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New predictions from old theory: Emergent effects of multiple stressors in a model of piscivorous fish

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ABSTRACT

Predicting cumulative effects is an important challenge of theoretical and management ecology. If a population will be exposed to multiple stressors (e.g., toxins, introduced competitors, climate change), will their cumulative effects be independent and hence multiplicative (the population survival rates due to each stressor can be multiplied together to determine the total reduction in abundance), synergistic (cumulative effects are greater than multiplicative), or antagonistic (stressors offset each other so cumulative effects are less than multiplicative)? Further, the effects of each stressor can vary with such factors as habitat quality, population density, and weather. It is difficult to predict cumulative effects with traditional population-level models because such models must assume the type and strength of stressor interactions *a priori*, and measuring stressor effects and interactions empirically is rarely practical. Instead, we used an individual-based model in which cumulative effects emerge from how each stressor affects the growth and survival of individuals, and how individuals interact. Our model is in fact based on theoretical concepts explored in the landmark 1980 paper of DeAngelis et al. (Cannibalism and size dispersal in young-of-the-year largemouth bass: experiment and model, Ecol. Model. 8, 133–148): in a community of fish that eat each other, initial differences in size among individuals have strong effects on subsequent abundance and size distributions. We model survival and growth of juvenile Colorado pikeminnow (*Ptychocheilus lucius*) during their first year, and two stressors they are subject to. The first stressor is a daily cycle of flow fluctuations imposed by an upstream hydroelectric dam; these fluctuations affect habitat area, food supply, and temperature, which then affect juvenile fish growth. Second is an introduced fish species that competes with pikeminnow for food, while both species can prey on each other via the size-based mechanism described by DeAngelis et al. We simulated the effects of the 36 combinations of six levels of these two stressors in each of 28 sites and weather year to produce 840 scenarios, using 7 weather year datasets as replicates. Emergent cumulative effects were multiplicative in 69% of these scenarios, synergistic in 22%, and antagonistic in 9%. Therefore, any *a priori* assumption about stressor interactions would be wrong in many situations. Synergistic effects were most common in deeper and larger habitats favorable to the introduced species; antagonistic effects were most common in smaller habitats where the introduced species had low growth, because flow fluctuations further reduced the small food supply.

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1. Introduction

In regulated systems, multiple stressors can combine to exert *cumulative effects* on species of concern. Despite legal requirements to include cumulative effects assessment (CEA) in many environmental impact studies and reports, they remain poorly understood (Duinker and Greig, 2006; Hegmann and Yarranton, 2011). Until recently, planning analysts might analyze the effect of each stressor individually and then use simple additive or multiplicative models to predict cumulative effects of multiple stressors acting together on organisms or ecological systems. This approach ignores the links between multiple drivers of an ecosystem and the potential for complex emergent stressor interactions. Recent studies suggest that stressor interactions are often *synergistic* (the combined effects of the multiple stressors are greater than

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predicted by a simple additive or multiplicative model) or *antagonistic* (the combined effects of the multiple stressors are less than predicted by a simple model).

For example, Hanazato and Dodson (1995) analyzed the individual and interacting effects of low oxygen concentration and chemicals on small crustaceans; synergistic effects were detected for all pairs of stressors. Folt et al. (1999) performed experiments with similar organisms but different stressors: high temperature, a chemical toxin, and low food supplies. Compared with predictions of several simple models, the effects of those simultaneous stressors were mostly antagonistic. Crain et al. (2008) performed a meta-analysis comparing experimental results to the additive effects model in 171 marine studies that varied two or more stressors. Overall, they detected significant synergistic effects across all studies, although many antagonistic results occurred, especially when the scope of the study was broadened to include community response.

Simulation modeling can be an important tool in CEA (Smit and Spaling, 1995). Rose (2000) used an individual-based model (IBM) to evaluate cumulative effects of prey composition, juvenile mortality due to water diversion, and adult mortality on the population dynamics of striped bass (*Morone saxatilis*) in the Sacramento–San Joaquin river basin. The cumulative effects of all three stressors were highly synergistic (mean simulated abundance was one-third of the multiplicative prediction). Harvey and Railsback (2007) used an individual-based model to predict the effect of multiple stressors associated with human use of forested watersheds (temperature, turbidity, and pool frequency) on cutthroat trout (*Oncorhynchus clarki*) in a creek in northwest California. Strong stressors tended to interact synergistically while lower stressor levels tended to have multiplicative effects.

