

## Spatial structuring within a reservoir fish population: implications for management

David R. Stewart<sup>A,D</sup>, James M. Long<sup>B</sup> and Daniel E. Shoup<sup>C</sup>

<sup>A</sup>Oklahoma Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Ecology and Management, Oklahoma State University, 007 Ag Hall, Stillwater, OK 74078, USA.

<sup>B</sup>US Geological Survey, Oklahoma Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Ecology and Management, Oklahoma State University, 007 Ag Hall, Stillwater, OK 74078, USA.

<sup>C</sup>Department of Natural Resource Ecology and Management, Oklahoma State University, 008 Ag Hall, Stillwater, OK 74078, USA.

<sup>D</sup>Corresponding author. Email: dstewa11@uwoyo.edu

**Abstract.** Spatial structuring in reservoir fish populations can exist because of environmental gradients, species-specific behaviour or even localised fishing effort. The present study investigated whether white crappie exhibited evidence of improved population structure where the northern more productive half of a lake is closed to fishing to provide waterfowl hunting opportunities. Population response to angling was modelled for each substock of white crappie (north (protected) and south (unprotected) areas), the entire lake (single-stock model) and by combining simulations of the two independent substock models (additive model). White crappie in the protected area were more abundant, consisting of larger, older individuals, and exhibited a lower total annual mortality rate than in the unprotected area. Population modelling found that fishing mortality rates between 0.1 and 0.3 resulted in sustainable populations (spawning potential ratios (SPR) > 0.30). The population in the unprotected area appeared to be more resilient (SPR > 0.30) at the higher fishing intensities (0.35–0.55). Considered additively, the whole-lake fishery appeared more resilient than when modelled as a single-pannmictic stock. These results provided evidence of spatial structuring in reservoir fish populations, and we recommend model assessments used to guide management decisions should consider those spatial differences in other populations where they exist.

**Additional keywords:** aquatic protected areas, environmental gradients, population dynamics, population model, spatial complexity, sustainability, yield.

Received 28 March 2014, accepted 10 June 2014, published online 23 October 2014

### Introduction

Stock-assessment strategies have commonly focussed on temporal variability in populations (Stephenson 1999; Kerr *et al.* 2010). The concept of defining and identifying spatial stock structure is a notion that until recently was not considered (Kerr *et al.* 2010). Historically, assessments have assumed that populations form discrete assemblages (i.e. single dynamic pool; Berger *et al.* 2012), even though biological phenomena and spatial scale can create heterogeneity within a stock (Wiens 1989; Stephenson 1999; Ames 2004; Walters and Martell 2004; Skjaeraasen *et al.* 2011). Spatial structuring has largely been ignored because of the complexity of alternatives, the lack of data for each management unit and because of the difficulty working across jurisdictional boundaries (Cope and Punt 2011; Berger *et al.* 2012). Ignoring the underlying spatial variability of populations can increase uncertainty in model assessments and result in biased approximations of stock productivity

(Stephenson 1999; Kerr *et al.* 2010). Although spatial stock complexity has only recently garnered attention in marine stock assessments, the concept of complex stocks is not surprising, given that fish are non-randomly distributed across the landscape of both marine and freshwater environments (Siler *et al.* 1986; Edds *et al.* 2002; Matthews *et al.* 2004; Vašek *et al.* 2004; Kerr *et al.* 2010).

Reservoir fishery management is not immune to spatial effects and, like many fishery systems, the local ichthyofauna is influenced by spatial and temporal heterogeneity (Siler *et al.* 1986; Matthews *et al.* 2004; Vašek *et al.* 2004). Fish abundance and composition in reservoirs is commonly associated with environmental gradients (Vašek *et al.* 2004; Prchalová *et al.* 2008), mostly owing to a decrease in productivity from upper to lower reservoir (Siler *et al.* 1986; Long and Fisher 2006; Prchalová *et al.* 2008). The upper portion of a reservoir is generally more productive and, in some instances, can support

higher abundances of both juveniles and adults (Matthews *et al.* 2004), likely increasing biotic interactions (Prchalová *et al.* 2008), and further affecting spatial distribution of fishes. Moreover, localised angler effort can work to create substructure in fish populations (Siler *et al.* 1986; Allen *et al.* 2012). These mechanisms collectively create spatial effects that could provide misleading survey estimates and undermine management efforts (Hutchings 1996; Kerr *et al.* 2010).

Fishery managers sometimes capitalise on spatial structuring by intentionally closing off aquatic areas to prevent overfishing or to protect biodiversity (i.e. aquatic protected areas; Suski and Cooke 2007). Aquatic protected areas (APAs) are a management tool used in the marine environment (Roberts and Hawkins 2000; NRC 2001) and have only recently been implemented in freshwater settings (Abell *et al.* 2007; Hedges *et al.* 2010). Marine protected areas, by definition, are any defined marine area set aside through spatial or temporal measures for special management by a management entity (Executive Order 13158) and this definition seems to adequately encompass APAs in freshwater as well. Protected areas can be designed to mitigate harvest (Abell *et al.* 2007), restrict fishing mortality (McClanahan 2010) or establish areas to facilitate protection of all species and habitats (Agardy 1994). More generally, APAs work to create substructure in fish populations where the population within the protected area receives fewer anthropogenic stressors, resulting in greater abundance, larger fish, lower mortality and increased longevity compared with the population outside the protected area (Suski and Cooke 2007).

Spatial differences can also occur as a result of other factors such as the biology of the organisms themselves (e.g. homing to natal areas by Pacific salmon *Oncorhynchus* spp.; Dittman and Quinn 1996), or as an artefact of setting aside an area for other uses (Hedges *et al.* 2010). When APAs are purposefully established or occur as a result of a fish species' behaviour or even because of environmental gradients, managers have generally been cognizant to incorporate substructure into conservation actions. When established through ancillary mechanisms (i.e. angler behaviour or areas set aside for other uses), unintended APAs may exist in numerous settings, creating substructure unknown to fisheries managers. This is particularly likely to occur with species that exhibit fairly little movement or have high site fidelity.

White crappie (*Pomoxis annularis*) is an important sportfish species in reservoirs, pursued by 6.1 million anglers annually (23% of all freshwater anglers) in the United States (USDOI–USFWS and USDOC–USCB 2011), and exhibits high site fidelity. White crappie typically establish small home ranges (Markham *et al.* 1991; Guy *et al.* 1994), and exhibits little, long-term movement from areas where it was originally found (Slipke and Maceina 2007). As a species susceptible to exploitation (Colvin 1991a, 1991b; Boxrucker 1999), white crappie appears susceptible to population substructuring should circumstances (e.g. environmental gradients or angler exploitation) produce sufficiently large spatial differences (Siler *et al.* 1986).

Minimum length limits (MLLs) and bag limits are used by agencies to prevent overharvest of some white crappie populations (Allen and Miranda 1995). Theoretical models (e.g. Beverton–Holt) are used in these evaluations and populations are assumed to consist of homogeneously distributed individuals

