Divergent population recovery trajectories following sex-biased perturbation in life history traits

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Abstract

Uncertainty in risks posed by emerging stressors such as synthetic hormones impedes the management and conservation of threatened and endangered long-lived vertebrate populations. Synthetic hormones often induce sex-biased perturbations in exposed animals by disrupting gonad development and early life-history stage transitions, threatening population persistence. We use a spatially-explicit biophysical model to evaluate how sex-biased perturbations in life history traits of individuals (maternal investment in egg production and sex determination) modulate year class strength and population recovery trajectories of a long-lived, migratory fish–shovelnose sturgeon (*Scaphirhynchus platorynchus*)–under spatially and temporally dynamic synthetic androgen exposure. Simulations revealed that reduced efficiency of maternal energetic investment in gonad development prolonged maturation time, increased the probability of skipped spawning, and, in turn, gradually shrunk spawner biomass, ultimately weakening year class strength and extending recovery time at higher exposure. Demographic perturbation in individuals emerged as vastly different population projection and recovery trajectories: the responses to skewed sex allocation were delayed at the population level by more than two decades, followed by an abrupt shift in year class strength and population size, ultimately reaching an alternate state without any sign of recovery. When energetics and demographics were both perturbed, they acted antagonistically, allowing the population to gradually recover without reaching a stable state. The emergent patterns in long-term population projections suggest the complexity of cumulative effects of sex-biased perturbation in life history traits of individuals exposed to low-level (often below detection) synthetic hormones, which can be further obscured by lagged responses and environmental stochasticity. Our study illustrates that the recovery from skewed sex allocation can pose greater conservation challenges than

diminished maternal investment in egg production–highlighting the importance of population monitoring for restoring depleted long-lived populations such as *Scaphirhynchus* sturgeon in ever-changing large rivers.

Keywords: early life history; endocrine disruptors; life history traits; endangered species; agent-based modeling; spatially explicit models; conservation

1. INTRODUCTION

Humans activities have uniquely shaped life history strategies of wild populations of animals by imposing unnatural stress for centuries (Crain, Kroeker & Halpern 2008; Hendry, Farrugia & Kinnison 2008). The symptoms of human-induced stressors, in turn, manifest in life history traits varyingly among individuals (Marr *et al.* 2006) over time and space (Hope 2005; Maxwell *et al.* 2013). Sexual dimorphism, for example, is prevalent in natural populations (Fairbairn 1997), often leading to sex-biased pressure (Coltman *et al.* 2003). As stress becomes intensified, these sources of intraspecific variation in fitness may emerge as a directional shift in demographic rates (Wedekind 2017), diminishing reproductive output (Knell & Martínez-Ruiz 2017). Because of sex-dependent differential investment in reproduction, sex-biased stresses may pose a unpredictable threat to persistence of wild populations (Coltman *et al.* 2003).

One emerging stressor with such effects is synthetic chemicals, which have been increasingly detected in aquatic systems around the globe (Bernhardt, Rosi & Gessner 2017). A rising demand for human food production has increased agricultural use of synthetic chemicals (Tilman 1999; Tilman *et al.* 2001), posing a greater risk to freshwater vertebrates (Bernhardt, Rosi & Gessner 2017). Synthetic hormones–often used as growth-promoters for farmed animals–are especially potent, impairing fish development and reproduction by disrupting energy allocation and maturation (del Carmen Alvarez & Fuiman 2005). These indirect processes thus stunt somatic and gonadal growth (Arcand Hoy & Benson 1998). In pre-spawning females, even low-dose (often below detection) exposure to synthetic hormones can disrupt maturation processes such as vitellogenin production–a critical step in egg production (Arcand Hoy & Benson 1998; Nash *et al.* 2004). Because maternal investment in egg production incur greater energetic costs than somatic growth, females may more likely experience reproductive impairment than males

from chemical perturbation in gonad development (Arukwe & Goksøyr 1998). Further, synthetic hormones can irreversibly perturb sex determination, skewing sex allocation in offspring (Mills & Chichester 2005). Modified demographic traits such as skewed sex ratio have been reported in wild animal populations with sex-biased mortality (McTavish, Stech & Stay 1998). However, it remains unclear how skewed sex allocation in early life stages resulting from exposure to synthetic hormones influence population persistence and recovery in nature (Ankley *et al.* 2008).

We here present a simulation study on how long-term sex-biased perturbations in life history traits can emerge and modify recovery potential of a migratory fish exposed to low-level synthetic androgens in a large river. Migratory animals are exposed to spatially and temporally dynamic flow-dependent exposure regimes as the chemicals move throughout networks of streams and rivers (O'Brien *et al.* 2016); variable exposure and subsequent symptoms among exposed individuals can obscure a causal link, if any, to population-level responses, delaying management actions (Peterson *et al.* 2003). We test varying exposure and effect scenarios on the Missouri River shovelnose sturgeon (*Scaphirhynchus platorynchus*) as an illustrative case study. Population sizes of *Scaphirhynchus* sturgeon have declined in many of their endemic habitats, and some are facing potential extirpation owing to extensive habitat modification (e.g., impoundments) (Bramblett & White 2001). Further, some of the Missouri River populations have shown signs of unsuccessful spawning (DeLonay *et al.* 2009a) and year class failure owing to low larval fish survival (Hrabik *et al.* 2007)–a threat to population persistence (DeLonay *et al.* 2009a). We use a spatially-explicit individual-based biophysical model to evaluate how modified energetics (reduced maternal investment in egg production) and demographics (skewed sex allocation)–two commonly reported symptoms of synthetic androgens–influence year class success, and population persistence and recovery of sturgeon.

