

# Simulated Influences of Hatching-Date Dependent Survival on Year Class Composition and Abundance

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**Abstract:** Juvenile fish survival is often strongly density dependent and results in relatively consistent average recruitment over a wide range of spawning stock biomasses. Hatching date-dependent mortality can limit contributions of individual hatching sub-cohorts (i.e., fish hatched in one period relative to another within the overall hatching distribution) to the year class and influence the potential for compensatory survival. We used trophic-based ecosystem models to evaluate effects of hatching date- dependent survival on the potential for compensation and regulation of year class strength and adult biomass by simulating variable early-life mortality. We built one model using data for north Florida lakes to represent a contracted spawning distribution and one model for south Florida lakes to represent a protracted spawning distribution using data for largemouth bass *Micropterus salmoides* with hatching-date dependent survival. Hatching date-dependent survival strongly influenced contributions of individual hatching sub-cohorts to year classes (up to 70+% change in sub-cohort biomass), but total effects on year class strength and adult biomass were small (range -9% to +13% total biomass change). Total survival to age-1 was largely regulated by predation such that increases in individual sub-cohort survival did not result in large increases in total recruitment. Ecosystem models indicated that spawning distributions affected sub-cohort interactions to influence compensation and regulation, which had implications for understanding adult spawning periodicity and fisheries management.

**Keywords:** recruitment, regulation, hatching date.

## INTRODUCTION

Density-dependent mortality causes compensatory juvenile survival at low egg production and regulation of juvenile survival at high egg production, thus causing stable average recruitment across a wide range in spawner abundances for many stocks [1]. Regulation can be influenced by multiple biotic (e.g., predation and starvation) and abiotic (e.g., temperature and water clarity) factors, which have greatest effects during early life stages (i.e., “crucial period,” [2]) and interact to affect survival. Although density-dependent mortality in juvenile fishes has received much attention, few cases exist where mechanisms causing regulation have been identified [2].

The relative effect of mechanisms influencing survival, and thus, resulting in compensation and regulation, have been shown to vary with hatching dates such that members of a year class born at different times may suffer from differing mortality forces. For example, Bestgen *et al.* [3] reported that early-hatched Colorado pikeminnow *Ptychocheilus lucius* had higher mortality during early life than later hatched members of a year class due to temporal habitat overlap with their predators. Alternately, early hatching may result in increased survival by enhanced foraging capability or reduced

predation mortality to gape-limited predators [4]. Hatch-date dependent survival has often been identified for both marine and freshwater fishes, but effects of hatching-date dependent survival on total year class abundance and composition (i.e., contributions of differing hatching sub-cohorts) are difficult to investigate.

We explored effects of sub-cohort-specific mortality and within-cohort interactions on recruitment to age-1 and adult biomass. We used largemouth bass *Micropterus salmoides* as an example because previous work in Florida showed that survival of age-0 largemouth bass was hatch-date specific [5]. We used trophic based ecosystem models to assess how largemouth bass year class composition, total recruitment (i.e., age-1), and adult biomass would change if juvenile mortality differed among hatching sub-cohorts. We included hatching duration effects on sub-cohort survival by comparing two models with differing spawning season lengths. One model represented a south Florida system (i.e., with a protracted largemouth bass spawning distribution) and the other represented a north Florida system (with a contracted largemouth bass spawning distribution). Using two models allowed us to incorporate the more pronounced observed differences in cohort dependent early survival at south lakes than at north lakes as well as observed ecological differences (e.g., prey abundance, diet composition) between lakes. Thus, we were interested in (1) the potential for compensation and regulation of recruitment and adult biomass in the presence of increased and decreased individual sub-cohort specific mortality and (2) how model predictions could vary

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among systems as a function of spawning season length and ecosystem characteristics.

## MATERIALS AND METHODS

We used Ecopath with Ecosim (EwE; www.ecopath.org) ecological modeling software to evaluate influences of hatching sub-cohort-specific survival on year class structure and biomass. Two EwE models were developed to explore how results could vary among populations (i.e., between a north Florida system and south Florida system). Models differed via observed differences in hatching distributions due to latitudinal (e.g., temperature [5]), source population (e.g., genetic composition [see 6]), and community composition (e.g., prey fish abundance [7]) differences. A mass-balance food web model was developed (Ecopath process) for each population and simulations were performed to predict effects of differential sub-cohort survival on age-1 biomass, adult biomass, and year class composition at equilibrium (Ecosim process).

An Ecopath model is a mass-balance representation of production and losses among living components (i.e., functional groups) of an ecosystem. Balance occurs when production is equal to predation mortality, non-predation mortality, and fishing harvests (i.e., in the absence of immigra-

tion or emigration) [8] for each prey functional group ( $i$ ) and predator functional group ( $j = 1$  to  $n$  predator groups). Eco-path balance occurs across all functional groups when:

$$B_i \cdot \left(\frac{P}{B}\right)_i \cdot EE_i = \sum_{j=1}^n B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} + Y_i$$

where  $B_i$  and  $B_j$  are biomasses of  $i$  and  $j$ ,  $(P/B)_i$  is the production/biomass ratio for  $i$  and should be entered as the total instantaneous mortality rate ( $Z_i$ ) for vertebrate groups or turnover rate for invertebrates and primary producers,  $EE_i$  is the fraction of  $(P/B)_i$  specified in the model,  $(Q/B)_j$  is the total food consumption per unit biomass of  $j$ ,  $DC_{ij}$  is the proportion of prey group  $i$  to predator group  $j$ 's total diet, and  $Y_i$  is harvest of group  $i$  [8]. Input rates (e.g.,  $P/B$ ) are entered using annual estimates. Functional groups in our ecosystems consisted of fish species groupings with similar foraging life histories (Table 1) and lower trophic level groups. Linkages among functional groups were input by a diet composition matrix for each model that described the percent weight of each prey functional group to each predator functional group's diet (i.e.,  $DC_{ij}$ ).