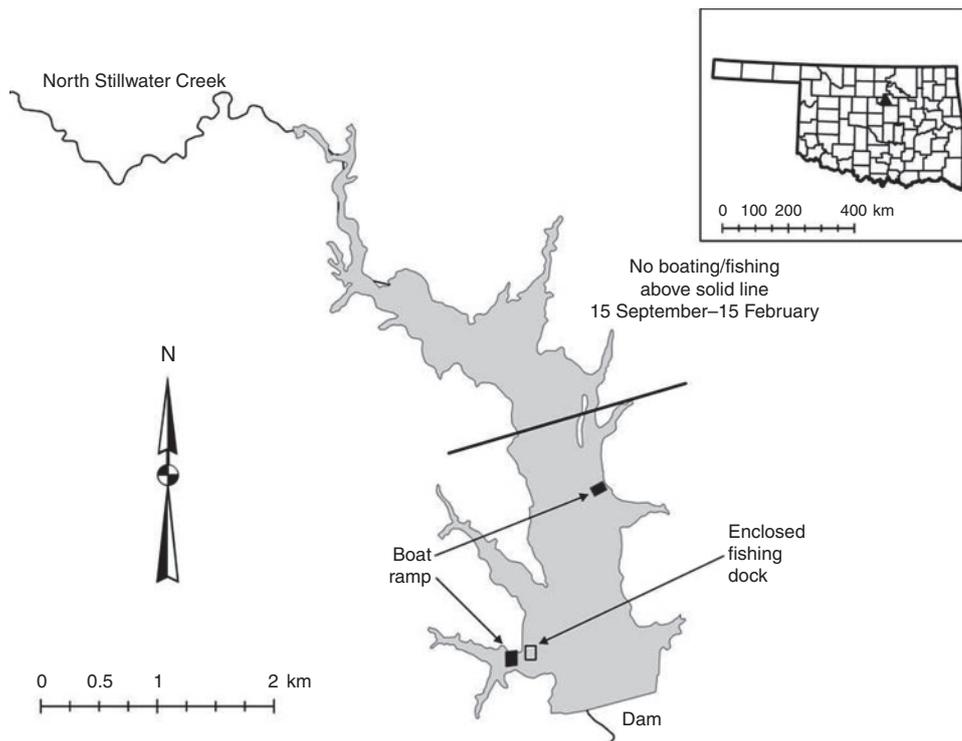
(Colvin 1991b; Allen and Miranda 1995; Boxrucker 1999; Isermann and Carlson 2009). However, MLLs often fail to improve size structure and yield (Boxrucker 1999; Isermann and Carlson 2009). The error in these models is often attributed to compensatory responses (i.e. mortality and recruitment; Boxrucker 1999), but the application of these models could also be burdened by complex spatial structuring. The goal of this research was to determine whether the cumulative effects of environmental gradients and the reservation of a large portion of a local reservoir for waterfowl hunting only (i.e. no fishing) could create spatial structuring within a white crappie population and, if so, to determine how this affects model assessments used to guide management decisions. Herein, evidence suggesting spatial structuring of the white crappie population is presented, along with the potential management consequences of failing to recognise the subsequent substructure.

### Study site

Lake McMurry is a 467-ha impoundment of North Stillwater Creek, located 10 km north-west of Stillwater, Oklahoma, USA (Fig. 1; Davies 2001; OWRB 2013). The reservoir was created in 1971, with the primary purposes of water supply, flood control and recreation (OWRB 2013). Mean and maximum depths in the reservoir were respectively 3.6 and 16.5 m, and water levels are fairly stable throughout the year (ODWC 2009). A significant nutrient (chlorophyll-*a*) gradient exists from the upper to lower lake (OWRB 2013). From *c.* 15 September each year through the following February, the northern half (protected area) of Lake McMurry is closed to boating and fishing to provide for waterfowl hunting at fixed blinds (<http://www.lakemcmurry.com>, accessed September 2014). The lower portion of the lake, where fishing is allowed year-round (unprotected area), contains the two boat ramps available at the lake and an enclosed fishing dock where crappie is the main fish species targeted even through the winter when the upper lake is closed to fishing (D. R. Stewart, Oklahoma State University, unpubl. creel data). The Oklahoma Department of Wildlife Conservation (ODWC) monitors the fishery and concluded that crappie abundance (total and harvestable size) in Lake McMurry had declined since 2001, but contained sufficient fish to provide a 'quality' fishery (ODWC 2009). However, ODWC (2009) also concluded that abundance of crappie  $\geq 254$ -mm TL had declined to 'unacceptable' levels since 2001. Furthermore, ODWC (2009) concluded that crappie had been 'stockpiling' (i.e. numerous young, small fish), which was a function of high recruitment of juveniles and slow growth of adults. As a result, ODWC (2009) stocked saugeye (sauger (*Sander canadensis*)  $\times$  walleye (*S. vitreus*)) to increase predation on crappie to improve crappie growth rates by reducing intraspecific competition (Boxrucker 2002; Galinat *et al.* 2002).

### Methods

White crappie were sampled using boat electrofishing (Smith-Root Model GGP 5.0, Vancouver, WA, USA; pulsed DC; 120 pulses  $s^{-1}$ ) from February to May 2011 using 20-min transects. In total, 37 transects were sampled in the protected area of Lake McMurry (north; closed to fishing) and 56 transects in the unprotected area (south; open to fishing year



**Fig. 1.** Map of Lake McMurtry, located 10 km north-west of Stillwater, Oklahoma (shown as triangle in inset map), depicting northern area (protected area) closed to boating and fishing for waterfowl hunting. The two boat ramps and the enclosed fishing dock, which are open year-round, are also shown.

around; Fig. 1). White crappie were measured (total length, mm), weighed (g) and the sagittal otoliths were removed from a subsample (i.e. 10 fish from each 10-mm length group) of fish to estimate age and then used to assign ages to unaged fish by means of an age-length key (Heidinger and Clodfelter 1987; Isermann *et al.* 2010; Coggins *et al.* 2013). Ages were assigned independently by two readers using a stereo-microscope (50 $\times$  magnification, side illumination). Discrepancies in age of the otoliths were reconciled in concert.

White crappie were marked during sampling with dorsal (protected area) or anal (unprotected area) fin clips and the Chapman-modified Schnabel mark-recapture equation was used to estimate population size with 95% confidence intervals (normally distributed) in each area (Ricker 1975). Marking mortality was estimated in each area of the reservoir on three separate occasions by holding marked and unmarked fish in wire-mesh pens for a 24-h period in Lake McMurtry. Fish were removed after 24 h and unmarked fish were marked with the appropriate fin clip and released. Fin clips of recaptured fish allowed us to determine the degree of mixing among areas of the lake.

Relative abundance (catch-per-unit-effort; number per transect), length-frequency histograms, growth, weight-length relationships and annual mortality were compared to determine whether statistical differences existed between the two potential subpopulations in the protected and unprotected areas. Relative abundance was  $\log(\text{count}+1)$ -transformed and a repeated-measures analysis using a generalised least-square

(GLS) model with an autoregressive-1 covariance structure (gls function within the nlme package in R; Pinheiro *et al.* 2011) was used to test for differences. Length-frequency histograms were tested with Kolmogorov-Smirnov (*KS*) tests, and proportional size distribution of preferred-size white crappie ( $\geq 250$  mm; Gabelhouse 1984) were calculated to determine the percentage of fish preferred by anglers present in each area. Length-at-age of white crappie was expressed using a von Bertalanffy growth model (Ricker 1975) and the parameters  $L_{\infty}$  (theoretical maximum size) and  $k$  (Brody growth coefficient) were estimated with maximum likelihood procedures and a Student's *t*-statistic (2-tailed) was used to test whether  $k$  differed between the protected and unprotected area (Zar 1999). Weight-length relationships were expressed using  $\log_{10}$ -transformed length and weight values and analysis of covariance (ANCOVA) was used to test for differences in the weight-length regression slopes ( $\beta$ ). Annual mortality was calculated using weighed catch curve analysis and ANCOVA was used to test for differences in annual mortality estimates between the two areas.

To determine the effect of spatial heterogeneity on management decisions, age-structured population models were constructed using R program (R Development Core Team 2011) to simulate the effect of fishing for each reservoir area separately (protected and unprotected), for the reservoir as a whole assuming a panmictic white crappie population (i.e. single stock with one averaged value for all population parameters), and additionally for the whole reservoir on the basis of results for the

**Table 1. Model and dynamic-state procedures used to describe equilibrium and time dynamics of white crappie at Lake McMurtry, Oklahoma**  
 Population variables and definitions are:  $L_{\infty}$ , theoretical maximum length;  $k$ , instantaneous growth rate;  $\beta$ , slope parameter of length-weight;  $\alpha$ , intercept parameter of length-weight;  $age_{mat}$ , age at 50% maturity;  $\sigma_{mat}$ , variation in age at maturity;  $age_{vul}$ , age at 50% first harvests;  $\sigma_{vul}$ , variation in age at first harvests;  $M$ , instantaneous natural mortality rate;  $U$ , annualised fishing mortality;  $\Omega$ , Goodyear compensation ratio;  $R_z$ , equilibrium recruitment; subscript ‘ $t$ ’ indicates time steps; subscript ‘ $a$ ’ indicates age class