2. MATERIALS AND METHODS

2.1. Study system

The study system is the lower 162 km of the Platte River (Nebraska, USA), one of the largest tributaries of the Missouri River basin (Fig. 1a and S1), providing spawning and nursing habitats essential for threatened and endategered fish populations such as *Scaphirhynchus* sturgeon (Peters & Parham 2008). Due to its proximity to wastewater treatment plants and agricultural fields, however, the lower Platte River is also one of the impaired water bodies in the region (NDEQ 2004). Fish that inhabit this river and its tributaries such as *Scaphirhynchus* sturgeon are exposed to elevated concentrations of synthetic hormones widely used at concentrated cattle feedlots near the lower Platte River watershed (Huntzinger & Ellis 1993) and exhibit symptoms of endocrine disruption (e.g., intersexuality and atresia, DeLonay *et al.* 2009a).

2.2. Sturgeon biophysical model

We use a spatially explicit individual-based biophysical model of shovelnsoe sturgoen previously developed for the Lower Platte River popuatlion; the model is fully described in Goto *et al.* (2015) and Goto *et al.* (2018). The model is designed to uncover ecological mechanisms underlying early life-history processes modified by natural and human-induced stressors, and their contributions to population persistence under spatially and temporally dynamic habitat conditions. The model primarily hinges on energetics principles to understand how maternal and environmental influences modulate year class variability through energy acquisition and allocation (Houde 1989). In this study, we evaluated sex-biased effects of synthetic androgen perturbation in maternal investment in gonad development and first-year sex allocation (Fig. 1b and S2). The following briefly describes the essetial features of the model relevant to this study.

The model river consists of 162 equally divided longitudinal rectangular segments (i.e., 1 rkm each). Model inputs include water temperature (°C), mean gauge height (depth, m), channel width (m), discharge rate (m^3 s^{-1}), and photoperiod (hrs). Water temperature, gauge height, channel width, and discharge rate (1995–2011) were derived from the USGS National Water Information System (http://waterdata.usgs.gov/nwis). Further details on derivation of physical and hydrological input data are described in Goto *et al.* (2018).

The sturgeon model keeps track of state variables of the entire life cycle (Fig. 1b). Early life stages (fertilized eggs, yolk-sac larvae, and feeding larvae, and age-0 juveniles) are represented as super-individuals (Scheffer *et al.* 1995), whereas age 1+ juveniles and adults are represented as individuals. Each super-individual is a collection of individuals ("cohorts") from the same mother. We initialized simulations with 60 000 age 1+ individuals on January 1st. The initial location of each sturgeon was randomly assigned to a cell with non-extreme water velocity (≤0.6 m s^{-1}) and depth (≥0.5 m). The initial age structure follows a Poisson distribution with mean age of 7, which is truncated at a maximum age of 16, and the initial sex ratio is 1:1. Sex was randomly assigned to each fish, assuming a binomial distribution. For age 1+ sturgeon, initial lengths-at-age were computed using the von Bertalanffy growth function (Ricker 1975) parameterized for the Platte River population (Goto *et al.* 2018). Once spawned, fertilized eggs were initialized as super-individuals; the number of super-individuals is the number of mothers, and the number of individuals in each super-individual is the total number of eggs spawned by each mother. After settlement, feeding larvae were initialized with individual-level processes (e.g., growth) and traits (e.g., body size).

The model simulates the population and updates state variables at discrete daily time steps over years and generations. The habitat conditions (including prey production) are first updated, and

then the model evaluates actions by sturgeon in the following order; (i) *spawning*, (ii) *hatching and larval development*, (iii) *movement*, (iv) *foraging*, (v) *growth*, and (vi) *mortality* (Fig. 1b). Density dependence is incorporated in directly foraging and indirectly in growth. Sturgeon's abilities to sense habitat conditions and prey density, capture prey, decide when to spawn, and survive are partially stochastic because of inherent uncertainty and randomness.

The model consists of one benthic prey submodel and six sturgeon submodels (Goto *et al.* 2018). Benthic prey production is computed using a mass-balance model described by Rashleigh & Grossman (2005) with modifications described in Goto *et al.* (2018). The early stages of larval development are computed using temperature-dependent nonlinear functions (Goto *et al.* 2018). Foraging is computed using a modified version of the Beddington–DeAngelis functional response model (Beddington 1975; DeAngelis, Goldstein & O'neill 1975). Growth is simulated by the bioenergetics model (Hanson *et al.* 1997) modified so that the assimilated energy is allocated to storage (reversible) and structure (irreversible) (Gurney *et al.* 2003). Sturgeon mature based on sex-specific probability, which is length-dependent functions parameterized for the Platte River population (Goto *et al.* 2018). Reproductive adults further allocate energy to gonad incrementally between spawning events. Adults initiate the reproductive cycle only when their physiological condition is above a threshold based on relative storage mass. The amount of daily energy allocated to gonad is further adjusted when the physiological condition is below the threshold (Goto *et al.* 2018). Spawning is simulated as a stochastic event and occurs only when spawning cues–water temperature, river discharge rate, daylight hours, and gonad development (gonadosomatic index or GSI), concurrently meet the thresholds (Delonay *et al.* 2016). Water temperature suitable for the female *Scaphirhynchus* sturgeon spawning ranges is set at 12.6–24.9ºC (DeLonay *et al.* 2009b). A minimum threshold for river discharge rate was set at 141.6

