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# The Relationship of Bluegill Population Dynamics and Submerged Aquatic Vegetation in Minnesota Lakes[1]

Cynthia M. Tomcko
Minnesota Department of Natural Resources
Division of Fish and Wildlife
1201 East Highway 2
Grand Rapids, Minnesota 55744 USA

and

Donald L. Pereira
Minnesota Department of Natural Resources
Division of Fish and Wildlife
500 Lafayette Road
St. Paul, MN 55155 USA

*Abstract*. —Increasing shoreland development is altering submerged aquatic vegetation with potential negative effects on fish species dependent on submerged vegetation, such as bluegill. We evaluated the relationship of bluegill growth, recruitment, size structure, mortality, maturity, production, and relative abundance to submerged aquatic vegetation species richness, quality, value to fish and occurrence using data from 2,571 surveys on Minnesota lakes to better understand how bluegill population dynamics are affected by alterations in submerged aquatic vegetation. Bluegill populations exhibited fast juvenile growth, high mortality and production in lakes where plant communities were less susceptible to disturbance and had low diversity, compared to diverse, susceptible plant communities. Adult bluegill grew faster in diverse, susceptible plant communities. The susceptibility and diversity of submerged aquatic vegetation communities explained variation in bluegill growth, mortality, and production based on Akaike and Bayes Information Criteria. These results serve to clarify the relationships between bluegill population dynamics and submerged aquatic vegetation, and provide a foundation for further research into causal mechanisms.

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Lakeshore is being developed at an increasing rate in Minnesota (Kelly and Stinchfield 1998; Jakes et al. 2003; Radomski and Schultz 2006), with potential negative effects on the nearshore habitat used by fish. Engel and Pederson (1998) reported that as lakeshore was developed, lakeshore owners removed riparian vegetation, including submerged aquatic vegetation, in an attempt to 'improve' the shoreline. Declines in emergent and floating-leaf aquatic vegetation have been documented at developed lakeshores in Minnesota (Radomski and Goeman 2001) and Wisconsin (Meyer et al. 1997). In addition, excessive phosphorus loading in developed watersheds resulting from increased amounts of impervious surfaces and replacement of shoreline vegetation with lawn (Waschbucsh et al. 1999) promotes the growth of dense aquatic vegetation. Given the importance to fish of submerged aquatic vegetation for predator refuge (Werner et al. 1983; Werner and Hall 1988), feeding (Engel 1985; Keast et al.1978; Keast 1985; Osenberg et al. 1994), spawning (Scott and Crossman 1973), and nursery habitat (Bryan and Scarnecchia 1992; Brazner and Beals 1997), altered submerged aquatic vegetation due to shoreland development is expected to have negative impacts on fish population dynamics.

Bluegill *Lepomis macrochirus* are dependent throughout their life cycle on submerged aquatic vegetation. Bluegill nests are typically excavated in the littoral zone of lakes (Scott and Crossman 1973; Beard 1982; Schneider 1993), confining male bluegill to the littoral zone where they guard eggs and fry (Gross 1982; Bain and Helfrich 1983). Juvenile bluegill migrate to the littoral zone (Beard 1982) to feed on the macroinvertebrates (Gerking 1962; Engel 1985; Werner and Hall 1988; Schramm and Jirka 1989) concentrated in submerged aquatic vegetation (Gerking 1962; Gilinsky 1984; Engel 1985). Juvenile bluegill remain in submerged vegetation to reduce predation risk (Werner et al. 1983; Werner and Hall 1988; Shoup et al. 2003), choosing the densest vegetation available (Gotceitas and Colgan 1987). Though adult bluegill feed on limnetic zooplankton (Werner and Hall 1988), they feed heavily on epiphytic macroinvertebrates in some lakes (Schramm and Jirka 1989). The dependence of bluegill on submerged aquatic vegetation makes it likely that bluegill population dynamics will respond to altered submerged aquatic vegetation.

The relationship of bluegill population dynamics, such as relative abundance and production, to submerged aquatic vegetation has been studied previously. Bluegill relative abundance (DiConstanzo 1957; Hinch and Collins 1993; Hayse and Wissing 1996; Cross and McInerny 2001; Carden 2002; Cross and McInerny 2005) and production (Wiley et al. 1984) increased with submerged aquatic vegetation in most studies. In contrast, Paukert et al. (2002), who focused on dynamics of large bluegill, and Hatzenbeler et al. (2000) found bluegill relative abundance unrelated to submerged vegetation cover. Large, tagged male bluegill selected emergent vegetation instead (Paukert and Willis 2002).

