# Development of a Regional Stock–Recruitment Model for Understanding Factors Affecting Walleye Recruitment in Northern Wisconsin Lakes

T. DOUGLAS BEARD, JR.\*

Wisconsin Department of Natural Resources, Bureau of Fisheries Management and Habitat Protection, 101 South Webster Street, Madison, Wisconsin 53505-7921, USA

### MICHAEL J. HANSEN

University of Wisconsin–Stevens Point, College of Natural Resources, 1900 Franklin Street, Stevens Point, Wisconsin 54481-3897, USA

## STEPHEN R. CARPENTER

University of Wisconsin–Madison, Center for Limnology, 680 North Park Street, Madison, Wisconsin 53706, USA

Abstract.—We used data from 162 lakes in northern Wisconsin during 1990–1999 to develop a stock-recruitment model for walleye Stizostedion vitreum and to identify important factors affecting recruitment. We used the linear version of the Ricker stock-recruit model and regression tree analysis to model age-0 walleye density, which ranged from 0.24 to 505 per km of shoreline (mean = 51.2). Adult walleye density ranged from .040 to 5.9 per surface hectare (mean = 1.5). The density of adult (sexually mature) walleyes, calendar year, and angling harvest rate of yellow perch Perca flavescens were significant descriptors of age-0 walleye density. Adult walleye density explained 10% of the variation in age-0 walleye abundance, which exhibited significant compensatory density dependence. Calendar year and yellow perch density explained nearly 32% of the residual variation in age-0 walleye density. The average age-0 walleye density in high-recruitment years (1991, 1994, and 1995) was 74.2/km, whereas the average age-0 walleye density in lowrecruitment years (1990, 1992, 1993, and 1996-1999) was 38.5/km. Yellow perch harvest rates influenced walleye recruitment in low-recruitment years, as lakes with angler harvest rates of yellow perch lower than 0.79/h had lower recruitment of age-0 walleyes; in high-recruitment years, by contrast, yellow perch density did not affect recruitment. Combining data from many walleye stocks within a region allowed us to determine regional factors affecting walleye recruitment. The combined data can be used to develop walleye harvest forecasting models.

Models for estimating the allowable harvest of fisheries often depend on stock-recruitment relationships (Hilborn and Walters 1992; Myers et al. 1995a, 1995b). Development of stock-recruitment relationships is one of the most difficult tasks facing fisheries biologists (Hilborn and Walters 1992; Myers and Barrowman 1996). Substantial effort has been spent developing and quantifying stockrecruitment relationships for many marine and most commercially harvested fish stocks (Hilborn and Walters 1992; Quinn and Deriso 1999); however, stock-recruitment relationships have not been quantified for many inland fisheries and noncommercially harvested species. Agencies have generally not set harvest goals for inland recreational species but have instead relied on densityindependent catchability to protect stocks (Peterman and Steer 1981; Bannerot and Austin 1983; Hansen et al. 2000). Stock-recruitment relationships may be useful in recreational fisheries management to avoid problems caused by targeted angler effort or habitat changes (Walters and Cox 1999; Cox et al. 2002).

Identification of stock-recruitment relationships can be difficult because both density-dependent and density-independent factors often affect survival (Sissenwine et al. 1988). Density-indepen-

<sup>\*</sup> Corresponding author: beardt@dnr.state.wi.us

Received November 27, 2001; accepted September 4, 2002

dent factors such as climate, prey density, predation pressure, or changes in spawning habitat often cause variability in recruitment when stocks are at intermediate abundance (Ricker 1975; Getz and Swartzman 1981; Hilborn and Walters 1992; Quinn and Deriso 1999). Such density-independent variability may lead to the conclusion that a stock-recruitment relationship does not exist (Koslow et al. 1987; Wooster and Bailey 1989; Gilbert 1997), but ignorance of a stock-recruitment relationship can lead to recruitment overfishing if spawning stocks are not adequately protected (Hilborn and Walters 1992). Stock-recruitment relationships that are based on the life history of a species, but that include density-independent variables to explain the residual variance, may allow better understanding of the mix of factors that affect recruitment of the species targeted by inland recreational fisheries (Madenjian et al. 1996; Hansen et al. 1998).

