



Effects of source–sink dynamics on harvest policy performance for yellow perch in southern Lake Michigan

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ABSTRACT

We used a spatially explicit stochastic simulation model to evaluate whether source–sink population dynamics would affect performance of alternative harvest policies for yellow perch, *Perca flavescens*, in southern Lake Michigan. The model contained four management areas in southern Lake Michigan representing each U.S. state's waters. We parameterized the model such that all recruitment was produced by only one management area, considering each of the four areas to be the sole source in turn, and contrasted results with a base scenario where all areas produced recruits. We evaluated three types of harvest policies: constant- F , where fishing mortality was constant, and two state-dependent policies, where fishing mortality was constant above either 40% or 70% of unfished spawning stock biomass (B_0) and decreased to 0 at 0% B_0 . We used four performance statistics to evaluate policies: (1) average percentage of B_0 remaining, (2) percentage of years with low spawning stock biomass, (3) average recreational harvest, and (4) percentage of years with low recreational harvest. Performance of harvest policies differed predictably depending on which management area was the source because relative productivity of stock–recruitment relationships and growth patterns differed among source areas. Thus, if management areas on the western side of Lake Michigan were the source of most of the recruits, the fishery could support higher fishing mortality rates than if areas on the eastern side of the lake were sources. State-dependent harvest policies were less sensitive to assumptions about the source of recruits than were constant fishing mortality rate policies. The 0–70 policy was most robust to source–sink dynamics across most of the performance statistics and levels of fishing mortality.

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1. Introduction

Harvest policy evaluation often does not consider spatial structure of the population or stock (Deroba and Bence, 2008), and evaluation of harvest policies on spatially structured populations has largely focused on exploring effects of marine protected areas (reviewed in Pelletier and Mahévas, 2005). Spatial structure can have important effects on performance of management when productivity differs spatially (Tuck and Possingham, 2000; Sanchirico et al., 2006). Most studies that have evaluated how spatial structure influences performance of harvest policies have only explored equilibrium solutions (e.g., Neubert, 2003; Sanchirico et al., 2006; Armstrong, 2007), and some standard policies, such as state-dependent policies, which scale fishing mortality rate with population biomass, have not been evaluated for cases with spatial structure consisting of sources and sinks. How state-dependent policies perform in the presence of spatial structure

with source–sink population dynamics is an important question because these dynamics have been theorized as important regulatory mechanisms for natural populations (Pulliam, 1988), and are thought to be extremely important in some fisheries (e.g., Lipcius et al., 1997; Roberts, 1997). Frank and Leggett (1994) suggest that collapses of stocks of north Atlantic cod (*Gadus morhua*), Atlantic salmon (*Salmo salar*), and Pacific salmon (*Oncorhynchus* spp.) may have been caused by not recognizing structure of these populations and overfishing sources. Generally, sources are considered areas where the per capita rate of population growth is positive and emigration exceeds immigration; sinks are areas where the per capita rate of population growth is negative and immigration exceeds emigration (Figueira and Crowder, 2006).

Yellow perch (*Perca flavescens*) is an ecologically and economically important species in Lake Michigan (Francis et al., 1996) and has supported recreational and commercial fisheries since the late 1800s (Wells and McLain, 1972). The yellow perch population has undergone large fluctuations during the last half century (Francis et al., 1996). Management of yellow perch in southern Lake Michigan is shared among four U.S. states, with Wisconsin and Illinois on the western side of Lake Michigan, and Indiana and Michigan

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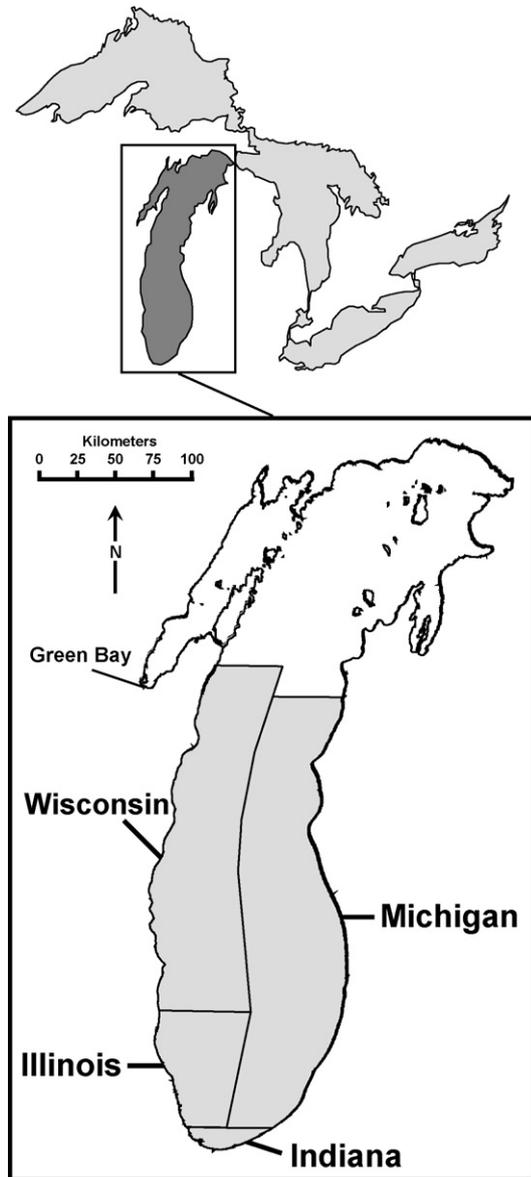