**Table 1. Species Composition of Fish Functional Groups**

Functional Group	Species Common Name	Species Taxonomic Name	North Model	South Model
other predators	Atlantic needlefish	<i>Strongylura marina</i>	x	x
	Black acara	<i>Cichlasoma bimaculatum</i>		x
	Black crappie (> 200 mm TL)	<i>Pomoxis nigromaculatus</i>	x	x
	Bowfin	<i>Amia calva</i>	x	x
	Chain pickerel	<i>Esox niger</i>	x	x
	Florida gar	<i>Lepisosteus platyrhincus</i>	x	x
	Longnose gar	<i>Lepisosteus osseus</i>		x
	White catfish (> 250 mm TL)	<i>Ameiurus catus</i>	x	x
	Yellow bullhead (>250 mm TL)	<i>Ameiurus natalis</i>	x	
	LMB	Largemouth bass	<i>Micropterus salmoides</i>	x
killifish-topminnows	Bluefin killifish	<i>Lucania goodei</i>	x	x
	Eastern starhead topminnow	<i>Fundulus escambiae</i>	x	
	Golden topminnow	<i>Fundulus chrysotus</i>	x	x
	Least killifish	<i>Heterandria formosa</i>	x	x
	Lined topminnow	<i>Fundulus lineolatus</i>	x	
	Mosquitofish	<i>Gambusia holbrooki</i>	x	x
	Sailfin molly	<i>Poecilia latipinna</i>		x
	Seminole killifish	<i>Fundulus seminolis</i>	x	x
sunfish	Banded pygmy sunfish	<i>Elassoma zonatum</i>	x	
	Black crappie	<i>Pomoxis nigromaculatus</i>	x	x
	Bluegill	<i>Lepomis macrochirus</i>	x	x

Table 1. contd....

Functional Group	Species Common Name	Species Taxonomic Name	North Model	South Model
	Bluespotted sunfish	<i>Enneacanthus gloriosus</i>	x	x
	Dollar sunfish	<i>Lepomis marginatus</i>	x	x
	Everglades pygmy sunfish	<i>Elassoma evergladei</i>		x
	Okefenokee pygmy sunfish	<i>Elassoma okefenokee</i>	x	
	Redbreast sunfish	<i>Lepomis auritus</i>	x	
	Redear sunfish	<i>Lepomis microlophus</i>	x	x
	Spotted sunfish	<i>Lepomis punctatus</i>	x	x
	Warmouth	<i>Lepomis gulosus</i>	x	x
generalists/minnows	Brook silverside	<i>Labidesthes sicculus</i>	x	x
	Coastal shiner	<i>Notropis petersoni</i>	x	
	Flagfish	<i>Jordanella floridae</i>		x
	Golden shiner	<i>Notemigonus crysoleucas</i>	x	x
	Inland silverside	<i>Menidia beryllina</i>	x	x
	Pugnose minnow	<i>Opsopoeodus emiliae</i>	x	x
	Taillight shiner	<i>Notropis maculatus</i>	x	x
benthic fish	Blue tilapia	<i>Tilapia aurea</i>		x
	Brown bullhead	<i>Ameiurus nebulosus</i>	x	x
	Channel catfish	<i>Ictalurus punctatus</i>	x	x
	Clown goby	<i>Microgobius gulosus</i>		x
	Gizzard shad	<i>Dorosoma cepedianum</i>	x	x
	Lake chubsucker	<i>Erimyzon sucetta</i>	x	x
	Pirate perch	<i>Aphredoderus sayanus</i>	x	
	Plated catfish	<i>Hoplosternum littorale</i>		x
	Suckermouth catfish	<i>Hypostomus plecostomus</i>		x
	Swamp darter	<i>Etheostoma fusiforme</i>	x	x
	Tadpole madtom	<i>Noturus gyrinus</i>	x	x
	Threadfin shad	<i>Dorosoma petenense</i>	x	x
	White catfish	<i>Ameiurus catus</i>	x	x
	Yellow bullhead	<i>Ameiurus natalis</i>	x	

mm TL = total length in millimeters, x indicates that species was collected in that region and is represented in the model

Each of our models (i.e., one for north Florida and one for south Florida) included age-structured largemouth bass hatching sub-cohort groups (i.e., early, middle, and late-hatched) and other fish and non-fish functional groups (Tables 2 and 3). Sub-cohorts were determined by grouping fish with similar hatching dates estimated from otolith daily rings (see [5]). For the north lake model, early, middle, and late hatching sub-cohorts had estimated hatch dates occurring in March, April and May-early June, respectively, for a total of

about 100 days of total hatching duration [5]. For the south lake model, early, middle, and late hatching sub-cohorts had estimated hatch dates occurring in December-January, February-March, and April-May, respectively, for a total of 150 days of total hatching duration [5].