Traditional stock-recruitment analyses have focused on long time series of data for a single stock (Hilborn and Walters 1992). Such data sets are common for marine commercial fisheries but are available for only a few inland recreational fisheries (Forney 1980; Madenjian et al. 1996; Hansen et al. 1998). Nonetheless, similar processes may regulate the recruitment of inland recreational fishes, especially if the stocks inhabit similar systems and have similar forces structuring their stock-recruitment relationships (Myers et al. 1999). If broad-scale environmental factors cause recruitment variability (Busch et al. 1975; Forney 1980; Madenjian et al. 1996; Hansen et al. 1998) or recruitment variability is mitigated by similar factors within individual stocks (Forney 1980; Madenjian et al. 1996; Hansen et al. 1998), a single stock-recruitment relationship may apply across a broad region. Although a stockrecruitment model based on such a relationship would likely not allow the prediction of recruitment or the setting of harvest goals for any one stock, it would quantify broad-scale features that affect individual stocks, which can then be studied if recruitment problems arise. Such a broad-scale model would help to guide analyses of individual stocks and might be useful for setting regional harvest targets.

Our objective was to develop a broad-scale, stock-recruitment model for walleye *Stizostedion vitreum* in northern Wisconsin by combining data from several stocks across the region. We wished to determine whether broad-scale, density-independent factors affected walleye recruitment and whether walleye recruitment was synchronous across northern Wisconsin. The cornerstone of a regional management scheme would be a stock–recruitment relationship that can be used to examine recruitment within a lake or stock and aid in developing regional management strategies.

#### Methods

Study area.---Numerous small lakes (most less than 400 surface hectares) predominate in northern Wisconsin, where walleyes are a primary target species. In this region, walleyes are harvested through both tribal spearing and recreational angling, so walleye stocks are managed as a regional resource to accommodate both fisheries (Staggs et al. 1990; Beard et al. 1997). Some walleye fisheries in the area are maintained through stocking, but most are sustained by natural reproduction (Nate et al. 2000). Although the management system accounts for variability in stock size when estimating the total allowable catch, the system does not rely on a quantitative model to understand regional stock-recruitment dynamics, prescribe management strategies, or forecast regional harvest goals (Hansen et al. 1991).

Data were collected as part of a larger project that began in 1990 to monitor walleye populations in response to a mixed angling and spearing harvest (Hansen et al. 1991). About 25 lakes each year were randomly selected for monitoring from among those walleye lakes in Wisconsin's ceded territory that were subject to both spearing and angler harvest (Beard et al. 1997). In this analysis, we used data from 162 lakes that were surveyed during 1990-1999. The lakes ranged from 41 to 6,181 surface hectares. Lakes that are part of a chain of lakes were not included unless it was known that there was movement by adult walleyes among them (Rasmussen et al., in press). Walleye recruitment in the lakes in this region is maintained by either natural reproduction or stocking (Nate et al. 2000); we analyzed data only for lakes where recruitment was solely from natural reproduction. Regulations on walleye angling varied among lakes and years. For example, the length limits during 1990-1997 consisted of either a 38.1-cm minimum length or no minimum length. In 1998, three more length limit categories were added, including one fish per day over 71.1 cm, a 35.6-45.7-cm protected slot limit, and one fish per day over 45.7 cm. Bag limits for walleyes in the region ranged from two to five fish per day and varied with spearing harvest on each lake each year (Fayram 2000).

Data collection.-Adult walleye populations

were estimated in spring using the Chapman modification of the Petersen mark-recapture estimator (Ricker 1975; Beard et al. 1997). Immediately after ice-out, fyke nets were used to capture and mark adult walleyes. Adult walleyes were defined as sexually mature fish plus fish of unknown sex longer than 38.1 cm (Beard et al. 1997). To ensure that all walleyes were vulnerable to capture during recapture sampling, walleyes were sampled along the entire shoreline 1-3 d after the marking period ended with 230-V AC electrofishing boats to estimate the proportion of adults that were marked. Population abundance was estimated for each sex and four length categories: 0-30.2, 30.3-38.0, 38.1-50.5, and 50.6 cm and longer (Beard et al. 1997). Estimates for each length category and associated variance were summed by sex to obtain a population estimate and variance for all mature adult walleyes in each lake (Beard et al. 1997). If the coefficient of variation of the population estimate  $(100 \cdot \text{SD/estimate})$  was greater than 40%, the estimate was not used. Population estimates were divided by lake surface acres to standardize for lake size.