Bluegill growth was also related to submerged aquatic vegetation. Most research focused on the relationship of bluegill growth to vegetation density, or related aspects such as coverage, rather than vegetation diversity. Bluegill have been found to grow slowly in dense vegetation; however, conflicting information has been collected about the density that supported fast growth. Crowder and Cooper (1979) found bluegill grew fast at intermediate densities of aquatic vegetation. In contrast, other studies show bluegill growth was negatively related (Theiling 1990; Cheruvelil et al. 2005) or unrelated (Engel 1985; Savino et al. 1992; Hayse and Wissing 1996) to submerged vegetation estimates.

Abundance and thus growth of bluegill is likely related to submerged vegetation density because vegetation affects predator-prey interactions. Dense vegetation reduced the predatory success of largemouth bass *Micropterus salmoides* (Savino and Stein 1982; Gotceitas and Colgan 1989), but not esocid predators (Tomcko et al. 1984, Savino and Stein 1989). Dense vegetation also reduced bluegill vulnerability to bass predation (Savino and Stein 1982) and predation risk (Hayse and

Wissing 1996). Bluegill consumption of invertebrate prey was reduced in dense vegetation (Crowder and Cooper 1979). Plant structure mediated bluegill predator-prey interactions, both bass predation on bluegill (Valley and Bremigan 2002) and bluegill predation of invertebrates (Engel 1985). Bluegill predation was reduced in leafy compared to cylindrical vegetation (Dionne and Folt 1991), and foraging duration was reduced in *Potamogeton robbinsii* and *P. illinoensis* compared to *Ceratophyllum demersum* (Harrel and Dibble 2001). Bluegill predation was reduced even though invertebrates were more abundant in vegetation with high biomass (Cyr and Downing 1988) and dissected leaf architecture (Cheruvelil et al. 2000).

Other research evaluated how removal of dense submerged vegetation affected bluegill population dynamics. The effects were inconsistent, possibly because of different locations and experimental conditions. Bluegill condition (Colle and Shireman 1980) and relative abundance (Bettoli et al. 1993) declined when submerged vegetation was removed. However, other research found that bluegill relative abundance, size structure, and/or growth was unaffected by the harvest of aquatic vegetation (Cross et al. 1992; Radomski et al. 1995; Slade 2005), or that growth and size structure were improved when aquatic vegetation was eliminated with herbicide (Pothoven et al. 1999). Submerged vegetation harvested in a channelized pattern increased largemouth bass predation on bluegill (Smith 1995), improved the growth of bluegill aged 3-4 (Olson et al. 1998), and improved bluegill survival and population size structure, but not growth (Unmuth et al. 1999). The number of lakes used for harvest experiments is often limited because of the expense, and the logistical and political difficulties in manipulating aquatic vegetation in lakes. Yet, a large sample size is critical to effectively reduce the variability.

Expanding the scope of previous studies to include a large sample of lakes from a broad geographical area using data from Minnesota's lake surveys would address the problems inherent in smaller-scale experimental manipulations of vegetation in lakes, clarify the magnitude of different sources of variation in bluegill population dynamics, and contribute to understanding the general relationships between aquatic vegetation and bluegill population dynamics. We used data collected from bluegill sampled in Minnesota lake surveys to evaluate the relationships among bluegill population dynamics and submerged aquatic vegetation on a broad scale (Schlagenhaft 1993). We evaluated bluegill growth, relative abundance, recruitment, size structure, mortality, maturity, and production. The estimates of submerged vegetation we used included plant species richness, the floristic quality index (FQI), an index developed to estimate plant density, and the frequency of occurrence of plant species. We hypothesized that bluegill population dynamics would be related to the diversity and amount of vegetation in a lake, negatively impacted by dense or sparse vegetation, and enhanced by intermediate densities of diverse vegetation. The relationships between bluegill population dynamics and submerged aquatic vegetation, and the relative importance of aquatic vegetation compared to other factors affecting bluegill population dynamics were explored in this study. The results could be used to enhance bluegill growth rates, and develop management strategies for producing harvestable-sized bluegill.