Age stanzas for each sub-cohort were used to track fish through their ontogeny and allowed stage-specific model inputs (e.g., P/B, diet composition, etc.) for each sub-cohort. Thus, our stanza structure allowed representation of sub-

**Table 2. Ecopath Inputs for a North Florida Eutrophic Lake Based on Data from Lakes Seminole and Talquin Collected in 2003 and 2004. Values in Parentheses Indicate Life Stages for Each Sub-Cohort of Largemouth Bass**

Group		Biomass	P/B	Q/B	EE
number	Functional group (stage)	(kg/ha)	(yr <sup>-1</sup> )	(yr <sup>-1</sup> )	
1	Other predators	2.56 <sup>a</sup>	0.40 <sup>c</sup>	3.20 <sup>c</sup>	
2	LMB late-hatched (to summer)	0.19 <sup>b</sup>	8.51 <sup>a</sup>	41.04 <sup>b</sup>	
3	LMB late-hatched (to fall)	1.46 <sup>a</sup>	4.16 <sup>a</sup>	13.70 <sup>b</sup>	
4	LMB late-hatched (age-1)	1.78 <sup>b</sup>	2.00 <sup>j</sup>	6.51 <sup>b</sup>	
5	LMB late-hatched (adult)	5.29 <sup>b</sup>	0.71 <sup>e</sup>	3.34 <sup>c</sup>	
6	LMB middle-hatched (to summer)	0.19 <sup>b</sup>	8.77 <sup>a</sup>	41.26 <sup>b</sup>	
7	LMB middle-hatched (to fall)	1.37 <sup>a</sup>	4.16 <sup>d</sup>	13.70 <sup>b</sup>	
8	LMB middle-hatched (age-1)	1.67 <sup>b</sup>	2.00 <sup>j</sup>	6.51 <sup>b</sup>	
9	LMB middle-hatched (adult)	4.96 <sup>b</sup>	0.71 <sup>e</sup>	3.34 <sup>c</sup>	
10	LMB early-hatched (to summer)	0.15 <sup>b</sup>	7.48 <sup>a</sup>	40.18 <sup>b</sup>	
11	LMB early-hatched (to fall)	1.29 <sup>a</sup>	4.16 <sup>d</sup>	13.70 <sup>b</sup>	
12	LMB early-hatched (age-1)	1.58 <sup>b</sup>	2.00 <sup>j</sup>	6.51 <sup>b</sup>	
13	LMB early-hatched (adult)	4.67 <sup>b</sup>	0.71 <sup>e</sup>	3.34 <sup>c</sup>	
14	killifish / topminnows	3.49 <sup>a</sup>	2.82 <sup>c</sup>	44.00 <sup>c</sup>	
15	sunfish	53.50 <sup>a</sup>	1.30 <sup>c</sup>	19.38 <sup>c</sup>	
16	generalists/minnows	9.25 <sup>a</sup>	1.60 <sup>c</sup>	27.80 <sup>c</sup>	
17	benthic fish	37.00 <sup>a</sup>	1.39 <sup>c</sup>	18.68 <sup>c</sup>	
18	crustaceans	26.00 <sup>b*</sup>	13.90 <sup>b*</sup>	22.00 <sup>i</sup>	
19	insects		30.20 <sup>f</sup>	38.00 <sup>b</sup>	0.70 <sup>h</sup>
20	zooplankton		15.00 <sup>i</sup>	35.00 <sup>i</sup>	0.80 <sup>i</sup>
21	macrophytes	61824.00 <sup>a</sup>	2.60 <sup>g</sup>	-	
22	phytoplankton		35.00 <sup>i</sup>	-	0.75 <sup>i</sup>
23	detritus	100.00 <sup>j</sup>	-	-	-

P = production, B = biomass, Q = consumption, EE = ecotrophic efficiency. <sup>a</sup>measured in this study. <sup>b</sup>estimated by Ecopath. <sup>b\*</sup>estimated by Ecopath based on inputs from [43, 44]. <sup>c</sup>derived from www.fishbase.org. <sup>d</sup>derived from [45]. <sup>e</sup>[46]. <sup>f</sup>[47]. <sup>g</sup>within range reported in [48]. <sup>h</sup>[49]. <sup>i</sup>within range reported from published Ecopath models (e.g., [50]), <sup>j</sup>[51].

cohort-specific ages at a given sampling period due to differences in hatching dates among sub-cohorts. Because the onset of spawning at north lakes did not occur until much later in the calendar year relative to south lakes (March versus the previous December or January, respectively), our earliest age-0 largemouth bass stage for the north region model is “to summer”. For each functional group, the model required three of the four following inputs: *B* (kg/ha), *P/B* (year<sup>-1</sup>), *Q/B* (year<sup>-1</sup>), and *EE* and solved for the other parameter [9]. Because late hatched fish were not present at the beginning of the year in the south model, their biomass was entered as a very small number with a *P/B* close to zero and then *P/B* was increased starting in the age/time stanza when they became present in the system which increased their biomasses to field observed levels (see Tables 2 and 3). Thus, our age

stanza structure allowed us to mimic hatching date chronology where early hatched largemouth bass were the oldest members of the year class in the model.