Model procedures		Dynamic state procedures	
Length at age	$L_a = L_{\infty}(1 - \exp^{-k(age_i)})$	Number of fish at age one	$N_{t+1,age_1} = \frac{aE_t}{1 + \beta E_t}$
Weight at age	$w_a = \exp^{(\beta(\log_{10}(L_a)) + \alpha)}$	Number of eggs	$E_t = \sum_{age} N_{t,age} w_a m_a$
Maturity at age	$m_a = \frac{1}{1 + \exp^{-(age_i - age_{mat})/\sigma_{mat}}}$	Numbers of fish at age for age-2+	$N_{t+1,age+1} = N_{t,age} \exp^{-M}(1 - Uv_{a-1})$
Vulnerability at age	$v_a = \frac{1}{1 + \exp^{-(age_i - age_{vul})/\sigma_{vul}}}$	Yield	$Y_t = U \sum_{age} N_{t,age} w_a v_a$
Number of survivors in the absence of fishing	$l_a = \exp^{-M(age_i - 1)}$	Vulnerable biomass	$VB_t = \sum_{age} N_{t,age} w_a v_a$
Number of survivors in the presence of fishing	$l_{fa} = \begin{cases} 1, & age = 1 \\ l_{a-1} \exp^{-(M - Uv_{a-1})}, & age > 1 \end{cases}$	Spawning potential ratio	$SPR = \frac{\phi_e}{\phi_E}$
Beverton–Holt productivity parameter	$a = \Omega \left( \frac{R_z}{E_0} \right)$		
Number of eggs fished in unfished state	$E_0 = R_z \sum_{age} l_a m_a$		
Beverton–Holt scaling parameter	$\beta = \frac{\Omega - 1}{E_0}$		
Equilibrium eggs per recruit in unfished state	$\phi_E = \sum_{age} l_a w_a m_a$		
Equilibrium eggs per recruit in fished state	$\phi_e = \sum_{age} l_{fa} w_a m_a$		

protected area and unprotected area subpopulations (Kerr *et al.* 2010). The model framework uses a series of Botsford’s incidence functions (e.g. survival and fecundity schedules) to integrate per-recruit dynamics and a stock-recruitment function formulated using Botsfords’ method of the Beverton–Holt function to simulate equilibrium recruitment and age-class abundance (Botsford and Wickham 1979; Botsford (1981a, 1981b); Walters and Martell 2004; Allen *et al.* 2012). Each modelling scenario was simulated for a 100-year period.

The model was structured to account for the impact of fishing on the basis of age at maturation ( $m_a$ ), weight at age ( $w_a$ ) and vulnerability at age ( $v_a$ ) to harvest (Table 1). Age-specific survivorship schedules were calculated to estimate the number of survivors in the absence ( $l_a$ ) and presence ( $l_{fa}$ ) of fishing. Incidence functions ( $\Phi$ ) were weighted by the survivorship schedules (i.e.  $l_a$  or  $l_{fa}$ ) (Walters and Martell 2004) and summed across all age classes to account for the cumulative effects of fishing (Allen *et al.* 2012). Equilibrium lifetime egg production per recruit was calculated to estimate age-specific fecundity ( $f_a$ ) for both unfished ( $\Phi_E$ ) and fished ( $\Phi_e$ ) conditions,  $f_a$  was set to zero if age was less than age at maturation. To consider differences in mortality between the protected area, unprotected area and overall model simulations, instantaneous natural

mortality ( $M$ ) was calculated as the mean value from four estimation methods, including Pauly (1980), Hoenig (1983), Jensen (1996), and Hewitt and Hoenig (2005).

The age-structured population model was linked to a Beverton–Holt stock-recruitment relationship (Table 1). Recruitment of white crappie to age-1 ( $N_{t+1,age_1}$ ) was calculated as part of the dynamic simulations (1–100 years), with parameters derived using the compensation ratio ( $\Omega$ ) that describes how much juvenile survival changes from unfished stock size to very low adult abundances that typically accompany high fishing pressure (Walters and Martell 2004). The number of eggs produced in an unfished state is  $E_0$ , where  $R_z$  is defined as the proportional difference in estimated biomass based on Chapman-modified continuous Schnabel mark–recapture population estimates used to simulate the unfished state (Tables 1, 2). The equilibrium abundance for older age classes of white crappie were calculated by including age-specific harvest and death rates as part of the dynamic time-step (Table 1; Walters and Martell 2004).

Fishery performance was assessed by evaluating the response of yield ( $Y_t$ ) and vulnerable biomass ( $VB$ ) across a range of fishing mortality rates ( $U$ ) (Table 1). Equilibrium yield was calculated as

**Table 2. Abundance characteristic of white crappie in different areas of Lake McMurry, Oklahoma, measured during a survey conducted February to May 2011**

The northern area (protected area) is closed to boating and fishing for ~5 months each year to allow waterfowl hunting

Location	Number of 20-min electrofishing transects	CPUE ± 95% CI (number per transect)	Population estimate (n) ± 95% CI
Protected	37	29.4 ± 4.19	14 696 ± 3267
Unprotected	56	17.7 ± 6.76	4636 ± 797
Whole-lake	93	22.4 ± 3.84	18 563 ± 2688

$$Y_t = U \sum_{age}^{\infty} N_{t,a} w_a v_a$$

Vulnerable biomass was used to assess the performance of each scenario on harvest and calculated as

$$VB_t = \sum_{age}^{\infty} N_{t,a} w_a v_a$$

and spawning potential ratio (SPR; Goodyear 1993) was used to assess the sustainability (SPR values of 0.30 or higher) of each stock in relation to fishing mortality rate *U*:

$$SPR = \frac{\phi_e}{\phi_E}$$

We conducted sensitivity analyses to evaluate how model estimates responded to variation in key parameters (*M*, *L<sub>∞</sub>*, *k*, *α*, *β*, *Ω*). Sensitivity analyses were performed by increasing and decreasing each of these parameters and then refitting the model (Allen et al. 2009; Brenden et al. 2012). We then examined the change in yield and SPR estimated by the model in response to the change in each parameter.

**Results**

In total, 2082 white crappie individuals were collected and marked in approximate equal numbers between reservoir areas (*n* = 1089 in the protected area, *n* = 993 in unprotected area), and only one fish was found outside the area in which it was marked, suggesting negligible movement between areas. Further, additional white crappie sampling was conducted in summer 2011 and spring 2012 for an unrelated project and all marked crappie fish captured during these sampling events were still in the area where they were originally marked. Catch rates of white crappie were significantly different between the protected and unprotected areas (Table 2; *F*<sub>1,91</sub> = 5.47, *P* < 0.05). Marking survival during the study was 100%, and a total of 132 white crappie was recaptured, resulting in an overall reservoir-wide population estimate of 18 563 (95% CI; 15 875–22 347); 79% of which were from the protected area.

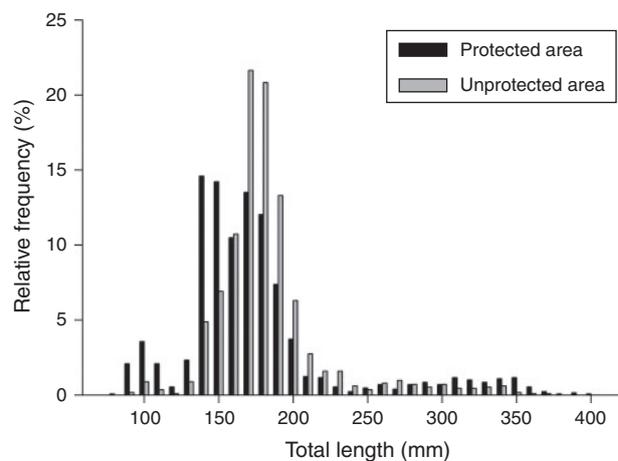
All population characteristics were significantly different between the protected and unprotected areas of Lake McMurry (Table 3). Size distributions of white crappie were significantly different (*KS* = 0.30, *P* < 0.01; Fig. 2), with a greater proportions of fish in the 170–240-mm length classes in the

**Table 3. Life-history characteristics and population parameters used in model simulations of the white crappie population at Lake McMurry, Oklahoma, during a survey conducted February to May 2011**

Single represents population parameters of a panmictic stock. Significant differences between protected and unprotected are indicated by different lower-case letters (at *P* = 0.05)