## Methods

Fish were collected by Minnesota Department of Natural Resources' (MNDNR) fisheries staff during 2,571 lake surveys conducted on 1,477 Minnesota lakes from 1982-1997 (Schlagenhaft 1993). Bluegill were sampled from 19 mm bar mesh trap nets, weighed, measured for total length, and had scales removed for age analysis. Trap netting was conducted using standardized procedures (Schlagenhaft 1993) to reduce measurement error among collectors.

Previous papers (Tomcko and Pierce 1997, 2001, 2005) described three of the bluegill population dynamics estimated - growth, recruitment, and population size structure. Measures of growth were mean back-calculated lengths at ages 2-6 (Tomcko and Pierce 1997, 2001), and mean growth increments for ages 1-6. We estimated bluegill recruitment as relative density (numbers/trap net night), ages 2-6, using year class strength indices (YCSI) developed for walleye by Li et al. (1996) and adapted for bluegill (Tomcko and Pierce 2005). Relative stock density (RSD; Anderson and Gutreuter 1983) was used as an index of population size structure (Tomcko and Pierce 2005).

We estimated mortality using three methods. First, instantaneous total mortality was calculated using a maximum age equation derived for all taxonomic groups (Hoenig 1983). Second, instantaneous total mortality was estimated from the slope of catch-at-age curves (Ricker 1975), using samples containing more than 100 bluegills (*N* = 559). Third, natural mortality was derived from mean annual air temperature and von Bertalanffy parameters using the model developed by Pauly (1980). Mean annual air temperatures were estimated for each lake in the year the survey was conducted, by spatially joining lake locations to temperature grids created by G. Spoden (climatologist, Minnesota State Climatology Office, MNDNR). We estimated von Bertalanffy parameters for individual bluegill using FishParm software (Prager et al. 1987), which was adapted to accept files of annuli data. Parameters for individual bluegill were used to preserve individual growth differences. We calculated omega ($L_{infinity} * K$; Gallucci and Quinn 1979), which has been recommended as an index of growth because of the interdependence of von Bertalanffy parameters.

We estimated age-at-maturity using three techniques. First, we estimated age-of-maturity as the inflection point of the age-length curve (Trippel and Harvey 1991), when bluegill divert energy from growth to reproduction. We found the age at the inflection point using the first derivative of the von Bertalanffy curve. We set the slope of the tangent at the point to the value of the slope that best approximated age-of-maturity for bluegill of know maturity. Second, age-of-maturity was estimated using He and Stewart's (2001, 2002) age-at-first-reproduction, $t_R$, for invertebrate-eating fish. Third, a series of eight piecewise linear models were compared to estimate the breakpoint of two lines fit to the age-length curve (Barrowman and Myers 2000). We set the first model breakpoint at age 2, the next at age 3, and so on until the last model breakpoint was set at age 9. The age for the model with the lowest error sum of squares was the estimated age-of-maturity. We attempted to validate all three maturity estimates (Appendix 1) using aged bluegill whose maturity status had been determined by dissection (Drake et al. 1997).

Production was estimated from the morphoedaphic index, MEI (Ryder et al. 1974), CPUE * growth, biomass * growth, and an adaptation of the Habitat Productivity Index (HPI; Randall et al. 1996) for bluegill. Few estimates of mean depth were available to calculate MEI (*N* = 68) so we estimated mean depth as maximum depth/3. Biomass equaled CPUE times mean bluegill weight in kg. HPI is the product of bluegill biomass and a production/biomass ratio for bluegill, which was derived by Randall and Minns (2000).