The densities of age-0 and age-1 walleyes were estimated between mid-September and mid-October of each year in which a spring population estimate was obtained. In most cases, the entire shoreline of each lake was sampled on one night with 230-V AC electrofishing boats when water temperatures were between 10°C and 18°C. In some lakes, when the entire shoreline could not be sampled, randomly selected sections were sampled and the distance sampled recorded. The age of each walleye collected was estimated by examining the length-frequency distribution for modal lengths, and when length-frequency analysis was inconclusive scale annuli were analyzed. The numbers of age-0 and age-1 walleyes were divided by the shoreline length (kilometers) sampled to estimate density. Lakes in which no age-0 or age-1 walleyes were collected were not used.

We examined several density-independent factors to see whether we could explain significant residual variation in recruitment using a Ricker stock-recruitment model (Ricker 1975). Because we were interested in regional patterns in walleye recruitment variation, we chose to analyze variables for which data were available for all lakes and which could cause regional variation in recruitment. The variables included were the calendar year (a surrogate for climate variation), drainage basin (Lake Superior, Lake Michigan, or the Mississippi River), angler bag limit (2, 3, or 5 fish/d), whether the lake was exempt from the regional 38.1-cm size limit (a surrogate for growth because lakes were exempted if walleyes exhibited slow growth), lake surface acres, shoreline development factor (SDF), angler-hours per hectare (a surrogate for interest in and use of the lake), angler catch and harvest rates of yellow perch Perca flavescens (a surrogate for yellow perch density), and walleye cohort density (age-1 density from the same sampling year). Year, drainage basin, bag limit, size limit, and surface acres were taken from Wisconsin's surface water inventory data files and Wisconsin Department of Natural Resources Fisheries Management databases. The shoreline development factor, the ratio of actual shoreline length to that expected if the lake were a perfect circle (Wetzel 1983), was calculated as follows:

$$SDF = \frac{\text{shoreline length}}{[2 \cdot (\pi \cdot \text{lake surface area})^{1/2}]}$$

A year-round creel survey was conducted on most lakes for which spring walleye abundance was estimated by mark-recapture. Creel surveys ran from the first Saturday in May through March 1 of the following year but were not conducted in November due to dangerous ice conditions and the lack of angler effort (Beard et al. 1997). Estimates of angler effort, catch rate, and harvest rate for each species were calculated using a Wisconsin hybrid creel survey design (Beard et al. 1997; Rasmussen et al. 1998). Angling effort, catch rate, and harvest rate were estimated separately for each stratum and then combined into annual estimates (Beard et al. 1997; Rasmussen et al. 1998).

*Recruitment modeling.*—Because walleyes can be cannibalistic (Forney 1980; Hansen et al. 1998), we used a Ricker recruitment model to describe age-0 density as a function of adult density:

$$R = S \cdot e^{a - bS},$$

where R is the number of age-0 recruits per kilometer, S is the number of adult walleyes per hectare, a is the background density-independent mortality and b is a coefficient that describes the density-dependent mortality rate. The model was transformed into its linear form and least squares regression was used to estimate parameters a and b (Hilborn and Walters 1992; Hansen et al. 1998):

$$\log_e(R/S) = a - bS + \epsilon,$$

where  $\varepsilon$  is the error term. The linear transformation

of the Ricker stock-recruitment model assumes that the model being fitted has lognormal errors (Hilborn and Walters 1992). The model was considered significant when the model *F*-test and the Ricker parameter estimates (*a*, *b*) were significant ( $P \le 0.05$ ). To assure proper scaling between adult and age-0 densities for purposes of model analysis, we converted the number of age-0 fish per kilometer to the number per hectare by dividing the total catch of age-0 walleyes by the number of lake surface hectares. However, we report descriptive statistics about age-0 densities (i.e., the mean and range) in terms of the number per kilometer because this is the most common practice in the literature.

To determine whether external factors would significantly improve the fit of the simple Ricker stock-recruitment model, we used the residuals from the simple model for age-0 fish to see whether density-independent factors would explain a significant amount of the residual variation. As the density-independent variables were both continuous and class variables, we used regression tree analysis to identify those that were significant descriptors of residual recruitment variation ( $P \leq$ 0.05 for both inclusion and exclusion). Regression trees have an advantage over the traditional methods used to identify correlative factors, such as general linear models, because both categorical and continuous variables can be combined in one nonparametric, multivariate analysis (Clark and Pregibon 1992). Unlike general linear models, regression trees automatically detect interactions between independent variables while conserving statistical degrees of freedom. Regression trees begin with all the data and split them into smaller and less variable nodes through recursive partitioning until the variability in each node (or tree branching point) is less than a predetermined level (Clark and Pregibon 1992). We used the least-squares method of fitting the regression tree. The criteria for node formation in the analysis were (1) that the proportional reduction in error (PRE) due to any independent variable be greater than 0.05 of the total and (2) that the PRE for each node be greater than 0.05. A minimum of five data points were required for a split to occur. Only observations that contained all values were used in the analysis (N = 105).