Parameter	Protected	Unprotected	Single
<i>L<sub>∞</sub></i> (mm)	333 ± 61	255 ± 22	337 ± 57
<i>k</i> (year <sup>-1</sup> )	0.25 ± 0.10b	0.41 ± 0.10c	0.24 ± 0.09
<i>α</i>	-5.96 ± 0.04	-5.79 ± 0.04	-5.93 ± 0.05
<i>β</i>	3.45 ± 0.02b	3.37 ± 0.02c	3.44 ± 0.02
<i>age<sub>max</sub></i>	12	10	12
<i>age<sub>mat</sub></i>	3	3	3
<i>σ<sub>mat</sub></i>	0.5	0.5	0.5
<i>age<sub>vul</sub></i>	2	2	2
<i>σ<sub>vul</sub></i>	0.5	0.5	0.5
<i>M</i>	0.33	0.43	0.32
<i>U</i>	{0,0.1,...1}	{0,0.1,...1}	{0,0.1,...1}
<i>Ω</i>	15	15	15
<i>R<sub>i</sub></i> (× 10 <sup>3</sup> ) <sup>A</sup>	4200	1650	5100
Annual Mortality	0.39 ± 0.07b	0.51 ± 0.04c	0.48 ± 0.07

<sup>A</sup>Estimates based on Chapman-modified continuous Schnabel population estimates.



**Fig. 2.** Length–frequency of white crappie in the protected and unprotected areas of Lake McMurry, Oklahoma, during a survey conducted February to May 2011. The north (protected) area is closed to boating and fishing for ~5 months each year, to allow waterfowl hunting.

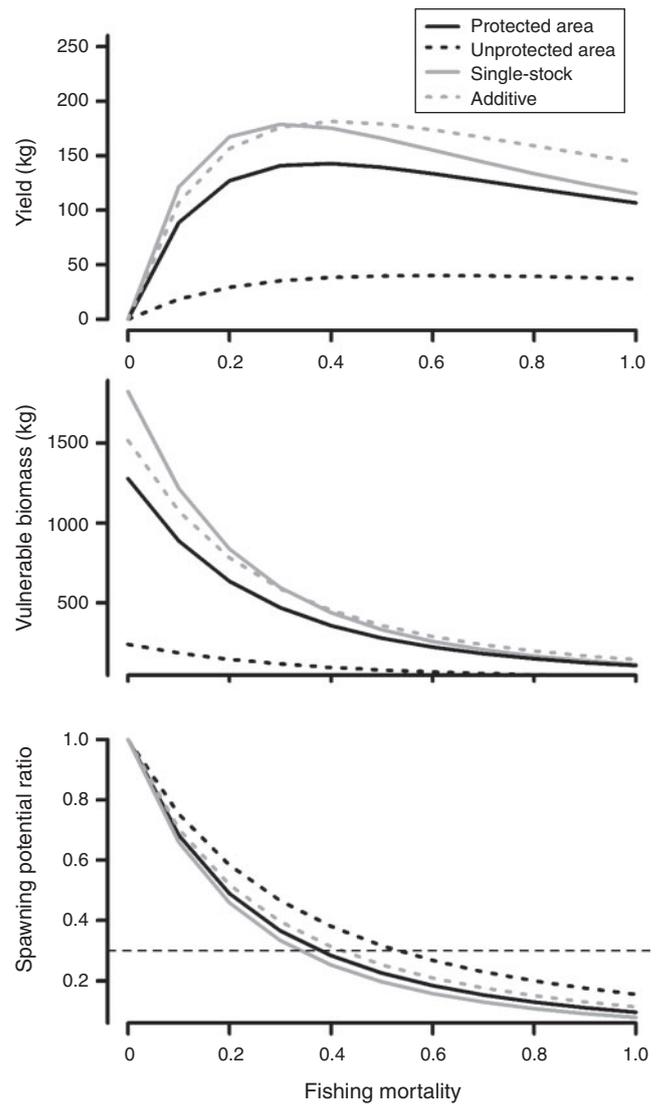
unprotected area ( $n = 116$ ;  $PSD-P = 0.08$ ) than in the protected area ( $n = 76$ ;  $PSD-P = 0.12$ ). The instantaneous growth rate ( $k$ ) was significantly higher for fish in the unprotected area ( $t_{0.05(2),9} = 27.57$ ,  $P < 0.01$ ; Table 3). Protected-area fish gained weight per increase in body length more rapidly (significantly larger  $\beta$  from the length–weight regression) than fish in the unprotected area ( $F_{1,2075} = 32.24$ ,  $P < 0.001$ ). White crappie in the protected area lived longer (up to 12 years) and exhibited a lower total annual mortality rate of 0.39 than those in the unprotected area, which had a maximum age of 10 years and a total annual mortality rate of 0.51 ( $F_{1,12} = 87.74$ ,  $P < 0.05$ ).

Model simulations indicated that yield estimates decreased with increasing fishing mortality, although at different rates for each of the models considered (Fig. 3). The two models that simulated estimates for the whole lake (single-stock and additive models) produced very different results. The single-stock model (which modelled the entire lake using a single averaged set of population parameters) predicted lower yield than the additive model (which accounted for the unequal population vital rates between the protected and unprotected area). The two substock models also differed. Yield was predicted to be ~70% higher in the protected area than in the unprotected area when both were harvested at moderate fishing mortality levels (i.e. 0.1–0.5). Across all four models tested, the change in yield in response to increasing fishing intensity was highest for the single-stock model, although the additive model and the protected area subpopulation model had yield that was only slightly lower. The unprotected stock subpopulation model had a much smaller response to changes in fishing intensity and the maximum yield predicted for this model was considerably lower than for any of the other models.

The models that had higher yield also had higher vulnerable-biomass estimates (Fig. 3). The protected area substock model predicted vulnerable biomass to be 81% higher than for the unprotected area substock model. The unprotected area substock model always predicted considerably less vulnerable biomass than the other models. As expected, vulnerable biomass declined significantly with fishing pressure, but estimates from the two substock models were still different even at the highest fishing intensities.

Fishing mortality between 0.1 and 0.3 resulted in SPR of  $>0.30$  for all model simulations, whereas fishing mortality estimates  $>0.55$  always resulted in SPR of  $<0.30$  (Fig. 3). The unprotected area appeared the most resilient, withstanding the highest amount of fishing intensities (i.e. up to 0.55) before SPR declined below the 0.30 threshold for sustainability. Considered as a single stock (which modelled the entire lake using a single averaged set of population parameters), the white crappie population was least resilient, reaching below the sustainability threshold at the lowest level of fishing mortality. Considering the protected and unprotected areas additively resulted in a model suggesting that the white crappie population is more resilient than estimated as a single stock.

Sensitivity analyses indicated that the age-structured assessment models were most sensitive to natural mortality and growth parameters (Figs 4, 5). The relationships between yield and key model parameters were both linear and non-linearly related,  $k$  exhibiting the only linear trend (Fig. 3). Non-linear trends for the remaining parameters  $L_{\infty}$ ,  $\alpha$ ,  $\beta$ ,  $M$ ,  $\Omega$  were evident