$m^3 s^{-1}$, which is expected to reach roughly 50% connectivity (migratory pathway connectedness) in the Lower Platte River (Peters & Parham 2008) and directly influences movement and subsequently habitat conditions for other individual-level actions. A minimum GSI to initiate spawning is set at 0.18 for females and 0.03 for males (Wildhaber *et al.* 2007a). After spawning, fish lose all gonad mass, and their physiological condition and total mass are updated; fish do not re-enter the reproductive cycle until the physiological condition meets the threshold. When either temperature or discharge rate does not meet the thresholds, fish skip spawning. We assume that when the physiological condition does not meet the threshold to remain in the reproductive cycle, gonadal energy is reabsorbed and reallocated to storage. Movement is tracked in the longitudinal direction only. The planktonic life stage fish (eggs and yolk-sac larvae) move by passive drift with water currents (Braaten *et al.* 2008). Feeding larvae, juveniles, and adults move in the direction with probability of attaining higher habitat quality using the empirical models developed for the Lower Platte River population (Peters & Parham 2008). Mortality results from thermal stress (eggs and yolk-sac larvae), predation (eggs, larvae, and juveniles), starvation, and recreational fishing (age 3+). We assume that a constant proportion of eggs and yolk-sac larvae die when water temperature rises above 24 °C (Kappenman, Webb & Greenwood 2013). Realized predation, starvation, and fishing mortality are a stochastic event. Starvation mortality depends on relative storage mass (Goto *et al.* 2018).

2.3. Simulation scenarios for sex-biased purtubations by synthetic androgens

We ran 57-year (27-year exposure + 30-year recovery) simulations for the following four scenarios to assess the population performance under two types of perturbations in life history traits of individuals induced by low-level synthetic androgens, energetics and demorgraphics;

1) No sex-biased purtubation–baseline;

2) Synthetic androgens perturb maternal energetic investment in egg production by imposing reduction in vitellogenin production rate;

3) Synthetic androgens perturb sex allocation by imposing skewness in sex ratio at recruitment; and

4) Synthetic androgens perturb both maternal energetic investment and sex allocation. We assumed no direct mortality caused by synthetic androgen exposure. Further, we assumed that: a) synthetic androgens are released between May 1st and October 31st (a six-month growing season); b) androgens affect only fish located below the confluence with the Elkhorn River (~51 rkm from Plattsmouth, NE, Fig 1a), where a number of cattle feedlots are located; and c) because the androgen concentration varies with stream flow rate, the realized exposure level for individual fish is spatially and temporally dynamic, and is thus adusted based on flow rate in a grid cell in which the given fish is located.

Energetic perturbation. We explicitly evaluated the mechanism underlying synthetic androgen-induced reduction in egg production by simulating the dose-dependent reduction of vitellogenin production in individual fish based on an exponential decay function (Ankley *et al.* 2003). Vitellogenin (VTG) concentration (mg ml^{-1}) is converted to relative gonad mass (GSI) using an empirically derived linear function based on field survey data on the Missouri River shovelnose sturgeon reported by Wildhaber *et al.* (2007b) (Fig. S2) as GSI = 0.984VTG + 35.103. Reduction in daily energy allocation to gonad (g d^{-1}) in exposed females was then computed based on somatic mass on the given day.

We tested the scenarios of 15%, 25%, and 35% reduction in daily vitellogenin production in fish that are located at the Elkhorn River–Platte River confluence; these reduction rates in vitelogenin production approximately corresspond to the responses in fish exposed to

environmentally realistic, low level sysnthetic androgens (e.g., <~15 ng l^{-1} 17β-trenbolone, a synthetic androgen commonly used in cattle feedlots, Ankley *et al.* 2003). For fish that are located in cells below the confluence, the reduction rates were proportionally adjuted by the difference in flow rate (e.g., if flow rates at the confluence and in the cell where a fish is located are 100 and 120 m^3 s^{-1}, respectively, the realized reduction rate for this fish is 12.5% under the 15% reduction scenario). Because the model sturgeon cannot detect low-level synthetic androgens in water, we assumed that their movement and energy acquisition (foraging) vary independently of synthetic androgens.

Demographic perturbation. We implemented synthetic androgen-induced skewness in sex allocation by proportionally reducing the probability of being female. We tested the scenarios of 20%, 60%, and 80% reduction in probability of being females for post-hatch fish that remain in the cell at the Elkhorn River–Platte River confluence; these rates approximately corresspond to the responses in fish exposed to environmentally realistic concentrations (e.g., <~15 ng l^{-1} 17β-trenbolone, Morthorst, Holbech & Bjerregaard 2010). We assumed that the probability of being female incrementally declines by remaining in the exposure area each day (i.e., 0.11%, 0.33%, and 0.44%, respectively). For fish in cells below the confluence, the probability was proportionally adjuted by the difference in flow rates (as above).

For all the scenarios, we used hydrological and temperature inputs empirically derived from the lower Platte River field surveys during 1995–2011 (Goto *et al.* 2018), from which we randomly selected each year; we assumed no systematic change or shift in hydrological and thermal conditions in this study. Further, we assumed no change in turbidity, channel geomorphology, and photoperiod. We ran ten simulations for each exposure scenario and

computed summary statistics and % deviations in demographic and life-history traits from the baseline simulations.