We estimated various aspects of submerged vegetation using plant species richness (Spp), FQI (Nichols 1999), and a value index (VI) that we developed. We also evaluated the correlation of the frequency of occurrence of common plant species and bluegill population dynamics. Estimates of the frequency of occurrence and relative abundance of the plant species were obtained from aquatic vegetation surveys made by MNDNR fisheries staff, 1993-2002. Staff estimated the relative abundance of aquatic plant species at 5 m points along transects, regularly spaced around a lake. The frequency of occurrence for a plant species equaled the number of transects where a species was present divided by the total number of transects. We obtained estimates of plant species richness and FQI (D. Perleberg, MNDNR, personal communication), which is composed of an estimate of a species response to disturbance and the square root of species richness. FQI was developed to estimate disturbance of a plant community, and has been used to designate lakes of outstanding quality (Nichols 1999). We developed a value index (VI) to estimate biovolume (Thomas et al. 1990), an estimate of plant density and the value of plants to bluegill. We hypothesized that plants would have higher value to bluegill and enhance their dynamics if plant density was intermediate and if plant species had high biovolume, typically filled the water column. For each plant species surveyed, we assigned scores for relative abundance, frequency of occurrence, and value. We assigned high scores to plant species occurring at intermediate relative abundance and frequency. We assigned value scores to a plant species based on knowledge of their growth form and structure, and our understanding of bluegill predator-prey interactions in vegetation. We assigned a value of 4 to plant species that fill the water column, have large or dissected leaves that support abundant prey, and provide a visual barrier from predators (eg. *Potamageton* spp., *Myriophyllum sibiricum*, and coontail *Ceratophyllum demersum*). A species scored a 3 if it had small leaves (e.g. *Ranunculus* spp.) or incompletely filled the water column (e.g., *Polygonum*, *Sagittaria*, or *Zosterella* spp.). Species scored a 2 if they had narrow leaves (e.g., *Vallisineria americanus, Scirpus* spp.), incompletely filled the water column, or primarily consisted of stem (e.g., *Nuphar* spp., *Brasenia schreberi*, *Nymphaea odorata*). A species scored a 1 if they had small leaves and filled little of the water column (e.g. *Chara* (muskgrass), *Nitella*, *Isoetes*, or *Najas* spp.). We summed occurrence, relative abundance and value scores for each plant species encountered in the survey, and then summed the scores for all plant species surveyed to create the VI for each lake. To evaluate a different scoring scheme, we increased the value of low relative to intermediate relative abundance and frequency of occurrence. We also evaluated what plant species occurred in lakes of different FQI by comparing frequency of occurrence for common plant species between lakes that had FQI $\leq$ 10 or $\geq$ 30.

Associations between bluegill population dynamics and submerged aquatic vegetation were determined with Pearson correlation coefficients. The alpha level was reduced for multiple comparisons (Bonferroni adjustment; Trippel and Hubert 1990). For building multiple regression models, the square of the sample correlation coefficient for pairs of candidate independent variables was used as an approximate test for multicollinearity (Weisberg 1985). We assessed scatter plots and analyzed residuals to determine if transformations were required. Year class strength, relative stock density, total mortality derived from maximum age, MEI, HPI, and maximum depth were $\log_e$ transformed. Secchi depth was square-root transformed. Variables in models included bluegill population dynamics, submerged vegetation estimates, mean annual air temperature, lake morphometry, and water chemistry from MNDNR lake surveys (Tomcko and Pierce 2001, 2005). Models were chosen *a priori* based on available information. Analysis was exploratory; variables were removed from models *post hoc* if collinearity was suspected. Models were compared using Akaike Information Criteria (AIC) and Bayes Information Criteria (BIC; Burnham and Anderson 2002). The model with the lowest criterion had the greatest weight of evidence. Both AIC and BIC were reported because BIC does not overfit models with many variables, but may underfit models (Burnham and Anderson 2002). Comparison of models was possible only if data was available on all variables. This precluded examining the effect of fishing pressure, which has an important effect on bluegill population dynamics, but for which limited data exists. Only 86 sunfish fishing pressure estimates existed for the 2,571 surveys in the bluegill database and no pressure estimates were available for records used for modeling.

## Results

We estimated 32 bluegill population dynamic and three submerged aquatic vegetation variables from bluegill populations and vegetation sampled in 2,571 surveys in 1,477 lakes (Table 1). Data from nearly 70,000 individual bluegill were included in the analysis. Surveys occurred over a period spanning more than a decade, 1982-1997.

The three submerged vegetation variables were highly correlated (Spp vs FQI, $r$ = 0.95; Spp vs. VI, $r$ = 0.92; FQI vs VI, $r$ = 0.87). FQI tended to have stronger correlations with bluegill population dynamics (Table 2). When we changed the formulation of the value index, the correlation coefficient decreased between mean increment at age 2 and VI from –0.57 to –0.39, and between mean backcalculated length at age 3 and VI, from –0.54 to –0.36.