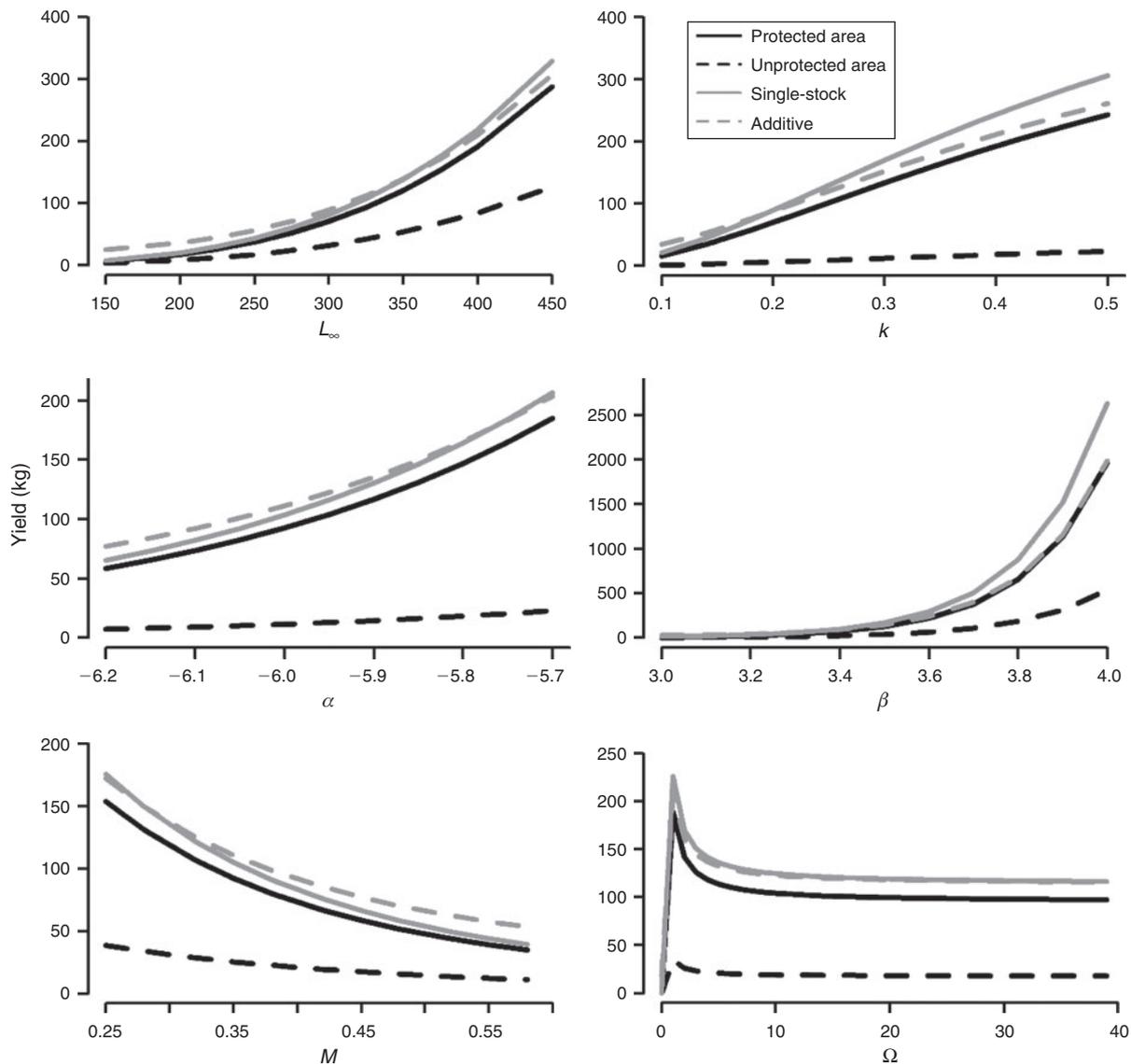


**Fig. 3.** Yield, biomass and spawning-potential ratio modelling results in relation to varying levels of fishing mortality of white crappie at Lake McMurtry, Oklahoma. The north (protected) area is closed to boating and fishing for 5 months each year. Models were constructed for the protected area, unprotected (south) area, whole lake as a single stock (averaged population parameters from protected and unprotected areas), and whole lake as additive (accounting for unequal vital rates of the protected and unprotected models).

and strongly influenced by low and high values of each parameter, except for  $\Omega$  where yield estimates were similar for values higher than 10. There were few relationships between key model parameters and SPR (Fig. 4). Increasing values of  $M$  and  $K$  resulted in increasing SPR estimates, whereas SPR was highest for low  $\beta$  values. The additive model was the least sensitive to changing parameter values.

**Discussion**

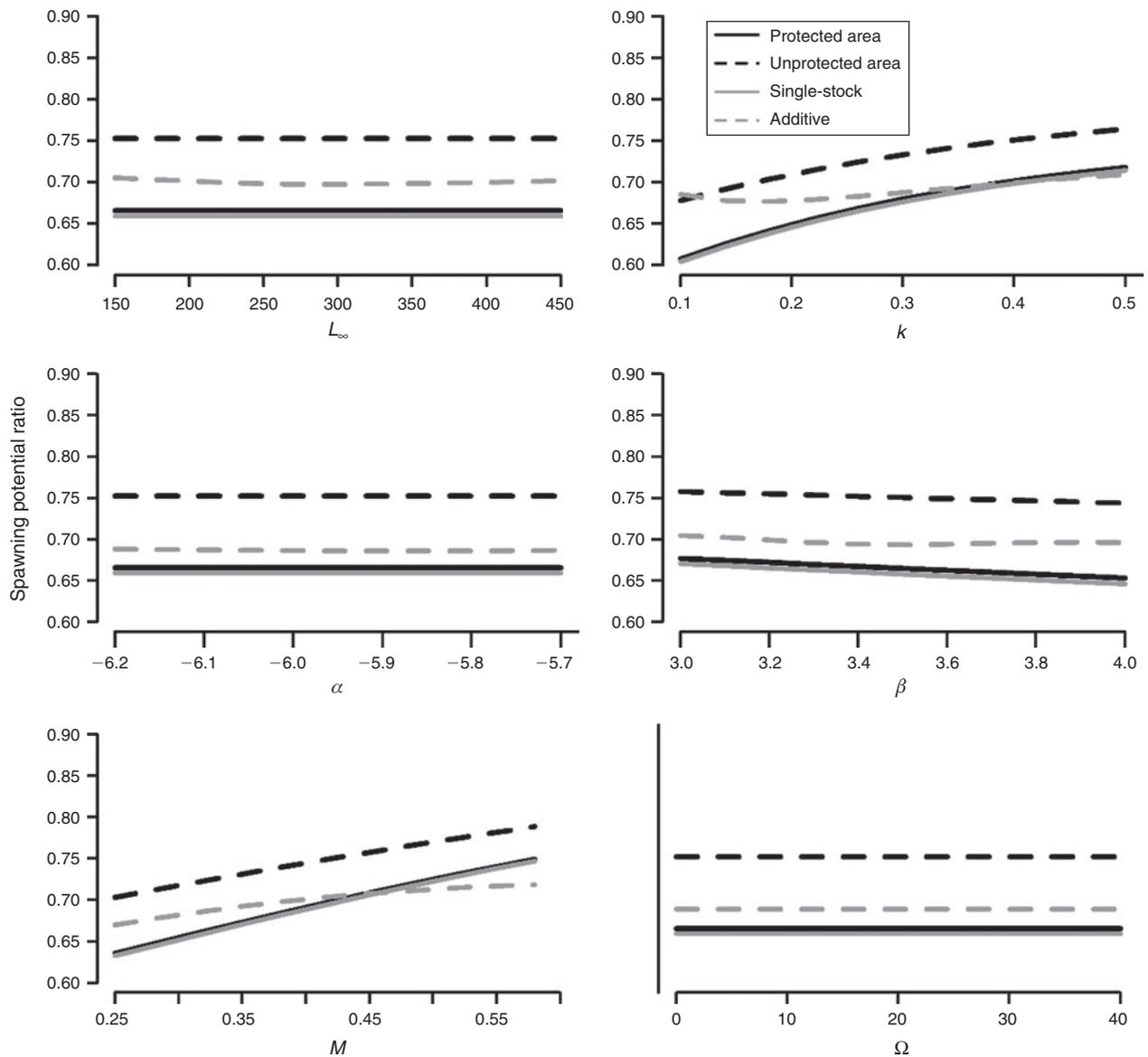
This is one of the first studies to consider a considerably finer spatial scale than what is normally used to sample sportfish in



**Fig. 4.** Results of sensitivity analyses showing associations between parameter values and yield (kg) for the single-stock (protected and unprotected areas) and whole-lake (single-stock and additive models) age-structured population assessments.

freshwater for management purposes. Management decisions are normally based on coarse data collected at the lake scale, assuming fish are randomly distributed and ignoring spatial heterogeneity within the stock. This can be problematic because in the present study, we illustrated the potential impact of failing to recognise the spatial heterogeneity within the white crappie population (whether that heterogeneity is nutrient-, habitat-, predation- or harvest-mediated). Knowing which factors contributed to the spatial structure could affect management decisions. For example, if nutrient mediated, then the different crappie population characteristics we found in the protected area of Lake McMurtry may be associated with trophic interactions, because a strong nutrient gradient (measured by chlorophyll-*a*) was evident, decreasing toward the dam (OWRB 2013). The nutrient gradient likely did not affect mortality but rather was an important factor affecting growth patterns (McInerney and Cross