3. RESULTS

3.1. Baseline sturgeon population dynamics

Under the baseline conditions, the sturgeon population remained stable over 57 years (Fig. 2 and S3). The population maintained, on average, ~32% of adults being female, ~15.8 metric ton spawner biomass, and ~7100 recruits (Fig. S3, Table S1 and S2). Adult females allocated, on average, ~9.4 % of total mass to gonad while they were in the reproductive cycle; ~22% of reproductive females eventually spawned, producing, on average, 23 million eggs (or ~33000 eggs spawner^{-1}) annually (Table S1 and S2). Most spawning and subsequent larval settlement occurred below the confluence of the Elkhorn River and the Platte River (112 rkm) in late April to early May (Table S1 and S2). Although the recruit numbers highly varied among years, a non-linear (hump-shaped) density-dependent relationship emerged between spawners and recruits (Fig. S3); on average, 0.11% of first-year fish survived (Table S1 and S2).

3.2. Recovery from reduced vitellogenin production efficiency

Simulated reduction in vitellogenin production rate gradually lowered reproductive capacities and, in turn, biomass production of the sturgeon population exposed to synthetic androgens (Fig. 2 and 3). The proportion of energy allocated to gonad mass (10%) or storage mass (24%) in reproductive females under exposure did not differ from those under baseline (Table S1). However, the number of adult females in the reproductive cycle declined by 7.5–34% during exposure (Fig. 4a,b). Further, spawner biomass and recruit numbers declined especially when exposed to moderate and high levels of the perturbation (6.8–25% and 23–38%, respectively, Fig. 3b, c), which were linearly correlated with relative changes in reproductive female

abundance (Fig. 3e). Lowered reproductive capacities and year class resulted in 8.6–43% reduction (relative to baseline) in population biomass during exposure (Fig. 2b and 3d).

Similar relationships remained during recovery; reproductive females, spawners, and recruits of the population with moderate exposures returned to the baseline levels with population size fully recovered (i.e., mean population size returns to the baseline level) within five years (Fig. 2b and 3), whereas the reproductive females, spawners, and recruits of the population with high exposure continued to decline, ultimately reducing mean population biomass by up to 83% before showing a sign of recovery after 15 years (~year 42, Fig. 2b).

3.3. Recovery from skewed recruit sex ratio

Sturgeon spawner biomass abruptly declined by up to 67% by ~year 22 under all scenarios of simulated skewed sex ratios during the first year of life (Fig. 2c). Skewed sex ratios in recruits were reflected in adults within ~6 years with relative female numbers declining, on average, by 6.3–25% during exposure (Fig. 3g). Subsequently, the number of adult females entering the reproductive cycle and spawner biomass both started declining by ~year 8. During exposure, mean reproductive female abundance declined by 19–21%; mean spawner biomass declined by up to 29% under high exposure (Fig. 3h and 3i). In contrast, mean recruit number declined under low and moderate exposure (by 15% and 23%, respectively), but differed little from the baseline population under high exposure (Fig. 3j).

During recovery, mean sex ratios under all the exposure scenarios remained slightly (by 9.3–16%) skewed toward males with high interannual variation (Fig. 3g). However, only the low-exposure population fully recovered, whereas the moderate and high exposure populations continued to show declining reproductive female abundance, spawner biomass, and recruit number (Fig. 3). Despite large year class in early recovery years (year 31–33), more than 85% of

adults were males under high exposure and did not contribute to spawner biomass (Fig. 3). The moderate and high exposure spawner biomass ultimately reached a stable state with less than 20% of the baseline population (Fig. 2c).

3.4. Recovery from combined effects of reduced vitellogenin production and skewed sex ratio

Concurrently simulating reduction in vitellogenin production and skewed sex ratios modulated the sturgeon population dynamics additively under low exposure, but antagonistically under moderate and high exposure (Fig. 2d). Spawner biomass declined within 5 years and remained relatively stable and then declined further during the last five years (Fig. 2d). During exposure, adult sex ratio differed little under low exposure, but skewness toward males increased by 11% under medium and high exposure (Fig. 4a). Further, reproductive female abundance, spawner biomass, and recruit number declined by 31%, 23%, and 31% (respectively) under low and moderate exposure, and declined by 46%, 29%, and 47% (respectively) under high exposure (Fig. 4b-d).

During recovery, adult sex ratios remained skewed toward males (by ~11%) under all the exposure scenarios (Fig. 4a). Mean reproductive female number, spawner biomass, and recruit number (except for reproductive females with low exposure) recovered after low and moderate exposures but remained low under high exposure (Fig. 4b-d). Spawner biomass under low and moderate exposure recovered within ~25 years of recovery, whereas the biomass of the population under high exposure reached a stable state in ~22 years at ~44% lower than the baseline population (Fig. 2d).

4. DISCUSSION

Simulations revealed that energetic (gonad maturation) and demographic (sex allocation) perturbations in life history traits of long-lived, migratory freshwater vertebrates such as

Scaphirhynchus sturgeon can emerge as vastly different response and recovery patterns in population projection in a spatially and temporally dynamic environment. We find that lowered vitellogenin production rate prolongs maturation and, in turn, reduces spawner biomass, ultimately weakening year class strength. Further, the energetic perturbation operates as exposure-dependent processes–the higher the exposure level, the more severe the impacts, thereby resulting in longer recovery time. In contrast, skewed sex allocation emerges as delayed (by more than two decades) population-level responses, followed by an abrupt shift in year class strength and population trajectory under higher exposures, ultimately reaching an alternative (stable) state without any sign of recovery. When energetics and demographics are concurrently perturbed, however, they act antagonistically as the exposure level increases, allowing it to gradually recover without reaching a stable state. These contrasting emergent patterns at the population level highlight the complexity of cumulative effects of stochastic perturbations in life history traits by long-term, low-level exposure to stressors, posing challenges to conservation efforts to restore the depleted vertebrate population.

