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[Article]

Determining Optimal Stocking Rates Using a Stock–Recruitment Model: An Example Using Walleye in Northern Wisconsin

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Abstract.—We propose that stock–recruitment models can be used to estimate optimal stocking rates. Data to estimate the optimal stocking rates can be obtained in a relatively short amount of time by sampling similar populations over a few years. Whether the goal of stocking is endangered species recovery or supplementation of recreational fisheries, accurately determining the optimal stocking rate is of ecological and financial importance. As an example, we applied this approach using a Ricker stock–recruitment model to walleye *Sander vitreus* stocking in northern Wisconsin lakes. Using June stocking data and fall age-0 survey data for 39 lakes over a 14-year time period, we found that the stocking rate resulting in the greatest number of age-0 walleyes was 60 age-0 walleyes/ha. Similarly, using June stocking data and fall age-1 survey data in 18 lakes over a 9-year time period we found that the stocking rate resulting in the greatest number of age-1 walleyes was 75 age-0 walleyes/ha. About 16% of the variation in fall age-0 walleye density was explained by the stocking rate, and 28% of the variation in fall age-1 walleye density was explained by the stocking rate. Density-dependent survival was apparent and significant, as low and high stocking densities resulted in lower age-0 and age-1 juvenile walleye densities. The lake surface area explained a significant amount of the residual variation in the age-1 stock–recruitment relationship such that stocked walleyes generally survived at lower rates in large lakes than in small lakes, which may be due to a greater diversity of predators in larger lakes. Based on our analysis, we recommend stocking small fingerling walleyes at a rate of 75 fish/ha in northern Wisconsin lakes.

Fishery management agencies stock billions of fish annually. The rationale for stocking fish into different systems ranges from recovery of an endangered species or collapsed fishery to providing recreational opportunities for anglers. Stocking of fish is often controversial because of its potential genetic, ecological, and financial impacts (Schramm and Piper 1995). Even in cases that involve endangered species, where there seems to be a reasonable rationale for at least considering the use of stocked fish, their exact role is subject to debate (Brannon et al. 2004; Myers et al. 2004). In spite of the controversy, large-scale hatchery programs exist in virtually every state and province in North America. The financial investment in hatchery infrastructure and annual fish production is tremendous. Given that hatcheries will continue to operate on this large scale into the foreseeable future, it is imperative that appropriate stocking levels are quantitatively established.

Generally, agencies establish target stocking rates to achieve various objectives for the fish they produce. Stocking rates are often based on the projected carrying capacity of the system being stocked (MDNR 1996; OMNR 2002; NDGFD 2002), the production capacity of the hatchery system (Whalen and LaBar 1994), or past evaluations of stocking success or failure in individual waters (Mathias et al. 1992; Santucci and Wahl 1993; Larscheid 1995). As the capability of hatcheries to produce fish has continued to increase, the carrying capacity of the aquatic systems being stocked and the suitability of recommended stock-

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ing densities have become a greater concern. Many governmental agencies suggest that the carrying capacity of the system be considered when determining stocking rates for a given water body (MDNR 1996; Flagg and Nash 1999; OMNR 2002; NDGFD 2002). Guidance (such as limiting the number of predator species stocked into a system) indicates that agencies are aware of the importance of carrying capacity, although it is often only qualitatively assessed (MDNR 1996; OMNR 2002; NDGFD 2002). In large, intensively studied systems, stocking rates have been tied to quantitative measures thought to be associated with carrying capacity (Flagg and Nash 1999), and carrying capacity has been estimated using prey consumption models (Kitchell and Hewett 1987; Stewart and Ibarra 1991; Jones et al. 1993; Johnson et al. 1999). Similarly, stocking strategies for relatively small individual water bodies have been developed when large amounts of data are available (Madenjian et al. 1991; Johnson et al. 1996). However, in circumstances when numerous small systems require management (such as is often the case with inland lakes), the data necessary for such quantitative evaluations of each individual water body may be impossible to collect due to the immense amount of sampling effort necessary. Other methods of quantifying system carrying capacity are needed to help prevent wasteful and potentially ecologically damaging use of hatchery fish.

