning relationship (Barber, 2008). Habitat effects can then be incorporated into an survival rate by assuming that the species' self thinning exponent b, which represents mortality loss, increases with decreasing habitat suitability (h) and decreases with increasing habitat suitability. Assuming a simple linear relationship between these two parameters, Barber (2008) proposed that survival for age class a of species s in segment i ($\sigma_{a,s,i}$) can be calculated based on the species-specific growth rate γ and the exponent b:

$$\sigma_{a,s,i}=\gamma_{a,s}exp-([1-h_{s,i}(t)] \cdot [(b_{max,s}-b_{min,s})+b_{min,s}]) \quad (3)$$
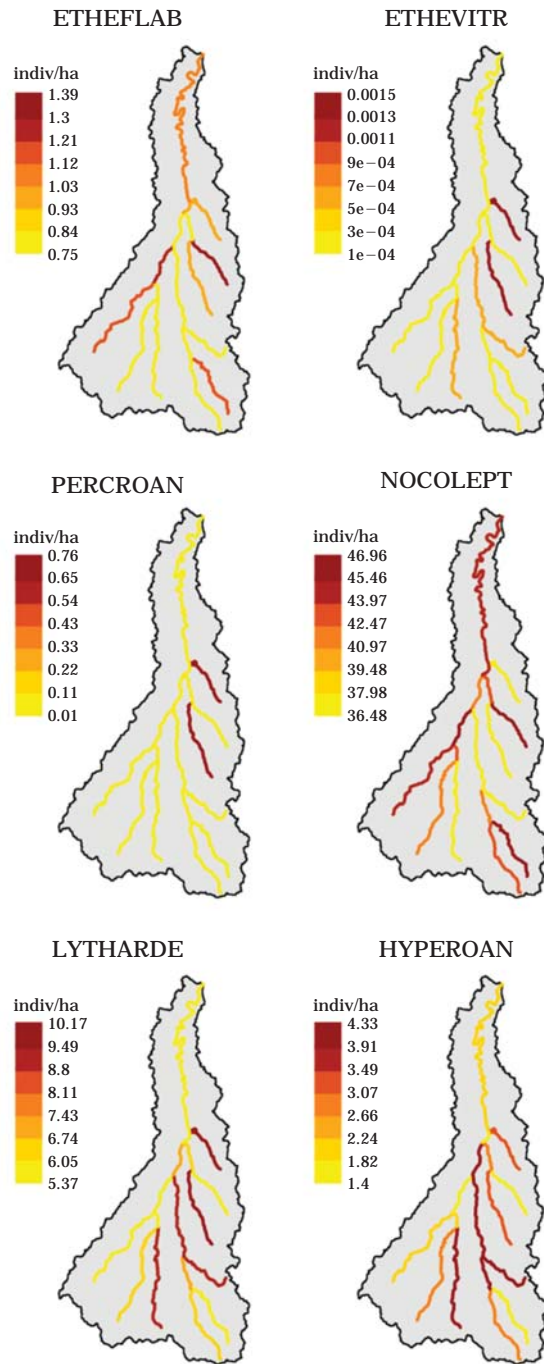

Fig. 1. Map of mean predicted densities of six fish species across the 17 river segments at the end of a 40-year simulation of the Hyco Creek watershed under current conditions (species coded by first four letters of genus and species names).

Although it is also possible to simply multiply the habitat factor $h(t)$ by a survival rate, we chose to use the self-thinning approach so that the effects

of habitat on survival would not be so severe.

Survival of the eggs to age class one for species j in a particular river segment accounts for effects of density dependence and competition on survival, and is calculated as:

$$\sigma_{0(j)}=1/[1+(\sum_{s=1}^{S} \alpha_{sj}\sum_{a=a_{m,s}}^{A_s} N_{a,s}/K_j)]^{\beta}, \text{ or}$$
$$1/[1+(\sum_{a_{m,j}}^{A_s} N_{a,j}/K_j)]^{\beta} \text{ for one species} \quad (4)$$

where S is the number of fish species in the system; A and K are the maximum age and carrying capacity of the species s, respectively; α represents the interaction of species 1 on species 2 ($a_{s,s}=1$); and β is a compensation factor (default $\beta=1$) (Hassell, 1975).