Input data for Ecopath models were obtained from field data and published literature (see Tables 2 and 3 for specific sources). Field data were collected at two south Florida lakes (i.e., Lakes Istokpoga and Okeechobee) and two north Florida lakes (i.e., Lakes Seminole and Talquin) during 2003 and 2004 and these data were combined within each region to derive model inputs [10]. Biomass for each functional group was estimated from average summer (i.e., June/July) block-net catches for each region where we sampled each lake with 12-0.01 ha blocknets treated with rotenone across the range of available habitats at each lake and year. Produc-

**Table 3. Ecopath Inputs for a South Florida Eutrophic Lake Based on Data from Lakes Istokpoga and Okeechobee Collected in 2003 and 2004. Values in Parentheses Indicate Life Stages for Each Sub-Cohort of Largemouth Bass**

Group		Biomass	P/B	Q/B	EE
number	Functional group (stage)	(kg/ha)	(yr <sup>-1</sup> )	(yr <sup>-1</sup> )	
1	Other predators	8.27 <sup>a</sup>	0.22 <sup>c</sup>	3.50 <sup>c</sup>	
2	LMB late-hatched (to spring)	0.03 <sup>b</sup>	0.00 <sup>a</sup>	48.99 <sup>b</sup>	
3	LMB late-hatched (to summer)	0.45 <sup>b</sup>	6.31 <sup>a</sup>	20.73 <sup>b</sup>	
4	LMB late-hatched (to fall)	0.54 <sup>a</sup>	4.16 <sup>d</sup>	11.00 <sup>b</sup>	
5	LMB late-hatched (age-1)	0.98 <sup>b</sup>	2.00 <sup>j</sup>	6.35 <sup>b</sup>	
6	LMB late-hatched (adult)	2.90 <sup>b</sup>	0.71 <sup>e</sup>	3.26 <sup>c</sup>	
7	LMB middle-hatched (to spring)	0.11 <sup>b</sup>	5.82 <sup>a</sup>	50.07 <sup>b</sup>	
8	LMB middle-hatched (to summer)	0.75 <sup>b</sup>	5.94 <sup>a</sup>	22.01 <sup>b</sup>	
9	LMB middle-hatched (to fall)	2.12 <sup>a</sup>	4.16 <sup>d</sup>	11.00 <sup>b</sup>	
10	LMB middle-hatched (age-1)	2.17 <sup>b</sup>	2.00 <sup>j</sup>	5.99 <sup>b</sup>	
11	LMB middle-hatched (adult)	7.04 <sup>b</sup>	0.71 <sup>e</sup>	3.17 <sup>c</sup>	
12	LMB early-hatched (to spring)	0.16 <sup>b</sup>	12.72 <sup>a</sup>	52.35 <sup>b</sup>	
13	LMB early-hatched (to summer)	0.48 <sup>b</sup>	6.72 <sup>a</sup>	21.48 <sup>b</sup>	
14	LMB early-hatched (to fall)	1.06 <sup>a</sup>	4.16 <sup>d</sup>	11.00 <sup>b</sup>	
15	LMB early-hatched (age-1)	1.61 <sup>b</sup>	2.00 <sup>j</sup>	5.96 <sup>b</sup>	
16	LMB early-hatched (adult)	4.77 <sup>b</sup>	0.71 <sup>e</sup>	3.06 <sup>c</sup>	
17	killifish / topminnows	10.40 <sup>a</sup>	2.32 <sup>c</sup>	44.00 <sup>c</sup>	
18	sunfish	73.15 <sup>a</sup>	0.85 <sup>c</sup>	17.17 <sup>c</sup>	
19	generalists/minnows	11.30 <sup>a</sup>	2.00 <sup>c</sup>	39.00 <sup>c</sup>	
20	benthic fish	12.00 <sup>a</sup>	1.15 <sup>c</sup>	22.30 <sup>c</sup>	
21	crustaceans	31.00 <sup>b*</sup>	11.00 <sup>b*</sup>	22.00 <sup>i</sup>	
22	insects		30.20 <sup>f</sup>	38.00 <sup>h</sup>	0.70 <sup>h</sup>
23	zooplankton		15.00 <sup>i</sup>	35.00 <sup>i</sup>	0.80 <sup>i</sup>
24	macrophytes	91232.00 <sup>a</sup>	2.60 <sup>g</sup>	-	
25	phytoplankton		35.00 <sup>i</sup>	-	0.75 <sup>i</sup>
26	detritus	100.00 <sup>i</sup>	-	-	-

P = production, B = biomass, Q = consumption, EE = ecotrophic efficiency. <sup>a</sup>measured in this study. <sup>b</sup>estimated by Ecopath. <sup>b\*</sup>estimated by Ecopath based on inputs from [43, 44]. <sup>c</sup>derived from www.fishbase.org. <sup>d</sup>derived from [45]. <sup>e</sup>[46]. <sup>f</sup>[47]. <sup>g</sup>within range reported in [48]. <sup>h</sup>[49]. <sup>i</sup>within range reported from published Ecopath models (e.g., [50]), <sup>j</sup>[51].