Stocking rates that are either too low or too high may negatively affect the cohort of stocked fish or the fish community in the receiving water. Stocking rates that are too low may prevent substantial survival of the stocked fish if depensatory mortality occurs. For example, if the fish species being stocked acts as prey for another species in the system, a minimum density of the prey species may be necessary to prevent predators from consuming the entire prey population (Hilborn and Walters 1992). This scenario may be of particular importance when attempting to recover an endangered species or a rebuild collapsed fish population. Conversely, stocking rates that are too high may lead to density-dependent reductions in growth (Fox and Flowers 1990; Close and Anderson 1992; Banks and LaMotte 2002; Bohlin et al. 2002) or cannibalism (Forney 1976; Hansen et al. 1996; Hansen et al. 1998), which decrease the survival of stocked fish and increase costs. In fish populations with some degree of natural reproduction, increased stocking may not add to the population (Whalen and LaBar 1994; Li et al. 1996; Kampa and Jennings 1998; NDGFD 2002; 1998; Sutela et al. 2004) or may reduce the productivity of the naturally reproducing portion of the population (Chilcote 2003; Nickelson 2003).

Stock–recruitment relationships are generally used to describe the relationship between the number of adults and the number of younger fish that they produce from estimates of spawner and recruit abundance through time. Understanding the relationship between the current number of adults and the number of young that they are likely to produce is one of the most important challenges in fisheries management (Myers 2002; Hilborn and Walters 1992). Because adults are necessary to produce juveniles, stock size is likely to be related to the number of juveniles produced. Similarly, when stocking sustains the future fish population, the number of fish stocked is related to the size of the future population. Therefore, we suggest that stock–recruitment relationships may be useful for estimating optimal stocking rates.

Our objective was to demonstrate the utility of stock–recruitment relationships in determining optimal stocking rates using walleye *Sander vitreus* in northern Wisconsin as an example. Beard et al. (2003) used a walleye stock–recruitment model to evaluate the survival of self-sustaining walleye populations in northern Wisconsin lakes and demonstrated that broad-scale factors influenced the generalized stock–recruitment relationship. We used a similar approach, based on numbers of walleye stocked and estimates of age-0 and age-1 walleye in autumn from northern Wisconsin lakes, to construct a Ricker stock–recruitment model to estimate the optimal stocking rate for small fingerling walleyes in northern Wisconsin.

Methods

Study area.—Lakes are a common feature of the landscape of northern Wisconsin and generally range from about 10 to 6,000 ha in size. Our data sets consisted of 39 lakes that ranged in area from 22 to 716 ha, and 22 lakes that ranged in area from 30 and 236 ha (Tables 1, 2). Natural reproduction supports most walleye populations in northern Wisconsin lakes (Nate et al. 2000). However, among lakes that contain walleye, about 30% have walleye populations supported primarily by stocking. To estimate the contribution of stocked walleyes to the population, we needed to know the origin (wild or hatchery) of all age-0 or age-1 walleyes. We did this by restricting our data set to lakes whose walleye populations were fully supported through stocking (i.e., we excluded lakes with any natural reproduction by walleyes).

TABLE 1.—Number of juvenile walleyes stocked per hectare in June and estimated number of age-0 walleyes per hectare in the fall in lakes in northern Wisconsin whose walleye populations are supported entirely through stocking.