3. Movement

Movement occurs among river segments in the network. The number of individuals (m) that move from segment i to j at time t is calculated separately for each species and age class as

$$m_{a,s,r(i,j)}(t)=\delta(1-\sigma_{a,s,i})N_{a,s,i}/L \text{ for all } d_{i,j}\le\mu_s, \quad (5)$$

where δ is the fraction of individuals that move, as opposed to die, $d_{i,j}$ is the network distance bet-ween midpoints of segments i and j, μ_s is the maximum adult movement distance for species s, and L is the number of segments meeting the movement distance criterion. We assume that only adults move, that movement in one timestep only occurs to segments within the species-specific maximum movement distance, that emigration is equally distributed among segments within range, and that movement occurs equally in both directions (Gatz and Adams, 1994; Skalski and Gilliam, 2000). A final parameter is $I_{a,s}$, the number of immigrants of age a of species s that immigrate from outside the metacommunity to the most downstream river segment.

EXAMPLE APPLICATION: HYCO CREEK

We applied the model to Hyco Creek, a 126 km^2 watershed in North Carolina, for a 40-year simulation with a yearly timestep. The CRAN-R package, stream.net was used to generate topology for the network (17 segments averaging 4.1 km in length, Fig. 1), and set constant input of three envi-

Table 2. Traits and parameters for fish species used in example, and sensitivity results.