Fig. 1. Map of Lake Michigan with modeled management areas of the southern basin identified by U.S. state name. Green Bay lies outside of the modeled region and is also identified on the map. The inset shows the location of Lake Michigan in a regional map of the Laurentian Great Lakes.

on the eastern side (Fig. 1). Prior to 1969, all the states bordering Lake Michigan had commercial fisheries for yellow perch (Baldwin et al., 1979). In 1969, the state of Michigan was the first to close their commercial fishery (Wells, 1977). Abundance declined to low levels during the 1990s with a series of weak year-classes during 1989–1997 and 1999–2000 (Wilberg et al., 2005). As the abundance of yellow perch declined in southern Lake Michigan during the mid to late 1990s, commercial fisheries in Indiana, Illinois, and southern Wisconsin were restricted to smaller quotas (Francis et al., 1996) and were eventually closed during 1996–1997; these fisheries remain closed. Stricter regulations were also imposed on the recreational fishery with reductions in daily bag limits implemented in all states during 1996–1998, the incorporation of a slot size limit in Illinois during 1997–2000, and seasonal closures of the fishery (Francis et al., 1996). Failed recruitment has been implicated as the primary cause of the population collapse (Francis et al., 1996; Heyer et al., 2001; Marsden and Robillard, 2004), but

high fishing mortality rates are also thought to have been a contributing cause (Wilberg et al., 2005). Each state has independent management jurisdiction over its own waters, but fishery managers in each of these states believe management decisions in one area could affect the population in other areas (Francis et al., 1996; Clapp and Dettmers, 2004).

Some authors have suggested that areas on the western shore of southern Lake Michigan may contribute disproportionately to basin-wide recruitment, thus resulting in recruitment sources and sinks (Dettmers et al., 2005; Beletsky et al., 2007). Yellow perch have an unusual early life history for a freshwater fish in that they spawn demersally in near-shore habitats, and larvae have an extended off-shore pelagic period (typically lasting 30–40 days) after hatching in small and medium sized lakes (Forney, 1971; Whiteside et al., 1985). In Lake Michigan, the larval period may extend even longer than in smaller systems, and larvae have been captured in the pelagia after about 75 days post hatch (Dettmers et al., 2005). This pelagic period may be extended in Lake Michigan because larval swimming speed shortly after hatching (1 cm s^{-1} ; Houde, 1969) is substantially slower than average current velocities (10 cm s^{-1} ; Beletsky et al., 2007). Janssen et al. (2005) suggested that favorable spawning habitat, and preferred habitat of juveniles (Janssen and Leubke, 2004) and adults (Wells, 1977), is concentrated on the western shore of Lake Michigan. This spatial distribution of rocky habitat may cause adults on the western side of Lake Michigan to contribute disproportionately more to total recruitment in southern Lake Michigan than adults on the eastern side of Lake Michigan. Additionally, in southern Lake Michigan, predominant currents would likely transport yellow perch from the western side of the lake to the eastern side (Beletsky et al., 2004, 2007; Dettmers et al., 2005). Coupled physical–biological modeling and observations of larval yellow perch in the middle of Lake Michigan have indicated that larval yellow perch are transported long distances by these currents (Beletsky et al., 2004, 2007; Dettmers et al., 2005; Höök et al., 2006).

Alternative harvest policies have been evaluated for yellow perch in the southern basin of Lake Michigan (Irwin et al., 2008). The yellow perch population model used by Irwin et al. (2008) included two potential source–sink recruitment hypotheses: no source–sink dynamics and moderate source–sink dynamics where Wisconsin and Illinois were sources for recruitment and Indiana and Michigan were sinks. However, the source–sink scenarios evaluated by Irwin et al. (2008) were based on the assumption that production of recruits per unit spawning stock biomass (SSB) was the same across management areas. In this paper, our objective was to determine whether extreme source–sink dynamics affect the performance of harvest policies for yellow perch in southern Lake Michigan. We considered several alternative scenarios that differed from those presented in Irwin et al. (2008) in their assumptions about recruitment dynamics to evaluate how harvest policy performance was affected by population sources and sinks. We did this by separately considering each management area as a sole source of recruits and simulating the entire population over a range of harvest policies. We contrasted these results with those obtained for a base scenario where all areas contributed to recruitment in proportion to their SSB.

2. Methods

2.1. Modeling approach

We contrasted results from five simulation scenarios that made different assumptions about where adults that produced recruitment reside. In four of these source–sink scenarios, annual

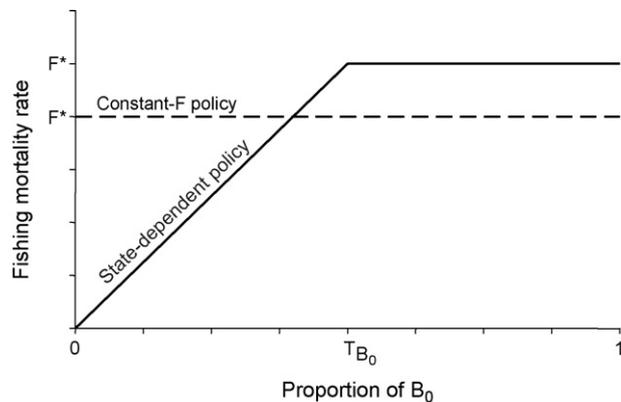


Fig. 2. Graphical representation of potential harvest policies. The dashed line represents a constant fishing mortality policy, for which target fishing mortality (F^*) is independent of stock size. The solid line represents a state-dependent policy where fishing mortality is constant at F^* above an upper threshold of spawning stock biomass (T_{B_0}) and declines if spawning stock biomass falls below that threshold.

recruitment was produced by adults residing in a single management area, considering each area in turn. The fifth scenario, which we refer to as the base scenario, assumed that offspring from all four areas contribute to basin-wide recruitment in proportion to the SSB in that area, following the same assumptions as Irwin et al. (2008). For each of these five scenarios we considered two alternative hypotheses about recruitment productivity.