Here, we use a mechanistic IBM to explore when and why some stressor interactions can be synergistic, while other interactions in the same system are multiplicative or even antagonistic. The system we study is juvenile Colorado pikeminnow (*Pytchocheilus lucius*), a fish now considered endangered in its native habitat of large rivers of the American Colorado River basin (Minckley et al., 2003). These fish are believed to spend their first summer and autumn rearing in *backwaters* (shallow, low-velocity side channels connected to the main river). The populations we address are on the Green River, downstream of Flaming Gorge Dam in Colorado and Utah. The Green River in this vicinity has a bed primarily of sand, so many backwaters form and are re-arranged during the spring high flows of many years.

We model two stressors. Flow fluctuations caused by hydroelectric power generation at the dam (a daily cycle of flow increase and decrease resulting from higher power generation during peak energy demand hours) alter the physical habitat and food supply of backwaters, with effects depending on the magnitude of daily flow cycles. The second stressor is interaction with exotic fish that have invaded the Green River; we represent exotic fish as the most abundant species, red shiner (*Cyprinella lutrensis*). Red shiners stress pikeminnow by competing for invertebrate prey and by preying directly on pikeminnow (Ruppert et al., 1993; Karp and Tyus, 1990) but can also serve as prey for larger pikeminnow. The model's purpose is to predict and understand effects of flow fluctuations and their interactions with the exotic fish stressor: How does the magnitude of flow fluctuations affect the survival and growth of pikeminnow? Does this flow stressor magnify the effects of red shiners, or offset them, or act independently?

Unlike the previous IBM-based studies, we apply our model to a wide range of sites and weather conditions so we can also examine how stressor interactions emerge from habitat conditions as well as biological interactions. Effects of both flow fluctuations and exotic fish on pikeminnow are highly dependent on backwater habitat characteristics; simulating many different backwaters allows us to ask not whether stressors interactions are multiplicative, synergistic, or antagonistic, but instead to determine the conditions under which each type of interaction emerges.

2. Methods

Our overall approach was to parameterize the IBM for 28 unique sites on the Green River, and then conduct simulation experiments that varied the strength of each stressor. For each site, we simulated stressor levels from zero to high, using seven weather scenarios as replicates. We then determined how often the simulated stressor effects were synergistic, antagonistic, and multiplicative. Finally, we investigated the habitat characteristics that caused the variation in interaction type.

2.1. Model description

Grand et al. (2006) described the habitat component of the pikeminnow IBM—how a backwater's daily size, temperature, and invertebrate prey production emerge from its bathymetry, river flows, weather, and the physical processes driving heat exchange between air and water. The biological component—how pikeminnow survival and growth emerge from physical habitat and interactions with shiners—was described in the on-line appendix to Grimm et al. (2006) and in the Supplementary Material for this article. The Supplementary Material also includes an archive of the backwater geometry and weather input files. Therefore we summarize model characteristics especially relevant to our analyses and the themes of this special issue by providing the "Entities, state variables, and scales," "Process overview and scheduling," and "Design concepts" elements of the ODD model description protocol (Grimm et al., 2010).

2.1.1. Entities, state variables, and scales

Space is modeled at two scales: a backwater, and the square grid cells that represent spatial variation within the backwater. Time is also modeled at two scales: physical processes are simulated at a one-hour time step but fish actions are simulated once per day and are driven by daily mean physical conditions.

Each simulation represents one backwater site, with dynamic state variables for its water surface elevation (a function of river flow), wetted area, volume, mean depth, temperature, and the number of invertebrates available as prey for fish. These backwater-scale variables are modeled by simulating a backwater as a collection of square ($1\ m^2$) grid cells. These cells have static variables for their elevation and whether they are part of the backwater or the river mainstem. Cells have a dynamic variable for depth, updated hourly from water surface elevation. Physical variables of the backwater are calculated from the depth of each cell.

Fish are represented as unique individuals with state variables for species, length, weight, and condition (weight relative to length). The two species are assumed identical in behavior and physiology except for two important differences. The first difference is in initial size at the beginning of a simulation: pikeminnow lengths are drawn from a normal distribution with mean of 12 mm and standard deviation of 2 mm, while red shiners start larger, with mean of 43 mm and standard deviation of 4 mm. Second, the two species have different values of the parameters relating length to weight, reflecting their different body shapes (pikeminnow are thinner, so an increment in weight produces more growth in length for pikeminnow than for shiners).

Because fish can forage over large areas in a day, fish simulations are non-spatial: they depend on characteristics of the entire backwater and fish have no location variables.

Simulations start on 10 July, approximately when pikeminnow juveniles first appear. Simulations stop at 5 December, the onset of

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