tion/biomass for juvenile largemouth bass stanzas were estimated from hatching sub-cohort specific survival rates in consecutive block-netting samples (see [5]). Other functional group *P/B* and all *Q/B* estimates were derived from www.fishbase.org and published literature (Tables 2 and 3). A weighted average (weighted by species abundance) was used for each non-largemouth bass fish functional group's *B*, *P/B*, and *Q/B* inputs. Juvenile largemouth bass diet inputs were obtained from diet content analysis of fish captured in blocknetting samples in spring and summer and electrofishing samples collected in the fall and at age-1 [10]. Diet contents were specified for each largemouth bass sub-cohort

through their first summer. We could not estimate ages (i.e., specify sub-cohorts) for age-0 largemouth bass after summer, and thus, we assumed that all sub-cohort diet matrices and survival were the same for a given age stanza after their first summer through their adult stanza. This implicitly assumed that no among sub-cohort gape limitation or capture efficiency differences existed after summer, which was plausible because later hatched sub-cohorts often had the highest mean daily growth rates among sub-cohorts that acted to reduce total length ranges [see 5]. Diet composition inputs for species other than largemouth bass were derived from www.fishbase.org and published literature (see [11]).

Four fisheries were established in each of our Ecopath models. A recreational fishery exploited each adult largemouth bass group at 20%, assuming that fishing mortality in these ecosystems was similar to fishing rates from other Florida and southeast black bass fisheries [12, 13, 14]. An individual fishery was created to target each largemouth bass hatching sub-cohort soon after hatching, which allowed us to vary early life mortality in simulations. Fisheries targeting sub-cohorts at their youngest age imposed minimal mortality for the baseline Ecopath model. Thus, we used fishing mortality rates to modify total mortality of each juvenile largemouth bass hatching sub-cohort in Ecosim (see below).

Ecopath models did not initially balance because *EE* estimates exceeded one for some functional groups, thus indicating that losses were greater for those groups than production using initial inputs. Model balances were achieved following suggestions by Christensen *et al.* [9] and Guénette *et al.* [15], rather than using the automated mass-balance routine [16]. We modified input values (i.e., *B*, *P/B*, *Q/B*, or *DC<sub>ij</sub>*) for fish functional groups using diagnostics (e.g., *P/Q* and *M*) recommended by Christensen *et al.* [9], C. Walters (personal communication), and personal knowledge of field data. We used Ecopath's sensitivity analysis to evaluate how changes to input parameter values for the balanced models would affect basic Ecopath parameters estimates.

The balanced Ecopath model was used in Ecosim to increase and decrease hatching sub-cohort specific mortality by  $\pm 50\%$  relative to baseline conditions. Simulated mortality changes were incorporated by changing sub-cohort specific fishing mortality, which resulted in changes to *Z* for a sub-cohort. Mortality was applied until the system re-equilibrated. Changes to mortality were applied to the first age stanza for each sub-cohort to represent an early-life mortality source, where that early mortality could have represented multiple factors commonly reported to result in early juvenile mortality (e.g., predation, [3]; or environmental factors, [17]). Simulated changes in mortality were applied to juvenile biomasses estimated from block-net samples (all  $> 15$  mm total length, TL), and thus, the 50% mortality was additional to mortality acting on these hatching sub-cohorts from their hatching date to 15 mm TL. Largemouth bass exhibit extensive male parental guarding until fry are 15-20 mm TL and density-dependent processes were expected to occur after parental care ceased. We used hatching sub-cohort specific biomass estimates at age-1 and adult stages as evaluation metrics for the relative effects of hatching-date dependent mortality and compensation potential on year class abundance and composition.

Vulnerabilities are required inputs of Ecosim and represent the maximum predation mortality a predator can exert on a prey functional group relative to baseline (i.e., Ecopath) predation mortality [9]. Low vulnerabilities (i.e., one) for a prey functional group represent slow flows from the invulnerable to the vulnerable state and make prey availability to predators largely independent of predator biomasses. High vulnerabilities (e.g., 100) represent fast flows from the invulnerable to vulnerable state and result in large changes to predation mortality for a prey functional group following predator biomass increases [9]. Vulnerabilities for the earliest age-stanzas of all largemouth bass sub-cohorts were low

(i.e., close to one) to emulate factors resulting in very low vulnerability to predators shortly after hatching (e.g., a spatial refuge, schooling, or parental nest guarding), thus resulted in reduced recruits-per-spawner at increased spawner biomasses. We allowed Ecosim to estimate the vulnerabilities for the most abundant LMB hatching sub-cohorts for each model and then used a scaling factor to estimate vulnerabilities for other LMB hatching sub-cohorts. Sub-cohort vulnerabilities were scaled such that the vulnerability value for a sub-cohort stanza times their base biomass was equal across all sub-cohorts, thus allowing for similar influences on prey functional groups as individual predator functional group biomasses changed (Carl Walters, personal communication). In general, all functional group vulnerabilities were entered such that  $1 < v < 10$ .

## RESULTS

In general, biomass and production inputs had greater effects than consumption inputs on estimates of *EE*, such that a  $\pm 30\%$  change in input values could result in up to a 43% change in *EE* estimates for that functional group. Underestimating *B* and *P/B* input values resulted in stronger effects on Ecopath estimates for that functional group than overestimating those values within the range of variation we evaluated. Varying *Q/B* values only had strong effects (i.e., 20-30% change) for *EE* estimates of other predators, sunfish, and insect prey functional groups. Sensitivity of Ecopath estimates to other fish functional group inputs including adult largemouth bass, when varied  $\pm 30\%$ , were less than 10%. Sensitivity analyses suggested that inputs for lowest trophic levels could have large effects on Ecopath's estimates for those trophic levels, but those inputs had very little effect on estimates of upper trophic level biomasses (generally less than 0.02 kg/ha) with large changes in lower trophic level inputs (i.e.,  $\pm 100\%$ ). Thus, input values of a given functional group had more effect on Ecopath's estimates for that functional group than estimates for other functional groups, and input values for top predators had more influence on Ecopath estimates than input values for lower trophic levels.