Delayed gonad maturation in energetically perturbed females prolongs the spawning cycle of our model sturgeon population instead of reducing fecundity. Sex-biased differences in energy allocation to gonadal maturation often determine life-history strategies such as foraging and mate selection, shaping sexual dimorphism in animal populations (Huse 1998; Rennie *et al.* 2008). For a capital spawner such as sturgeon, slowed female gonad maturation delays spawning timing. Although sturgeon are iteroparous, because of infrequent spawning and long maturation time, delayed spawning events can reduce lifetime reproductive output (our simulations show that some individuals spawned only once). Inefficient energy use triggered by synthetic hormones in animals with long maturation time may thus threaten population persistence. Our simulations,

however, also suggest that the energetic perturbation triggers plastic responses. Although reproductive and spawning females decline by up to 25%, the population eventually recovers, indicating the reproductive capacity diminished during androgen exposure can be restored if energy allocation to gonad resumes.

Delayed spawning events may also increase the probability of year class failures owing to environmental stochasticity. We find that exposed (energetically challenged) female sturgeon are more likely to abort the reproductive cycle as they divert energy to meet metabolic needs when poor environmental conditions persist. Although energetic tradeoffs between migration and fecundity are beyond the scope of our study, animals with long spawning migration such as sturgeon likely skip spawning or produce offspring with lower survival rate owing to reduced energy reserves (Glebe & Leggett 1981). Sufficient energy reserves in eggs are vital to larval development and survival; maternal investment in egg production determines the nutritional status of post-hatching larvae (Kjesbu *et al.* 1996). Our model assumes that individual eggs do not vary in energy content; however, energetic tradeoffs in maternal investment in egg production and offspring survival can arise and vary greatly among taxa (Jönsson 1997; McBride *et al.* 2015) and thus need further investigation for *Scaphirhynchus* sturgeon.

Our study suggests that the recovery from demographic perturbation can pose greater conservation challenges than energetic perturbation. We find that a long-lived animal population such as sturgeon experiencing skewed sex allocation can remain in a small population size for long time. Although skewed sex ratio has been widely reported for a variety of vertebrate taxa (Donald 2007), causes of the skewness vary; it can result from phenotypic sex-biased differences in physiology, dispersal, and (natural or human-induced) mortality (Weimerskirch, Lallemand & Martin 2005; Pen *et al.* 2010). In our baseline model population, adult sex ratios are skewed

toward males (~1:2.2), primarily resulting from 1) a longer maturation time for females than males and 2) more energy investment for reproduction in females, resulting in higher probability of starvation in poor years. Simulations, however, show that further deviation (by 13–23%) in adult sex ratio skewness result in long-lasting threats to year class success and population viability. Consequences of skewed adult sex ratio may not immediately emerge for long-lived species (Holmes & York 2003; Lawson *et al.* 2010). Once the skewness reaches a tipping point (Scheffer *et al.* 2009), however, it often becomes difficult for a population to recover (Scheffer *et al.* 2001) as it may stabilize in an alternative state facilitated by a positive feedback (Van Nes & Scheffer 2007; Dai *et al.* 2012). In conservation planning for long-lived migratory species such as sturgeon, thus, to prevent the shifts and minimize recovery cost, it is critical to identify early warnings that signal impending demographic shifts; skewness in adult sex ratio can be a sensitive metric for assessing viability of stressed populations (Ancona *et al.* 2017).

Long-term, low-level exposure to stressors such as synthetic hormones often obscures causative relationships (Windsor, Ormerod & Tyler 2018). Establishing ecologically relevant indicators such as deviation in adult sex ratio and vitellogenin production rate would guide the risk assessment of synthetic hormones and habitat conservation planning for depleted populations. Further, given potential time lags across biological hierarchy, continued biological monitoring of individual-level traits would help detect early signals that may indicate population-level changes. Although our study was designed to evaluate consequences of low-level exposure, our findings indicate larger implications of among-individual variation in sex-biased perturbations for population persistence and recovery of threatened and endangered species. Population models widely used in risk assessments often assume no individual-level variation in each size or age group. These models may not only gloss over individual variation in fertility and

age at maturity that may contribute to population viability, but also under- or over- estimate effects of synthetic hormones and other stressors (Jobling & Tyler 2003).

Large-river migratory populations such as *Scaphirhynchus* sturgeon likely experience multiple synthetic hormones over agriculturally rich landscapes in regions such as the Midwestern United States (Welcomme 1995). Further confounding factors in conservation and management efforts can arise in hydrologically altered systems such as the Platte River. Precipitation can affect the amount of agrichemicals released into rivers. Assessing the likelihood of ecological risks of agrichemicals for long-lived species requires the development of trait-based predictive models using anticipated scenarios. With expected trends in climate variability, which can have considerable effects on river hydrology and water chemistry, these forecasting tools are critical for fisheries and water resource management.

AUTHORS' CONTRIBUTIONS

DG, VEF, and MAP conceived the ideas; MJH, JJH and MLR collected and managed the data; DG led the writing of the manuscript. All authors contributed to revisions and gave final approval for publication.

