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[Article]

Yellow Perch Dynamics in Southwestern Lake Michigan during 1986–2002

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Abstract.—We examined the role of harvest in the collapse of the population of yellow perch *Perca flavescens* in southwestern Lake Michigan during the mid to late 1990s. After the great decrease in this population at that time, commercial fisheries in Illinois and Wisconsin were closed during 1996–1997 (and have remained closed), and stricter regulations were placed on recreational fisheries. Reproductive failure has been implicated as the primary cause of the population collapse, but the role of fishing in the collapse was not rigorously investigated in previous studies. We conducted an age-, size-, and sex-structured stock assessment of yellow perch to estimate population size and examine historical trends in fishing mortality in Illinois and Wisconsin waters of southwestern Lake Michigan. Model estimates indicated that yellow perch abundance in 2002 was less than 10% of the 1986 abundance in Wisconsin and about 20% of the respective population in Illinois. Annual mortality rates for females age 4 and older averaged 69% during 1986–1996 in Wisconsin and 60% in Illinois during 1986–1997, rates that are quite high for a species like yellow perch, which can live longer than 10 years. The estimated fishing mortality rates of adult females during 1986–1996 exceeded widely used reference points, suggesting that overfishing may have occurred. Fishing mortality rates decreased substantially in the late 1990s after stricter regulations were imposed on recreational fisheries and commercial fisheries were closed. We believe that unsustainably high mortality rates from fishing were a substantial contributing cause of the rapid decline of mature females in the mid-1990s. Spawning stock biomass in 2002 was at its highest level since the early 1990s despite relatively poor recruitment during the past decade. In part, this development reflects the fact that management actions have successfully reduced fishing mortality.

Yellow perch *Perca flavescens* is an ecologically and economically important species in Lake Michigan (Wells and McLain 1972). Yellow perch are native to Lake Michigan, play an important role in near-shore energy cycling and transfer (Evans 1986), and have provided a fishery on Lake Michigan since the late 1800s (Wells and McLain 1972; Wells 1977). Yellow perch is the only native species in Lake Michigan that has supported a commercial fishery continuously during the last century (Baldwin et al. 1979), although since 1998 the only commercial fishery remaining is in Green Bay, Wisconsin. During the 1980s and 1990s, the recreational fishery harvested more yellow perch than any other species in Lake Michigan (Bence and Smith 1999).

In southern Lake Michigan, yellow perch abundance underwent periodic fluctuations during 1934–1964 and declined greatly during the 1960s (Francis et al. 1996). Because the decline in yellow perch abundance in the 1960s coincided with a large increase in alewife *Alosa pseudoharengus* abundance, alewife interference with yellow perch reproduction (either through competition or predation) was considered the primary cause of the

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decline (Wells 1977). However, exploitation was also considered a contributing factor to the overall decline and the primary cause of the decline of adults (Wells 1977). Before 1969, all the states bordering Lake Michigan (Indiana, Illinois, Michigan, and Wisconsin) 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). During the 1970s, yellow perch populations in southern Lake Michigan began to recover (Wells and Jorgenson 1983), and abundance was high during the 1980s with strong year-classes in 1980 and 1983–1988 (Jude and Tesar 1985; Makauskas and Clapp 2000). Abundance declined to low levels during the 1990s, however, with a series of weak year-classes during 1989–1997 and 1999–2000. As yellow perch abundance declined, the sex ratio became skewed toward males, perhaps because of intense fishing attention targeted on large females (Madenjian et al. 2002). The selective removal of large females may have led to further declines in yellow perch recruitment. 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 eventually were closed during 1996–1997; these fisheries remain closed. Stricter regulations were also imposed on the recreational fishery, reductions in daily bag limits being implemented in all states during 1996–1998, as well as incorporation of a slot size limit in Illinois during 1997–2000 and seasonal closures of the fishery (Francis et al. 1996). Reproductive failure has been implicated as the primary cause of the population collapse (Francis et al. 1996; Heyer et al. 2001; Marsden and Robillard 2004), but the role of fishing in the collapse has not been rigorously investigated.

Our objectives were to estimate fishing mortality rates and the abundance of yellow perch in Wisconsin and Illinois waters of southwestern Lake Michigan during 1986–2002 to determine the contribution of fishing to the collapse of yellow perch in southern Lake Michigan. We also wanted to determine whether fishing mortality rates exceeded the maximum rates that could be supported and to integrate diverse sources of data to get the best estimates of recruitment and population size. Our approach was to fit age-, size-, and sex-structured population models to fishery and survey data. No previous population model–based stock assessments have been conducted for yellow perch in southern Lake Michigan. Similar age-structured assessments have been applied to lake trout *Salvelinus namaycush* (Sitar et al. 1999), lake whitefish *Coregonus clupeaformis* (Ebener et al. 2005), walleye *Sander vitreus* (Deriso et al. 1988), and yellow perch (Lake Erie Yellow Perch Task Group 2001) in other areas of the Great Lakes.

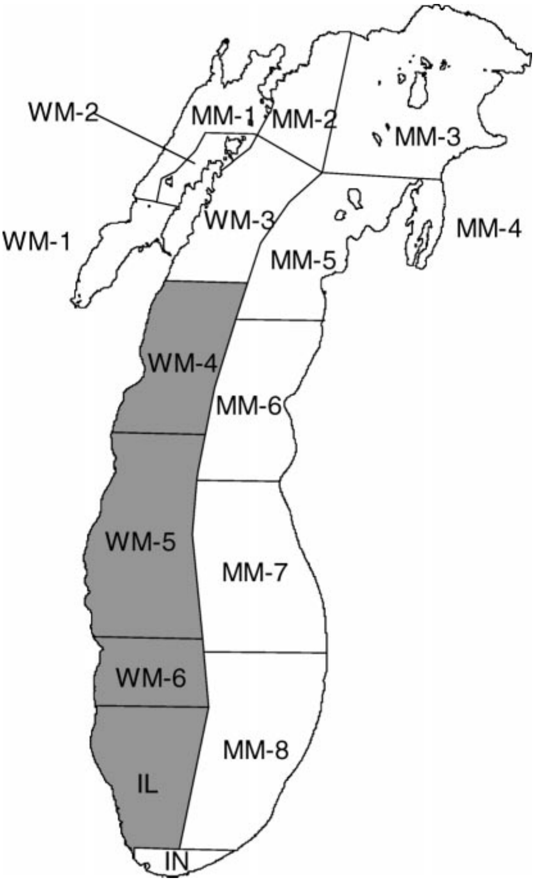

FIGURE 1.—Map of Lake Michigan statistical districts with modeled areas shaded; WM indicates Wisconsin waters, IL indicates Illinois waters, IN indicates Indiana waters, and MM indicates Michigan waters.

Methods

We implemented statistical catch-at-age models (detailed description in Appendix A) for yellow perch in southwestern Lake Michigan (Figure 1). Statistical catch-at-age models are age-structured models that follow cohorts of fish over time and consider the catch-at-age data to be measured with error (Megrey 1989). Such models consist of population and observation submodels, where the model parameters are estimated by fitting the models to data (Megrey 1989). Our assessment models considered annual time intervals, the period from 1986 to 2002, and ages 2 through 9 (age 9 was an aggregate age-class that included all fish age 9 and older). We began our models in 1986 because recreational fishery data were not available for earlier years. During model development, we tested the effect of sequentially lowering the aggregate age-class (down to age 6) and obtained results similar to those we report here. Our models also contained two fisheries, recreational and commercial, and a fishery-independent gill-net survey. Our models produced estimates of fishing mortality rates, abundance, biomass, and spawning stock biomass (SSB). We defined SSB as the biomass of mature females in the population and calculated this on the basis of a length-based maturation curve derived outside our model-fitting process (see Appendix A).

Our assessment model was age, size, and sex structured. In statistical catch-at-age models, relative vulnerability (i.e., selectivity) to the fisheries is usually modeled as a time-invariant function of age (Quinn and Deriso 1999). However, this assumption does not appear to be reasonable for yellow perch, because these fisheries are highly size-selective (Kraft and Johnson 1992) and yellow perch size at age has changed substantially over time (Marsden and Robillard 2004). Also, yellow perch show sexually dimorphic growth—the females growing faster and to larger sizes than the males—which is suspected to cause higher fishing mortality rates for females than for males (Wells and Jorgenson 1983; Madenjian et al. 2002). We modeled selectivity of the fisheries and surveys as functions of length and allowed growth to change over time with a time-varying von Bertalanffy growth model (Szalai et al. 2003). We accounted for temporal variations in growth by allowing the von Bertalanffy parameters to change in accord with random walk submodels (see Appendix A). Our approach allowed the relative vulnerability of different age–sex categories of yellow perch to change over time as their mean length at age changed, even though relative vulnerability was a constant function of length that did not differ between the sexes (Methot 1990; Hampton and Fournier 2001). We also included a different selectivity pattern to capture changes in recreational fishery selectivity during 1997–2000, when a slot size limit was implemented in Illinois. We assumed a time-, sex-, and age-invariant natural mortality rate, M, of 0.37, which was consistent with estimates of M for yellow perch in Indiana waters of southern Lake Michigan (Allen 2000) and with values used for stock assessments of yellow perch in Lake Erie (Lake Erie Yellow Perch Task Group 2001).

As well as allowing for changes in the relative vulnerability of different ages in response to changes in growth, our model allowed for temporal changes in the vulnerability of the most selected size of yellow perch, so that the fishing mortality imposed by a given amount of fishing effort could change over time. As with the growth model, this was done by varying fishery catchability parameters according to random walk models (see Appendix A).

Genetic analyses have found that yellow perch in the southern basin of Lake Michigan form a single genetic stock (Miller 2003). However, our approach implicitly assumed that there was no net migration for either of the model areas (Illinois, and Wisconsin WM-4 to WM-6; Figure 1). We believe this assumption is a reasonable approximation because preliminary tagging data suggest a relatively low median dispersal distance for adult yellow perch in southwestern Lake Michigan (<30 km; D. Glover, University of Illinois at Urbana-Champaign, personal communication). Also, Horns (2001) attributed differences in growth patterns among yellow perch stocks in southern Lake Michigan to geographic segregation. Evidence from current physical modeling studies suggests that genetic structure of the yellow perch population of southern Lake Michigan may be caused by mixing during the larval stage (Beletsky et al. 2004).