Lake	County	Area (ma)	Year	Number stocked/ha	Age-0 walleyes/ha
Poskin	Barron	61	2002	124	1.26
Diamond	Bayfield	138	2000	124	0.09
Poquettes	Burnett	39	1998	131	0.03
Lipsett	Burnett	159	2002	134	0.44
Big McKenzie	Burnett	480	1999	91	2.28
Red	Douglas	104	1994	62	0.37
Fay	Florence	100	1998	140	7.25
Stevens	Forest	120	2002	123	4.72
Boot	Iron	78	1992	185	65.92
Mercer	Iron	74	1989	247	0.01
Fisher	Iron	183	2000	132	0.03
Long	Oneida	46	1999	248	0.05
Lower Kaubashine	Oneida	76	1996	127	1.49
Jennie Webber	Oneida	91	2002	124	0.16
Gilmore	Oneida	122	2001	248	0.07
Pickerel	Oneida	298	1989	217	0.03
Thunder	Oneida	716	1997	63	0.00
Magnor	Polk	91	2000	124	0.14
Half Moon	Polk	234	2000	247	0.00
Big Round	Polk	411	1991	203	0.03
Musser	Price	228	2002	124	0.28
Amacoy	Rusk	113	1999	247	0.01
Kathryn	Taylor	25	1999	124	0.02
Alma	Vilas	22	1999	134	0.11
Brandy	Vilas	45	2001	254	0.03
Towanda	Vilas	59	2001	124	8.96
Sparkling	Vilas	62	2001	101	0.77
Muskellunge	Vilas	110	1994	60	6.75
Pickerel	Vilas	119	2001	118	0.02
Dead Pike	Vilas	120	2002	124	0.09
Deerskin	Vilas	125	2002	124	1.56
Found	Vilas	132	1998	246	3.95
Upper Gresham	Vilas	148	2002	124	0.73
Allequash	Vilas	172	1991	57	0.00
Lost	Vilas	220	2002	124	8.77
Cable	Washburn	75	1997	247	0.02
Horseshoe	Washburn	79	1991	64	0.38
Island	Washburn	112	1997	247	0.10
Gilmore	Washburn	157	2000	159	3.02

Determining an optimal stocking rate requires information collected from lakes stocked at a wide range of stocking densities. Guidelines of the Wisconsin Department of Natural Resources (WDNR) suggest stocking juvenile walleyes into lakes at a density of 124/ha. Although many lakes were stocked at the recommended density of 124/ha, several lakes were also stocked at densities higher and lower than recommended (range = 57–254/ha; Table 1).

Data collection.—Abundance of age-0 walleye in fall was estimated in 39 lakes during 1989–2002 by electrofishing the entire shoreline of each lake, including islands, when water temperatures were between 7°C and 18°C (September–October). All age-0 and age-1 walleyes were collected and measured. Scale samples were collected from juvenile walleye that encompassed the expected length breakpoint between age-0 and age-1 walleyes (e.g., 18–23 cm) to facilitate separation of the two age-classes. Numbers of age-0 walleyes captured in each lake were divided by the shoreline length sampled in each lake to calculate age-0 population catch per effort (Hansen et al. 2004). We estimated age-0 walleye density in each lake using the relationship between catch per effort from fall electrofishing surveys and density of age-0 walleye developed by Hansen et al. (2004). Specifically, we used the following equation:

$$W = 0.0852 \cdot (N \cdot 1.61)^{1.564},$$

where W is the number of age-0 walleyes per hectare, and N is the number of age-0 walleyes caught

TABLE 2.—Number of juvenile walleyes stocked per hectare in June and estimated number of age-1 walleyes per hectare in the following fall in lakes in northern Wisconsin whose walleye populations are supported entirely through stocking.

Lake	County	Area (ha)	Survey year	Number stocked/ha	Age-1 walleyes/ha
English	Ashland	99	1995	125	0.99
Diamond	Bayfield	138	2001	124	0.10
Lipsett	Burnett	159	2001	124	0.15
Fisher	Iron	166	2000	145	0.54
Mercer	Iron	74	2000	247	0.54
Mayflower	Marathon	40	2000	124	0.54
Julia	Oneida	162	2000	124	0.59
Long	Oneida	46	1998	65	1.97
Half Moon	Polk	234	2000	247	0.05
Magnor	Polk	94	2001	120	0.20
Amacoy	Rusk	113	2000	247	0.15
Black Oak	Vilas	236	2001	124	0.05
Circle Lily	Vilas	90	1995	122	1.28
Deerskin	Vilas	125	1993	57	1.13
Moon	Vilas	53	1999	245	2.66
Muskellunge	Vilas	110	1995	60	1.28
Wildcat	Vilas	123	1995	126	3.55
Little Sand	Washburn	30	1998	124	3.20

per kilometer of electrofishing. The equation we used to estimate age-0 walleye density was the same as the equation suggested by Hansen et al. (2004) except terms have been altered to convert to metric units.