The model forecasted population dynamics for 50 years under constant fishing mortality rate and state-dependent harvest policies (Fig. 2). We compared the performance of harvest policies using average harvest per year (in numbers), average percent of unfished SSB (B_0) remaining in the population, and the percentage of years that each of these performance statistics fell below a critical threshold, where each performance statistic was calculated over the 50-year time horizon. The model structure and performance statistics were developed through a series of workshops with managers and scientists interested in yellow perch management in Lake Michigan (see Irwin et al., 2008 for details), and are consistent with those used in Irwin et al. (2008).

Details of the simulation model are documented in Irwin et al. (2008). The model was age-, length-, sex-, and spatially-structured and contained four management areas. These management areas represented jurisdictional waters of each state (Fig. 1). Within each area, yellow perch recruited to the population at age-2, with a 1:1 sex ratio. Growth followed a time-varying von Bertalanffy model with separate sets of parameters for males and females in each state. The growth model allowed for density-dependent (Headley and Lauer, 2008) and density-independent (Horns, 2001) interannual variation. Values of the parameters for the growth model were chosen to match observed spatial and temporal patterns of yellow perch growth (Irwin et al., 2008). Females grew faster and to larger sizes than males (Wells, 1977; Wilberg et al., 2005), and yellow perch in Wisconsin and Illinois grew faster than fish in Michigan or Indiana (Horns, 2001). The model also included modest rates of post-recruitment migration among management areas. These migration rates were developed from tag recovery data of yellow perch in southern Lake Michigan. Post recruitment migration rates are thought to be low because the median dispersal distance of tagged fish was less than 30 km.¹

Total per capita instantaneous mortality rates for each age and sex in each management area were the sum of the age-, sex-, and

area-specific fishing mortality rate and a natural mortality rate, ($M=0.37 \text{ year}^{-1}$). Fishing mortality was a function of the harvest policy, selectivity-at-age and -sex, and was affected by assessment and implementation errors. Selectivity was length-based and represented the selectivity pattern of the recreational fishery (Wilberg et al., 2005). Assessment and implementation errors were included so that application of the policy would be made with imperfect information and the policy would be imperfectly implemented. Assessment errors were modeled as a first order autoregressive process, whereas implementation errors were assumed to be independent among years (Irwin et al., 2008).

2.2. Stock-recruitment model

Total recruitment (summed over management areas) was modeled using a Ricker stock-recruitment relationship with multiplicative lognormal annual error. The log-scale stock-recruitment parameters used in individual simulations were drawn from a multivariate normal distribution. For the scenarios assuming a single area as the source, stock size used in the relationship was SSB for that area, whereas for the base scenario stock size was SSB summed over the areas. For each of the five scenarios of source-sink dynamics, stock-recruitment parameters were needed for each of the two hypotheses regarding recruitment productivity (Fig. 3). The two productivity hypotheses were (1) productivity will continue to be low as has been seen since the early 1990s (the “recent” recruitment hypothesis), and (2) the system retains the potential for high recruitment (the “variable” hypothesis). The variable recruitment hypothesis switched randomly from year to year between high and low productivity regimes. After total recruitment was determined, the recruits were allocated among the four management areas based on the expected proportion of recruits returning to each management area during 1996–2004, and process error that allowed for variation in the proportion returning to each management area (Irwin et al., 2008). We are not suggesting the single source hypotheses are equally plausible, but that they represent useful extremes with which we can contrast performance of harvest policies.

We required eight sets of parameter values (two productivity hypotheses for each of the four scenarios assuming a single management area was the source) in addition to the values for the base scenario. Parameters for the recent hypothesis were based on analysis of a recruitment and SSB time series from 1993 to 2002, whereas parameters for the variable recruitment hypothesis were based on analysis of a time-series for 1986–2002, where each year was assigned to one of the two regimes. Recruitment and SSB time series were compiled from updated versions of assessment models in Wilberg et al. (2005) for Illinois and Wisconsin, and similar unpublished models for Indiana and Michigan. A longer time series of relative recruitment was used to estimate the probability of a high versus low productivity year (Irwin et al., 2008). SSB values for Indiana and Michigan were estimated from average time series of SSB in the other areas rescaled to estimated average SSB in Michigan and Indiana because assessment estimates were from substantially shorter time series (1996–2004) and assessment results were heavily influenced by equilibrium assumptions about initial age composition that were necessary to obtain estimates.

All recruitment hypotheses and source-sink scenarios include parameter uncertainty and stochastic annual variability. Stock-recruitment parameter means, standard deviations, and correlations were estimated on a log-scale by the point estimates, and the asymptotic variance-covariance matrix obtained using maximum likelihood. For the four single management area source scenarios these regressions used total estimated recruitment in southern

¹ Glover (2005).