Model fitting.—We took a Bayesian approach to obtain posterior probability estimates for the parameter values and quantities of interest, such as fishing mortality rates, abundance, biomass, and SSB. We fitted our models to commercial yield, recreational harvest, commercial length frequency, recreational length frequency, commercial effort, recreational effort, mean length at age in the survey, age composition of the survey by sex, total survey catch per unit effort (CPE) by sex, and survey length composition by sex. The objective function contained 11 additive components for the Wisconsin model and 12 additive components for the Illinois model (Appendix). Each component represented a type of data or a specified informative distribution (i.e., prior distribution) for parameters. Variations in catchability and growth model parameters followed random walks and were included as components. We estimated 149 parameters for the Wisconsin model and 151 parameters for the Illinois model. We used Markov Chain Monte Carlo (MCMC) simulations with a Metropolis–Hastings algorithm to estimate posterior probability intervals (the Bayesian analog of confidence intervals) of several model parameters and estimates (Otter Research 2000). We ran the MCMC chain for 2×10^6 steps, sampling every 250 steps, and discarded samples from the initial 2.5×10^5 steps as a burn-in period, which reduces the effect of the starting values on the MCMC results (Gelman et al. 2004). To determine whether the length of our burn-in period was long enough, we separated the MCMC chains (of the objective function) into several smaller chains and compared the distributions of these blocks (Gelman et al. 2004); the distribution of each block was nearly identical to that of the other blocks.

We assumed that total catch for all fisheries was median-unbiased and that the coefficient of variation (CV = SD/mean) of the catches was constant for each fishery (i.e., we assumed lognormal errors). We set the CV for the commercial fishery by assuming that recorded yield was accurate to within approximately 10% in Illinois and 20% in Wisconsin 95% of the time. The CV for the recreational fishery was set to approximately 10% based on estimates of the CV from the Wisconsin recreational fishery during 1998–2001 (Wisconsin Department of Natural Resources [WDNR], unpublished data). Independent estimates for the CV of the Illinois recreational fishery were not available. The CVs of survey CPEs and effective sample sizes of the age and length compositions of the surveys and of the recreational and commercial fisheries were estimated by an iterative approach, in which we adjusted the assumed initial CVs and effective sample sizes of the objective function components to match the residual variance (McAllister and Ianelli 1997). Effective sample sizes for survey age composition determined by otoliths or anal fin spines were weighted five times higher than those determined by scales because scale-aging is thought to be less accurate than the other methods for aging yellow perch (Robillard and Marsden 1996; Baker and McComish 1998; WDNR, unpublished data). For the Illinois model, we set the CVs of the random walk deviations for commercial and recreational catchability to about 25%. For the Wisconsin model, we used the same CV for recreational fishery catchability but a higher CV of about 40% for commercial catchability because, given the potential for large amounts of unreported catch, we thought the commercial effort data were less accurate for Wisconsin than for Illinois. For the Wisconsin model, we set the CVs to about 5% for the random walk deviations for the L_∞ and K parameters of the growth model because mean length at age of the older age groups rarely changed rapidly from year to year. In contrast, we set the CV of the random walk deviations for mean length at age 2 to 10% because mean length at age 2 showed more variation from year to year than did older ages. Using the same CV values for L_∞ and K in the Illinois model as in the Wisconsin model resulted in poor convergence. Therefore, we set the CVs for L_∞ and K to about 2.5% to further constrain the growth model for Illinois, but the CV for deviations in mean length at age 2 was the same as in the Wisconsin model.

Sensitivity analyses.—We performed sensitivity analyses to determine the effects of some of our assumptions on the results of the analysis. To test the sensitivity of the model estimates to the weighting factors for each data source, we increased and decreased the weighting factors for each data source fivefold and refitted the models. We also tested the sensitivity of our estimates to our assumed value of M by increasing and decreasing M by 20% and refitting our models. We then evaluated the sensitivity of the model estimates to these changes by comparing model estimates of abundance, biomass, and mean fishing mortality rates for females and males at ages 4 and older in 2002 with those obtained with the baseline weighting factors and natural mortality rate. Also, because of large suspected amounts of unreported commercial harvest in Wisconsin during 1989–1992, we tested the effects of three amounts (one to three times the reported amount) of commercial harvest during those years on our results.

Data.—Commercial yield and effort were estimated from mandatory bimonthly reports submitted by commercial fishermen. In some cases, these reports were validated by law enforcement officials, but underreporting may have been a large problem, especially in Wisconsin. The exact magnitude of underreporting is unknown, but during 1990–1992 the commercial yield in Wisconsin was underreported by at least 44%, as documented by law enforcement officials during a multiyear sting operation (WDNR, unpublished data). Two commercial fishermen indicted for unreported harvest testified that unreported harvest was two to three times the reported harvest. Because Wisconsin first implemented a commercial quota for yellow perch in the summer of 1989, there had been less incen-

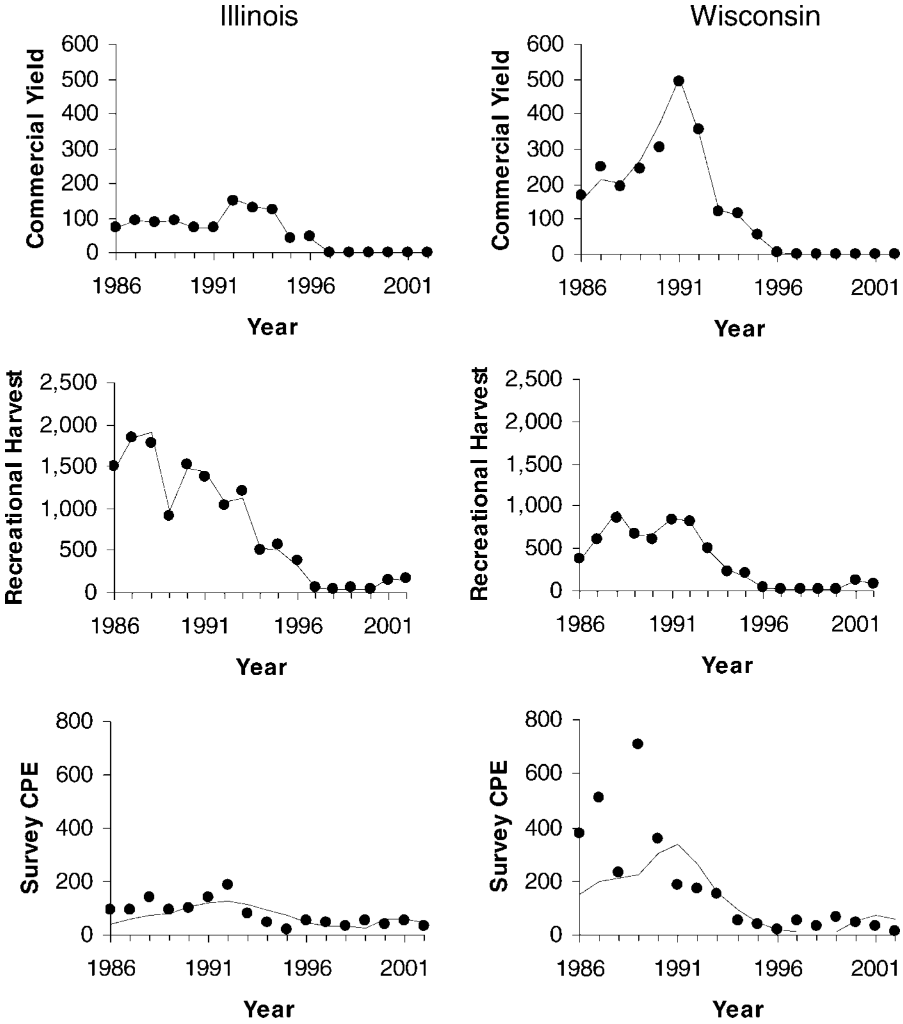

FIGURE 2.—Model fits to commercial yield (1,000 kg), recreational harvest (in thousands), and survey catch per effort (CPE; number per 30.5 m) in Illinois and Wisconsin waters of southwestern Lake Michigan during 1986–2002. Model predictions are represented by solid lines, observed values by dots.

tive for commercial fishermen to underreport before then. For observed commercial yield in Wisconsin during 1989–1992, we added the reported commercial yield and the verified illegal yield and multiplied the sum by two. In Illinois, unreported commercial harvest was thought to be relatively low (Illinois Department of Natural Resources [IDNR], unpublished data). Length-frequency estimates of the commercial catch were collected by dockside monitoring. Sampling did not occur for most lifts.

Creel surveys were conducted by the WDNR and the IDNR to estimate recreational fishery harvest, effort, and composition of the harvest (details in Austen et al. 1995). Creel clerks visited access points and interviewed anglers to determine target species and angler effort. Anglers' catches were examined for species composition and length frequency.

Graded-mesh gill-net surveys were conducted in Wisconsin (2.54–7.62-cm stretch-measure with 0.64-cm increments) in the winter and in Illinois (2.54–8.89-cm stretch-measure with 1.27-cm increments) in June of each year to obtain fishery-independent data on relative abundance. Nets were set overnight in the same locations each year at multiple depths. CPE was measured as the number of yellow perch per 30.5-m gill net.

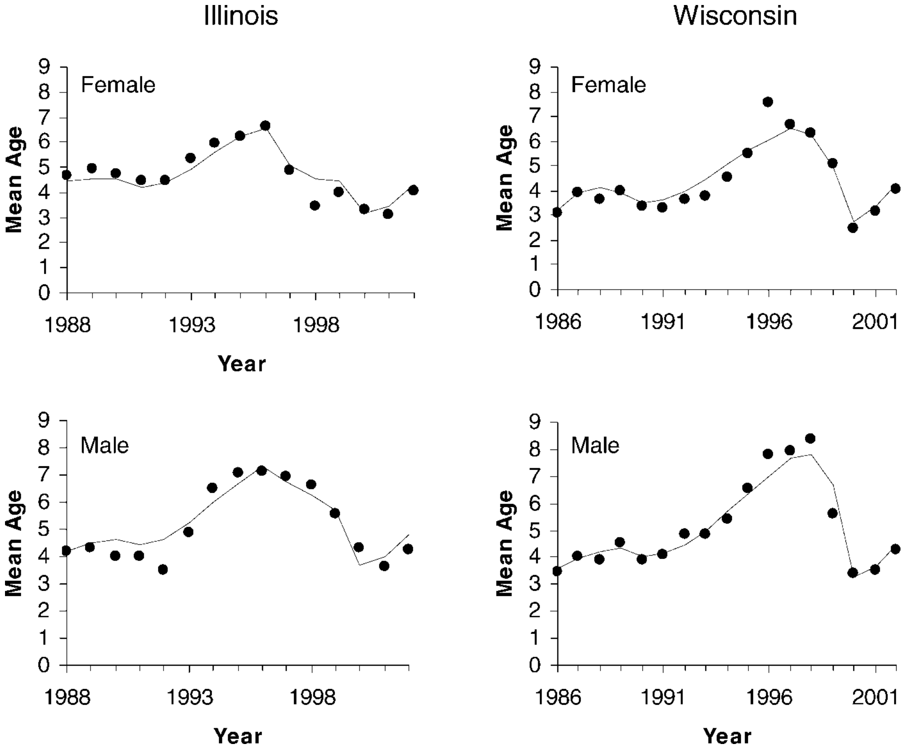

FIGURE 3.—Mean age of yellow perch caught in gill-net surveys in Illinois and Wisconsin waters of southwestern Lake Michigan during 1986–2002. Lines represent model predictions and dots represent observed values.