Similarly, we estimated age-1 walleye density in a different set of 18 lakes using the relationship between catch per effort from fall electrofishing surveys and density of age-1 walleye developed by Serns (1983), namely,

$$W = 0.821 \cdot N,$$

where W is the number of age-1 walleyes per hectare, and N is the number of age-1 walleye caught per kilometer of electrofishing. The equation we used to estimate age-1 walleye density was the same as the equation suggested by Serns (1983) except terms have been altered to convert to metric units.

The number of juvenile walleyes stocked into each lake was determined by calculating the mean weight of fingerlings in a given hatchery pond and then stocking the number of kilograms that yielded the desired number of walleyes to be stocked into the lake. A sample of several hundred walleyes from each hatchery pond was weighed cumulatively and then enumerated. The mean weight per walleye was then used to estimate the weight corresponding to the appropriate number of juvenile walleyes to be stocked. Although the number of walleyes stocked is estimated with some error, the measurement error for numbers of walleyes stocked is much less than that of population densities estimated from sampling (e.g., electrofishing surveys). Therefore, we treated the number stocked as being measured without error. Juvenile walleyes were stocked in June and were approximately 5 cm in length. We divided the number of walleyes stocked in each lake by the area of the lake so that stocking densities and age-0 and age-1 population densities were in the same units (number/ha). Of the 39 lakes included in our analysis of age-0 recruitment, 14 were sampled in more than 1 year. Similarly, of the 18 lakes included in our analysis of age-1 recruitment, three were sampled in more than 1 year. To reduce the possibility that one lake might unduly influence the analysis, we randomly selected one survey from each lake with multiple surveys for analysis.

Recruitment modeling.—We used a Ricker stock–recruitment model to describe the relationship between density of juvenile walleyes stocked (S) and density of age-0 or age-1 walleyes in the fall (R). We chose the Ricker model to determine if compensatory density-dependent mortality was likely. In particular, we were interested in testing whether high stocking rates yielded a low number of total recruits, which can be determined by examining the β coefficient in the Ricker equation (Quinn and Deriso 1999). We used the following form of the Ricker stock–recruitment model:

$$R = \alpha S e^{-\beta S - cX},$$

where R is the estimated number of age-0 or age-

1 walleyes per hectare in fall, S is the number of juvenile walleyes stocked per hectare, α describes the survival from stocking to fall at low stocking rates, β describes the rate at which survival from stocking to fall declines with stocking rate, and c describes the influence of other explanatory variables X on poststocking survival.

We attempted to describe residual variance in the relationship between numbers of stocked walleyes and numbers surviving to fall with variables that have been associated with juvenile walleye survival. Spring water temperatures explain a significant amount of variation in the relationship between walleye stock size and number of recruits (Madenjian et al. 1996; Hansen et al. 1998), but spring water temperatures were not available for our study lakes. However, Beard et al. (2003) found that calendar year, a surrogate for climatic effects, also described a significant amount of residual variance in the stock–recruitment relationship for 162 northern Wisconsin lakes with self-sustaining walleye populations. Although spring water temperatures are unlikely to affect survival of walleyes stocked in summer, we used calendar year as a potential explanatory indicator variable for annual climatic effects that may affect the survival of stocked walleyes. Nate et al. (2003) used lake depth and lake area to discriminate between lakes with and without walleyes and suggested that these variables represented physical factors important to the survival of walleyes. Therefore, we examined mean lake depth and lake area as explanatory variables in our analysis.

We transformed the Ricker model to its linear form to estimate model parameters, namely,

$$\log_e(R/S) = a - \beta S + cX + \varepsilon,$$

where a equals $\log_e(\alpha)$, other terms are as previously defined, and ε is residual error. The addition of the error term (ε) in this form of the model treats the errors of the model as lognormally distributed, which is a common assumption supported by empirical data and theoretical arguments (Hilborn and Walters 1992; Haddon 2001). This form of the model allows model parameters (a, β, and c) to be estimated by multiple linear regression (Hilborn and Walters 1992; SPSS 2000). A significant negative value for β suggests compensatory density-dependent survival, a significant positive value for β suggests depensatory density-dependent survival, and a nonsignificant value for β suggests density-independent survival (Hilborn and Walters 1992). We used an alpha level of 0.05 to judge significance. Partial correlations between residuals and environmental explanatory variables (including all two-way interaction terms) were tested as each was added to ($P \leq 0.05$) or removed from ($P > 0.05$) the model (SPSS 2000). The value of the stocking rate at which age-0 or age-1 population density is maximized in autumn occurs at $1/\beta$, and the maximum return associated with this stocking rate is $\alpha/\beta \cdot e^{-1}$(Ricker 1975).

