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Density dependent functional forms drive compensation in populations exposed to stressors

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ABSTRACT

The interaction between density dependence (DD) and environmental stressors can result in responses that range from compensatory to synergistic impacts to population growth. Models that exclude DD or use generic DD functions for populations in which density may be an important form of regulation may introduce bias into management decisions. Understanding the interaction between DD and stressors on demographic endpoints is needed to ensure models applied in management have the potential to detect compensatory or synergistic interactions between the two. This relationship was explored through the development of a DD demographic model for the sheepshead minnow (*Cyprinodon variegatus*) containing data-defined functions of DD for adult survival, fecundity, and growth. Concentration response curves were developed for organism-level effects from chronic laboratory studies with four chemicals (estradiol, trenbolone, trifluralin, chlordane) causing impacts that vary in endpoint and magnitude. Concentration–response curves were also developed for three hypothetical chemicals (HC) that affected only adult survival (HC-A), fecundity (HC-B), or juvenile growth (HC-C). Population growth rate (PGR) was determined across a range of densities and concentrations for each chemical. PGR contours revealed potential DD–stressor interactions ranging from compensatory to synergistic, which were a function of the combination of DD forms applied in the model and the organism-level impacts of the stressor. Simulations of population projections verified the potential compensatory and synergistic interactions of density and stressors depicted by the PGR contours. The strongest compensation occurred where survival was both DD and impacted by the stressor. When DD survival was omitted, DD fecundity and growth were drivers of PGR, but had limited compensatory influence. These interactions reflect the importance of DD demographic rates to population projections, which should be incorporated into models applied in the management of species in which density may be an important population driver.
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1. Introduction

Density dependence (DD) has historically been a contentious issue among ecologists, who have disagreed on the degree to which a population is self-regulated. While evidence for DD is difficult to identify amongst the noise of population time series (Freckleton et al., 2006), numerous studies have demonstrated significant relationships of demographic rates and density (e.g., Coulson et al., 2001; Samhouri et al., 2009). The inclusion of DD in population models has profound impacts on projected outcomes used for management of endangered species (Todd et al., 2004), harvested or pest populations (Rose et al., 2001), or in toxicological risk assessment (Moe, 2008). Within toxicity assessment, the early suggestion that DD buffers the negative effects of a toxicant (Grant, 1998) has been demonstrated experimentally (e.g. Barata et al., 2002; Moe et al., 2002). Understanding DD influences on a population exposed to a stressor is critical to an evaluation of exposure risk in natural populations that may fluctuate widely in density. While recommendations exist to evaluate DD and toxicological effects together (Forbes et al., 2001), further understanding of the general patterns of this interaction is a high research priority for population-level toxicological assessment (Munns, 2006).

The most ecologically relevant model-based assessment of toxic exposure on wildlife populations integrates organism-level effects (e.g. altered survival, reproduction) and population-level effects (e.g. fluctuation in population size through time; Akcakaya et al., 2008). Population growth rate (PGR; e.g., λ = finite rate of increase, r = instantaneous rate of change) is a favorable model-based index of population level effects because it integrates complex interactions of individuals (i.e., toxicant exposure and DD) to describe potential temporal changes in population size. Although PGR is a point estimate, it is the most commonly used metric for baseline assessments of potential toxicant impacts on a population (Schmolke et al., 2010). The functional form of DD, defined here

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as the mathematical relationship of how a demographic endpoint (e.g., survival, growth, reproduction) varies with density, is generally unknown for most species. As such, model-based assessments of the impact of a stressor either omit DD completely (Raimondo et al., 2009), use a generic function such as a Ricker model (Hayashi et al., 2009), or define it with a simplistic scalar (e.g. carrying capacity; Tucker et al., 2008). While applying simple descriptions of DD may provide more ecological realism than density independent models, the functional form of DD may be critical in determining how a population responds to a stressor (Moe, 2008).

The interactions between population density and stressors can be additive, compensatory, or synergistic and incorporating the appropriate response is necessary to understand how a population may respond to environmental challenges (Forbes et al., 2001). Additive effects occur when incremental increases in density have the same effect across incremental increases in toxicant level. Compensatory DD results from favorable changes in demographic rates (e.g. survival, reproduction) when density is reduced, possibly due to less competition or predation pressure (Hixon and Jones, 2005). This mechanism provides improved demographic rates that help to offset losses of individuals (Rose et al., 2001). Synergism occurs when interactions of DD and toxicant stressors increase population decline beyond that observed from either one independently. This may result when additional stressors affect moderate to high-density populations where individuals already have reduced fitness resulting from intra-specific competition (Sibly, 1999).