Table 1. Mean, standard deviation (SD), and number of surveys (*N*) for bluegill population dynamic and submerged aquatic vegetation variables. Bluegill population dynamic (BG pop dyn) variables included mean backcalculated length (XL) at ages 2-6, mean increment (XIncr) at ages 1-6, year class strength index (YCSI) at ages 2-6, relative stock densities for bluegill of 150 (NEWSD), 175 (RSDPM), 200 (RSDPR), 225 (RSDBIG), and 250 mm (RSDMEM), total mortality estimated using catch curves (Zcatch) and maximum age (ZmaxAge), natural mortality (PaulysM), maturity estimated using von Bertalanffy curves (MatVB), age at first reproduction ($t_R$), maturity estimated using piecewise linear models (MatPiece), morphoedaphic index (MEI), catch per unit effort * mean backcalculated length at age 3 (CPUE*XL3), biomass * mean backcalculated length at age 3 (BIO*XL3), and habitat productivity index (HPI). Submerged aquatic vegetation variables included plant species richness (Spp), floristic quality index (FQI), and value index (VI).

| Variable | Mean | SD | *N* |
|---|---|---|---|
| Length at age (mm) | | | |
| XL2 | 75.8 | 18.5 | 1,660 |
| XL3 | 105.5 | 26.7 | 2,136 |
| XL4 | 129.4 | 30.0 | 2,190 |
| XL5 | 149.6 | 29.4 | 2,169 |
| XL6 | 164.5 | 26.9 | 1,956 |
| XIncr1 | 32.5 | 13.0 | 2,528 |
| XIncr2 | 30.0 | 12.9 | 2,522 |
| XIncr3 | 30.3 | 10.8 | 2,497 |
| XIncr4 | 27.4 | 7.7 | 2,427 |
| XIncr5 | 23.6 | 6.0 | 2,286 |
| XIncr6 | 19.7 | 5.2 | 2,015 |
| YCSI at age | | | |
| YCSI2 | 3.4 | 10.1 | 2,142 |
| YCSI3 | 4.2 | 12.0 | 2,142 |
| YCSI4 | 4.5 | 15.6 | 2,142 |
| YCSI5 | 4.5 | 10.6 | 2,142 |
| YCSI6 | 4.5 | 10.4 | 2,142 |
| RSD | | | |
| NEWSD | 49.7 | 27.8 | 1,715 |
| RSDPM | 25.3 | 25.6 | 1,584 |
| RSDPR | 12.0 | 19.1 | 1,024 |
| RSDBIG | 8.8 | 16.6 | 349 |
| RSDMEM | 9.6 | 21.5 | 62 |
| Mortality | | | |
| Zcatch | 0.02 | 0.57 | 1,436 |
| ZmaxAge | 0.67 | 0.31 | 2,180 |
| PaulysM | 0.20 | 0.19 | 2,089 |
| Maturity (yrs) | | | |
| MatVB | 5.3 | 1.6 | 1,817 |
| tR | 3.7 | 0.3 | 1,817 |
| MatPiece | 4.0 | 0.7 | 1,737 |
| Production | | | |
| MEI (mg/l/m) | 83.6 | 120.8 | 502 |
| CPUE*XL3 | 421.5 | 669.3 | 1,719 |
| BIO*XL3 | 21.0 | 59.7 | 1,774 |
| HPI | 195.3 | 371.2 | 1,307 |
| CPUE (number/net) | 4.24 | 8.55 | 2,155 |
| Submerged aquatic vegetation | | | |
| Spp | 19.3 | 8.0 | 1,130 |
| FQI | 23.1 | 7.0 | 1,130 |
| VI | 151.2 | 64.2 | 459 |

Table 2. Pairwise correlation coefficients for bluegill population dynamic variables and submerged aquatic vegetation variables. Bluegill population dynamic (BG pop dyn) variables included mean backcalculated length (XL) at ages 2-6, mean increment (XIncr) at ages 1-6, year class strength index (YCSI) at ages 2-6, relative stock densities for bluegill of 150 (NEWSD), 175 (RSDPM), 200 (RSDPR), 225 (RSDBIG), and 250 mm (RSDMEM), total mortality estimated using catch curves (Zcatch) and maximum age (ZmaxAge), natural mortality (PaulysM), maturity estimated using von Bertalanffy curves (MatVB), age at first reproduction ($t_R$), maturity estimated using piecewise linear models (MatPiece), morphoedaphic index (MEI), catch per unit effort * mean backcalculated length at age 3 (CPUE*XL3), biomass * mean backcalculated length at age 3 (BIO*XL3), and habitat productivity index (HPI). Submerged aquatic vegetation variables included floristic quality index (FQI), plant species richness (Spp), and value index (VI). Significant correlations are designated by an asterisk (Bonferroni adjustment for 32 comparisons; $P < 0.0016$).