Several age-0 and age-1 walleye electrofishing surveys caught no walleyes; this posed a problem when estimating the stock–recruitment relationship as defined above because $\log_e(R/S)$ is undefined when R equals 0. However, lakes with zero walleye recruits in the first fall must be included to accurately predict the optimal stocking rate. A common solution to this problem is to add one or another arbitrarily small number to the term being transformed (Zar 1984). In our case, however, the ratio of age-0 or age-1 walleyes per hectare (R) to stocked walleye per hectare (S) was often quite small, so adding one or another small number would substantially affect parameter estimate values for the relationship. Consequently, to transform survey catches of zero walleyes so they were defined but were affected as little as possible by the transformation, we added one to the total catch of age-0 or age-1 walleyes in each survey. Essentially, this transformation reduced the value of recruits per hectare to the detection limit of electrofishing surveys. Adding one to the total walleye catch in each lake changed the estimated density (number/ha) by a slightly different amount in each lake since walleye density was estimated based on the number of juvenile walleyes captured per kilometer of shoreline by electrofishing (Hansen et al. 2004). Therefore, the estimated population density depended on the total length of shoreline sampled in each lake. We felt that the addition of one walleye to the total number captured in each lake would have little effect on the value of $\log_e(R/S)$ and represented a biologically meaningful transformation (i.e., one walleye was the smallest number other than zero that could have been sampled).

Results

The density of juvenile walleyes stocked in summer explained 16% of the variation in age-0 walleye population density in autumn ($F = 7.07$; df = 1, 37; $P = 0.01$; Figure 1). The estimated equation was

$$R = 0.01971Se^{-0.01664S}.$$

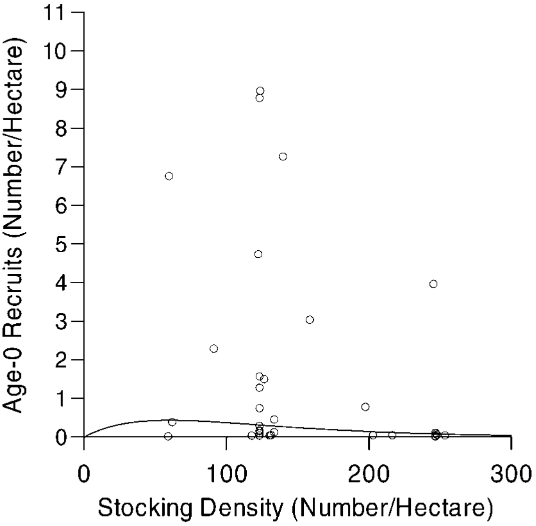

FIGURE 1.—Number of age-0 walleyes as a function of juvenile walleye stocking density in northern Wisconsin lakes whose walleye populations are sustained by stocking. Stocking density and age-0 recruit data were collected in 1989–2002. The Boot Lake data point was excluded for visual clarity.

The β coefficient was negative and significant, which suggests density-dependent mortality as fewer age-0 walleyes were produced at both high and low stocking densities. The optimal stocking rate (i.e., the stocking rate that resulted in the highest number of age-0 walleyes in autumn) occurred at 60 walleyes/ha. The 95% confidence interval for the optimal stocking rate (i.e., the 95% confidence interval for β) was 34–253 walleyes/ha. The maximum return associated with the optimal stocking rate of 60 walleye/ha was 0.4 walleyes/ha, which translates to a 0.7% survival rate from time of stocking in June to sampling in September–October. The 95% confidence interval for the maximum return was 0.03–14.94 age-0 walleyes/ha. Of the environmental variables that we explored to describe residual variation in the relationship between stocking density and fall age-0 density, none added significantly to the model.