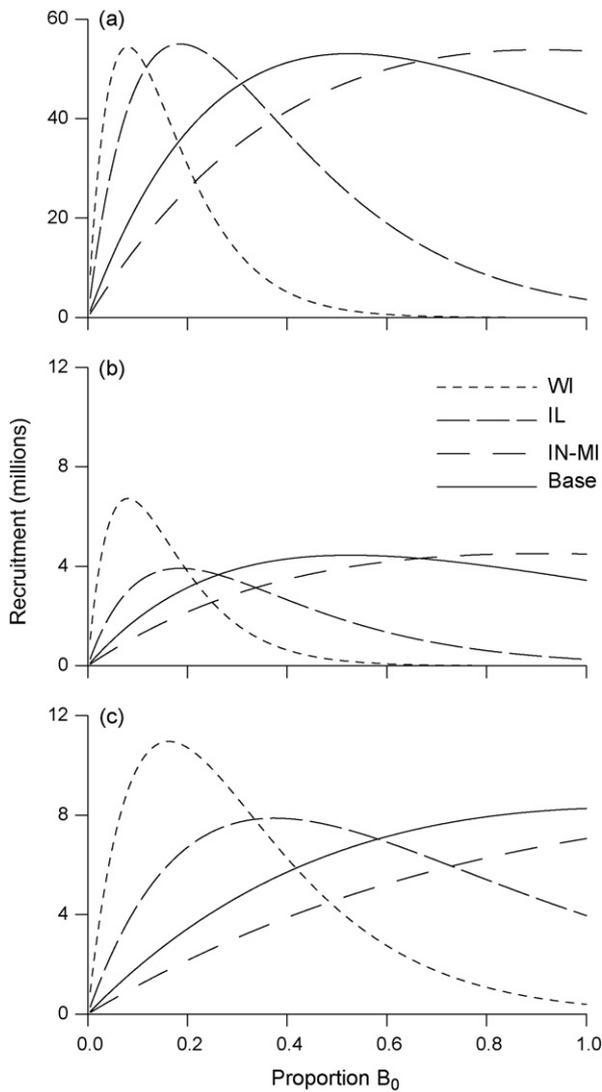


Fig. 3. Stock-recruitment relationships based on mean parameters and ignoring stochasticity for alternative assumptions about source management areas that produced recruits: all recruits produced in Wisconsin (WI), Illinois (IL), Michigan or Indiana (IN-MI), or the base scenario (where some recruits were produced in all areas; Base). Panels a and b indicate high and low productivity relationships used under the “variable” recruitment hypothesis, and panel c indicates productivity used under the “recent” recruitment hypothesis. Curves are scaled relative to unfished SSB, B_0 , used in the harvest policies.

Lake Michigan and SSB estimates for each management area one at a time. These estimates defined the multivariate normal distributions used to generate parameter values for each simulation. The base scenario parameter estimates from Irwin et al. (2008) were calculated similarly based on total estimated stock size in southern Lake Michigan.

For the variable recruitment hypothesis, a productivity regime was selected based on a Bernoulli random variable (Irwin et al., 2008). The Ricker parameters included an adjustment to the Ricker “alpha” to account for the productivity regime. The same Ricker parameters were used each year throughout a 50-year simulation for the “recent” recruitment hypothesis.

2.3. Harvest policies

We considered a range of constant fishing mortality rate (constant- F) and state-dependent policies. For state-dependent

policies, target fishing mortality (\bar{F}) was constant at the maximum target fishing mortality (F^*) above a threshold level of SSB (T_{B_0}) and decreased linearly below that threshold, reaching a value of zero for SSB of zero (Fig. 2). We evaluated three threshold values in our analysis, 0% (constant- F), 40%, and 70% of B_0 , and seven levels of F^* , 0.1, 0.3, 0.5, 0.7, 1.0, 1.5, and 2.0 year⁻¹, for a total of 21 alternative harvest policies. We thus refer to constant- F , 0–40 and 0–70 policies. F^* was defined in terms of average age-based fishing mortality rates for females age-4 and older. We estimated B_0 for each area as the weighted average biomass across simulations in year 50 weighted by recruitment hypothesis with no fishing mortality (Irwin et al., 2008). Harvest policies were applied in the same way in each management area (i.e., managers would be naive about the source–sink dynamics), and only the value of B_0 varied among the harvest policies used in the different management areas.

2.4. Simulation details

We used a factorial design for this simulation study. We ran 250 simulations for each type of policy (constant- F , 0–40, 0–70), at seven levels of F^* , for both stock-recruitment hypotheses, and for each of the five source–sink scenarios. Each set of 250 simulations used the same 250 sets of random numbers, a common approach to increase simulation efficiency.

2.5. Policy performance comparisons

Performance statistics for each simulation were calculated by summarizing over the 50 year time-horizon. We evaluated four performance statistics of importance to yellow perch managers: total harvest (numbers), total SSB across all areas as a percentage of average B_0 , risk of low harvest (<1.5 million fish per year) and risk of low stock size (<20% mean B_0) (see Irwin et al. (2008) for background on the choice of performance statistics). We generated distributions for the performance statistics for each harvest policy and source–sink scenario by combining results across the two recruitment hypotheses. We did this by weighting performance statistics from each simulation by the presumed probability (0.8 for the variable recruitment hypothesis and 0.2 for the recent recruitment hypothesis) that each was true (Irwin et al., 2008). We then summarized the weighted distributions, so each distribution for a given F^* and control rule in each source–sink scenario reflects results from 500 simulations.

To compare performance of policies under source–sink dynamics with those under the base scenario, we calculated the proportional root mean square error (RMSE) for each simulation using the same random number seed for a given policy and productivity hypothesis,

$$RMSE_i = \sqrt{\frac{\sum_A ((X_{A,i} - X_{B,i}) / X_{B,i})^2}{4}}$$

where $X_{A,i}$ is the value of any particular performance statistic (calculated over years within a simulation) for simulation i assuming that all recruits were produced in area A , and $X_{B,i}$ is the same statistic calculated for the base model. This version of RMSE calculates relative variation because the differences are scaled by the results from the base scenario. Smaller RMSE values indicate performance of a harvest policy was more similar among alternative source–sink models and more similar to the base scenario than larger values. These RMSEs were then combined over productivity hypotheses to obtain the distribution for a given policy in the same way as the individual performance statistics.