The length of each fish was measured, and the age composition of the catch was estimated by estimating ages for a randomly chosen subsample and applying the subsequent age–length key to the length frequency. Ages were estimated by counting the annuli on scales during 1986–1999 in Wisconsin and during 1986–1993 in Illinois. However, because this method was found to be fairly unreliable (Robillard and Marsden 1996; Baker and McComish 1998; WDNR, unpublished data), Illinois estimated ages of fish by counting annuli in otoliths during 1994–2002, and Wisconsin estimated ages of fish by counting the annuli in anal fin spines during 2000–2002. Ages estimated by different readers of spines and otoliths agreed 86% of the time (WDNR, unpublished data).

Results

Model Fits

Most of our data sources contained relatively large amounts of contrast and our models produced reasonable fits to all data sources. Fishery and survey catch was relatively high in the beginning of our time series and decreased to low levels during the mid-1990s. Our models predicted observed commercial yield and recreational harvest within 5% of observed values in most years (Figure 2). For total survey CPE, our models produced the same declining trend as the observed total survey CPE but predicted survey CPE lower than observed values in most years before 1991 (Figure 2). This may reflect decreases in survey catchability caused by increases in water clarity since the colonization of Lake Michigan by zebra mussels *Dreissena polymorpha.* Relative differences between observed and predicted survey CPE tended to be larger than fishery catch residuals (especially for the Wisconsin survey); this result is not surprising given that CVs for the survey CPE were relatively high and were higher for the Wisconsin survey than for the Illinois survey. Mean age in the survey was relatively stable during 1986–1992, increased during 1992–1997, and decreased thereafter (Figure 3). Deviations between model predictions and observations of mean age in the survey were usually less than 15%. Mean length in the recreational fishery and surveys increased during 1986–2002 but did not show a trend

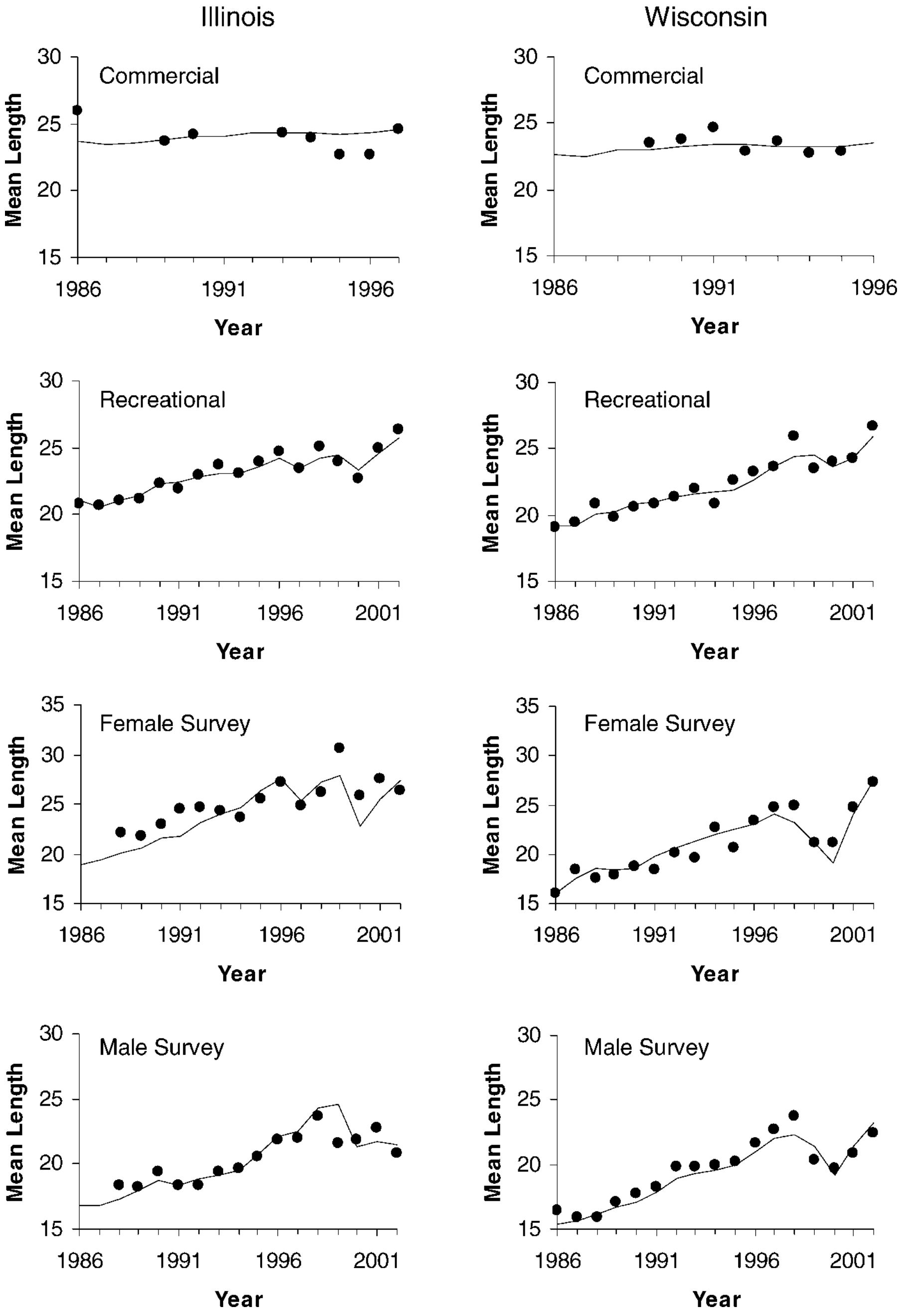

FIGURE 4.—Mean length of yellow perch caught in the commercial and recreational fisheries and gill-net surveys in Illinois and Wisconsin waters of southwestern Lake Michigan during 1986–2002. Lines represent model predictions and dots represent observed values.

for commercial fisheries (Figure 4). Predicted mean length was usually within 10% of the observed value for the commercial fishery and surveys and within 5% of observed values for the recreational fishery (Figure 4). Predicted mean length of females in the Illinois survey during 1986–1992 was lower than observed values, possibly because the survey mainly targets mature fish; after 1990, the proportion of immature females in the population was smaller.

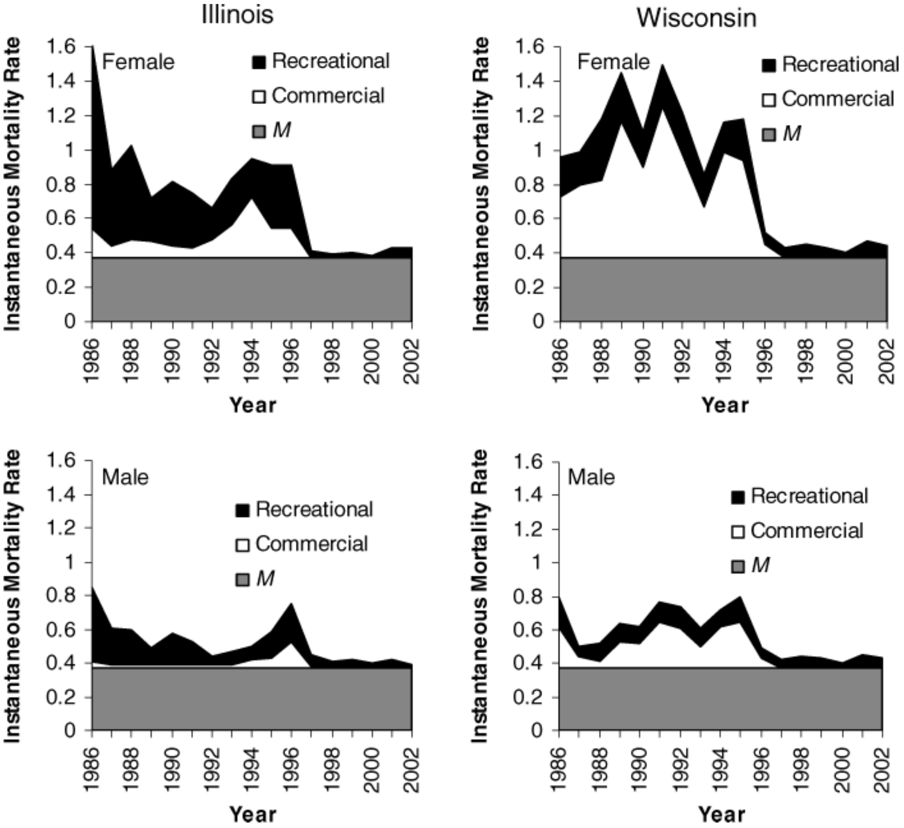

FIGURE 5.—Model estimates of average instantaneous mortality rates for yellow perch age 4 and older in Illinois and Wisconsin waters of southwestern Lake Michigan during 1986–2002; the symbol *M* stands for natural mortality.