The variables that were significant in explaining the variance in the residuals were then added back to the generalized Ricker stock–recruitment model as follows:

$$R = S \cdot e^{a - bS + cX},$$

where *X* are significant independent variables identified in the regression tree analysis. The model was estimated from the linear version, namely,

$$\log_e(R/S) = a - bS + cX + \epsilon.$$

To guard against overfitting the model, the regression parameters in the new linear model that were not significant ( $P \le 0.05$ ) were dropped. Important density-independent variables identified by the regression tree analysis were added to the Ricker model in the same order in which they appeared in the regression tree. If X was a categorical variable, we used a general-linear-model approach to add it to the expanded model. When a class variable such as calendar year or drainage basin was identified as significant by the regression tree analysis, we performed analysis of covariance (AN-COVA) to ensure that the b coefficient was homogeneous among classes.

We examined possible bias in the expanded Ricker model by comparing a plot of the residuals of the expanded Ricker stock—recruitment model with residual plots generated by the simple mean model  $(\log_e[R/S] = \text{mean}[\log_e\{R/S\}])$  and the Ricker stock—recruitment model. If the residuals appeared to contain outliers or systematic departures across the predicted values, the model may have been biased (Sokal and Rohlf 1995). As all three models were nested, the general *F*-test of the full versus the reduced models was calculated during model formation and significance testing (Yandell 1997).

#### Results

The densities of adult, age-0, and age-1 walleyes did not appear to increase or decrease through time during 1990–1999. The estimates of adult walleye density in the 162 study lakes ranged from 0.04 to 5.9/hectare during this period, averaging 1.5/ hectare (Figure 1). Estimates of age-0 walleye density ranged from 0. 24 to 505/km, averaging 51.2/ km, and were highest during 1994 and 1995 (Figure 2); age-1 walleye density ranged from 0.54 to 127.5/km, averaging 16.4/km.

Adult walleye density (S) explained 10% of the recruitment variation in study lakes (F = 17.64; df = 1, 160; P < 0.001; Figure 3):

$$R = S \cdot e^{-.556 - 0.484S}$$

The highest number of recruits was produced at an adult density of about 2 fish/hectare, and low



FIGURE 1.—Frequency of the estimated numbers of adult walleyes per hectare used for estimating stock-recruitment models for 162 lakes in northern Wisconsin during 1990–1999. The histogram bars are offset slightly for easier interpretation.

numbers of recruits were produced at adult densities greater than about 4 fish/hectare (Figure 3). The *b*-coefficient was significantly different from zero and negative, which indicates compensatory density-dependent mortality (Hilborn and Walters 1992). Although the Ricker model explained only 10% of the variation in age-0 walleye density, recruitment was density dependent, with low recruitment at both high and low adult walleye densities. Further, recruitment variation was substantial across adult densities, which suggests that density-independent factors were also significant contributors to recruitment variation.

Regression tree analysis identified the calendar year and yellow perch harvest per hour as the main effects in explaining nearly 39% of the residual variation in age-0 walleye density (Figure 4). The initial split was on year, with the residuals from the high-recruitment years of 1991, 1994, and 1995 generally being larger than those from the low-recruitment years of 1990, 1992, 1993, and 1996-1999 (Figure 4). Average age-0 density during high-recruitment years was 74 walleyes/km, whereas average age-0 density in low-recruitment years was 38.4 walleyes/km (Figure 2). In lowrecruitment years, the strength of recruitment was decreased by low yellow perch harvest rates because lakes with angler harvest rates lower than 0.79 yellow perch/h experienced lower recruitment of age-0 walleyes (Figure 4). Lakes with higher yellow perch harvest rates were split again by year, with recruitment in 1992 and 1996 being lower than that in other years. In high-recruitment years, yellow perch did not seem to affect recruitment



FIGURE 2.—Estimated numbers of age-0 walleyes per kilometer in 162 lakes in northern Wisconsin during 1990–1999. The horizontal lines within the boxes represent means, the vertical lines outside the boxes SDs. Observations marked by stars are located within one interquartile of the box; observations marked by circles are located more than two interquartiles from the box.

because the regression tree showed no further nodal splitting.