3. Results

3.1. Performance among source scenarios

Not surprisingly, SSB decreased as F^* increased regardless of which area was the source, as was the case for the base scenario (Fig. 4). Constant- F policies resulted in lower levels of SSB than either of the state-dependent policies for all levels of F^* for all source-sink scenarios, a result that is expected because the actual fishing mortality rate applied was higher, on average, for the constant- F policy. Likewise, the average percentage of years when SSB was below 20% of B_0 increased with increasing F^* for each harvest policy we considered for each source-area scenario (Fig. 5).

For state-dependent policies, average harvest increased with increasing F^* over the range of F^* examined (Table 1, Fig. 6). Conversely, recreational harvest peaked at an intermediate F^* for constant- F policies, although the associated F^* where average harvest was maximized varied depending upon the source area. This qualitative difference was also observed for the base scenario. The maximum average basin-wide harvest (over all four management areas combined) occurred at $F^* = 1.5 \text{ year}^{-1}$ when yellow perch recruits were derived from either Wisconsin or Illinois; whereas, the maximum occurred at $F^* = 0.7 \text{ year}^{-1}$ when either Indiana or Michigan were the source area. However, average harvest showed a marked decrease for F^* above 0.7 year^{-1} in Indiana and Michigan, but remained relatively flat for Illinois and Wisconsin. For the base scenario, average harvest peaked for $F^* = 1.0 \text{ year}^{-1}$ and median harvest peaked at 0.7 year^{-1} for the constant- F policies. Maximum average harvest was substantially

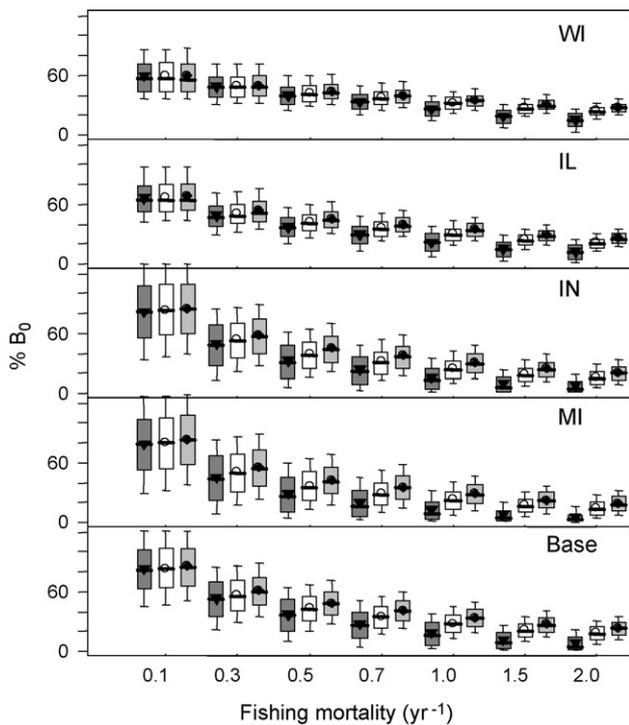


Fig. 4. Box plots of average percentage of spawning stock biomass (SSB) relative to unfished SSB (B_0) for each source-sink scenario. Boxes indicate, 25th and 75th percentiles, whiskers indicate the 10th and 90th percentiles, horizontal line indicates the median, and symbols indicate the mean. Dark gray boxes indicate constant fishing mortality rate, white boxes indicate 0–40 state-dependent, and light gray boxes indicate 0–70 state-dependent harvest policies. WI indicates Wisconsin as the source of all recruitment, IL: Illinois, IN: Indiana, MI: Michigan, and Base: base scenario where all areas contribute to recruitment in proportion to their SSB.

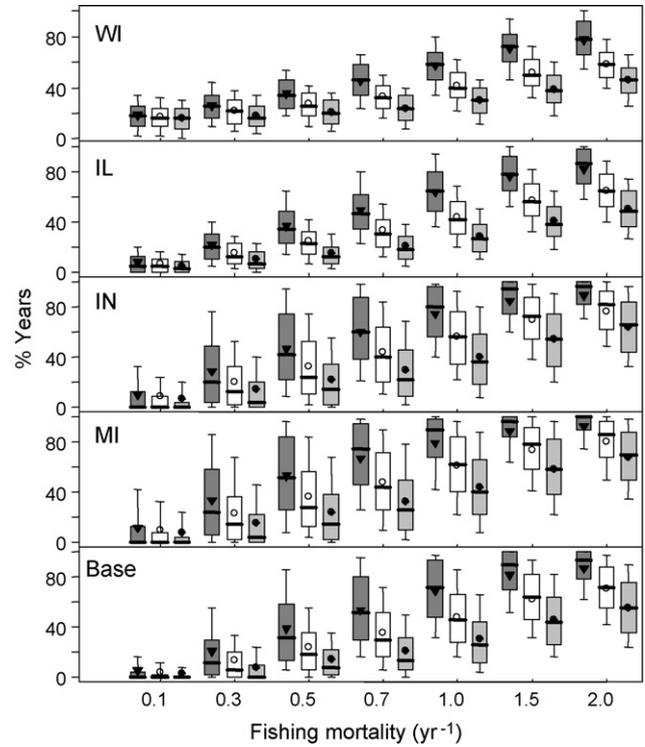


Fig. 5. As for Fig. 4, except results are shown for percentage of years with spawning stock biomass (SSB) less than 20% of unfished SSB (B_0) for each source-sink scenario.

higher if Illinois or Wisconsin was the source area, in comparison with either the base scenario or when Indiana or Michigan was the source.