| | Submerged aquatic vegetation | | | | | |
|---|---|---|---|---|---|---|
| BG Pop Dyn | FQI | *N* | Spp | *N* | VI | *N* |
| Growth at age | | | | | | |
| XL2 | -0.58* | 761 | -0.52* | 761 | -0.50* | 305 |
| XL3 | -0.56* | 978 | -0.49* | 978 | -0.54* | 391 |
| XL4 | -0.49* | 979 | -0.42* | 979 | -0.51* | 390 |
| XL5 | -0.39* | 960 | -0.33* | 960 | -0.40* | 387 |
| XL6 | -0.22* | 862 | -0.17* | 862 | -0.22* | 360 |
| XIncr1 | -0.16* | 1,101 | -0.13* | 1,101 | -0.35* | 448 |
| XIncr2 | -0.58* | 1,096 | -0.50* | 1,096 | -0.57* | 447 |
| XIncr3 | -0.38* | 1,086 | -0.32* | 1,086 | -0.41* | 445 |
| XIncr4 | <0.01 | 1,053 | <0.01 | 1,053 | -0.09 | 431 |
| XIncr5 | 0.18* | 991 | 0.16* | 991 | 0.19* | 408 |
| XIncr6 | 0.18* | 871 | 0.18* | 871 | 0.28* | 363 |
| CPUE (#/trapnet) | 0.14* | 984 | 0.11* | 984 | 0.23* | 451 |
| YCSI at age | | | | | | |
| lnYCSI2 | -0.11 | 665 | -0.13* | 665 | 0.01 | 298 |
| lnYCSI3 | <0.01 | 854 | -0.02 | 854 | 0.07 | 384 |
| lnYCSI4 | 0.08 | 853 | 0.05 | 853 | 0.15 | 382 |
| lnYCSI5 | 0.12* | 835 | 0.08 | 835 | 0.20* | 380 |
| lnYCSI6 | 0.05 | 757 | 0.02 | 757 | 0.08 | 355 |
| RSD | | | | | | |
| lnNEWSD | -0.04 | 844 | -0.02 | 844 | 0.03 | 444 |
| lnRSDPM | -0.09 | 775 | -0.06 | 775 | -0.11 | 414 |
| lnRSDPR | -0.20* | 512 | -0.17* | 512 | -0.29* | 289 |
| lnRSDBIG | -0.21 | 160 | -0.20 | 160 | -0.32 | 92 |
| lnRSDMEM | -0.33 | 31 | -0.36 | 31 | -0.23 | 19 |
| Mortality | | | | | | |
| Zcatch | -0.16* | 662 | -0.12 | 662 | -0.12 | 258 |
| lnZmaxAge | -0.40* | 990 | -0.36* | 990 | -0.39* | 449 |
| PaulysM | -0.49* | 943 | -0.44* | 943 | -0.50* | 431 |
| Maturity | | | | | | |
| MatVB | -0.06 | 812 | -0.05 | 812 | <0.01 | 377 |
| $t_R$ | 0.41* | 812 | 0.37* | 812 | 0.44* | 377 |
| MatPiece | 0.08 | 780 | 0.03 | 780 | 0.02 | 363 |
| Production | | | | | | |
| lnMEI | -0.60* | 366 | -0.52* | 366 | -0.50* | 280 |
| lnCPUExGro | 0.04 | 853 | 0.01 | 853 | 0.13 | 383 |
| lnBioXGro | 0.13 | 528 | 0.11 | 528 | 0.19 | 227 |
| lnHPIkgPha | 0.22* | 616 | 0.18* | 616 | 0.27* | 270 |

Bluegill population dynamics were related to submerged aquatic vegetation estimates (Table 2). Juvenile bluegill growth (mean increment at age 2), total mortality based on maximum age, natural mortality, $t_R$, and MEI were correlated to vegetation estimates. Bluegill exhibited fast juvenile growth, high total and natural mortality, high production, and early maturation in low diversity compared to diverse plant communities.