The addition of the calendar year as a categorical predictor variable increased the variability explained in age-0 walleye density to 32% (F = 7.24; df = 9, 151; P < 0.001). The interaction between year and adult density was not significant, which indicates that the degree of density dependence



FIGURE 3.—Estimated numbers of age-0 walleyes per kilometer versus estimated numbers of adult walleyes per hectare for 162 lakes surveyed in northern Wisconsin during 1990–1999. The curve is the Ricker stock–recruitment curve, and circles are individual observations.





FIGURE 4.—Results of a regression tree analysis of the residuals from a Ricker stock-recruitment model for walleyes in 105 lakes in northern Wisconsin during 1990–1999. The variables on which splits occurred, the number of observations in each split, and the values for the variables are shown adjacent to the split line. The mean values for all residuals residuals residuals residuals node are shown; where a node represents a termination point, the mean residual value is enclosed in a box.

between adult and age-0 walleyes did not differ significantly among years (F = 0.74; df = 9, 142; P = 0.67).

The addition of yellow perch harvest per hour increased the explained variability in age-0 walleye densities to 36%. However, the coefficient for this variable was not significantly different from zero (F = 2.15; df = 1, 134; P = 0.145). Because yellow perch harvest rates can be limited by length and bag limits at each lake, we substituted yellow perch catch per hour for yellow perch harvest per hour. The model with the yellow perch catch rate explained a similar amount of the variation in age-0 walleye densities (36%), even though the coefficient for yellow perch catch rate was still not significantly different from zero (F = 2.53; df = 1, 134;  $P \le 0.11$ ).

Other potential independent variables were not significant descriptors of walleye recruitment. The shoreline development factor was significantly and negatively correlated with the age-0 walleye residuals (r = -0.28; n = 112; P < 0.001), but it was not important in the regression tree analysis. Also, the shoreline development factor did not explain significantly more of the variation in walleye recruitment in a stock-recruitment model that included the adult walleye density, yellow perch catch rate, and year.

The expanded Ricker model resulted in less var-

iation in the residuals than the simple mean or simple Ricker model (Figure 5). However, even the full model tended to underestimate large recruitment events and overestimate small recruitment events. Plots of residuals against predicted values did not suggest any mechanisms for improving the fit of the model (Sokal and Rohlf 1995). Because parameter estimates for the full, expanded model were significantly larger than zero, we chose this model as the best model for the data.

#### Discussion

Our results suggest that walleye recruitment in northern Wisconsin lakes is regulated by a mix of factors that include compensatory, density-dependent interactions between adult and age-0 walleyes, density-independent factors that operate across a broad regional scale, and density-dependent interactions between yellow perch and age-0 walleyes. These findings are similar to those of other work on walleye stock-recruitment (Forney 1980; Madenjian et al. 1996; Hansen et al. 1998). Walleye recruitment showed a high degree of synchrony across northern Wisconsin, which suggests that overall climatic effects strongly influenced walleye reproductive success. Although synchrony across regions is common for physical and chemical variables, it has generally not been common



# Predicted Values

FIGURE 5.—Observed and predicted values for (A) a simple mean model, (B) a simple Ricker stock-recruitment model, and (C) an expanded Ricker stock-recruitment model for 162 lakes in northern Wisconsin during 1990–1999. The 45° lines show 1:1 relationships between the observed and predicted values.

for biological variables (Magnuson et al. 1990; Kratz et al. 1998; Baines et al. 2000). Calendar year served as a surrogate for density-independent factors that appear to regulate walleye recruitment, such as the spring warming rate (Busch et al. 1975; Madenjian et al. 1996) or variation in May water temperature (Hansen et al. 1998). Because temperature appears to be synchronous across lakes within a region (Baines et al. 2000) and walleye recruitment is influenced by temperature, the relationship between temperature and recruitment may lead to synchrony in regional walleye recruitment. The yellow perch angling harvest rate served as an index of density-dependent interactions with other prey or predator species (Forney 1980; Madenjian et al. 1996; Hansen et al. 1998) and seemed to have a similar effect on walleye recruitment across the region.