The density of juvenile walleyes stocked in the previous summer explained 28% of the variation in age-1 walleye population density in autumn ($F = 6.18$; df = 1, 16; $P = 0.02$; Figure 2). The estimated equation was

$$R = 0.02683Se^{-0.01327S}.$$

The β coefficient was negative and significant, which suggests density-dependent mortality as fewer age-1 walleyes were produced at both high and low stocking densities. The optimal stocking rate occurred at 75 walleyes/ha. The 95% confidence interval for the optimal stocking rate was 41–510 walleyes/ha. The maximum return associated with the optimal stocking rate of 75 walleye/ha was 0.74 age-1 walleyes/ha. The 95% confidence interval for the maximum return of age-1 walleyes was 0.09–28.79 walleyes/ha.

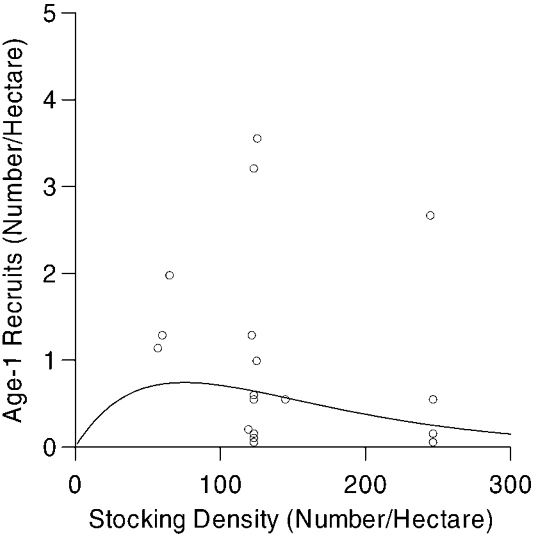

FIGURE 2.—Number of age-1 walleyes as a function of juvenile walleye stocking density in northern Wisconsin lakes whose walleye populations are sustained by stocking. Stocking density and age-0 recruit data were collected in 1993–2001.

Among the environmental variables we tested, only the lake area added significantly to the model. The model that included H explained 65% of the variability in age-1 density ($F = 13.73$; df = 2, 15; $p < 0.001$). The estimated equation was

$$R = 0.1396Se^{-0.01174S-0.01605H}.$$

The relationship between lake size and age-1 walleye density is negative, which suggests that survival is lowest in lakes that are large and highest in lakes that are small (Figure 3).

Discussion

We use the term ‘‘optimal stocking rate’’ to indicate the stocking rate that yields the highest number of recruits per hectare. Fish stocking is conducted for various reasons, and maximizing the number of recruits may not always be the goal of a stocking program. However, for propagation of endangered species, the importance of this optimization is apparent. Determining the optimal

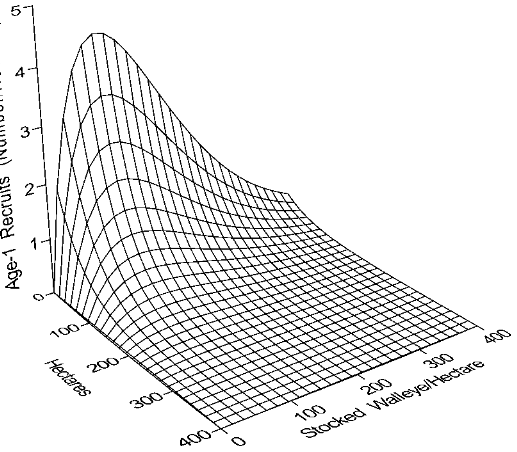

FIGURE 3.—Number of age-1 walleyes as a function of juvenile walleye stocking density and lake area in northern Wisconsin lakes whose walleye populations are sustained by stocking.

stocking rate is also important for economic reasons. The mean cost to produce an adult walleye through stocking in Wisconsin is US$7.44 (WDNR 1999). If thousands of walleyes are stocked in any lake and hundreds of lakes in Wisconsin are stocked with walleyes, the total cost of stocking can be substantial. Similarly, costs of other species of stocked fish (such as Chinook salmon *Oncorhynchus tshawytscha*) range to over $200 per adult return (IEAB 2002). Given the relatively high cost of adult fish produced through stocking, the need to determine the optimal stocking rate is of obvious financial importance.