For all harvest policies and levels of F^* considered, the average percentage of years with harvest below 1.5 million fish was lowest with a constant- F policy regardless of the source-sink scenario, but the associated F^* again varied among source areas (Fig. 7): the risk of low harvests was minimized with an F^* of 0.3 year^{-1} in Indiana and Michigan, 0.5 year^{-1} in Illinois, and 0.7 year^{-1} in Wisconsin. Additionally, if either Illinois or Wisconsin was the source area, the average proportion of years with low harvest was lower over a wider range of fishing mortality than if the source area was in Michigan or Indiana. However, the base scenario had higher average harvest and lower probability of low harvest at the lowest two levels of F^* than any of the source-area scenarios.

Table 1

Target fishing mortality rates (F^*) that achieve maximum mean harvest and associated levels of maximum mean harvest for source-sink scenarios and the base scenario. Constant fishing mortality rate policies are denoted as Constant- F , and state-dependent harvest policies are denoted by the proportion of unfished spawning stock biomass at which fishing mortality is decreased (0–40 and 0–70). Scenarios indicate the source of all recruits for the model and base indicates the scenario where all areas contribute to recruitment in proportion to spawning stock biomass

Scenario	Harvest policy			Mean harvest (millions)		
	Constant- F	F^* (year ⁻¹)		Constant- F	0–40	0–70
Wisconsin	1.5	2.0	2.0	9.5	11.5	10.5
Illinois	1.5	2.0	2.0	7.9	9.4	9.1
Indiana	0.7	2.0	2.0	5.6	6.7	6.9
Michigan	0.7	2.0	2.0	4.8	5.9	6.2
Base	1.0	2.0	2.0	6.6	8.1	8.3

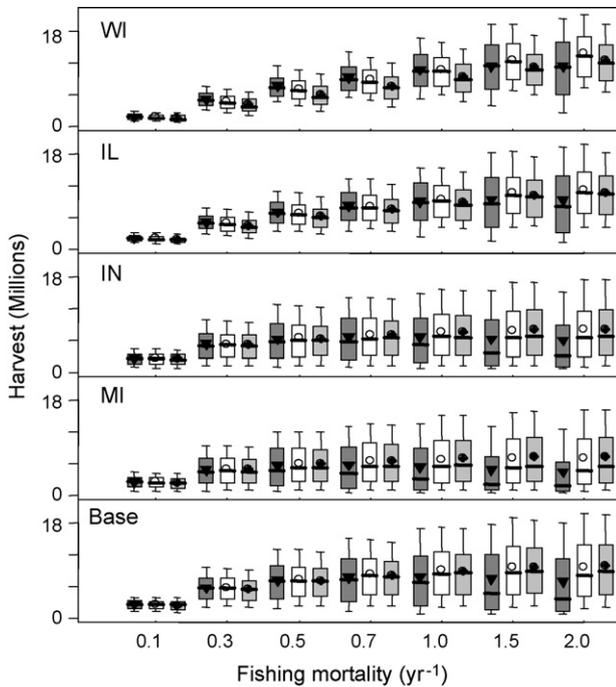


Fig. 6. As for Fig. 4, except results are shown for harvest (millions of fish) for each source–sink scenario.

3.2. Sensitivity across source areas

Consistency of harvest policy performance over source areas, as indicated by RMSEs, followed different patterns for the four performance statistics (Fig. 8). The mean RMSE for average SSB was highest across harvest policies for the highest level of fishing mor-

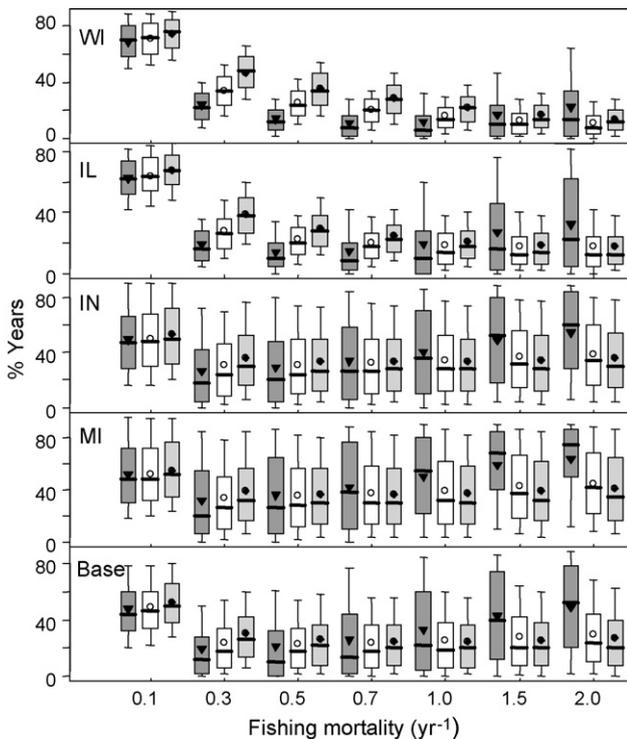


Fig. 7. As for Fig. 4, except results are shown for percentage of years with harvest less than 1.5 million fish for each source–sink scenario.