Years with high recruitment of age-0 walleyes (1994 and 1995) were characterized by relatively warm and stable water temperatures following 2 years of relatively poor walleye reproduction, which suggests that broad-scale climatic patterns can strongly influence recruitment patterns. Such regional synchrony can be discerned by examining data from many walleye stocks. In the absence of such regional synchrony, we would have concluded that local processes were the most important factors regulating walleye recruitment in northern Wisconsin. Walleye recruitment also appears to be synchronous in Minnesota's large walleye lakes (Donald Pereira, Minnesota Department of Natural Resources, personal communication). Our results from northern Wisconsin suggest that walleye recruitment is synchronous in small lakes across a large region. If the lakes in this region are synchronous, a few sentinel stocks could be used to indicate regional variation or yellow perch harvest per unit effort could be monitored as an indicator of prey abundance.

Year effects may be strong enough to override the effects of density-dependent interactions among juvenile walleyes, adult walleyes, and other species such as yellow perch. In years with favorable weather, recruitment may be sufficient to overcome cannibalism by adult walleyes, competition with other species, or predation by other species (Hansen et al. 1998). Conversely, in other years, unfavorable weather may enhance the strength of density-dependent interactions with adult walleyes (Forney 1980; Madenjian et al. 1996; Hansen et al. 1998) and other species (Hansen et al. 1998). The regression tree analysis identified the yellow perch harvest rate as being an important factor in characterizing age-0 walleye densities but one that was nested among a subgroup of poor reproductive years. Linear modeling, however, did not show the effect of the yellow perch harvest rate to be significant. From a management perspective, the fact that walleye recruitment is strongly regulated by variable climatic effects makes it hard to predict or manage harvest for future abundance. Recruitment models that include large stochastic variation will lead to management policies that are necessarily conservative.

Our results confirmed the importance of several factors that were previously shown to influence walleye recruitment, but many other factors that are thought to affect walleye recruitment were not found to be important. For example, stocking walleyes in waters where walleye abundance is sustained through natural reproduction can have a detrimental effect on adjacent year-classes (Li et al. 1996). In northern Wisconsin lakes in which recruitment comes entirely from natural reproduction, the strongest year-classes were in adjacent years (1994 and 1995), which suggests that unlike stocking, natural recruitment does not suppress adjacent year-classes. Also, three genetically distinct stocks of walleyes occupy the three major drainage basins in northern Wisconsin (Fields et al. 1997), suggesting that genetic differences can translate into different recruitment patterns. However, our analyses did not indicate that recruitment patterns varied significantly among drainage basins.

Our analysis did not use a traditional stockrecruitment approach; whereas most stock-recruitment analyses have used data for one species over a long time period (Anderson and Wilen 1985), we used data from many different stocks. Myers et al. (1999) also estimated recruitment parameters for individual species from an analysis of multiple stocks and suggested that this approach allows improved estimates of stock-recruitment parameters. Recruitment parameters should be interpreted cautiously in developing harvest policies, however, because the models from which they come assume that all populations in a taxon are comparable (Myers et al. 1999). Even though we made an assumption about population commonality between different walleye stocks, combining data across many stocks may allow us to reduce the uncertainty of the biological processes affecting these stocks (Myers et al. 1999).

Because our data were not a single time series for one stock, we did not need to account for autocorrelation in stock estimates, which is a serious problem with stock-recruitment analyses (Walters 1985; Caputi 1988; Hilborn and Walters 1992; Myers and Barrowman 1996). Another serious problem with many stock-recruitment analyses is that the errors in stock estimates are not taken into account (Hilborn and Walters 1992). Failure to address the autocorrelation or error in stock estimates may lead to bias in harvest policies developed from stock-recruitment relationships. If we were to use this analysis in a broader process of setting harvest policy, we would employ techniques such as geometric mean regression (Ricker 1975), measurement error models (Fuller 1987), or Monte Carlo simulation (Hilborn and Walters 1992) to determine the effect of errors in stock estimates. Further, correcting for time series bias would be necessary to ensure that autocorrelation issues are

addressed (Walters 1985; Hilborn and Walters 1992). The data from our study were independent among years and randomly selected from a suite of different lakes each year, which allowed us to identify factors affecting walleye recruitment free from time series bias. Because we were not using this model for setting harvest policy, we did not address possible errors in the stock estimates. This type of analysis should only be used to identify factors affecting stock-recruitment relationships and not to set harvest policy.