Ecopath used a modification of Pianka's [18] niche overlap index and diet proportion inputs from field data to describe similarities in prey use between predator functional groups [9]. We expected highest diet similarities between closest aged sub-cohorts because of gape limited predation. However, estimates of prey niche overlap indicated high similarities in prey types among LMB hatching sub-cohorts in spring and summer, but niche overlap values were not always intuitive based on hatching sequence. For example, prey niche overlap estimates for the north lakes model indicated that the early hatched sub-cohort had lower prey niche overlap with the middle hatched sub-cohort (estimate = 0.57) than with the late hatched sub-cohort in July (estimate = 0.84, Table 4). At south lakes, early and middle hatched sub-cohorts had high prey niche overlap in May (estimate = 0.82, Table 4). There were no estimates for the late-hatched sub-cohort's diet overlap with other hatching sub-cohorts in May because these fish were just beginning to enter the population at this time. At south lakes, the early hatched sub-cohort had similar diet overlap with both late and middle-hatched sub-cohorts (estimates = 0.78 and 0.79, respectively) and middle and late-hatched sub-cohorts had very high prey

**Table 4. Ecopath Estimates of Diet Niche Overlap Among Age-0 Largemouth Bass Hatching Sub-Cohorts**

Model	Stage		Late	Middle
North	In July	Late	1.000	
		Middle	0.734	1.000
		Early	0.838	0.574
South	In May	Late	1.000	
		Middle	-	1.000
		Early	-	0.823
	In July	Late	1.000	
		Middle	0.965	1.000
		Early	0.783	0.793

niche overlap in July (estimate = 0.97, Table 4). Observed diet proportions resulted in prey niche overlap estimates that could not solely be explained by hatching sequence.

Hatching-date specific mortality influenced contributions of hatching sub-cohorts to the year class, but effects on age-1 biomass and adult biomass were small. For the north lakes model, contributions of each hatching cohort to the year class were similar (range = 31% to 35%) at Ecopath balance. Simulations that changed one hatching sub-cohort's mortality strongly affected that sub-cohort and other unaltered sub-cohorts responded similarly to each other. For example, increased mortality for the early-hatched sub-cohort reduced their contribution at age-1 to 12% (i.e., a 62% change in their biomass) and resulted in middle and late-hatched cohorts contributing 43% and 45% of the year class (24-25% biomass increases), respectively (Table 5). Increased mortality for individual sub-cohorts greatly reduced their contributions to as little as 10%, whereas reduced mortality allowed for great increases in contributions to the years class by other unaltered sub-cohorts (up to 56%, Table 5). Total age-1 and adult biomasses showed small changes ranging from -7% to +9%. For the south lakes model, contributions of each hatching cohort to age-1 biomass were more variable (range = 21% to 46%) at Ecopath balance than for the north lakes model (Table 5). This variation influenced responses of hatching sub-cohorts to mortality in simulations such that unaltered sub-cohorts did not respond as similarly to each other as in the north lakes model. For example, increased mortality for the middle-hatched sub-cohort reduced their contribution to age-1 biomass from 46% to 33% (i.e., a 34% reduction in biomass) and resulted in early and late-hatched cohorts contributing 41% and 26% of the year class (10% and 15% biomass increases), respectively. Increased mortality for individual sub-cohorts decreased contributions to as little as 7% of the year class (e.g., late-hatched sub-cohort) and decreased mortality increased contributions up to 57% of the year class (e.g., middle-hatched sub-cohort). Late-hatched fish had the strongest responses to mortality simulations in the south lakes model because of their low contribution to the year class at Ecopath balance (Table 5). Similar responses among unaltered sub-cohorts in the north lakes

model resulted from the contracted spawning distribution and high similarity between the groups. In contrast, the protracted spawning distribution at south lakes caused greater differences among sub-cohorts and influenced responses in mortality simulations. Total age-1 biomass was affected by as much as 9% across simulations and adult biomass was predicted to increase by up to 13% and decrease by as much as 7% across simulations. Despite large changes in year class composition relative to contributions of individual hatching sub-cohorts, we saw small effects on total year classes and adult biomass. Thus, the model predicted that large changes in mortality for some portion of the juveniles would not cause large changes to year class biomass and indicated strong compensation and regulation in recruitment.

## DISCUSSION AND CONCLUSION

Ecosystem models predicted that persistent changes in mortality of hatching sub-cohorts could affect equilibrium year class composition and revealed high compensation in juvenile survival under differing mortality treatments. Our models also showed strong regulation of total age-1 biomass with changes in sub-cohort mortality, via predation and cannibalism. Model predictions indicated that effects of individual sub-cohort survival on year class composition will likely vary among systems due to differences in population and community characteristics. Results of our models were somewhat expected based on ecological theory, but suggested that these types of models can be useful for exploring population dynamics and recruitment questions within an ecosystem context. Hatch date-specific offspring survival is an important component in the evolution of reproductive strategies [19], and simulation models that explore intra-cohort dynamics can help refine hypotheses on the importance of spawning season length [20] and ecological interactions [21] affecting recruitment and population composition.