Low diversity plant communities tended to occur in southern rather than northern Minnesota, and in warmer temperatures (Figure 1). Plant species richness and FQI increased then flattened out at northern latitudes and temperatures. This may reflect impacts of the human disturbance gradient, with both urban and agricultural watershed impacts being greater at southern latitudes. The relationship between the plant value index and both latitude and temperature was dome- shaped, with higher value index at moderate latitudes and temperature (Figure 1). Two estimates of early bluegill growth, mean increment at age 2 (*N* = 2,513) and mean backcalculated length at age 3 (*N* = 2,128) were correlated with latitude (*r* = -0.37 and -0.32, respectively) and temperature (*r* = 0.28 and 0.22, respectively).

Low FQI lakes were not common in the database. There were 60 lakes with FQI ≤10 and 12 lakes with FQI ≤ 5. This is in contrast to 171 lakes with FQI ≤ 30.

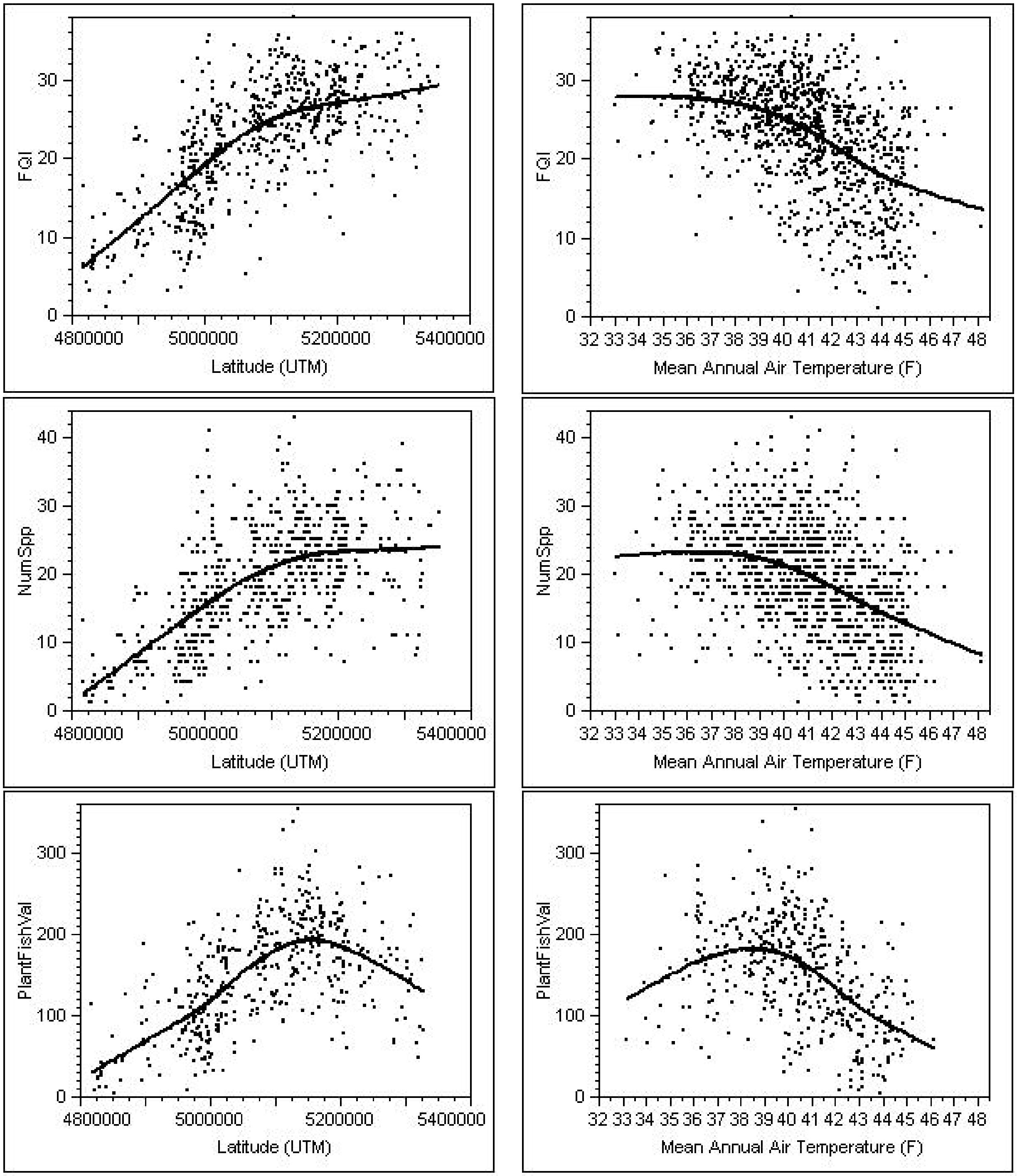
Lakes with high FQI not only had greater number of species, but each plant species occurred more frequently throughout a lake. Analysis of the mean frequency of occurrence of different species by lake showed that the mean was higher for all species, except *Elodea canadensis,* in lakes with FQI ≥ 30 than in lakes with FQI ≤ 10 (Table 3).