1999; Paukert and Willis 2001), as illustrated by crappie in the protected area having greater weight than fish in the unprotected area. If differences were habitat mediated, managers could decide to employ habitat-improvement projects to affect the subpopulations of crappie in the lower portion of the reservoir. Few differences in near-shore habitat or adjacent land use between the protected and unprotected portions of Lake McMurtry were apparent (D. R. Stewart and J. M. Long, unpubl. data). The protected portion contained approximately twice as much area of woody debris as the lower end, which is a habitat type used extensively by white crappie (Markham *et al.* 1991; Slipke and Maceina 2007). Alternatively, differential habitat use by saugeye, a major predator stocked to control overabundance of crappie (Boxrucker 2002; Galinat *et al.* 2002), could potentially be a contributing factor. But for this to occur, saugeye would need to be more abundant in the protected area of the lake



**Fig. 5.** Results of sensitivity analyses showing associations between parameter values and the spawning-potential ratio for the single-stock (protected and unprotected areas) and whole-lake (single-stock and additive models) age-structured population assessments.

than the unprotected area, reducing abundance of smaller individuals and allowing the remainder to grow faster and reach larger sizes. Previous research has demonstrated that saugeye exhibits seasonal movement, inhabiting upper ends of reservoirs in spring, but otherwise being located near deep, open water areas (Leeds 1990; Neely *et al.* 2011; May *et al.* 2012). Moreover, only large saugeye individuals (>400-mm TL) tend to prey on crappie to a great degree (Horton and Gilliland 1990). Although fish >400 mm dominate the saugeye population in Lake McMurtry, their abundance had been in decline since 2001 (ODWC 2009), suggesting that their influence on the crappie population would be minor. However, if closing the upper area to fishing for hunting purposes directly decreased exploitation of the protected area crappie subpopulation and caused the observed differences in population characteristics, then

managers can use APAs as a tool to help further fishery goals at this reservoir or others that are similar. The population characteristics of the unprotected subpopulation were indicative of an exploited stock, having truncated age and size structure that lacked larger and older individuals (Conover and Munch 2002), and higher mortality possibly related to angler harvest (Paukert and Willis 2001). In contrast, the protected area population had characteristics indicative of an unexploited stock (Paukert and Willis 2001; Stewart *et al.* 2009), with lower mortality, slower growth and higher abundance of larger-size fish. Regardless of which factor produced the observed differences between the protected and unprotected area, our results showed strong evidence for spatial structuring that should be considered when managing species that move little and show strong site fidelity so as to improve management of the whole population.

Spatial structuring resulting from high site fidelity and low dispersal behaviour is not a new phenomenon and has been documented in numerous fish stocks, although mostly marine species (Quinn 1996; Ames 2004; Kerr *et al.* 2010). The present study was conducted in spring and during a period when white crappie moves large distances to spawn and then moves to its summer home ranges (Guy *et al.* 1994), but we observed little mixing during this time when the likelihood of mixing would be highest. We sampled white crappie again in August 2011 and again in February–March 2012, and observed 2011 north-end marked and south-end marked crappie in the protected and unprotected areas respectively. These additional observations further supported that mixing is not occurring. Our observation of segregated subpopulations in the protected and unprotected areas of Lake McMurtry are probably not unique to this lake, but rather a reflection of the paucity of studies conducted on white crappie movement. For example, at Lake Goldsmith (116 ha), South Dakota, white crappie home ranges were largest during July, but still small with a median area of ~30 ha (~300-m radius of a circle, Guy *et al.* 1994), whereas at Delaware Reservoir (532 ha), Ohio, the median home range of white crappie was ~0.63 ha (~45-m radius of a circle, Markham *et al.* 1991). The small home ranges and high spawning-site fidelity of this species in general (Fryda *et al.* 2008) suggest that complex spatial structuring may exist in other systems and be even more prominent in larger systems. Our additive model did not consider dispersal; however, with a better understanding of the movement patterns of the resident white crappie stock, this model could be modified to link the two subpopulations by incorporating a dispersal-rate coefficient (see Kerr *et al.* 2010). At that point, fishery scientists could use this model to account for the spatial complexity within the population and consider management decisions that would benefit both subpopulations.

It is not surprising that spatial differences in population characteristics existed between the upper and lower areas of Lake McMurtry. Spatial heterogeneity in reservoirs is common and is likely to be evident in other systems. Lake McMurtry is only 455 ha in surface area, so similar spatial heterogeneity could be even more likely in the larger systems typical across the southern United States. Nutrient gradients, species-specific behaviour and habitat preferences could create geographically separate groups, especially with species that exhibit high site fidelity such as white crappie (Fryda *et al.* 2008). A fishery manager could incorporate spatial variability into their management assessments to increase the effectiveness of management decisions (Siler *et al.* 1986). Otherwise, regulations that benefit population characteristics of one substock may not work for other substocks (e.g. if they have characteristics making them more vulnerable to overharvest). For example, in the present study the protected area substock appears to be driving the results of the single-stock model, typically predicting the highest yield and lowest sustainability levels. Although, in this instance, the single-stock assessment would provide a conservative management recommendation (i.e. model suggests the population is least resilient to fishing mortality), the results could have easily been driven by population characteristics of a substock that was more resilient to fishing mortality and lead to more liberal harvest rates, which in some cases could result in declines of less-productive substocks (Kerr *et al.* 2010).

An interesting finding was that the unprotected substock could withstand the highest fishing mortality rates. We used a static SPR, which is a function of survivorship, maturation and weight schedules, to estimate the effect of harvest on reproductive potential (Goodyear 1993). Sensitivity analyses indicated that SPR was significantly related to  $k$ ,  $\beta$  and  $M$  and may explain why the unprotected area was estimated to be the most resilient to fishing mortality. Fish in the unprotected area added weight per increase in body length at a much slower rate, and had a higher  $k$  and  $M$  that collectively contributed to a higher SPR value. The sensitivity to these values highlights the need to better understand natural mortality and attain robust estimates of growth when using biological reference points, to guide management decisions when using single-stock models that do not account for unequal vital rates. However, the SPR calculated from the additive model (accounts for unequal population vital rates between the protected and unprotected area) was the least sensitive to changing parameters on the basis of sensitivity analyses, likely because the calculation is based on vital rates from not one but both the protected and unprotected substocks.

The model simulations did not explicitly account for the different mortality estimates between subpopulations found in the protected and unprotected areas. We calculated mean natural mortality estimates using four commonly used methods (Pauly 1980; Hoenig 1983; Jensen 1996; Hewitt and Hoenig 2005), because data for Lake McMurtry did not exist that would have allowed us to partition total mortality into natural and fishing subcomponents. Although the difference in mortality between the protected and unprotected area could have been assumed to be solely related to fishing mortality alone, the protected area does receive some exploitation for at least 6 months of the year and other compensatory mechanisms affecting total mortality might be involved. Certainly, a fine-scale exploitation assessment would allow one to better determine percentage reduction in harvest contributed to the spatial structuring caused by either environmental gradients or the unintended APA at Lake McMurtry.

The present study demonstrated the effects of spatial structuring on intra-reservoir population characteristics and the potential management consequences of managing the reservoir as a single homogeneous biological entity. More importantly, the study highlighted the importance of spatial scale and how it relates to fisheries management. Identifying the scale of the population and determining whether specific groups exist is fundamental to understanding how to manage a particular species influenced by environmental gradients, or other spatial environmental conditions such as unintended APAs. These results suggest that the environmental gradient in combination with the hunting restrictions at Lake McMurtry played a role in creating spatial complexity within the crappie population.

### Acknowledgements

Financial support for this publication was provided by Oklahoma State University and Oklahoma Cooperative Fish and Wildlife Research Unit (US Geological Survey, Oklahoma State University, the Oklahoma Department of Wildlife Conservation, the Wildlife Management Institute, and the US Fish and Wildlife Service cooperating). We thank M. Allen for constructive comments regarding this manuscript and J. Duck, N. Gonsoulin and M. Porta for help with field sampling. Any use of trade, firm or product

names is for descriptive purposes only and does not imply endorsement by the US Government. This study was performed under the auspices of a protocol approved by the Institutional Animal Care and Use Committee at Oklahoma State University.