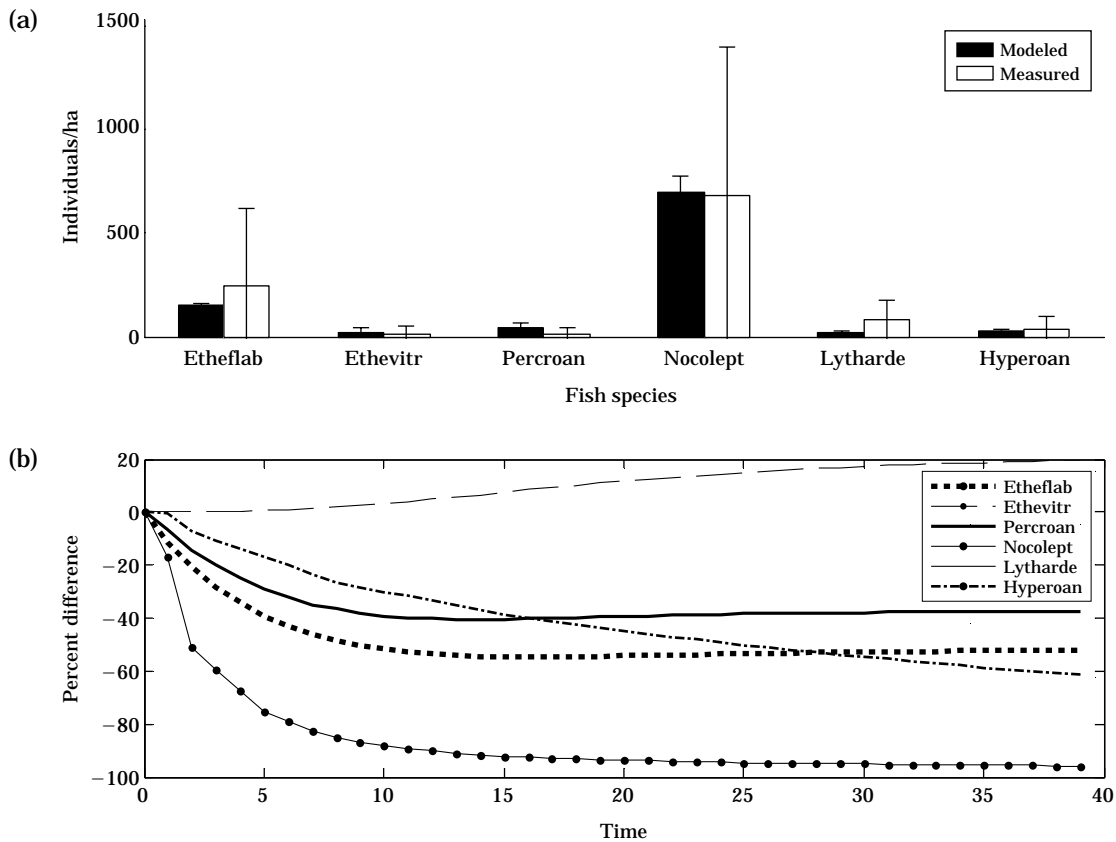| Traits/ Parameters	Fish species					
	Etheostoma flabellare	*Etheostoma vitreum*	*Percina roanoka*	*Nocomis leptocephalus*	*Lythrurus ardens*	*Hypentelium roanokense*
Common name	Fantail darter	Glassy darter	Roanoke darter	Bluehead Chub	Rosefin shiner	Roanoke Hogsucker
Family	Percidae	Percidae	Percidae	Cyprinidae	Cyprinidae	Catostomidae
Individuals per hectare	12.4	11.9	6.8	40.1	5.1	6.2
b_{min}, b_{max}	0.6, 1	0.6, 1	0.6, 1	0.6, 1	0.4, 0.8	0.6, 1
a_m, A	2, 4	3, 4	2, 4	2, 4	2, 5	5, 9
γ	0.0013~0.0034	0.0012~0.0034	0.0015~0.0067	0.0015~0.0256	0.0021~0.0034	0.0005~0.4837
f	0.70~2.10	1.58~2.37	1.54~6.85	8.56~46.48	0.77~9.84	347.20~354.40
Habitat regression coefficients (from Rashleigh *et al.*, in review)						
c_0	−88.123	−10.7064	−52.8484	−82.4953	−66.0891	−64.2873
c_{flow}	−1.2015	1.9754	3.5855	−0.5204	1.0692	6.5122
$c_{velocity}$	0	12.5542	2.6262	0	0	0
$c_{temperature}$	14.3009	0	7.3856	13.3358	10.1208	10.3559
c_{flow}^2	0.5206	0	−0.5852	0	0	−2.5418
$c_{velocity}^2$	0	−5.4729	0	0	0	0
c_{temp}^2	−0.5644	0	−0.2914	−0.5195	−0.3937	−0.4372
Sensitivity of final fish species densities (%) to 10% increase in parameters						
f	18	52	14	4	18	4
γ	1	5	1	0	0	−4
K	10	7	10	10	9	11
d	0	0	0	0	0	0
α	−9	−7	−9	−9	−9	−10
β	−13	3	−18	−15	−20	−28

Fig. 2. (a) Mean predicted final densities of six fish species under current conditions, compared to measured data (species coded as in Fig. 1); (b) Percent change in species densities over the 40 year simulation in response to an assumed 1° C water temperature increase, as compared to baseline.

ronmental factors (water temperature, flow, velocity) from the NHDPlus database (http://www.horizon-systems.com/NHDPlus/).The Hyco Creek model was set up and parameterized for the six most common fish species (Tables 1, 2). Initial conditions were estimated based on available analyses (Cyterski and Barber, unpublished data); output fish densities were compared to data collected by the North Carolina Department of Environment and Natural Resources from the same ecoregion and basin (N=28, NCDENR, 2006). Model results were quite accurate for four of the six species, with less accuracy for the two rarest species (Fig. 2a). We ran a sensitivity analysis as a 10% increase in selected parameters, which showed reasonable sensitivities; fecundity and the compensation parameter were most sensitive to this change (Table 2). We also ran a 1°C temperature increase scenario based on Intergovernmental Panel on Climate Change (IPCC) predictions for this region. In response to temperature, all species declined

except one (Ethevitr), some declining more than others, and one species (Lytharde) increased through time due to release from competition with other species (Fig. 2b).