ACKNOWLEDGEMENTS

We greatly appreciate comments by Maxime Vaugeois (University of Minnesota) and anonymous reviewers on the earlier version of this manuscript. This project was partially funded by University of Nebraska–Lincoln and the Nebraska Game and Parks Commission (Project F-180-R).

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Figures

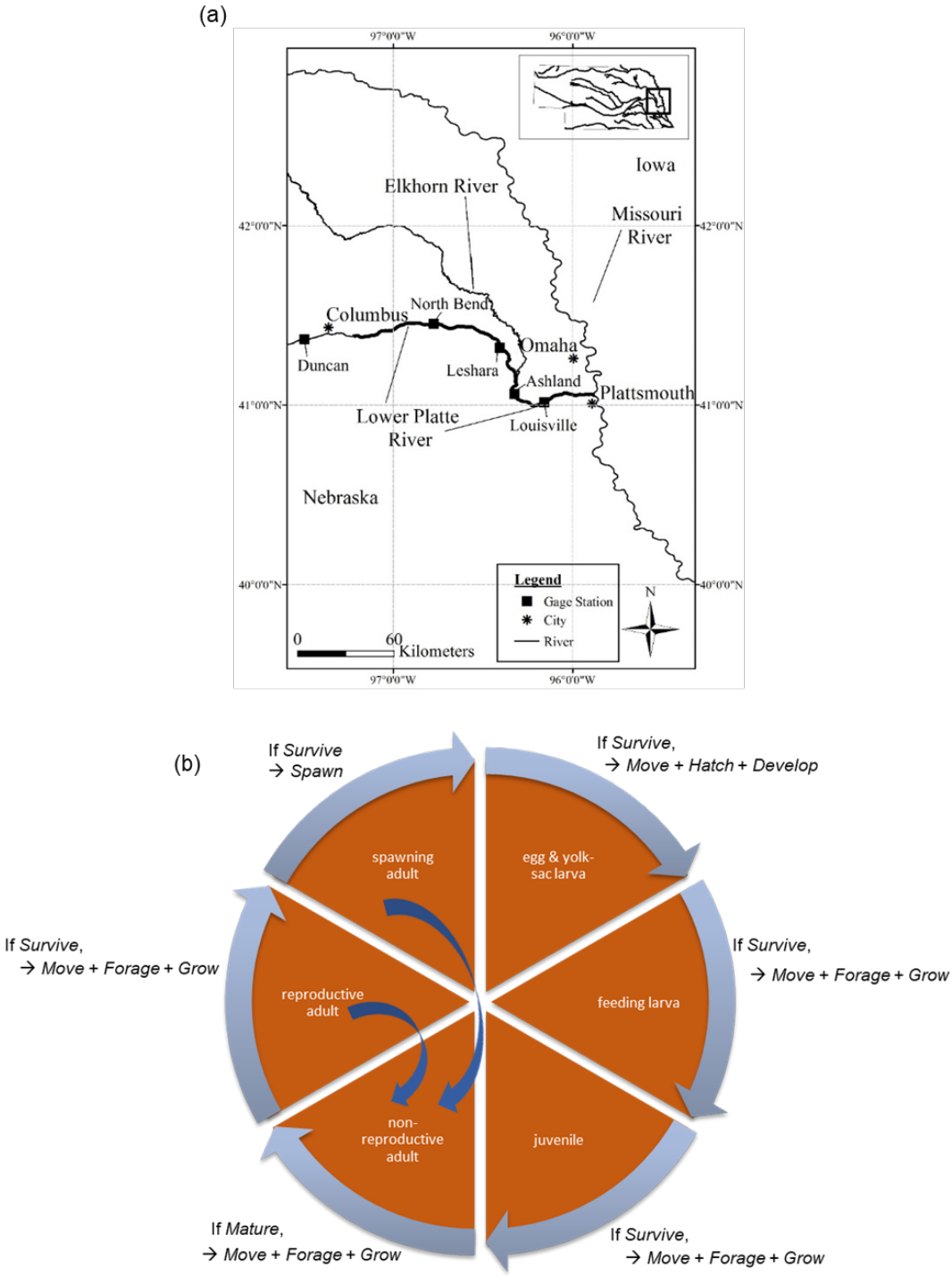

Fig. 1. Study system and model structure. a) a map of the study system, Lower Platte River (Nebraska–NE, USA) and b) a schematic of the spatially explicit individual-based biophysical model for shovelnose sturgeon.