Model Estimates

Model estimates of mortality rates were generally higher for females than males and were higher during the mid-1980s through the mid-1990s than in the late 1990s and after (Figure 5). In Wisconsin, the commercial fishery was the predominant source of fishing mortality until the commercial fishery was closed; in Illinois, the recreational fishery was the predominant source of fishing mortality. Estimated instantaneous fishing mortality rates for females age 4 and older exceeded 1.0 in most modeled years before 1996 in Wisconsin waters and averaged 1.16, which corresponds to an annual mortality rate of about 69%. In Illinois, estimated fishing mortality rates were not as high as in Wisconsin, although total mortality rates averaged about 0.92 (annual mortality rate of about 60%) for females age 4 and older during 1986–1997. In Wisconsin during 1986–1996, instantaneous total mortality rates for males age 4 and older averaged 0.67 (annual mortality rate of about 49%), and in Illinois during 1986–1997, instantaneous total mortality rates for this group of males averaged 0.57 (annual mortality rate of about 44%). Until severe restrictions were placed on commercial and recreational fisheries (1996–1997), fishing was the predominant source of mortality for female yellow perch age 4 and older in Wisconsin and Illinois. After the fisheries were considerably restricted—in 1996 in Wisconsin and 1997 in Illinois—fishing mortality rates declined substantially and natural mortality became the predominant source of mortality.

Model estimates of recruitment in Illinois and Wisconsin showed similar patterns, recruitment being generally higher in Illinois than in Wisconsin (Table 1; Figure 6). Recruitment was relatively high during 1984–1989 and was substantially lower than 1980s levels thereafter, except for the 1998 year-class. The largest year-class during the 1980s was in 1988 and the largest year-class during the 1990s was in 1998. Model estimates of average recruitment of the 1984–1989 year-classes were 13 times higher in Illinois and 23 times higher in

TABLE 1.—Model estimates of yellow perch abundance at age (in thousands) during 1986–2002 in Illinois and Wisconsin waters of southwestern Lake Michigan.

	Age							
Year	2	3	4	5	6	7	8	9+
Illinois								
1986	9,674	11,417	2,082	769	284	105	39	14
1987	9,598	6,682	7,518	862	146	33	10	4
1988	6,807	6,629	4,518	3,715	247	32	6	2
1989	7,255	4,701	4,457	2,567	1,245	67	8	2
1990	17,535	5,011	3,180	2,759	1,370	545	30	4
1991	5,432	12,110	3,322	1,837	1,383	633	231	15
1992	2,521	3,726	8,070	1,949	969	694	311	116
1993	444	1,718	2,401	4,930	1,090	526	371	224
1994	22	302	1,070	1,370	2,691	573	270	295
1995	190	15	188	598	727	1,434	298	284
1996	325	127	9	102	310	378	747	292
1997	1,153	216	70	4	48	144	175	476
1998	130	787	143	45	3	31	93	420
1999	879	89	529	96	30	2	21	342
2000	8,911	599	59	349	63	20	1	240
2001	38	6,144	404	40	235	43	14	163
2002	38	26	4,139	265	26	153	28	115
Wisconsin								
1986	5,863	11,702	1,490	300	101	40	16	6
1987	5,083	4,050	7,922	741	106	21	5	2
1988	8,757	3,510	2,776	4,246	195	20	2	0
1989	8,438	6,045	2,353	1,676	1,718	71	5	0
1990	11,935	5,826	3,994	1,250	694	578	19	1
1991	5,221	8,230	3,786	2,020	530	287	204	6
1992	1,237	3,603	4,964	1,665	682	161	78	47
1993	310	853	2,315	2,227	627	225	48	34
1994	102	214	572	1,327	1,043	285	96	33
1995	83	71	144	336	579	408	108	44
1996	60	57	49	85	158	231	153	53
1997	289	42	39	33	54	96	139	122
1998	128	200	29	27	22	35	63	170
1999	373	88	138	20	18	14	22	147
2000	3,115	258	61	93	13	11	9	107
2001	29	2,147	175	41	62	9	8	77
2002	29	20	1,405	111	26	39	5	53

Wisconsin than the estimated average recruitment of the 1990–1997 year-classes. Recruitment was not strongly related to stock size; yellow perch produced weak year-classes across a wide range of stock size (Figure 6).

Estimated abundance of yellow perch in Wisconsin waters of southwestern Lake Michigan increased from 1986 to 1990 and then decreased from 1991 to 2002 except for a small increase in 2000 (Figure 7). Estimated abundance of yellow perch in Illinois waters declined from 1986 to 2002, except during 1990 and 2000. In 2002, yellow perch abundance was approximately 8% of 1986 abundance in Wisconsin and approximately 20% of 1986 abundance in Illinois. Model estimates of relatively high abundance throughout the 1980s resulted from high estimated recruitment during that period. Abundance decreased drastically during the 1990s because recruitment declined and fishing mortality rates were relatively high.

Changes in estimated biomass were smaller than changes in abundance; estimated biomass in 2002 was approximately 74% of 1986 biomass in Wisconsin and 123% of 1986 biomass in Illinois (Figure 6). Estimated biomass showed somewhat different trends over time than abundance because the age structure of the population changed and growth rates increased. In 1986, the population was composed of mostly age-2 and −3 yellow perch. In 2002, the majority of the population was age 4 and substantially larger at a given age because of their faster growth.

Patterns of estimated SSB were similar to patterns of biomass (Figure 6). Model estimates of SSB increased during 1986–1992 in Illinois and

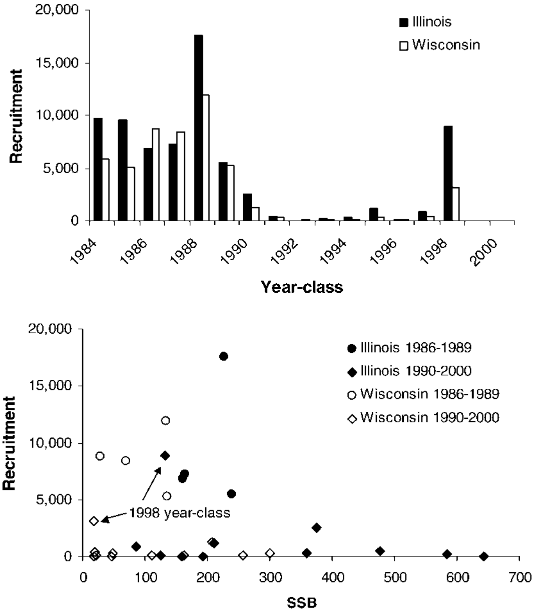

FIGURE 6.—Model estimates of yellow perch recruitment (in thousands) in Illinois and Wisconsin waters of southwestern Lake Michigan for the 1984–2000 year-classes (upper panel) and estimates of recruitment plotted against yellow perch spawning stock biomass (SSB; in 1,000-kg increments; lower panel).

during 1986–1991 in Wisconsin, and decreased until the late 1990s. Estimated SSB increased greatly during 1997–2002 in Illinois and during 1999–2002 in Wisconsin. In 2002, SSB was at its highest level since the early 1990s, being 346% and 854% of 1986 levels in Illinois and Wisconsin, respectively. The large increase in SSB during 1999–2002 was attributable to the relatively good recruitment of the 1998 year-class, low fishing mortality rates, and rapid growth and maturity of females. We estimated that spawning stock biomass per recruit (SSB/R) was approximately 0.46 kg in Wisconsin and 0.44 kg in Illinois in 2002. Comparing these SSB/R values with those in scenarios with no fishing mortality, we estimated that 2002 SSB/R was approximately 84% of the unexploited scenario in Wisconsin and 87% of the unexploited scenario in Illinois. In contrast, SSB/R during 1986–1995 was approximately 0.03 kg (18% of the unexploited scenario) in Wisconsin and 0.06 kg (33% of the unexploited scenario) in Illinois. These dramatic differences in SSB/R occurred because fishing mortality rates were much lower during 2002 than during 1986–1995 and because yellow perch were growing faster, and therefore maturing at younger ages, during 2002 than during 1986–1995.

Females grew faster and to larger sizes than males (Figure 8); the mean lengths at age of females at all ages older than age 2 were higher than for males of the same age. Estimated mean length at age remained relatively stable during 1986–1994 and increased substantially during 1994–2000. During 2000–2002, mean length at age decreased slightly but was still higher than during the 1980s and early 1990s. In Wisconsin, yellow perch were generally smaller at a given age than in Illinois.

Selectivity patterns of the recreational fisheries in Wisconsin and Illinois were quite similar to one another when no length-based regulations were in effect (Figure 9). Commercial selectivity patterns were also similar. This latter result was not surprising because the scarcity of biological data for the Illinois commercial catch had led us to assume an informative prior for the selectivity parameters, based on the results of the Wisconsin assessment (see Appendix A). Given the differences in selectivity of commercial and recreational fisheries, yellow perch recruited to the recreational fishery at smaller sizes than to the commercial fishery. Selectivity of the Illinois recreational fishery changed substantially when a slot size limit was implemented during 1997–2000. In Illinois during 1997–2000, average mortality rates for males age 4 and older were slightly higher than for females, reflecting the selectivity pattern of the recreational fishery. Selectivity patterns in the survey were substantially different between Illinois and Wisconsin. Differences in selectivity patterns are probably attributable to differences in the surveys such as mesh sizes of assessment gill nets and time of year of the survey.