Our model indicates significant density dependence in poststocking survival of stocked walleyes. Density dependent mortality occurs in many self-sustaining fish populations of many species (Myers and Cadigan 1993; Myers et al. 1997), and also occurs with stocking density in individual waters (McKeown et al. 1999; Sutlea et al. 2004). Our findings agree with those of McKeown et al. (1999), who suggested that carrying capacity may limit the success of stocked fish if the stocking density is above some level in any individual water. Our results suggest that density-dependent mortality associated with walleye stocking rate may be generalized across waters.

We found that the greatest number of age-0 walleyes/ha was produced in Wisconsin lakes at a stocking density of 60 age-0 walleyes/ha, and the greatest number of age-1 walleyes was produced at a stocking density of 75 age-0 walleyes/ha. The optimal stocking rates we found are somewhat close to the stocking rate used most often by the WDNR (124 juvenile walleyes/ha; WDNR 1999). Although the confidence intervals for the optimal stocking rates for walleye are wide, the point estimates are still the most likely rate to result in the maximum return.

Estimates of the optimal stocking rate that results in the highest number of age-0 recruits (60 walleyes/ha) is similar to the optimal stocking rate that is expected to produce the highest number of age-1 recruits (75 walleyes/ha). Given that estimates for the optimal stocking rate for age-0 and age-1 walleyes were calculated from different surveys and often in different lakes and years, the similarity of the optimal stocking rates associated with age-0 and age-1 walleyes suggests that the most appropriate stocking rate is near 75 juvenile walleyes/ha. In addition, the similarity of optimal stocking rates for age-0 and age-1 walleyes suggests that whatever mechanism causes density dependence for age-0 walleyes is still apparent when the walleyes are age 1. The similarity of the optimal stocking rates for age-0 and age-1 walleyes appears to conflict with one of the findings of Johnson et al. (1996) who found that survival to age 1 was not predicted by survival to first fall because of occasionally high overwinter survival. However, the lack of the ability of age-0 walleye survival to predict survival to age 1 may certainly exist in individual lakes (such as those examined by Johnson et al. [1996]), but across many lakes, the survival of age-0 walleyes seems to be associated with survival to age 1.

The fact that the relationship between stocking rate and survival of juvenile walleyes is stronger for age-1 walleyes than for age-0 walleyes may suggest that the density-dependent mechanism is present during the walleyes' first summer but continues to act between their first and second fall. The suggestion that the density-dependent mechanism intensifies between the walleyes' first and second fall agrees with the findings of Forney (1976) who suggested that higher growth rates are associated with high survival of walleyes through their first winter, and the findings of Fox and Flowers (1990) who found that age- 0 walleye growth was density dependent. In addition, Johnson et al. (1996) suggest that the first winter experienced by juvenile walleyes may result in high mortality. If high stocking rates decrease walleye growth, the associated mortality is likely to be the strongest during the first winter, thereby increasing the strength of the relationship between initial stocking density and the total number of recruits.

Survival of stocked juvenile walleyes to their second fall may have been lower in large lakes than in small lakes because more predator species were present in larger lakes. Species diversity is positively related to area of aquatic (Barbour and Brown 1974; Matuszek and Beggs 1988; Robinson and Tonn 1989) and terrestrial systems (MacArthur and Wilson 1967; Gotelli 1998). As species diversity increases, the diversity of piscivorous fishes likely increases. Nate et al. (2003) suggested that community structure may play a role in determining whether a walleye population was supported through natural reproduction or stocking. In particular, Nate et al. (2003) suggested that the absence of predators such as largemouth bass *Micropterus salmoides* and northern pike *Esox lucius* was associated with lakes whose walleye populations were sustained by natural reproduction rather than stocking. Santucci and Wahl (1993) found that predators such as largemouth bass limited the success of stocked walleyes. In addition, Johnson et al. (1996) suggested that predator density may limit the survival of stocked walleyes. Therefore, because piscivorous fish are thought to play a role in the survival of walleyes, stocked walleye survival may be limited by predation in large lakes.