## References

- Abell, R., Allan, J. D., and Lehner, B. (2007). Unlocking the potential of protected areas for freshwaters. *Biological Conservation* **134**, 48–63. doi:10.1016/J.BIOCON.2006.08.017
- Agardy, M. T. (1994). Advances in marine conservation: the role of marine protected areas. *Trends in Ecology & Evolution* **9**, 267–270. doi:10.1016/0169-5347(94)90297-6
- Allen, M. S., and Miranda, L. E. (1995). An evaluation of the value of harvest restrictions in managing crappie fisheries. *North American Journal of Fisheries Management* **15**, 766–772. doi:10.1577/1548-8675(1995)015<0766:AEOTVO>2.3.CO;2
- Allen, M. S., Brown, P., Douglas, J., Fulton, W., and Catalano, M. (2009). An assessment of recreational fishery harvest policies for Murray cod in southeast Australia. *Fisheries Research* **95**, 260–267. doi:10.1016/J.FISHRES.2008.09.028
- Allen, M. S., Ahrens, R. N. M., Hansen, M. J., and Arlinghaus, R. (2012). Dynamic angling effort influences the value of minimum-length limits to prevent recruitment overfishing. *Fisheries Management and Ecology*. doi:10.1111/J.1365-2400.2012.00871.X
- Ames, E. P. (2004). Atlantic cod stock structure in the Gulf of Maine. *Fisheries* **29**, 10–28. doi:10.1577/1548-8446(2004)29[10:ACSSIT]2.0.CO;2
- Berger, A. M., Jones, M. L., Zhao, Y., and Bence, J. R. (2012). Accounting for spatial population structure at scales relevant to life history improves stock assessment: the case for Lake Erie walleye *Sander vitreus*. *Fisheries Research* **115–116**, 44–59. doi:10.1016/J.FISHRES.2011.11.006
- Botsford, L. W. (1981a). Optimal fishery policy for size-specific density-dependent population models. *Journal of Mathematical Biology* **12**, 265–293. doi:10.1007/BF00276917
- Botsford, L. W. (1981b). The effects of increased individual growth rates on depressed population size. *American Naturalist* **117**, 38–63. doi:10.1086/283685
- Botsford, L. W., and Wickham, D. E. (1979). Population cycles caused by interage, density-dependent mortality in young fish and crustaceans. Cyclic phenomena in marine plants and animals. In 'Proceedings of the 13th European Marine Biology Symposium', 27 September–4 October 1978, Isle of Man, UK. (Eds E. Naylor and R. G. Hartnoll.) pp. 73–82. (Permagon: New York.)
- Boxrucker, J. (1999). Changes in crappie population structure following restrictive harvest regulations. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* **53**, 80–90.
- Boxrucker, J. (2002). Improved growth of a white crappie population following stocking of saugeyes (sauger × walleye): a top-down, density-dependent growth response. *North American Journal of Fisheries Management* **22**, 1425–1437. doi:10.1577/1548-8675(2002)022<1425:IGOAWC>2.0.CO;2
- Brenden, T. O., Bence, J. R., and Szalai, E. B. (2012). An age-structured integrated assessment of Chinook salmon population dynamics in Lake Huron's main basin since 1968. *Transactions of the American Fisheries Society* **141**, 919–933. doi:10.1080/00028487.2012.675910
- Coggins, L. G. Jr, Gwinn, D. C., and Allen, M. S. (2013). Evaluation of age-length key sample sizes required to estimate fish total mortality and growth. *Transactions of the American Fisheries Society* **142**, 832–840. doi:10.1080/00028487.2013.768550
- Colvin, M. A. (1991a). Population characteristics and angler harvest of white crappie in four large Missouri reservoirs. *North American Journal of Fisheries Management* **11**, 572–584. doi:10.1577/1548-8675(1991)011<0572:PCAAHO>2.3.CO;2
- Colvin, M. A. (1991b). Evaluation of minimum-size limits and reduced daily limits on the crappie populations and fisheries in five large Missouri reservoirs. *North American Journal of Fisheries Management* **11**, 585–597. doi:10.1577/1548-8675(1991)011<0585:EOMSLA>2.3.CO;2
- Conover, D. O., and Munch, S. B. (2002). Sustaining fisheries yields over evolutionary time scales. *Science* **297**, 94–96. doi:10.1126/SCIENCE.1074085
- Cope, J. M., and Punt, A. E. (2011). Reconciling stock assessment and management scales under conditions of spatially varying catch histories. *Fisheries Research* **107**, 22–38. doi:10.1016/J.FISHRES.2010.10.002
- Davies, S. L. (2001). A needs assessment of Lake McMurtry. M.Sc. Thesis, Oklahoma State University, Stillwater, OK.
- Dittman, A. H., and Quinn, T. P. (1996). Homing in Pacific salmon: mechanisms and ecological basis. *The Journal of Experimental Biology* **199**, 83–91.
- Edds, D. E., Matthews, W. J., and Gelwick, F. P. (2002). Resource use by large catfishes in a reservoir: is there evidence for interactive segregation and innate differences? *Journal of Fish Biology* **60**, 739–750. doi:10.1111/J.1095-8649.2002.TB01698.X
- Fryda, N. F., Koupal, K. D., and Hoback, W. W. (2008). Abundance and cove fidelity of adult crappies during spawning seasons in a Nebraska irrigation reservoir. In 'Balancing Fisheries Management and Water Uses for Impounded River Systems'. (Eds M. S. Allen, S. Sammons and M. J. Maciena.) pp. 587–594. American Fisheries Society Symposium 62, Bethesda, MD.
- Gabelhouse, D. W., Jr (1984). A length-categorization system to assess fish stocks. *North American Journal of Fisheries Management* **4**, 273–285. doi:10.1577/1548-8659(1984)4<273:ALSTAF>2.0.CO;2
- Galinat, G. F., Willis, D. W., Blackwell, B. G., and Hubers, M. J. (2002). Influence of a saugeye (Sauger × Walleye) introduction program on the black crappie population in Richmond Lake, South Dakota. *North American Journal of Fisheries Management* **22**, 1416–1424. doi:10.1577/1548-8675(2002)022<1416:IOASSW>2.0.CO;2
- Goodyear, C. P. (1993). Spawning stock biomass per recruit in fisheries management: foundation and current use. In 'Risk Evaluation and Biological Reference Points for Fisheries Management'. (Eds S. J. Smith, J. J. Hunt, and D. Rivard.) pp. 67–81. (Canadian Special Publication Fisheries Aquatic Science: Ottawa, ON.)
- Guy, C. S., Willis, D. W., and Jackson, J. J. (1994). Biotelemetry of white crappies in a South Dakota glacial lake. *Transactions of the American Fisheries Society* **123**, 63–70. doi:10.1577/1548-8659(1994)123<0063:BOWCIA>2.3.CO;2
- Hedges, K. J., Koops, M. A., Mandrak, N. E., and Johannsson, O. E. (2010). Use of aquatic protected areas in the management of large lakes. *Aquatic Ecosystem Health & Management* **13**, 135–142. doi:10.1080/14634981003788912
- Heidinger, R. C., and Clodfelter, K. (1987). Validity of the otolith for determining age and growth of walleye, striped bass, and smallmouth bass in power plant cooling ponds. In 'Age and Growth of Fish'. (Eds R. C. Summerfelt and G. E. Hall.) pp. 241–251. (Iowa State University Press: Ames, IA)
- Hewitt, D. A., and Hoenig, J. M. (2005). Comparison of two approaches for estimating natural mortality based on longevity. *Fishery Bulletin* **103**, 433–437.
- Hoenig, J. M. (1983). Empirical use of longevity data to estimate mortality rates. *Fish Bulletin* **82**, 820–822.
- Horton, R. A., and Gilliland, E. R. (1990). Diet overlap between saugeye and largemouth bass in Thunderbird Reservoir, Oklahoma. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* **44**, 98–104.
- Hutchings, J. A. (1996). Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 943–962. doi:10.1139/F96-097