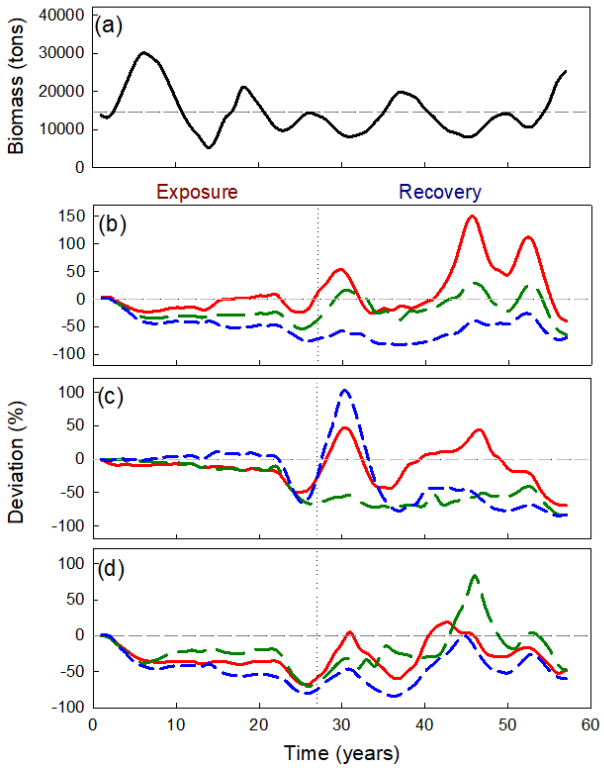

Fig. 2. Shovelnose sturgeon population projections during exposure and recovery under synthetic androgen scenarios – a) a baseline scenario, b) an energetic perturbation (reduced maternal investment in gonad development) scenario with three exposure levels (shown as biomass relative to the baseline scenario); c) a demographic perturbation (pre-recruit sex ratio skewness) scenario with three exposure levels; and d) a combined scenario of energetic and demographic perturbations with three exposure levels. Red solid, green dashed, and blue dotted lines indicate low, medium and high androgen exposure.

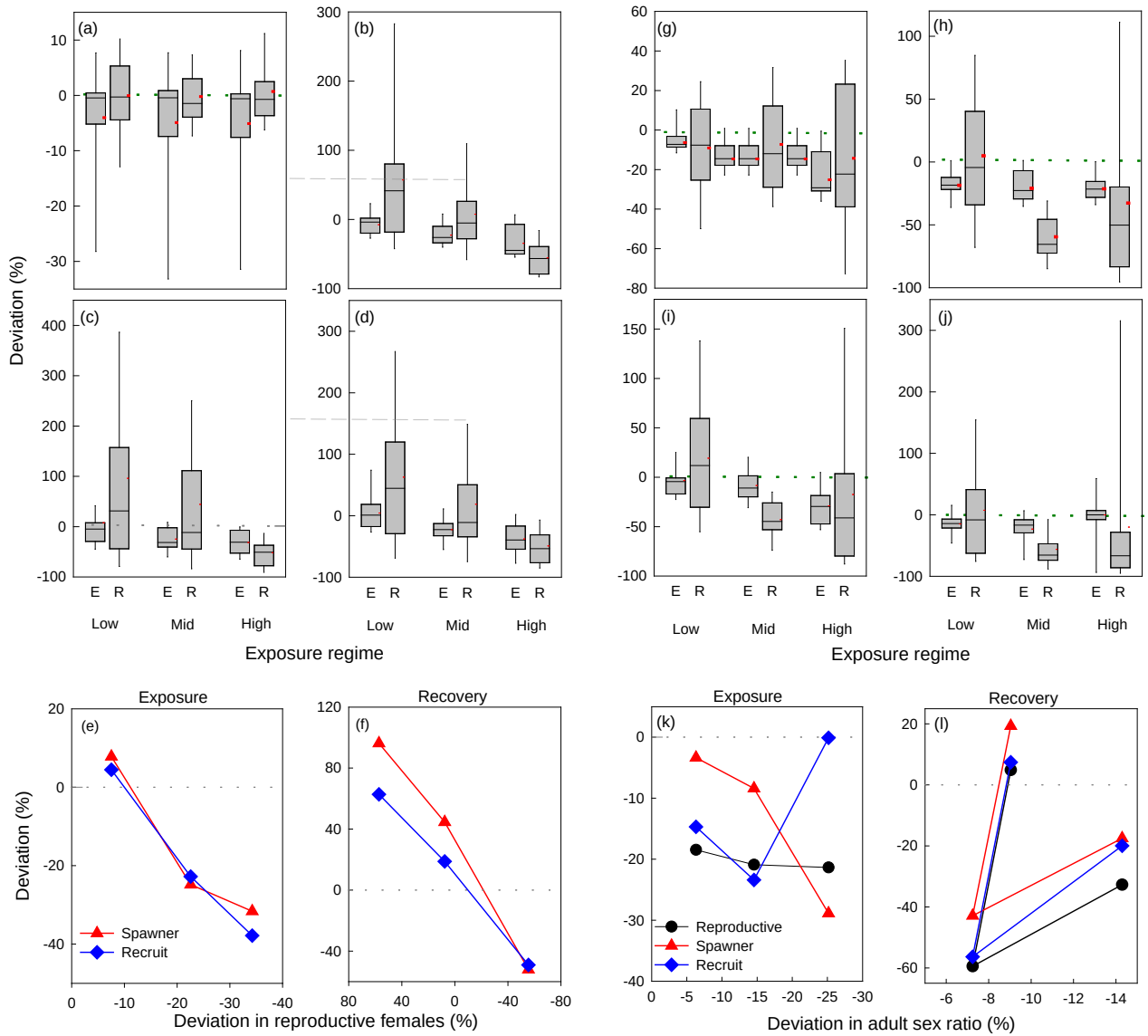
(a)
(b)
(c)
(d)
(g)
(h)
(i)
(j)
Deviation (%)
E R
Low
Mid
High
Exposure regime
Exposure
Recovery
(e)
(f)
(k)
(l)
Spawner
Recruit
Reproductive
Deviation in reproductive females (%)
Deviation in adult sex ratio (%)

Fig. 3. Changes (%, compared to the baseline scenario) in life history traits of shovelnose sturgeon populations– under energetic perturbation scenarios: a) proportion of mature females in the reproductive cycle, b) reproductive female number, c) spawner biomass, d) recruit number, e) relationship between reproductive female number and spawner biomass or recruit number during exposure, f) relationship between reproductive female number and spawner biomass or recruit number during recovery; and demographic perturbation scenarios: g) adult sex ratio, h) reproductive female number, i) spawner biomass, j) recruit number, k) relationship between adult sex ratio and reproductive female number, spawner biomass, or recruit number during exposure, and l) relationship between adult sex ratio and reproductive female number, spawner biomass, or recruit number during recovery. In, a–d and g–j, red solid lines in box plots indicate mean values and black solid lines show 25th, 50th, and 75th percentile (bottom to top). In e, f, k, and l, data points show mean values from low, moderate, and high androgen exposure levels.