Measures of diet niche overlap provide information on resource use among consumers, but are not reliable indices of competition because they could also indicate prey resource abundance [22, 23]. Ecopath estimated high prey niche overlap for all juvenile largemouth bass sub-cohorts in spring and summer except for middle versus early-hatched sub-cohorts from the north region. Prey resource use for gape-limited juvenile fishes is often limited by body size because larger offspring that were hatched earlier and/or had faster growth can use a larger range of prey species than smaller offspring that were later-hatched and/or slower growing [24]. In our models, the large overlap in prey resource use reflected field observations of similarity in TL ranges among sub-cohorts and large TL ranges for each sub-cohort due to hatch-date dependent growth differences [see 5]. For example, the early-hatched sub-cohort at north lakes in July were 46-128mm TL (median TL = 92 mm), whereas the late-hatched sub-cohort were 28-100 mm TL (median TL = 58 mm). Thus, high prey overlap would be expected based on gape limitation considerations, but length similarity did not explain the lower diet overlap estimated for middle and early-hatched sub-cohorts at north lakes in July. Diet overlap estimates indicated that largemouth bass hatching sub-cohorts used many of the same prey resources through summer, and thus, Foraging Arena Theory [1] would predict that

**Table 5. Ecosim Predicted Age-1 Year Class Composition after Inducing and Reducing Early Juvenile Mortality for Individual Hatching Sub-Cohorts**

Model	Age	Affected Sub-Cohort	Mortality Simulation	Proportion of Year Class			Total Age-1 Biomass Change (%)	Total Adult Biomass Change (%)
				Early	Middle	Late		
North	Age-1	Ecopath		0.31	0.33	0.35		
		Early	+ 50	0.12	0.43	0.45	-3	-5
			- 50	0.50	0.24	0.26	3	8
		Middle	+ 50	0.43	0.10	0.47	-7	-4
			- 50	0.20	0.56	0.24	9	8
		Late	+ 50	0.43	0.44	0.12	-5	-5
			- 50	0.20	0.22	0.57	7	9
South	Age-1	Ecopath		0.34	0.46	0.21		
		Early	+ 50	0.17	0.57	0.26	-9	-6
			- 50	0.52	0.34	0.14	9	13
		Middle	+ 50	0.41	0.33	0.26	-9	-7
			- 50	0.28	0.57	0.16	9	7
		Late	+ 50	0.39	0.54	0.07	-8	-6
			- 50	0.28	0.37	0.36	9	10

changes in sub-cohort abundance would influence predation risk due to foraging if prey abundances were limiting.

Processes that regulate juvenile fish survival have received much attention, and it is now recognized that survival to recruitment results from a series of interdependent events during larval and juvenile stages [4]. The severity of mortality along this series of life-stages can vary among hatching sub-cohorts and result in disproportionate contributions of specific hatching sub-cohorts to the year class relative to their proportion of total fry abundance [25]. Given the identification of hatching date specific mortality, remarkably little work has addressed how hatching date-dependent mortality may influence dynamics within cohorts. Our simulations showed weak effects of sub-cohort mortality on overall biomass at age 1 and adult biomass, because 50% changes in survival of a specific sub-cohort did not lead to large overall changes in other sub-cohort biomasses. Biomasses of unaltered sub-cohorts exhibited strong compensation and total

age-1 and adult biomass did not decline substantially as a result of higher mortality of a specific sub-cohort. Our simulations suggested weaker linkages among sub-cohorts than expected based on hatching-date sequence. For example, early and middle-hatched sub-cohorts responded similarly to simulated changes in late-hatched sub-cohort survival, whereas we expected sub-cohorts hatched consecutively to interact more strongly.

Complex interactions among predators and juvenile largemouth bass functional groups regulated proportional contributions of hatching sub-cohorts to the year class in the models. Predicted increases in sub-cohort biomasses via lower mortality resulted in increased numbers of adult bass acting as predators in the system, and thus, biomass reductions for other hatching sub-cohorts. Importantly, functional groups were modeled such that foraging times did not vary with prey or predator abundances, except for the youngest largemouth bass age stanzas which were assumed to restrict

feeding times rather than maximize growth when food was abundant [e.g., 26]. Increased mortality for individual hatching sub-cohorts decreased biomasses at all life stages for that sub-cohort, increased prey fish functional group biomasses, and therefore increased biomasses of other hatching sub-cohorts. Following increased mortality for a given sub-cohort, biomass increases via compensation for other unaltered hatching sub-cohorts were regulated by predators and suggested a “competitive juvenile bottleneck” [27, 28] between “other predators” and largemouth bass functional groups. Decreased survival of a given hatching sub-cohort resulted in decreased predation on “other predators” because there were fewer largemouth bass adults acting as predators at equilibrium. Thus, increasing “other predators” biomass via lower predation mortality and resulting in increased predation on the unaltered LMB hatching sub-cohorts. In contrast, the opposite phenomenon occurred under simulated increased survival of juvenile largemouth bass hatching sub-cohorts. Thus, the model suggested cultivation of largemouth bass juveniles through adult influences on “other predators” (see [29]). Evaluation of the hypothesized “competitive juvenile bottleneck” between juvenile largemouth bass functional groups and “other predators” would require more complex stage-structuring in the model, however this type of relationship has commonly been found in freshwater ecosystems (e.g., between bluegill and largemouth bass; [30, 31]).