To understand the interaction of population density and toxicant exposure, factorial design experiments have been performed that cross several toxicant concentrations with multiple density treatments, which may also include food limitation (Sibly, 1999). These studies have been performed with limited species and chemical diversity due to the size and cost of experiments. They have measured synergistic (Barata et al., 2002; Linke-Gamenick et al., 1999), compensatory (Barata et al., 2002; Liess, 2002; Linke-Gamenick et al., 1999; Moe et al., 2002), over-compensatory (Moe et al., 2005) and no detectable (Menezes-Oliveira et al., 2011) interactions of density and toxicant exposure. Effects assessment from such studies is limited to the densities and toxicant concentrations used and may not describe impacts outside the tested ranges. Importantly, results from these studies indicate that chronic tests conducted at a fixed density may not be representative of toxicant effects in field populations with DD vital rates.

Interactive effects of density and a stressor on PGR can be depicted through schematic contour diagrams (Fig. 1). Barata et al. (2002) interpolated PGR contours from factorial design laboratory studies and found verifying degrees of synergism and compensation. PGR contours can also identify changes to equilibrium population size ("carrying capacity"; $\lambda = 1$, $r = 0$) relative to stress and density, which provides the boundary of a population's tolerance to the model stressor. Understanding how the equilibrium population size changes in response to a stressor may be valuable in the application of ceiling type DD (Grant, 1998). In the absence of large-scale factorial experiments, modeled PGR contours may provide useful insight into how populations may respond to a chemical stressor in naturally fluctuating populations.

This study examines changes in PGR of sheepshead minnow (*Cyprinodon variegatus*) populations exposed to toxicants at various concentrations and densities with the objective of identifying the underlying pattern of their interaction. A DD matrix model is combined with chronic toxicity concentration-response models for three hypothetical and four real chemicals (estradiol, trenbolone, trifluralin, and chlordane). The population model contains laboratory-derived functional forms of DD for growth, adult survival, and reproduction, and the toxicity-response models are for a range of impacts to these and other demographic rates. For each chemical, simulated exposures to a wide range of densities and concentrations result in PGR contours with the potential to demonstrate additivity, compensation, or synergism. Temporal simulations of populations exposed to chemicals project changes to population size and demonstrate the linkage of PGR contours and dynamics of populations exposed to stressors. The objective of this analysis is to demonstrate that (1) model simulations can identify patterns of interaction between chemical stressors and density; (2) the functional form of DD is a critical mechanism driving these patterns; and (3) comprehensive model-based analyses may provide a cost-effective alternative to laboratory studies where interactions of population density with toxicant exposure are of concern.

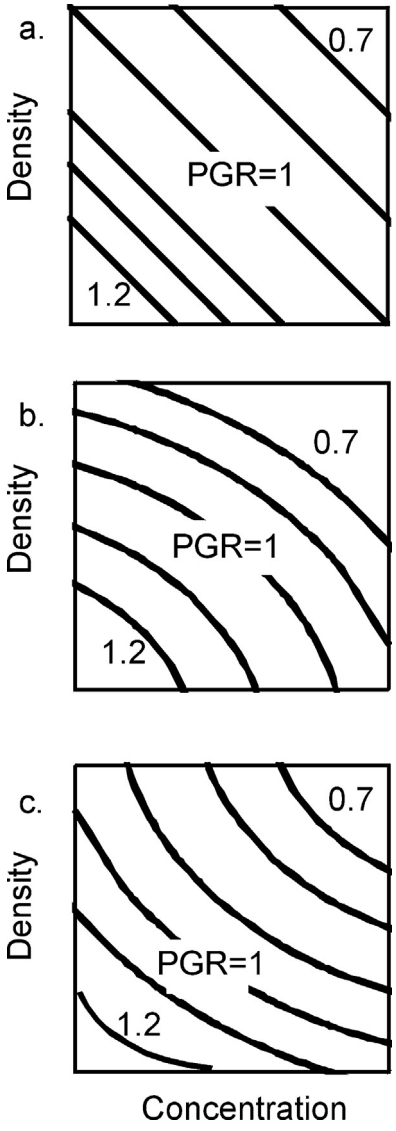

Fig. 1. Theoretical PGR (λ) contours depicting (a) additive, (b) compensatory, and (c) synergistic interactions of density and a chemical stressor.

2. Methods

2.1. Life history and density dependent demographic rates

The sheepshead minnow (Cyprinodontidae), a euryhaline fish distributed in coastal waters of the eastern and gulf coasts of the United States and Mexico, is a standard toxicity test species with a history of use in ecological risk assessments (Hansen and Parrish, 1977). As is typical for fish, the life cycle is composed of four life stages, *i*; 1 = embryo (within egg), 2 = larva (hatchling