- Isermann, D. A., and Carlson, A. J. (2009). Can minimum length limits improve size structure in Minnesota black crappie populations? Investigation Report 552. Minnesota Department of Natural Resources, Brainerd, MN.
- Isermann, D. A., Wolter, M. H., and Breeggemann, J. J. (2010). Estimating black crappie age: an assessment of dorsal spines and scales as nonlethal alternatives to otoliths. *North American Journal of Fisheries Management* **30**, 1591–1598. doi:10.1577/M10-133.1
- Jensen, A. L. (1996). Beverton and Holt life histories invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 820–822. doi:10.1139/F95-233
- Kerr, L. A., Cadrin, S. X., and Secor, D. H. (2010). Simulation modeling as a tool for examining the consequences of spatial structure and connectivity on local and regional population dynamics. *ICES Journal of Marine Science* **67**, 1631–1639. doi:10.1093/ICESJMS/FSQ053
- Leeds, L. G. (1990). Distribution, movement, and habitat preference of saugeye in Thunderbird Reservoir, Oklahoma. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* **44**, 27–35.
- Long, J. M., and Fisher, W. L. (2006). Analysis of environmental variation in a Great Plains reservoir using principal components analysis and geographic information systems. *Lake and Reservoir* **22**, 132–140. doi:10.1080/07438140609353890
- Markham, J. L., Johnson, D. L., and Petering, R. W. (1991). White crappie summer movements and habitat use in Delaware Reservoir, Ohio. *North American Journal of Fisheries Management* **11**, 504–512. doi:10.1577/1548-8675(1991)011<0504:WCSMAH>2.3.CO;2
- Matthews, W. J., Gido, K. B., and Gelwick, F. P. (2004). Fish assemblages of reservoirs, illustrated by Lake Texoma (Oklahoma–Texas, USA) as a representative system. *Lake and Reservoir Management* **20**, 219–239. doi:10.1080/07438140409354246
- May, C. J., Aday, D. D., Hale, R. S., Denlinger, J. C. S., and Marschall, E. A. (2012). Modeling habitat selection of a top predator: considering growth and physical environments in a spatial context. *Transactions of the American Fisheries Society* **141**, 215–223. doi:10.1080/00028487.2012.655122
- McClanahan, T. R. (2010). Effects of fisheries closures and gear restrictions on fishing income in a Kenyan Coral Reef. *Conservation Biology* **24**, 1519–1528. doi:10.1111/J.1523-1739.2010.01530.X
- McInerney, M. C., and Cross, T. C. (1999). Effects of lake productivity, climate warming, and intraspecific density on growth and growth patterns of black crappie in southern Minnesota lakes. *Journal of Freshwater Ecology* **14**, 255–264. doi:10.1080/02705060.1999.9663677
- National Research Council (NRC) (2001). ‘Marine Protected Areas: Tools for Sustaining Ocean Ecosystems.’ (National Academy Press: Washington, DC.)
- Neely, B. C., Dumont, S. C., Cole, R. L., and Farooqi, M. A. (2011). Seasonal home range estimates and habitat selection of saugeye in a small warmwater impoundment. *Fisheries Management and Ecology* **18**, 113–120. doi:10.1111/J.1365-2400.2010.00760.X
- Oklahoma Department of Wildlife Conservation (ODWC) (2009). Surveys and recommendations – Lake McMurtry. Performance Report F-79-D02, Oklahoma Department of Wildlife Conservation, Oklahoma City, OK.
- Oklahoma Water Resources Board (OWRB) (2013). Lakes of Oklahoma. Available at <http://www.owrb.ok.gov/news/publications/lok/lok.php> [Verified 7 November 2013].
- Paukert, C. P., and Willis, D. W. (2001). Comparison of exploited and unexploited yellow perch *Perca flavescens* (Mitchill) populations in Nebraska Sandhill lakes. *Fisheries Management and Ecology* **8**, 533–542. doi:10.1046/J.1365-2400.2001.00278.X
- Pauly, D. (1980). On the interrelationship between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil international pour l'Exploration de la Mer* **39**, 175–192. doi:10.1093/ICESJMS/39.2.175
- Pinheiro, J., Bates, D., DebRoy, S., and Sarkar, D. (2011). nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-98. Available at <http://CRAN.R-project.org/package=nlme> [Verified 11 October 2014].
- Prchalová, M., Kubečka, J., Vašek, M., Peterka, J., Sed'a, J., Jůza, T., Říha, M., Jarolím, O., Tušer, M., Kratochvíl, M., Čech, M., Drašík, V., Frouzová, J., and Hohausová, E. (2008). Distribution patterns of fishes in a canyon-shaped reservoir. *Journal of Fish Biology* **73**, 54–78. doi:10.1111/J.1095-8649.2008.01906.X
- Quinn, S. (1996). Trends in regulatory and voluntary catch-and-release fishing. In ‘Multidimensional Approaches to Reservoir Fishery Management’. (Eds L. E. Miranda and D. R. DeVries.) pp. 152–162. American Fisheries Society, Symposium 16, Bethesda, MD.
- R Development Core Team (2011). R: a language and environment for statistical computing. (R Foundation for Statistical Computing: Vienna, Austria.) Available at [www.R-project.org](http://www.R-project.org) [Verified September 2014].
- Ricker, W. E. (1975). ‘Computation and Interpretation of Biological Statistics of Fish Populations.’ Bulletin 191. (Fisheries Research Board of Canada: Ottawa, ON.)
- Roberts, C. M., and Hawkins, J. P. (2000). ‘Fully Protected Marine Reserves: a Guide.’ (World Wildlife Fund: Washington, DC.)
- Siler, J. R., Foris, W. J., and McInerney, M. C. (1986). Spatial heterogeneity in fish parameters within a reservoir. In ‘Reservoir Fisheries Management: Strategies for the 80’s’. (Eds G. E. Hall and M. J. Van Den Avyle.) pp. 122–136. American Fisheries Society Symposium, Bethesda, MD.
- Skjaeraasen, J. E., Meager, J. J., Karlsen, O., Hutchings, J. A., and Ferno, A. (2011). Extreme spawning-site fidelity in Atlantic cod. *ICES Journal of Marine Science* **68**, 1472–1477. doi:10.1093/ICESJMS/FSR055
- Slipke, J. W., and Maceina, M. J. (2007). Movement and use of backwater habitats by largemouth bass and white crappie in Demopolis Reservoir, Alabama. *Journal of Freshwater Ecology* **22**, 393–401. doi:10.1080/02705060.2007.9664169
- Stephenson, R. L. (1999). Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. *Fisheries Research* **43**, 247–249. doi:10.1016/S0165-7836(99)00076-4
- Stewart, D. R., Benz, G. W., and Scholten, G. D. (2009). Weight–length relationships and growth data for blue catfish from four Tennessee waterbodies. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* **63**, 140–146.
- Suski, C. D., and Cooke, S. J. (2007). Conservation of aquatic resources through the use of freshwater protected areas: opportunities and challenges. *Biodiversity and Conservation* **16**, 2015–2029. doi:10.1007/S10531-006-9060-7
- USDOI–USFWS, USDOC–USCB (2011). National survey of fishing, hunting, and wildlife-associated recreation. US Department of the Interior, US Fish and Wildlife Service (USDOI–USFWS) and US Department of Commerce, US Census Bureau, Washington, DC.
- Vašek, M., Kubečka, J., Peterka, J., Čech, M., Drašík, V., Hladík, M., Prchalová, M., and Frouzová, J. (2004). Longitudinal and vertical spatial gradients in the distribution of fish within a canyon-shaped reservoir. *International Review of Hydrobiology* **89**, 352–362. doi:10.1002/IROH.200410734
- Walters, C. J., and Martell, S. J. D. (2004). ‘Fisheries Ecology and Management.’ (Princeton University Press: Princeton, NJ.)
- Wiens, J. A. (1989). Spatial scaling in ecology. *Functional Ecology* **3**, 385–397. doi:10.2307/2389612
- Zar, J. H. (1999). ‘Biostatistical Analysis’, 4th edn. (Prentice Hall: Upper Saddle River, NJ.)