Sensitivity Analyses

The models were somewhat sensitive to changes in the assumed CVs and effective sample sizes for the different data sources (Table 2). The Illinois model was slightly less sensitive to these assumptions than the Wisconsin model was. In general, fivefold changes in the weights for each data source usually resulted in less than 15% changes in mean fishing mortality rates, abundance, and biomass. Weights that resulted in increased estimates of mean fishing mortality rates usually resulted in decreased estimates of abundance and biomass. The Illinois model was most sensitive to changes in the CV and effective sample sizes as-

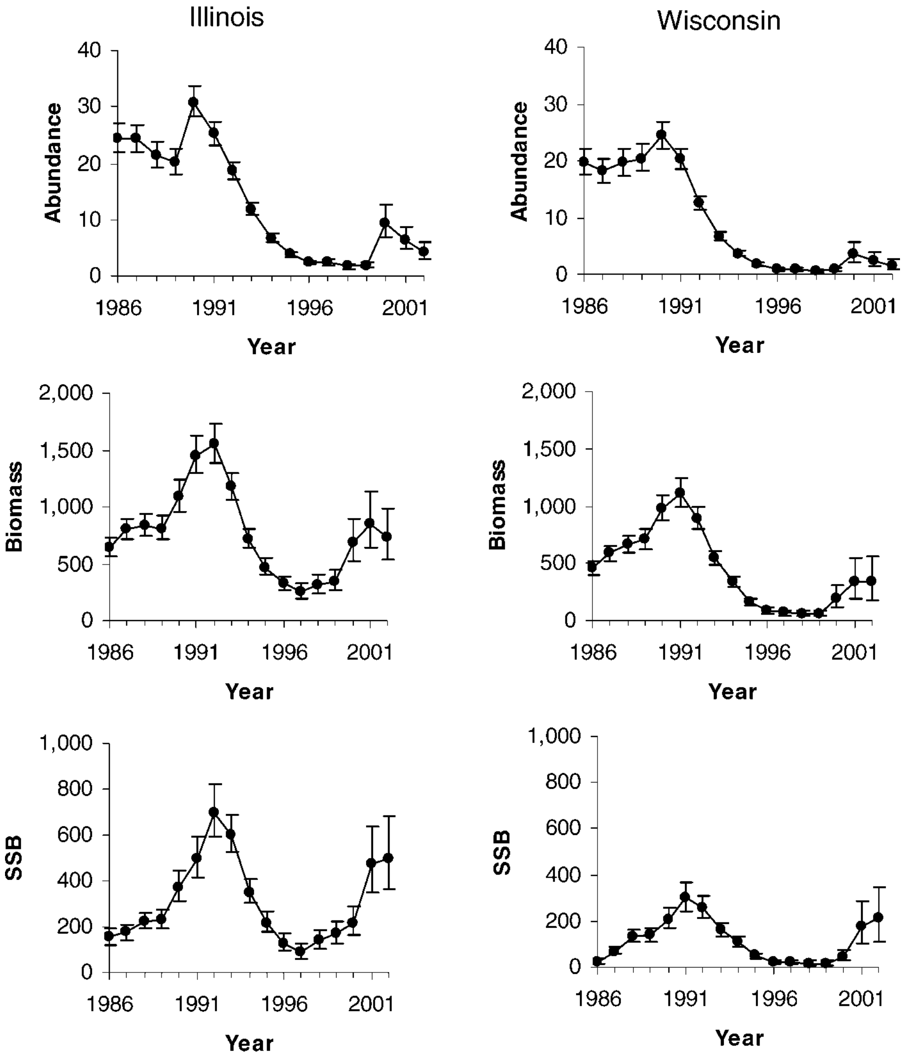

FIGURE 7.—Estimated abundance (in thousands), biomass (1,000 kg), and spawning stock biomass (SSB; 1,000 kg) of age-2 and older yellow perch in Illinois and Wisconsin waters of southern Lake Michigan during 1986–2002. Error bars represent 95% probability intervals (the Bayesian analog of confidence intervals).

sociated with females caught in the survey and to the effective sample size of the length composition from the recreational fishery. The Wisconsin model was most sensitive to CV and effective sample size associated with males caught in the survey and to the CV for catchability of the commercial fishery. Increasing *M* by 20% resulted in higher model estimates of average fishing mortality rates and lower estimates of abundance and biomass. The Illinois model was less sensitive to our assumed value of *M* than was the Wisconsin model; Illinois model estimates changed by approximately 12% and Wisconsin model estimates by approximately 47%.

The Wisconsin model estimates of abundance, biomass, and mean fishing mortality rates were also somewhat sensitive to the different levels of commercial harvest (Table 3). When we fit the model using only reported yield, the model estimates of abundance and biomass in 2002 were more than 20% below the baseline (2× what was reported during 1989–1992) scenario, and estimates of mean fishing mortality rates were about 27% higher than the baseline estimates. Under the 3× reported yield scenario, abundance and biomass were about 20% greater than the baseline scenario, but mean fishing mortality rates were about 17% lower than the baseline.

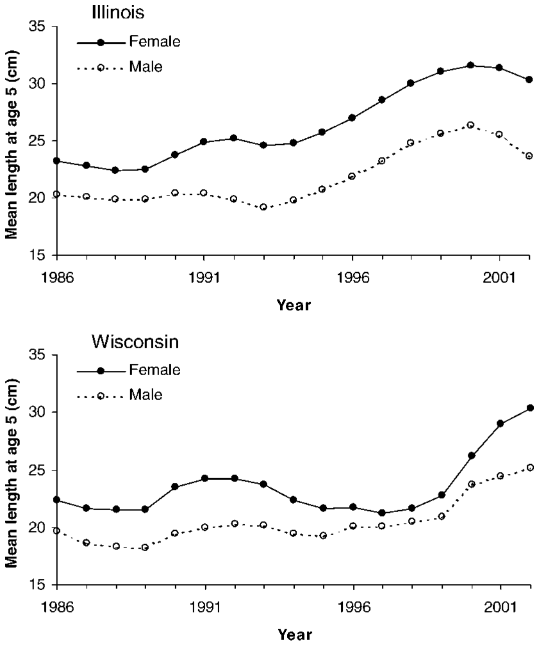

FIGURE 8.—Model estimates of yellow perch mean length at age 5 in Illinois and Wisconsin waters of southwestern Lake Michigan during 1986–2002.

Discussion

The decline in abundance of yellow perch in southwestern Lake Michigan during the 1990s was probably caused by a combination of recruitment failure and relatively high fishing mortality rates, and our results are consistent with other authors' descriptions of this decline. During 1989–1994, yellow perch larvae were abundant shortly after hatching, but recruitment to age 0 in the fall was poor, which led some researchers to propose that at least the initial decline in recruitment was not due to fishing (Francis et al. 1996; Robillard et al. 1999; Marsden and Robillard 2004). Our results also indicated that several successive year-classes failed despite relatively high SSB. However, after 1994, the relative abundance of yellow perch larvae was less than 10% of the relative abundance during the early 1990s, which may indicate that SSB had decreased to low enough levels to limit recruitment (Francis et al. 1996; Marsden and Robillard 2004). We estimated that between 1991 and 1996 yellow perch SSB in Wisconsin declined by almost 94% and between 1992 and 1997 yellow perch SSB in Illinois declined by almost 90%. The resulting low SSB may have prolonged the period of poor reproduction.

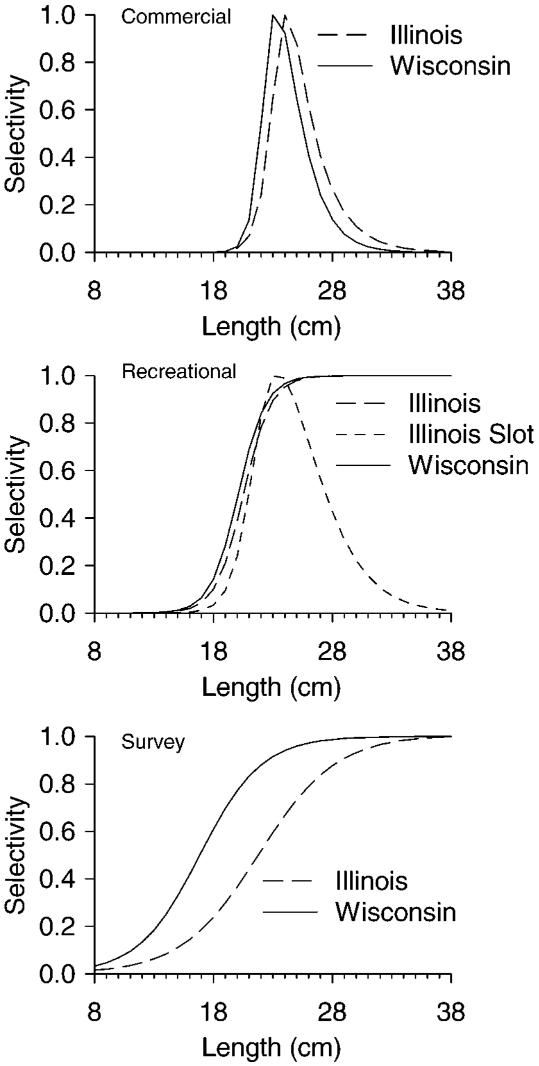

FIGURE 9.—Model estimates of selectivity of the commercial fishery, recreational fishery, and survey in Illinois and Wisconsin during 1986–2002.

The decline of yellow perch SSB in southern Lake Michigan would probably not have occurred at such a rapid pace if fishing mortality rates had been lower. We projected dynamics for 1986–1996, using our estimated recruitment time series and age-based selectivity estimates while changing the overall level of *F*. Our projections indicated that SSB in 1996 would have been more than five times higher than our model estimates in Wisconsin and nearly twice as high estimated in Illinois if fishing mortality rates for fully selected ages and sexes had been equal to the natural mortality rate (0.37) during 1986–1997. Although our simple projections do not account for compensatory

TABLE 2.—Results of sensitivity analyses of changes of weights of data sources in the objective function for yellow perch catch-at-age models for Illinois and Wisconsin waters of southwestern Lake Michigan. Differences from baseline estimates are displayed as percentages. Baseline model estimates of abundance (N; 1,000s), biomass (B; 1,000 kg), mean fishing mortality for females age 4 and older ($\bar{F}_{4+}$ females), and mean fishing mortality for males age 4 and older ($\bar{F}_{4+}$ males) for 2002 are displayed for comparison. Variables L_∞ and K are the asymptotic length and growth coefficient from the von Bertalanffy growth model; M is natural mortality. In two cases the model's parameter estimates failed to converge to values that minimized the objective function; these are denoted by NC.