Our results were dependent on Ecosim assumptions (e.g., Foraging Arena Theory), model constraints, and data from regions with differing aquatic communities. Our input values from field data and Ecopath outputs are only applicable to the time period that our data were collected. For example, winter and early spring water temperatures were colder than previous years at south lakes and likely increased growth and mortality differences among sub-cohorts relative to warmer years [5]. Foraging Arena Theory formulations in Ecosim imply that density-dependent processes influencing growth and diet composition would vary as a function of biomasses relative to baseline Ecopath relationships and did not incorporate extrinsic factors (e.g., variable water levels) that have been correlated to largemouth bass recruitment variability [e.g., 32]. Our model structure treated sub-cohorts as individual subpopulations constrained by their Ecopath inputs, and thus, did not incorporate plasticity in individual spawning times that could arise from biological factors (e.g., adult condition and size [33, 34]). Ecosim estimates follow Foraging Arena Theory formulations that determine how predator abundance and prey vulnerability result in mortality and consumption at varying biomasses [1, 9]. The vulnerabilities schedule for functional groups as predators on their prey is one of the most important parameters in Ecosim and one of the hardest to know with reliability [35]. In our models, increasing vulnerability values changed the magnitude of biomass responses, however the overall trends remained the same. Ecopath and Ecosim have undergone extensive modification, improvement, and review since their origination; however model estimates, their errors, and their application require scrutiny (see [35]). Essington [36] used simulations to show that the precision of Ecopath estimates for *B* and *EE* were equivalent to the precision of the input data and he concluded that “bad data led to bad predictions.” We collected all fish functional group biomasses for our models and at-

tempted to obtain other inputs from the same or similar systems, but inputs derived from other models and published literature certainly contributed to Ecopath estimates in ways that may not mirror the populations we simulated. Essington [36] also reported that Ecopath inputs were more sensitive to *B* and *P/B* inputs than to diet composition data. Uncertainties regarding EwE parameter inputs and estimates are similar to those reported for other commonly used ecosystem and bioenergetics-based models (e.g., [37, 38]).

## IMPLICATIONS

Much research has indicated that juvenile fish survival is strongly density-dependent as a result of regulating processes such as predation, starvation, and cannibalism [2]. Several authors have shown that the importance of the processes resulting in strong density dependence is rarely specified [39 and references therein], and Shepherd and Cushing [2] suggested that a weak regulatory process could result in regulation at high stock sizes and when fishing mortality is low (as is likely for largemouth bass, [14]). Our simulations suggested that hatching specific sub-cohort mortality could have large influences on relative contributions of individual hatching sub-cohorts to a year class, however total age-1 biomasses was relatively stable across all simulations. Simulations that induced and reduced mortality of individual largemouth bass hatching sub-cohorts had small effects on age-1 total biomass (maximum biomass increase = 13% and maximum biomass decrease = 9%) relative to Ecopath baseline estimates, thus suggesting high compensation following increased sub-cohort mortality and strong regulation following decreased sub-cohort mortality. Predation was the most important regulating process acting on recruitment. Although total biomass responses to variable hatching sub-cohort mortality were slightly stronger for the south Florida population than for the north Florida population, predation still acted strongly to regulate total recruitment to age-1 for both spawning strategies. Walters and Juanes [39] proposed that mortality should result in selection for a balance between growth and survival of juvenile fishes due to shorter foraging times and smaller foraging volumes in the presence of high predator abundance, and thus, increased competition and exaggerated density-dependent effects on growth rates. Sub-cohort-specific survival could largely influence predation risks and feeding activities to result in strong competition, which has implications for energy allocations that could affect life-history metrics such as age at maturity, overwinter condition, and lifetime fitness.

Our results also have implications for fisheries management. Several authors have proposed that fishing regulations should prevent removal of spawning adults during periods of assumed high juvenile survival (i.e., during parental care, [40, 41]) or when progeny from any spawning period may have survival advantages depending on inter-annual environmental variability. Similarly, previous studies have shown reduced egg and larval survival following the removal of nest guarding adults for black bass *Micropterus spp.* (e.g., [41, 42]). Our results suggested that loss of a portion of the reproductive output could largely influence year class composition relative to hatching sub-cohort contributions. However, we would not expect large effects on year-class strength because ecological interactions were predicted to

regulate total biomass and survival of other sub-cohorts should exhibit compensation if fishing greatly reduced survival of one portion of a year class. These results are likely dependent on the duration of spawning activities (i.e., production of multiple hatching sub-cohorts) and the proportion of the total annual reproductive output affected by increased mortality. Our results also indicated only small increases in total largemouth bass biomasses with large increases in hatching sub-cohort survival, which may extend to stocking practices assuming that stocking induces similar dynamics as increased sub-cohort survival in our simulations. Walters and Juanes [39] presented similar reasoning for failures in northwest Pacific salmonid stockings. Potential trade-offs between parental spawning times and inter-sub-cohort interactions affecting juvenile survival necessitate further investigation for understanding recruitment regulation, population level characteristics, and fisheries management.

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