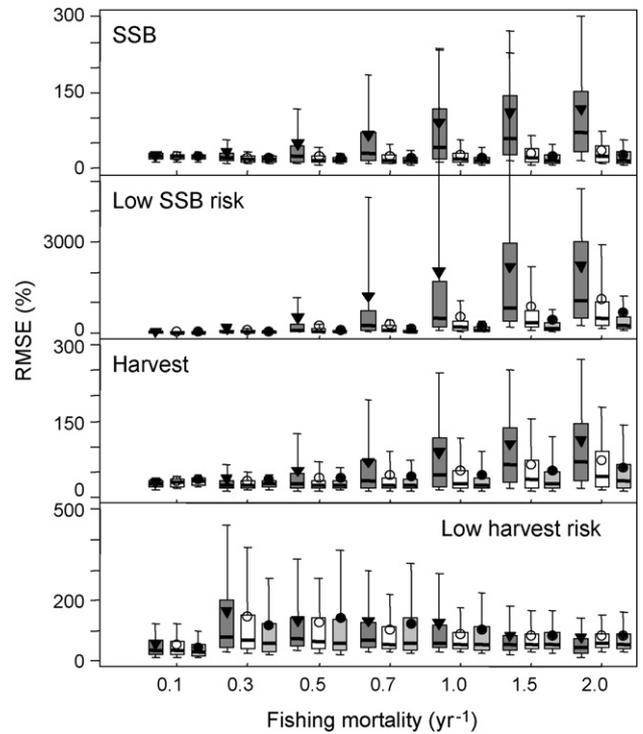


Fig. 8. Box plots of root mean square error (RMSE) of spawning stock biomass (SSB), percentage of years with low SSB (low SSB risk; less than $0.2 B_0$), harvest, and percentage of years with low harvest (low harvest risk; less than 1.5 million fish) based on comparing single source area scenarios to the base scenario. Boxes, whiskers, and symbols for box plots, and colors distinguishing types of harvest policies are as defined in Fig. 4.

tality and became similar for all assumed recruitment sources at low fishing mortality rates. Variability in RMSE of SSB, as indicated by the interquartile range of RMSE, showed the same pattern as mean RMSE. The increase in mean RMSE and variability in RMSE at higher levels of F^* probably occurred because variability in SSB becomes more closely tied to recruitment variability when SSB is depressed to quite low levels as it was under high fishing mortality. RMSE increased with increasing F^* for the constant- F policies, but decreased with increasing F^* between 0.1 year^{-1} and 0.3 year^{-1} for the 0–40 policy and between 0.1 year^{-1} and 0.5 year^{-1} for the 0–70 policy before increasing. The 0–70 policies had the lowest RMSE for average SSB, and a 0–70 policy also achieved the lowest overall RMSE (at $F^* = 0.5 \text{ year}^{-1}$). In contrast, mean RMSE and variability of low SSB risk increased for all policies with increasing F^* . As for SSB, mean RMSE and variability of RMSE of low SSB risk was lowest for the 0–70 policy for all levels of F^* . RMSE of low SSB risk was generally the highest of the performance statistics we evaluated.

Mean RMSEs for harvest increased with increasing F^* , and differences among harvest policies tended to increase with increasing F^* except for the highest level of F^* . For low harvest risk, RMSEs were lowest at the lowest level of F^* . The highest RMSEs for low harvest risk were at F^* s of 0.3 year^{-1} for the constant- F and 0–40 policies and at 0.5 year^{-1} for the 0–70 policy; RMSEs declined at higher values of F^* . The 0–70 policy achieved the lowest RMSE for low harvest risk at an F^* of 0.1 year^{-1} , but RMSEs were quite similar across harvest policies. Unlike RMSEs for SSB, low SSB risk, and harvest, differences among harvest policies in RMSE for low harvest risk generally decreased with increasing F^* except for the lowest level of F^* .

4. Discussion

We found that performance of state-dependent harvest policies with moderate levels of fishing mortality led to reasonable trade-offs between maintaining acceptable levels of recreational harvest and SSB on average while also minimizing the risk of low SSB and were more robust to uncertain source–sink dynamics than constant- F policies for three of our performance statistics. In particular, the 0–70 policies tended to have the most consistent performance across source–sink scenarios. Irwin et al. (2008) also found that harvest policies for yellow perch in Lake Michigan with relatively low fishing mortality rates provided a reasonable tradeoff between maintaining acceptable levels of recreational harvest and SSB on average while also minimizing the risk of low SSB. However, constant- F policies with low or moderate fishing mortality rates were better at reducing risk of low harvest than state-dependent policies (Irwin et al., 2008). Our evaluation of scenarios that assumed all recruits derived from a single management area support similar conclusions, but details of policy performance differed depending on which management area was the source of recruitment. That such differences exist is not surprising because stock–recruitment relationships and growth were assumed to be different among management areas and the B_0 s used in the state-dependent harvest policies differed substantially from the true B_0 s in Wisconsin and Illinois. We also conducted simulations to determine if different growth patterns among areas or post-recruitment migration influenced the results of our study by re-running the simulations with growth the same in all areas and with growth the same in all areas and no migration, respectively. Results from these simulations showed the same patterns as the simulations with area-specific growth and post-recruitment migration, indicating that these factors did not seem to cause differences in policy performance in different source–sink scenarios. Differences in policy performance among source–sink scenarios most likely stem from an interaction between the stock–recruitment function of the source area and how well our assumed level of B_0 matches the true B_0 of the scenario.