Our analysis was intended to identify factors that likely regulate recruitment of walleyes in northern Wisconsin. A strength of our approach was that it provided a large range in adult walleye densities with which to estimate stock-recruitment parameters. Analyses of this type can identify factors affecting recruitment and thereby guide future management. This type of analysis can also allow managers to develop forecasts of harvest potential. In addition, such analyses can be combined with other regional models to allow a fisheries program to manage walleyes or other inland game species across a broad region by either protecting spawning stocks or initiating stocking programs to offset recruitment problems. Analyses such as ours would allow fishery managers to identify factors that regulate recruitment across a regional pool of fish stocks, develop strategies to better manage the affected stocks, and forecast potential harvest across a wide region. Development of a broad regional harvest policy that incorporates large stochastic variation in recruitment would also ensure a high level of stock protection in each of the individual fisheries located in this region.

#### Acknowledgments

We thank the many crews of the Wisconsin DNR that helped to collect and process this data. We thank Tom Beard, Sr., Mike Coshun, Steve Gilbert, Steve Hewett, and Ruth King for coordinating all aspects of data collection. Andy Fayram, Greg Sass, Bob Carline, and two anonymous reviewers provided very helpful critical reviews of this manuscript. Partial funding for this project came from the Federal Aid in Sport Fish Restoration Program.

#### References

- Anderson, J. L., and J. E. Wilen. 1985. Estimating the population dynamics of coho salmon (*Oncorhynchus kisutch*) using pooled time-series and crosssectional data. Canadian Journal of Fisheries and Aquatic Sciences 42:459–467.
- Baines, S. B., K. E. Webster, T. K. Kratz, S. R. Carpenter, and J. J. Magnuson. 2000. Synchronous behavior

of temperature, calcium, and chlorophyll in lakes of northern Wisconsin. Ecology 81:815–825.

- Bannerot, S. P., and C. B. Austin. 1983. Using frequency distributions of catch per unit effort to measure fish stock abundance. Transactions of the American Fisheries Society 112:608–617.
- Beard, T. D., Jr., S. W. Hewett, Q. Yang, R. M. King, and S. J. Gilbert. 1997. Prediction of angler catch rates based on walleye population density. North American Journal of Fisheries Management 17: 621–627.
- Busch, W.-D. N., R. L. Scholl, and W. L. Hartman. 1975. Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in western Lake Erie, 1960–1970. Journal of the Fisheries Research Board of Canada 32:1733–1743.
- Caputi, N. 1988. Factors affecting the time series bias in stock-recruitment relationships and the interaction between time series and measurement error bias. Canadian Journal of Fisheries and Aquatic Sciences 45:178–184.
- Clark, L. A., and D. Pregibon. 1992. Tree based models. Pages 377–419 in J. M. Chambers and T. J. Hastie, editors. Statistical models. Wadsworth, Belmont, California.
- Cox, S., T. D. Beard, Jr., and C. J. Walters. 2002. Harvest control in open access sport fisheries: hot rod or asleep at the reel? Bulletin of Marine Science 70: 749–761.
- Fayram, A. H. 2000. 1999 ceded territory fishery assessment report. Wisconsin Department of Natural Resources, Fisheries Management Administrative Report 50, Madison.
- Fields, R. D., M. D. J. Desjardins, M. J. Hudson, T. W. Kassler, J. B. Ludden, J. V. Tranquilli, C. A. Toline, and D. P. Philipp. 1997. Genetic analyses of fish species in the upper Midwest. Illinois Natural History Survey, University of Illinois, Aquatic Ecology Technical Report 1997/5, Champaign–Urbana.
- Forney, J. L. 1980. Evolution of a management strategy for the walleye in Oneida Lake, New York. New York Fish and Game Journal 27:105–141.
- Fuller, W. A. 1987. Measurement error models. Wiley, New York.
- Getz, W. M., and G. L. Swartzman. 1981. A probability transition matrix model for yield estimation in fisheries with highly variable recruitment. Canadian Journal of Fisheries and Aquatic Sciences 38:847– 855.
- Gilbert, D. J. 1997. Towards a new recruitment paradigm for fish stocks. Canadian Journal of Fisheries and Aquatic Sciences 54:969–977.
- Hansen, M. J., T. D. Beard, Jr., and S. W. Hewett. 2000. Catch rates and catchability of walleye in angling and spearing fisheries in northern Wisconsin lakes. North American Journal of Fisheries Management 20:109–118.
- Hansen, M. J., M. A. Bozek, J. R. Newby, S. P. Newman, and M. D. Staggs. 1998. Factors affecting recruitment of walleyes in Escanaba Lake, Wisconsin, 1958–1996. North American Journal of Fisheries Management 18:764–774.