Variable	Baseline value	Adjustment factors	N	B	$\bar{F}_{4+}$	
					Females	Males
Illinois						
Baseline			4,790	818	0.058	0.025
Commercial yield	0.0025	5	−3.1	−3.1	3.3	3.2
	0.0025	0.2	0.7	0.7	−0.8	−0.7
Commercial catchability	0.06	5	−16.1	−16.6	12.8	5.8
	0.06	0.2	41.7	43.1	−30.5	−28.7
Commercial length	32	5	−10.2	−10.9	12.8	5.8
	32	0.2	−2.0	−0.7	0.4	5.0
Recreational harvest	0.01	5	2.3	2.0	−5.4	−6.7
	0.01	0.2	−0.7	−0.6	3.4	4.1
Recreational catchability	0.06	5	3.5	2.9	−0.5	−2.7
	0.06	0.2	−7.6	−6.2	3.4	9.5
Recreational length	367	5	−24.1	−24.4	34.1	7.6
	367	0.2	17.6	11.5	−15.1	−12.1
Survey CPE, females	0.19	5	30.7	29.3	−22.8	−25.8
	0.19	0.2	−32.6	−31.0	45.8	53.0
Survey female ages	27	5	17.2	11.0	−8.3	−30.7
	27	0.2	−10.1	−7.2	7.2	20.5
Survey female lengths	61	5	25.1	17.0	−20.4	−24.8
	61	0.2	−21.8	−17.1	23.2	40.1
Survey CPE, males	0.22	5	4.3	4.2	−4.0	−4.5
	0.22	0.2	−5.5	−5.3	5.4	6.4
Survey male ages	53	5	−9.7	−6.8	7.3	21.5
	53	0.2	−8.9	−5.9	6.2	14.0
Survey male lengths	58	5	−4.9	2.7	−2.8	15.3
	58	0.2	−17.0	−13.9	16.5	30.5
Female L_∞	0.0006	5	3.2	2.1	−3.8	−2.8
	0.0006	0.2	−0.5	−0.1	2.7	−1.9
Female K	0.0006	5	5.3	4.5	−4.4	−6.4
	0.0006	0.2	−1.4	−1.2	1.8	0.9
Male L_∞	0.0006	5	−2.9	−4.7	5.4	−8.6
	0.0006	0.2	−19.1	−15.2	19.6	37.8
Male K	0.0006	5	0.0	−0.9	1.0	−1.8
	0.0006	0.2	−0.2	0.2	−0.2	0.5
Length at age 2	0.01	5	−3.2	−3.1	3.2	5.0
	0.01	0.2	6.1	5.7	−5.4	−7.4
M	0.37	1.2	−9.3	−11.5	17.2	6.6
	0.37	0.8	12.8	16.3	−15.8	−9.3
Wisconsin						
Baseline			1,690	356	0.075	0.060
Commercial yield	0.0125	5	−3.7	−3.8	4.2	3.8
	0.0125	0.2	3.9	4.0	−4.0	−3.8
Commercial catchability	0.16	5	25.8	25.2	−20.3	−21.2
	0.16	0.2	−22.8	−22.1	28.2	31.4
Commercial length	43	5	−7.9	−7.7	8.3	9.0
	43	0.2	5.8	2.4	−0.8	−8.3
Recreational harvest	0.01	5	4.0	3.7	6.0	5.5
	0.01	0.2	−2.0	−1.9	0.6	0.7
Recreational catchability	0.06	5	6.6	6.3	−7.8	−8.2
	0.06	0.2	−16.1	−15.4	27.1	28.7
Recreational length	141	5	−1.4	3.2	−3.3	5.7
	141	0.2	−7.7	−8.5	9.4	7.8
Survey CPE, females	1.06	5	4.0	3.8	−3.8	−3.9
	1.06	0.2	−4.2	−3.8	4.0	4.6
Survey female ages	31	5	13.6	10.7	−10.0	−7.9
	31	0.2	−17.9	−17.2	21.8	20.1
Survey female lengths	45	5	NC	NC	NC	NC

TABLE 2.—Continued.

	45	0.2	0.2	−0.1	0.6	−0.1
Survey CPE, males	0.92	5	25.0	24.6	−20.1	−20.6
	0.92	0.2	−41.3	−40.9	72.0	74.1
Survey male ages	50	5	NC	NC	NC	NC
	50	0.2	−33.3	−33.3	50.6	52.5
Survey male lengths	63	5	20.0	14.4	−11.9	−19.6
	63	0.2	6.6	8.9	−8.4	−5.3
Female L_∞	0.0025	5	−1.2	−1.0	0.2	1.5
	0.0025	0.2	−0.4	−1.0	1.5	0.1
Female K	0.0025	5	−1.3	−2.5	0.9	1.7
	0.0025	0.2	−0.4	0.3	0.6	0.2
Male L_∞	0.0025	5	13.7	13.0	−11.8	−13.1
	0.0025	0.2	−18.7	−18.3	23.2	24.8
Male K	0.0025	5	−2.1	−2.0	2.0	2.0
	0.0025	0.2	1.9	1.8	−1.7	−1.9
Length at age 2	0.01	5	0.7	0.3	−1.2	0.0
	0.01	0.2	−5.7	−5.6	7.4	6.0
M	0.37	1.2	−34.3	−35.0	59.0	58.3
	0.37	0.8	49.4	50.8	−36.1	−35.5

changes that might have occurred if fishing mortality had been lower, we believe they do illustrate that high fishing mortality rates for adult females were a substantial contributor to the rapid decline in SSB that occurred. An alternative hypothesis to the effect of fishing on the dynamics of the yellow perch population is that natural mortality decreased concurrently with restrictions on the fisheries. In a supplemental analysis (detailed results not reported), we explored this possibility by adding one more estimated parameter to each model such that natural mortality changed from one level for the 1986–1996 period to another for 1997 and after. The estimated changes in M were opposite in sign for the Wisconsin and Illinois models and were much less than the estimated changes in fishing mortality for these periods.

The declines of yellow perch abundance in southern Lake Michigan were similar in the 1960s and 1990s, and recruitment failures of several successive year-classes may be probable in the future. In the early 1960s, yellow perch suffered a recruitment failure (Wells 1977) similar to the recruitment failure observed in the early 1990s (Robillard et al. 1999; Marsden and Robillard 2004). The recruitment failure in the 1960s was preceded by an increase in abundance during the late 1950s (Wells 1977), which was similar to the increase in abundance during the late 1980s (Francis et al. 1996). Adult abundance had decreased rapidly by the mid-1960s because of intense fishery activities (Wells 1977). Yellow perch growth in size was slow during the 1950s (Wells 1977) and the 1980s (Marsden and Robillard 2004). Extremely high fishery catches preceded both declines in abundance. However, the Lake Michigan community had two major differences regarding exotic species in these periods: Alewife abundance in Lake Michigan was extremely high during the 1960s but relatively low in the 1980s and 1990s, and zebra mussels were absent from Lake Michigan in the 1960s but abundant in the 1990s (Madenjian et al. 2002). Because the reproduction failure in the 1960s was associated with extremely high levels of alewife abundance, the decline in recruitment was blamed on alewives (Eck and Wells 1987). Schroyer and McComish (2000) found a negative correlation between alewife abundance and yellow perch recruitment in Indiana waters of Lake Michigan during 1988–1997, but little direct evidence of alewives preying on yellow perch larvae has been observed in southern Lake Michigan (Dettmers et al. 2003). Also, alewife abundance during the 1990s was substantially lower (perhaps more than 20 times lower) than during the mid-1960s (Madenjian et al. 2002), the period when alewife interference with yellow perch recruitment was originally proposed as a cause for yellow perch reproduction failure. Marsden and Robillard (2004) suggested that declines

TABLE 3.—Model estimates of abundance (N; 1,000s), biomass (B; 1,000 kg), mean rate of fishing mortality for females age 4 and older ($\bar{F}_{4+}$ females), and mean rate of fishing mortality for males age 4 and older ($\bar{F}_{4+}$ males) for 2002 under three scenarios of unreported commercial harvest in Wisconsin waters of southwestern Lake Michigan during 1989–1992.

Scenario	N	B	$\bar{F}_{4+}$ females	$\bar{F}_{4+}$ males
Reported	1,331	280	0.095	0.077
2 × Reported	1,690	356	0.075	0.060
3 × Reported	2,020	427	0.062	0.050

in yellow perch recruitment may be exacerbated by changes in the ecosystem caused by zebra mussel colonization, and Janssen and Leubke (2004) found that poor recruitment was correlated with the presence of zebra mussels in Indiana waters of Lake Michigan. Indeed, zebra mussels can alter the composition of the zooplankton community (MacIsaac et al. 1992), which may decrease food supplies for larval yellow perch. However, yellow perch recruitment did not collapse after invasion of zebra mussels in Oneida Lake (Mayer et al. 2000) or the western basin of Lake Erie (Tyson and Knight 2001).

Several reference points suggest that yellow perch experienced overfishing in southwestern Lake Michigan during 1986–1996. Beverton (1998) recommended using the F_{95} reference point (F at which yield is 95% of maximum sustainable yield) to manage fisheries sustainably. A rough estimate of F_{95} is usually near the M value for medium-lived species (Beverton 1998), which would be approximately 0.37 for yellow perch in southern Lake Michigan. Others have argued that M should be an upper bound on the fishing mortality rates that maximize yield (Deriso 1982; Quinn and Deriso 1999). Fishing mortality rates for adult females were well above M in Illinois (1–2 times M) and Wisconsin (2–4 times M). A number of U.S. marine commercial fisheries are managed so as to keep fishing mortality below levels that would reduce SSB/R below a set percentage of the unfished situation ($F_{X\%}$); typical percentages have been in the 35% to 45% range (Quinn and Deriso 1999). In Wisconsin and Illinois, F was higher than $F_{35\%}$ during 1986–1996.

Regulation changes probably helped reduce fishing mortality rates substantially. In 1996 in Wisconsin, the commercial quota was set to zero and a daily bag limit of five yellow perch per angler was implemented for recreational fishery (reduced from 50 to 25 in 1995). When these policies were introduced, fishing mortality decreased noticeably. Recreational effort decreased, but this may not have been a direct consequence of the implemented bag limit. When stricter bag limits were implemented in some inland Wisconsin lakes for walleyes, anglers preferred to fish in lakes that had less restrictive bag limits (Beard et al. 2003). In Illinois in 1995, the recreational daily bag limit was reduced from no limit to 25 yellow perch per angler. In 1997, the commercial quota was reduced to zero, and a daily bag limit of 15 yellow perch per angler and a slot size limit of 8–10 in (fish within this range could be kept) were implemented for the recreational fishery. Mortality rates also declined substantially in Illinois, as they did in Wisconsin; commercial effort was reduced to zero, and recreational fishing effort also decreased noticeably. In addition, the slot size limit caused the recreational fishery selectivity to change so that average fishing mortality rates were higher for age-4 and older males than for age-4 and older females.