DISCUSSION

We have assembled elements that exist in other models to create a fairly simple, open source model for representing multiple fish species in river networks. Advantages of this approach are the published approaches for existing model components, intermediate complexity, transparency, and transferability between modeling platforms. Our approach is flexible, for example, habitat suitability can be determined from any number of environmental factors, on any timescale. Using the same model formulation, habitat suitability may vary by age-class or season (e.g., distinct spawning requirements). Other methods, such as fuzzy models

(Mouton *et al.*, 2009) could be used to determine habitat suitability, however, the regression approach used here allows for straightforward links with dynamic environmental input.

Additional detail could be added as needed to the population model. For example, we could explicitly represent fish growth, including consumption and respiration; however, this would increase the complexity and parameters (Barber, 2008). Individual differences are not represented here, although individual-based models have often been used for fish (e.g., McDermott and Rose, 2000; van Nes *et al.*, 2002). Behavioral interactions such as territorial interactions are also omitted, but may be important (Petty and Grossman, 2004). Competition between species may be asymmetric, and may vary through time (Matthews, 1998). Also, predation is not included. We assumed here that speciation does not occur; we could expand the model to include evolutionary and genetic processes (e.g., Labonne *et al.*, 2008). Future work could incorporate the complexity outlined here, for now we include enough complexity to represent stressor effects in ecological timescales, and no more.

Because river segments are relatively large, we did not assume that fish had knowledge of neighboring segments (an approach used in more detailed fish movement models e.g., Giske *et al.*, 1998; Railsback *et al.*, 1999). However, more complex movement rules could easily be built in to the movement parameter. Also, the network structure could be specified by other methods, such as functional process zones (Thorp *et al.*, 2010) or river valley segments (Brenden *et al.*, 2008). Our model can also represent changes in network structure, due to loss of headwater streams (represented as survival of zero in these segments), or barriers to movement (represented as zero movement probability).

A user can implement the model in R, Matlab, or C, with minimum data of assumed initial fish densities and basic NHDPlus data: a stream network, and constant habitat values. Default fish parameters are available from the BASS model. The usefulness of our model lies in its ability to be linked with hydrology and water quality models for integrated analyses of river systems. Our model is currently linked with the WASP model (www.epa.gov/athens/wwqtsc/html/wasp.html) to receive spatial time series inputs of environmental factors. Links from hydrologic models to spatial fish mod-

els have been done for the Everglades of Florida (Gaff *et al.*, 2000) and the Murray-Darling Basin in Australia (Young *et al.*, 2000). Mid-complexity models for the dynamics of important fishery resources can form the basis of ecosystem services assessments and be incorporated into an integrated modeling system for watershed assessment and prediction. Our model represents one such promising approach.

APPLICATION IN KOREA

Aquatic ecological modeling is a future aim for Korea, to better understand and forecast the response of lotic ecosystems to anthropogenic disturbances (Lee *et al.*, 2011). Some form of the modeling presented here may provide a useful start to this endeavor. Although over 100 fish species have been identified from rivers in Korea, early modeling efforts can focus on the 38 more common species (Yoon *et al.*, 2011). An understanding exists for the relationship of fishes to environment (Bae *et al.*, 2011; Yoon *et al.*, 2011), and excellent data exist for calibrating and validating the model through the National Aquatic Ecological Monitoring Program (Lee *et al.*, 2011). However, challenges include obtaining adequate population parameters for these species, and characterizing their interactions. Obtaining basic life history data for the most common or important species will be a critical first step in this modeling approach. Possible sources for population parameters include the Fishbase (www.fishbase.org) and Fishwise (www.fishwise.co.za) databases, targeted studies (Hwa-Kun, 2011), and studies from nearby countries, possibly using species within similar guilds (e.g., Wang *et al.*, 1995).

The ecological model may be applied to the scale of the 110 base watershed management regions in the country (Park *et al.*, 2011), which is somewhat larger in scale than the example presented here, or at the four larger watersheds (Lee *et al.*, 2011). Time series of input water quality data for habitat relationships can be derived from watershed modeling currently underway in Korea (e.g., Park and Lee, 2002). Particular simulations may examine the effects of stressors such as climate change, urbanization, flow alteration, nutrient enrichment, and invasive species (Bae *et al.*, 2008; Yoon *et al.*, 2011).

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