In contrast to Madenjian et al. (1996), Hansen et al. (1998), and Beard et al. (2003), we did not find evidence of year effects (i.e., a surrogate for climatic effects) on the survival of stocked juvenile walleyes. Because juvenile walleyes in our study were stocked in June, climatic effects that are often associated with juvenile year-class strength, such as the spring warming rate (Madenjian et al. 1996) or May temperature variation (Hansen et al. 1998), occurred prior to the time of stocking in our study.

Other stock–recruitment models could be used to describe the relationship between stocking density and the number of recruits depending on the best fit and biology of the particular species (Hilborn and Walters 1992). We chose to use the Ricker stock–recruitment model for walleyes in northern Wisconsin because the lakes were all closed to immigration and emigration and we expected that stocked fish were likely to interact with each other and potentially cause ‘‘overcompensation’’ (Hilborn and Walters 1992). The Ricker stock–recruitment model also fit our data relatively well. The amount of variation in age-1 walleye population density explained by age-0 stocking density (28%) was similar to or higher than that of other studies where walleye recruit density was modeled as a function of adult population density (e.g., Madenjian et al. 1996; Hansen et al. 1998; Beard et al. 2003).

Lakes differ in size, productivity, species composition, degree of natural walleye production, and other factors that lead to variation in the carrying capacity of walleyes. Therefore, optimal stocking rates for specific lakes may be higher or lower than 75/ha. In lakes with self-sustaining walleye populations, stocked walleyes may not add to the walleye population at all (Li et al. 1996) possibly due to a limited carrying capacity for juvenile walleyes. If carrying capacity is limited, optimal stocking rates in lakes with some natural reproduction would likely be much lower than 75/ha. However, most of the lakes stocked with walleyes in Wisconsin are exclusively or heavily dependent on walleye stocking. Our analysis demonstrates generalities among lakes, such that stocking age-0 walleyes at a rate higher or lower than approximately 75/ha across all lakes would likely lead to fewer age-1 walleyes in the autumn of the following year.

Management Implications

We conclude that stock–recruitment models are useful for estimating the optimal stocking rate, are broadly applicable, and can avoid three common problems in stock–recruitment modeling: (1) a lack of contrast in the number of spawners, (2) too few data points, and (3) errors in measurement of stock size (Hilborn and Walters 1992). Lack of contrast in the number of fish stocked is more easily controllable than the number of spawners. Though the decision to stock fewer or more fish in particular lakes may be complicated and potentially politically unpopular, the advantage of obtaining large contrast in stocking densities minimizes the effects of environmental stochasticity and makes this approach to estimating optimal stocking rates appealing. Historically, stock–recruitment relationships have depended on relatively long time series of spawner recruit estimates. Determining the optimal stocking rate using multiple populations could potentially be accomplished in a single year. Finally, errors in the measurement of stock size can obscure the underlying stock–recruitment relationship (Walters and Ludwig 1981). When stocked fish are treated as the ‘‘spawners,’’ the stock size is known with little error. The utility of this method seems applicable in any situation where multiple populations of a fish species occur.

Based on our results, we suggest a stocking rate of 75 small fingerling walleyes/ha. Stocking at rates higher or lower than 75/ha will result in fewer age-1 walleyes in northern Wisconsin. Stocking juvenile walleyes at 60/ha will maximize their survival to their first fall, and stocking juvenile walleyes at 75/ha will maximize their survival to their second fall. The goal of stocking is generally to produce harvestable fish. Since age-1 fish are closer to harvestable length than age-0 fish, it seems more appropriate to stock at a rate that maximizes survival of walleyes to age 1.

Finally, we suggest that alternate stocking strategies may be necessary in larger lakes in order for a reasonable number of juvenile walleyes to survive to age 1. If predation limits the success of small fingerling walleyes in large lakes, it may be necessary to stock in ways to eliminate the impact of predation. Stocking adult walleyes, though expensive, would likely have the most success in this regard.

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