Our results show that in comparison with the base scenario, if Wisconsin or Illinois was the source of all or most of the recruits for southern Lake Michigan, then the yellow perch population would be able to support higher levels of fishing mortality and provide higher levels of average harvest, without higher risk of low stock size or harvest than we found in the base scenario. Indeed, if Illinois or Wisconsin was the source area, average harvest could be 9–61% higher than under the base scenario at the highest levels of F^* , depending on the source area and harvest policy. This result is due to the high productivity that these two areas could achieve at low stock sizes based on assumptions of single-source production (Fig. 3). However, higher average harvests when Wisconsin or Illinois was the source area were only seen above levels of F^* of 0.5 year⁻¹, 0.7 year⁻¹, and 1.0 year⁻¹ for constant- F , 0–40, and 0–70 policies in Wisconsin and above 0.7 year⁻¹, 1.0 year⁻¹, and 1.5 year⁻¹ in Illinois. Performance of harvest policies in the base scenario was more similar to cases where either Indiana or Michigan was the source area than when Illinois or Wisconsin was the source area, but the Indiana and Michigan source scenarios always indicated a higher risk of low SSB or low harvest for a given average harvest than the base scenario. This probably happens because Indiana usually has the largest SSB under the base scenario, growth of yellow perch in Michigan is similar to that in Indiana, and the Indiana and Michigan single-source scenarios have lower productivity at low stock size than the base scenario.

State-dependent policies, where fishing mortality rates decreased as SSB decreased below a threshold proportion of mean B_0 , were less sensitive to source–sink dynamics than constant- F

policies. Irwin et al. (2008) presented additional results for the base scenario suggesting that in many cases these types of policies could make more desirable tradeoffs than is possible with a constant- F policy. These results are consistent with Tuck and Possingham (2000), who suggested that a precautionary approach to management of stocks where source–sink dynamics are unknown may be to consider each subpopulation unconnected with surrounding subpopulations and manage to preserve adequate levels of SSB in each area. They found that in the face of unknown source–sink dynamics higher equilibrium yield and stock size occurred when areas were considered independently than when areas were considered a single stock. While we did not consider state-dependent policies that set the same fishing mortality in all areas based on the total SSB summed over areas, the constant- F policy can be viewed as a special case of such a policy.

We have relatively little information on the source–sink structure of yellow perch recruitment in Lake Michigan because attempts to estimate hatching locations of recruits have so far been unsuccessful. However, Janssen et al. (2005) and Dettmers et al. (2005) suggested that the western shore of Lake Michigan may be the source area for recruitment in southern Lake Michigan. The predominant wind direction is westerly and the predominant current is counter clockwise (Beletsky et al., 2004; Beletsky et al., 2007), thus larvae produced in western Lake Michigan would, on average, be transported eastward. Janssen et al. (2005) suggested that yellow perch eggs spawned on rocky habitat would survive better than eggs spawned on other types of habitats because egg skeins tended to stay in place in rocky habitat whereas they did not on other habitat types. In southern Lake Michigan, yellow perch appear to preferentially spawn on rocky habitat (Robillard and Marsden, 2001), and this habitat type is concentrated in Wisconsin and Illinois waters (Janssen et al., 2005). Other processes such as spatial differences in abundance of egg predators could also lead to similar dynamics as we included in our model, but these hypotheses have not been explored in the field. As a result of such spatial differences, our base scenario is qualitatively consistent with the hypothesis that the western side of Lake Michigan is a source, in that Indiana and Michigan were net sinks for recruitment under unfished conditions (Irwin et al., 2008). Because scenarios with Illinois or Wisconsin as the source seem more plausible and more productive than the other source scenarios considered, pursuit of policies allowing for higher rates of fishing could potentially be justified. However, the risks of misidentifying the source area are potentially large.

Our assumption of no reproductive contribution from sink areas was a limiting case and is obviously a simplification. This simplification implies that populations in sink areas are entirely dependent on recruitment from a subpopulation in another area. Our model did allow some amount of migration of post recruitment fish, but management areas differed in whether they were usually net exporters or importers depending on the specific recruitment hypotheses. Additionally, our model assumed that compensation in recruitment dynamics occurs before recruits were assigned to an area (i.e., it was not area-specific) because compensation only depended on the SSB in the source area. There is some evidence such compensation exists (Dettmers et al., 2005), but post-recruitment cannibalism may also be important. Truemper et al. (2006) found that small yellow perch were common diet items of larger yellow perch, and such cannibalism likely occurs after juveniles settle to demersal habitat because larger yellow perch generally feed demersally (Tyson and Knight, 2001).

Source–sink dynamics can have important effects on harvest policy performance, particularly with respect to the benefits of marine protected areas (Crowder et al., 2000; Sanchirico et al.,

2006; Armstrong, 2007). Other authors have found that use of alternative harvest policies in different areas can provide optimal performance if the source–sink dynamics are known (Tuck and Possingham, 2000; Neubert, 2003; Sanchirico et al., 2006; Armstrong, 2007). We did not evaluate cases where the source area was unfished. Theoretically, it would be beneficial to fish the source area in our simulations because the recruitment followed a Ricker model, where production of recruits peaks at an intermediate stock size. Under most conditions examined by others, fishing the sink area provides more benefits in terms of harvest and SSB remaining in the populations than fishing source areas (Crowder et al., 2000; Tuck and Possingham, 2000). However, under some conditions (differences in profitability among areas) profitability can be optimized by fishing the source area (Sanchirico et al., 2006). Additionally, the existence of source–sink dynamics can lead to scenarios where closing the fishery in some areas is optimal in terms of total harvest or profit. However, these studies have only focused on constant fishing mortality and escapement based policies under equilibrium conditions. We did not attempt to find optimal harvest policies in each management area because of Lake Michigan managers' strong preference for a common policy across areas and because such fine tuning would probably require much better knowledge regarding source–sink dynamics. The influence of uncertainty about spatial structure on the performance of area-specific policies is a topic which could benefit from further research.

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