We did not incorporate age-estimation error into our model, and this may bias our estimates of recruitment and mortality rates. Our results probably underestimate the amount of variability in recruitment because age-estimation error tends to blend strong and weak year-classes together (Richards and Schnute 1998). Specifically, our estimates of recruitment of the 1989 and 1990 year-classes are probably high because of age-estimation error associated with the 1988 year-class. However, our estimates of recruitment are consistent with external estimates of year-class strength from age-0 assessments (Pientka et al. 2003). Our mortality rate estimates are most likely biased low for the beginning of the time series, when ages of yellow perch were estimated from scales. Younger yellow perch tended to be estimated as older when ages were estimated from scales (Robillard and Mardsen 1996; Baker and McComish 1998; WDNR, unpublished data), and the overrepresentation of older fish in the data is most likely interpreted by the model as an indication that older fish were more abundant. Annual mortality rates in the late 1970s in Indiana and Illinois were estimated to be about 70% for males age 3 and older and substantially higher for females age 3 and older (Wells and Jorgenson 1983). These mortality rate estimates are similar to our estimates for Wisconsin in the late 1980s and for Illinois in the mid-1980s.

Yellow perch growth may be density dependent and may also have increased as a result of zebra mussel colonization. Patterns of growth during 1986–1998 resembled growth during 1954–1979 for yellow perch in southern Lake Michigan. Yellow perch growth may have been density-dependent during 1986–2002 and 1954–1975 (Wells 1977). We found similar growth patterns in Wisconsin and Illinois; growth was relatively slow when yellow perch were at high abundance and fastest when they were present at low abundance. However, growth during 1999–2002 (low abundance) was the fastest observed for yellow perch in southern Lake Michigan during the past five decades. This increased growth coincided with substantial changes in yellow perch habitat that were attributable to colonization by zebra mussels.

Thayer et al. (1997) found increased adult yellow perch growth associated with zebra mussels in pond enclosures, and Tyson and Knight (2001) found increased growth of age-2 and age-3 yellow perch in the western basin of Lake Erie after zebra mussel colonization; these increases in growth were attributed to increased food availability. However, Mayer et al. (2000) found no increase in adult yellow perch growth associated with zebra mussel colonization in Oneida Lake.

Management Implications

Since 1998, recruitment has continued to be poor in southern Lake Michigan except for the 2002 year-class (Pientka et al. 2003; Clapp and Dettmers 2004; Fitzgerald et al. 2004). Success of the 1998 year-class has renewed pressure on the agencies to implement less restrictive regulations. Partially on the basis of development of the models described here, the Lake Michigan Yellow Perch Task Group recommended that regulations remain unchanged for the time being. The models we developed will continue to be used to monitor changes in the population and to advise managers.

Overexploitation of yellow perch has not previously been considered a likely hypothesis for the decline of yellow perch in southern Lake Michigan (Francis et al. 1996). However, we found that SSB had reached very low levels by the mid-1990s, the rapidity of the decline in SSB probably being compounded by intense fishing. Although exotic species or climatic changes may have affected recruitment, fishing mortality rates during the late 1980s and early 1990s probably were above levels that would be sustainable over the long term. Therefore, management of yellow perch in Lake Michigan should focus on limiting fishing mortality and be flexible to adjust to future recruitment failures. Despite poor recruitment, SSB has increased to its highest point since the early 1990s in Wisconsin and Illinois. This is partly a response to extensive management actions taken by Wisconsin and Illinois, which have reduced fishing mortality rates. However, relatively few year-classes are represented in the population, and future increases in biomass and SSB will depend on relatively strong recruitment of future cohorts to the adult population.

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Appendix: Detailed Description of Assessment Models

The population submodel predicted how yellow perch numbers at age and size at age changed over time, whereas the observation submodel predicted observed quantities on the basis of the predicted dynamics. The symbols used in the population and observation submodels are presented in Table A.1, and equations for these submodels are in Table A.2. We used the posterior likelihood to determine the best-fit parameters.

Population Submodel

Total recruitment (defined as the number of age-2 fish) at the start of each year was estimated as a free parameter, and the sex ratio at recruitment was assumed to be 1:1 (equation A.2.1). The numbers at ages 3 and 4 for each sex in the first year (1986) were also estimated as parameters. The numbers at ages 5–9+ in 1986 were calculated on the assumption that each of those cohorts had the same abundance at age 4 as was estimated for age 4 in 1986 and an estimated mortality rate that was either sex-specific (Wisconsin; equation A.2.2) or the same for both sexes (Illinois; equation A.2.3). We used this approach because sample sizes for fish age 5 and older were low and these cohorts were not observed for many subsequent years. For Illinois we used a common mortality parameter for both sexes because sexes were aggregated in the Illinois survey data for 1986–1988. These assumptions about number at age in the first year have a relatively small effect on model estimates because there were few old yellow perch in 1986.

The abundance at age of these cohorts was then tracked over time by applying age- and sex-specific mortality rates (equation A.2.10). Biomass was simply the product of the number of fish in a given length bin and their length-specific weight summed over sexes, ages, and lengths. The biomass of the spawning stock (SSB) was calculated only for females and utilized a time-invariant maturity schedule based on length, which we estimated by fitting a logistic function to maturity-at-length data from Indiana waters of Lake Michigan (Paul Allen, Ball State University, unpublished data) outside the model-fitting process.

The total mortality rate for a given age and sex was the sum of the natural mortality rate and the age-, sex-, and year-specific fishing mortality rates for the two fisheries—recreational and commercial (equation A.2.5). Fishing mortality rates at age for a sex were calculated as a weighted average of the length-specific fishing mortality rates, the weights being equal to the proportion of fish that were a given age, sex, and length (equation A.2.6).

The age-specific rates were calculated from length-specific ones. For each fishery, the fishing mortality rate for a given length bin of yellow perch for the commercial and recreational fisheries was the product of catchability, effort, and selectivity; the natural logarithm of catchability followed a random walk (equation A.2.7) and therefore was year specific for each fishery. We modeled selectivity as a constant function of length, based on the midpoint for each length bin. Note that the fishing process influences fish of the same length in the same way, irrespective of their sex or age. We used a double logistic function to model the dome-shaped selectivity pattern (Quinn and Deriso 1999) for the commercial gill-net fisheries (Kraft and Johnson 1992) and for the Illinois recreational fishery during 1997–2000, when a slot limit was in effect (equation A.2.8). For the Illinois and Wisconsin recreational fisheries (except for the Illinois fishery during 1997–2000), we modeled the selectivity pattern with an asymptotic logistic function (equation A.2.9).

Growth was modeled by using a stochastic von Bertalanffy growth model, in which the parameters were allowed to vary over time (Szalai et al. 2003). For 1986, mean length at age (for the beginning of the year) was calculated with the assumption that these fish had lived under constant growth conditions and that all cohorts started with the same mean length at age 2 as in 1986, experiencing constant pre-1986 values for asymptotic length and the growth coefficient (L_∞ and K; equation A.2.4). Mean length at age 2 was equal for males and females, but this changed over time with a random walk (equation A.2.14). For the years after 1986, mean length at ages 3–8 was equal to the mean from the previous age and year plus the increments from the von Bertalanffy model (equation A.2.11). The same model was used to estimate the mean length for the aggregated age-9-and-older group, but this was based on a weighted average of growth expected for age-8 and age-9 fish, the weights being determined by the contribution of the two ages to this group in the next year (equation A.2.12). To estimate mean length at age in the fall, fish were grown for 0.8 year (equation A.2.13). As with length at age 2, asymptotic mean length and the Brody growth coefficient also changed over time with a random walk (equation A.2.14), which were modeled separately for males and females. The modeled length composition for a given age was normally distributed with a mean predicted by the von Bertalanffy equation. The proportion in each 1-cm length bin was calculated from the corresponding standard normal cumulative distribution function (Φ; equation A.2.15). The standard deviation of each normal distribution was the product of the mean length at age and an age- and sex-specific coefficient of variation (CV). We used a hockey stick function to describe how the CV decreased with increasing age for ages 2 to 5 and then remained constant after age 5. This pattern of decreasing variation in length at age with increasing age is common to many teleost fishes (Bowker 1995), and the CVs we used were based on the observed variation of length at age (WDNR, unpublished data).

Observation Submodel

Catch at length (in numbers) for the commercial and recreational fisheries was calculated with the Baranov catch equation (equations A.2.16 and A.2.17). For the commercial catch calculations we used numbers at length calculated from numbers at age reassigned to length categories based on the fall distribution of length at age, whereas the recreational catch calculations were based on the length distributions of the fishes in spring. This approximation is intended to account for the facts that the two fisheries are operating at different times during the year (the commercial fishery being centered in the fall, the recreational fishery in the spring and summer), that fish grow during the year, and that fishery selectivity is length based. Total catch in numbers was simply the sum over length bins of catch at length. Commercial yield was calculated by multiplying catch at length by weight at length (from fall lengths) and summing over length categories.

Length- and sex-specific CPE were calculated as the product of catchability, selectivity, and numbers at length (equation A.2.18). The catchability of the survey was sex-specific in Illinois but the same for males and females in Wisconsin, reflecting differences in survey design between the two surveys. We modeled survey selectivity by using the same logistic function of length used for recreational fishery selectivity (equation A.2.9). Total CPE by sex for the survey was the sum over lengths of the length-specific survey CPEs. Catch per unit effort at age and sex for the survey was calculated as the product of survey catchability, numbers at age and sex, and the age- and sex-specific survey selectivity (given by a weighted sum of length-specific selectivity values; equation A.2.19). For each year, the proportions of the catch for the fisheries and the survey falling into each length bin and the proportions of the survey catch at each age were calculated for comparison with observed proportions.

The model predictions of mean length at age seen in the survey were calculated by taking the modeled population length distribution at age and adjusting it for the estimated survey selectivity (equation A.2.20).

Likelihood Equations

Our objective function was the posterior negative log-likelihood, $\Delta = \Sigma_i \ell_i$, with individual negative log-likelihood components and priors (dropping some ignored constants) given by ℓ_i. Our point estimates minimized this function. One set of components had the general form

$$\ell_i = \frac{1}{2}\sum_j X_j^2, \qquad \text{(A.1)}$$

where X_j is an assumed standard normal variate and j is an index distinguishing the terms being summed for the ith component. These likelihood components were based on an assumed independent normal (mean length at age) or lognormal distribution (fishery total catch or survey total CPE) for deviations between observed quantities and model predictions or an informative normal prior distribution for random walk errors (for mean length at age 2, L_∞, K, and catchability for the commercial and recreational fisheries) and for two parameters of the Illinois commercial fishery selectivity function (Table A.3). We used an informative prior for two of the four Illinois commercial fishery selectivity parameters because the observed length composition of the Illinois commercial catch contained relatively few measurements; we based these priors on the point estimates and standard errors of the same parameters from the Wisconsin model. Small constants were added to observed and predicted values (for the lognormal distributions) to reduce the influence of very small values (Hampton and Fournier 2001).