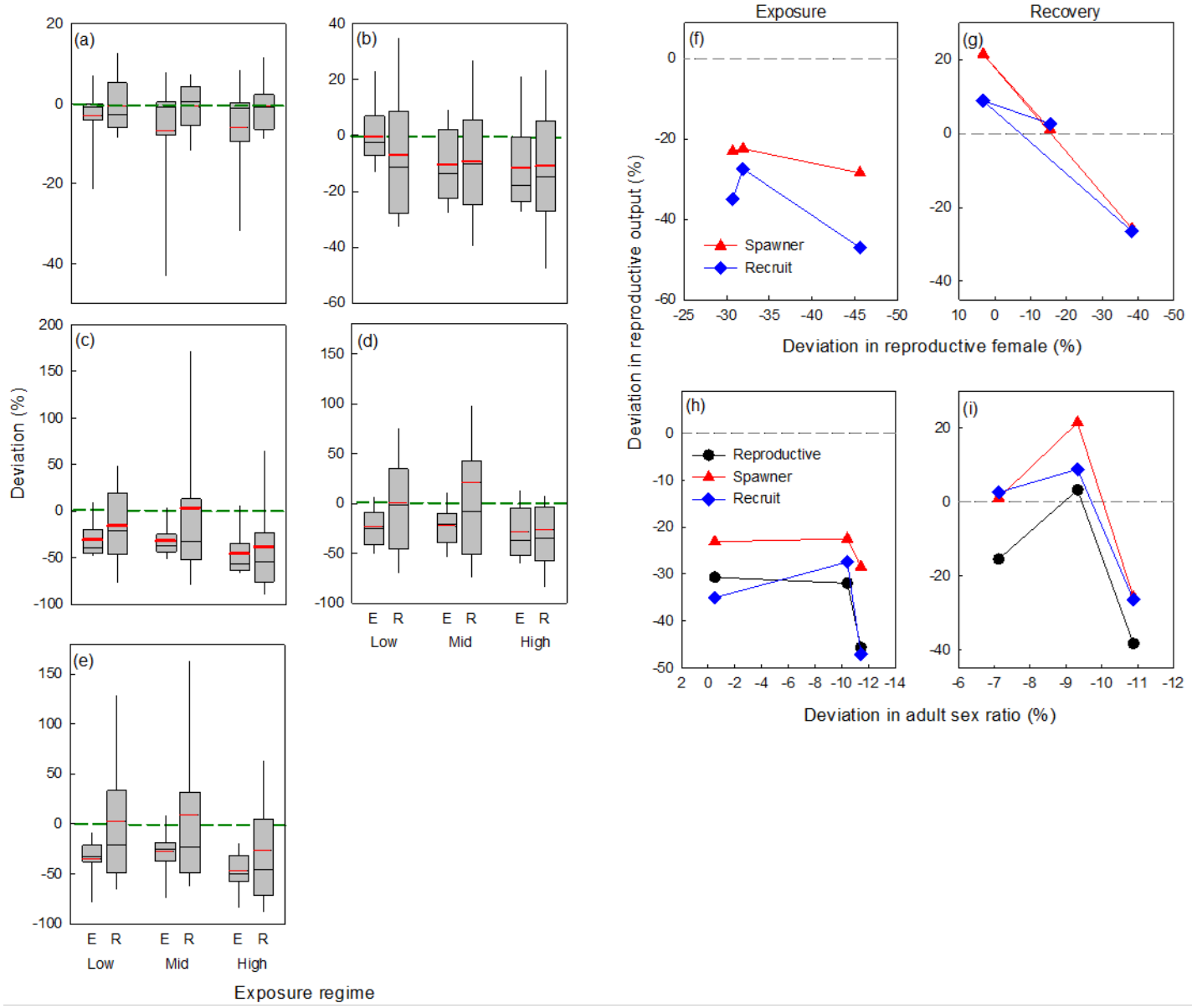
(a)
(b)
(c)
(d)
(e)
Deviation (%)
E R
Low
Mid
High
Exposure regime
Exposure
Recovery
(f)
(g)
(h)
(i)
Spawner
Recruit
Reproductive
Deviation in reproductive output (%)
Deviation in reproductive female (%)
Deviation in adult sex ratio (%)

Fig. 4. Changes (%, compared to the baseline scenario) in life history traits of shovelnose sturgeon populations under combined scenario of energetic and demographic perturbations – a) proportion of mature females in the reproductive cycle, b) adult sex ratio, c) reproductive female number, d) spawner biomass, e) recruit number, f) relationship between reproductive female number and spawner biomass or recruit number during exposure, g) relationship between reproductive female number and spawner biomass or recruit number during recovery, h) relationship between adult sex ratio and reproductive female number, spawner biomass, or recruit number during exposure, and i) relationship between adult sex ratio and reproductive female number, spawner biomass, or recruit number during recovery. In, a–e, red solid lines in box plots show mean values and black solid lines indicate 25th, 50th, and 75th percentile (bottom to top). In f–i, data points show mean values from low, moderate, and high androgen exposure levels.