- Hansen, M. J., M. D. Staggs, and M. H. Hoff. 1991. Derivation of safety factors for setting harvest quotas on adult walleyes from past estimates of abundance. Transactions of the American Fisheries Society 120:620–628.
- Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York.
- Koslow, J. A., K. R. Thompson, and W. Silvert. 1987. Recruitment to northwest Atlantic cod (*Gadus mor-hua*) and haddock (*Melanogrammus aeglefinus*) stocks: influence of stock size and climate. Canadian Journal of Fisheries and Aquatic Sciences 44: 26–39.
- Kratz, T. K., P. A. Sorrano, S. B. Baines, B. J. Benson, J. J. Magnuson, T. M. Frost, and R. L. Lathrop. 1998. Interannual synchronous dynamics in north temperate lakes in Northern Wisconsin, USA. Pages 273–287 in D. G. George, editor. Management of lakes and reservoirs during global climate change. Kluwer Academic, Amsterdam.
- Li, J., Y. Cohen, D. H. Schupp, and I. R. Adelman. 1996. Effects of walleye stocking on year-class strength. North American Journal of Fisheries Management 16:840-850.
- Madenjian, C. P., J. T. Tyson, R. L. Knight, M. W. Kershner, and M. J. Hansen. 1996. First year growth, recruitment, and maturity of walleyes in western Lake Erie. Transactions of the American Fisheries Society 125:821–830.
- Magnuson, J. J., B. J. Benson, and T. K. Kratz. 1990. Temporal coherence in the limnology of a suite of lakes in Wisconsin. Freshwater Biology 23:145– 159.
- Myers, R. A., and N. J. Barrowman. 1996. Is fish recruitment related to spawner abundance? U.S. National Marine Fisheries Service Fishery Bulletin 94: 707–724.
- Myers, R. A., N. J. Barrowman, J. A. Hutchings, and A. A. Rosenberg. 1995a. Population dynamics of exploited fish stocks at low population levels. Science 269:1106–1109.
- Myers, R. A., K. G. Bowen, and N. J. Barrowman. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences 56:2404–2419.
- Myers, R. A., J. Bridson, and N. J. Barrowman. 1995b. Summary of worldwide stock and recruitment data. Canadian Technical Report of Fisheries and Aquatic Sciences 2024.
- Nate, N. A., M. A. Bozek, M. J. Hansen, and S. W. Hewett. 2000. Variation in walleye abundance with

lake size and recruitment source. North American Journal of Fisheries Management 20:119–126.

- Peterman, R. M., and G. J. Steer. 1981. Relation between sport-fishing catchability coefficients and salmon abundance. Transactions of the American Fisheries Society 110:585–593.
- Quinn, T. J., and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.
- Rasmussen, P. W., M. D. Staggs, T. D. Beard, Jr., and S. P. Newman. 1998. Bias and confidence interval coverage of creel survey estimators evaluated by simulation. Transactions of the American Fisheries Society 127:469–480.
- Rasmussen, P. W., D. M. Heisey, S. J. Gilbert, R. M. King, and S. W. Hewett. 2002. Estimating postspawning movement of walleye among interconnected lakes of northern Wisconsin. Transactions of the American Fisheries Society 131:1020–1032.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.
- Sissenwine, M. P., M. J. Fogarty, and W. J. Overholtz. 1988. Some fisheries management implications of recruitment variability. Pages 129–152 in J. A. Gulland, editor. Fish population dynamics. Wiley, New York.
- Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics for biological research. Freeman, New York.
- Staggs, M. D., R. C. Moody, M. J. Hansen, and M. H. Hoff. 1990. Spearing and sport angling for walleye in Wisconsin's ceded territory. Wisconsin Department of Natural Resources, Fisheries Management Administrative Report 31, Madison.
- Walters, C., and S. Cox. 1999. Maintaining quality in recreational fisheries: how success breeds failure in the management of open-access sport fisheries: evaluating the benefits of recreational fisheries. University of British Columbia, Fisheries Centre Research Reports, volume 7, number 2, Vancouver.
- Walters, C. J. 1985. Bias in estimation of functional relationships from time series data. Canadian Journal of Fisheries and Aquatic Sciences 42:147–149.
- Wetzel, R. G. 1983. Limnology. Saunders, Philadelphia.
- Wooster, W. S., and K. M. Bailey. 1989. Recruitment in marine fishes revisited. Pages 153–159 in R. J. Beamish and G. A. MacFarlane, editors. Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Canadian Special Publication on Fisheries and Aquatic Sciences 108.
- Yandell, B. S. 1997. Practical data analysis for designed experiments. Chapman and Hall, New York.