An additional set of components took the general form

$$\ell_i = -\sum_k n_k \sum_y \sum_T u_{T,k} \log_e(\hat{u}_{T,k} + c) \qquad \text{(A.2)}$$

based on our assumption that multinomial distributions led to the observed proportions at length and age for all data sources for which there were observations. This included a component for the fishery length compositions and components for the survey length and age compositions. The outer sum is over categories of data (k), which were fisheries 1 and 2 (for the fishery length compositions) and sexes (for survey age and length compositions), and the inner sum was over types (T) of fish within a category and year (length bins or ages). Small constants ($c = 0.0001$ for length compositions and $c = 0.001$ for age compositions) were added to the likelihood functions to reduce the effect of small proportions during model fitting (Fournier and Archibald 1982).

For completeness we note that for parameters other than those with the normal priors described above, we assumed uniformly distributed priors on the scale with which they were estimated. These priors did not enter explicitly into the objective function because they were implemented by placing bounds on the allowed parameter range during estimation.

TABLE A.1.—Symbols representing parameters, data, and calculated quantities for assessment models.

Parameter	Definition
	Indicator variables
a	Age-class (2–9+)
y	Year (1986–2001)
l	Midpoint of each length bin (8–38 cm)
G	Sex (male or female)
f	Fishery (commercial = 1, recreational = 2, survey = 3)
	Estimated parameters
R_y	Recruitment for each year
$N_{1986,a,G}$	Numbers at age in 1986 for ages 3 and 4
Z_{init_G}	Mortality rates for the final five age-classes in the first year
q_f	Catchability
λ_f	Parameters for logistic and double logistic selectivity functions
$L_{\infty y,G}$	Asymptotic length
$K_{y,G}$	Brody growth coefficient
$L_{y,2}$	Mean length at age 2
M	Rate of natural mortality (time-, sex-, and age-invariant)
δ_y	Random walk deviations for mean length at age 2
$\gamma_{y,G}$	Random walk deviations for $L_{\infty y,G}$
$\varpi_{y,G}$	Random walk deviations for $K_{y,G}$
$\varepsilon_{y,f}$	Random walk deviations for catchability
	Calculated quantities
$Z_{y,a,l,G}$	Total instantaneous mortality rate
$F_{y,a,l,G,f}$	Instantaneous rate of fishing mortality
$p_{y,a,l,G}$	Proportions at length for each age
$N_{y,a,l,G}$	Numbers at age, length in the beginning of the year, and sex in year y
$\dot{N}_{y,a,l,G}$	Numbers at age, length in the fall of the year, and sex in year y
$L_{y,a,G}$	Mean length at age in population at beginning of year
$\hat{\tilde{L}}_{y,a,G}$	Model predicted mean length at age measured by survey
$\dot{L}_{y,a,G}$	Mean length at age in population in fall
s_f	Selectivity
$\hat{I}_{y,a,l,G}$	Survey index of abundance
$\hat{u}_{y,a,l,G,f}$	Model prediction of proportions of catch at age, length, and sex
$\hat{\tilde{C}}_{y,l,f}$	Model prediction of catch
$\hat{\tilde{W}}_{y,l}$	Model predicted commercial yield (kg)
	Likelihood weighting components
$n_{y,a,l,G}$	Sample size of fish aged for the mean length-at-age likelihood function and effective sample size for age and length compositions
σ_f	Coefficient of variation for fishery catches
σ_δ	Standard deviation for mean length-at-age-2 random walk deviations
$\sigma_{\gamma,G}$	Standard deviation for $L_{\infty y,G}$ random walk deviations
$\sigma_{\varpi,G}$	Standard deviation for $K_{y,G}$ random walk deviations
$\sigma_{\varepsilon,f}$	Standard deviation for fishery catchability random walk deviations
σ_{λ_t}	Standard deviation for commercial selectivity prior for Illinois
	Data
$\tilde{L}_{y,a,G}$	Observed mean length at age in the survey
$I_{y,a,l,G}$	Observed catch per effort in the survey
$u_{y,a,l,G,f}$	Observed proportions at age and length in the fisheries
$C_{y,l,f=2}$	Harvest (numbers) in the recreational fishery
$W_{y,l,f=1}$	Yield (kg) in the commercial fishery
$E_{y,f}$	Fishery effort
w_l	Weight at length
$\omega_{y,a,G}$	Number of fish aged by age, year, and sex
$\tilde{\lambda}_{i,f=1}$	Mean parameter for the prior of commercial selectivity function for Illinois
M	Instantaneous rate of natural mortality (age- and sex-independent)

TABLE A.2—Equations for population and observation submodels. See Table A.1 for variable definitions.

Equation		
Population submodel		
Recruitment, initial abundances at age, and initial mean length at age		
$N_{y,a=2,G} = \frac{R_y}{2}$		(A.2.1)
$N_{y=1986,a,G} = N_{y=1986,a=4,G}e^{-(a-4)Z_{\text{init}_G}}$	$a > 4$; Wisconsin	(A.2.2)
$N_{y=1986,a,G} = N_{y=1986,a=4,G}e^{-(a-4)Z_{\text{init}}}$	$a > 4$; Illinois	(A.2.3)
$L_{y=1986,a+1,G} = L_{y=1986,a,G} + (L_{\infty_{y=\text{pre}1986,G}} - L_{y=1986,a,G})$		(A.2.4)
$\times\ (1 - e^{-K_{y=\text{pre}1986,G}})$	$a > 2$	
Mortality rates		
$Z_{y,a,G} = M + \sum_{f=1}^{2} F_{y,a,G,f}$		(A.2.5)
$F_{y,a,G,f} = \sum_l p_{y,a,l,G}F_{y,l,f}; \qquad \sum_l p_{y,a,l,G} = 1$		(A.2.6)
$F_{y,l,f} = q_{y,f}E_{y,f}s_{l,f}; \qquad q_{y+1,f} = q_{y,f}e^{\varepsilon_{y,f}}$		(A.2.7)
$s_{l,f} = \left\{\frac{1}{1 + e^{-[\lambda_{1,f}(l)-\lambda_{3,f}]}}\right\}\left\{1 - \frac{1}{1 + e^{-[\lambda_{2,f}(l)-\lambda_{4,f}]}}\right\}$		(A.2.8)
$s_{l,f} = \frac{1}{1 + e^{-[\lambda_{1,f}(l)-\lambda_{2,f}]}}$		(A.2.9)
Population and length-at-age dynamics		
$N_{y+1,a+1,G} = N_{y,a,G}e^{-Z_{y,a,G}}$		(A.2.10)
$L_{y+1,a+1,G} = L_{y,a,G} + (L_{\infty_{y,G}} - L_{y,a,G})(1 - e^{-K_{y,G}})$		(A.2.11)
$L_{y+1,a=9,G} = \frac{N_{y,a=8,G}[L_{y,a=8,G} + (L_{\infty_{y,G}} - L_{y,a=8,G})(1 - e^{-K_{y,G}})]}{N_{y,a=8,G} + N_{y,a=9,G}}$		(A.2.12)
$+ \frac{N_{y,a=9,G}[L_{y,a=9,G} + (L_{\infty_{y,G}} - L_{y,a=9,G})(1 - e^{-K_{y,G}})]}{N_{y,a=8,G} + N_{y,a=9,G}}$		
$\dot{L}_{y,a,G} = L_{y,a,G} + (L_{\infty_{y,G}} - L_{y,a,G})(1 - e^{-0.8K_{y,G}})$		(A.2.13)
$L_{y+1,2} = L_{y,2}e^{\delta_y}; \qquad L_{\infty_{y+1,G}} = L_{\infty_{y,G}}e^{\gamma_{y,G}}; \qquad K_{y+1,G} = K_{y,G}e^{\varpi_{y,G}}$		(A.2.14)
$p_{y,a,l,G} = \Phi\left(\frac{(l + 1) - L_{y,a,G}}{\sigma_{l_{a,G}}}\right) - \Phi\left(\frac{l - L_{y,a,G}}{\sigma_{l_{a,G}}}\right)$		(A.2.15)
Observation submodel		
$\hat{C}_{y,l,f=1} = \frac{F_{y,l,f=1}}{Z_{y,l}}(1 - e^{-Z_{y,l}}) \sum_G \dot{N}_{y,l,G}$		(A.2.16)
$\hat{C}_{y,l,f=2} = \frac{F_{y,l,f=2}}{Z_{y,l}}(1 - e^{-Z_{y,l}}) \sum_G N_{y,l,G}$		(A.2.17)
$\hat{I}_{y,l,G} = q_{G,f=3}s_{l,f=3}N_{y,l,G}$		(A.2.18)
$\hat{I}_{y,a,G} = q_{G,f=3}N_{y,a,G} \sum_l s_{l,f=3}p_{y,a,l,G}$		(A.2.19)
$\hat{\hat{L}}_{y,a,G} = \frac{\sum_l s_{l,f=3}p_{y,a,l,G}(l)}{\sum_l s_{l,f=3}}$		(A.2.20)

TABLE A.3.—Specifications of terms for normal and lognormal negative log-likelihood components. See equation A.1 in the text to the appendix.

Standard normal variate	Squared variates summed over these indices
$(\tilde{L}_{y,a,G} - \hat{\tilde{L}}_{y,a,G})/(\sigma_{y,a,G}/\sqrt{\omega_{y,a,G}})$	y, a, G
$(\log_e W_{y,f=1} - \log_e \hat{W}_{y,f=1})/\sigma_{f=1}$	y
$[\log_e(C_{y,g=2}) - \log_e(\hat{C}_{y,f=2})]/\sigma_{f=2}$	y
$[\log_e(I_{y,G}) - \log_e(\hat{I}_{y,G})]/\sigma_{f=3}$	y, G
δ_y/σ_δ	y
$\gamma_{y,G}/\sigma_{\gamma,G}$ and $\varpi_{y,G}/\sigma_{\varpi,G}$	y, G
$\varepsilon_{y,f}/\sigma_{\varepsilon f}$	y, f
$(\lambda_{j,f=1} - \tilde{\lambda}_{j,f=1})/\sigma_{\lambda_j}$	$j; j < 3$