Few exotics, such as Eurasian milfoil *Myriophyllum spicatum* and curly-leaf pondweed *Potamogeton crispus* were encountered. Eurasian milfoil accounted for only 24 occurrences of the 13,996 individual plant species encountered in the 511 lakes on which vegetation surveys were done as less than 100 lakes were infested with Eurasian milfoil by 1997. Curly-leaf pondweed also occurred infrequently, accounting for 172 occurrences of the 13,996 individual plant species encountered.

Table 3. The mean, standard deviation (SD), and number of lakes (*N*) for the frequency of occurrence (FreqOccur) of aquatic plant species, *Scirpus acutus* (Bulrush), *Najas flexilis* (Bushy), *Ceratophyllum demersum* (Coontail), *Elodea canadensis* (Elodea), *Potamogeton zosteriformis* (FlatStem), *Potamogeton natans* (FloatP), *Myriophyllum sibiricum* (NMilfoil), *Chara* spp. (MuskGr), *Potamogeton amplifolius* (P Ampli), *Potamogeton richardsonii* (P Richa), *Potamogeton pectinatus* (Sago), *Vallisneria americana* (Vallis), *Nymphaea odorata* (WhitLily), and *Nuphar variegata* (YelLily).

| | FQI> 30 | | | FQI < 10 | | |
|---|---|---|---|---|---|---|
| FreqOccur | Mean | SD | *N* | Mean | SD | *N* |
| Bulrush | 40.1 | 25.8 | 41 | 30 | 28.3 | 4 |
| Bushy | 59.4 | 28.6 | 47 | | | |
| Coontail | 67.1 | 25.1 | 44 | 46.2 | 36.2 | 15 |
| Elodea | 46.4 | 24.7 | 45 | 56 | 41.4 | 6 |
| FlatStem | 76.1 | 24.0 | 46 | 10 | - | 1 |
| FloatP | 33.2 | 21.7 | 41 | 14.5 | 6.4 | 2 |
| MuskGr | 61.2 | 34.4 | 44 | | | |
| N.Milfoil | 54.8 | 28.9 | 38 | 5 | - | 1 |
| PAmpi | 45.3 | 31.9 | 47 | | | |
| PRicha | 53.5 | 25.6 | 48 | 10 | - | 1 |
| Sago | 42.2 | 23.6 | 31 | 32.0 | 27.2 | 20 |
| Vallis | 46.6 | 27.4 | 47 | | | |
| WhitLily | 41.4 | 24.6 | 50 | 10 | - | 1 |
| YelLily | 50.8 | 32.6 | 51 | 30 | 28.3 | 2 |

Figure 1. The floristic quality index (FQI), plant species richness (NumSpp), and plant fish value index versus latitude (UTM northerly coordinates) and mean annual air temperature (F) for Minnesota lakes, 1982-1997. Bold lines indicate cubic spline fits.



Bluegill population dynamics were correlated with the frequency of occurrence of plant species with a variety of growth-forms and leaf architecture (Table 4). Bluegill growth and morality declined when muskgrass was frequently encountered (mean increment at age 2, $r$ = -0.33; natural mortality, $r$ = -0.34). Mean backcalculated length at age 2, declined as flatstem pondweed *Potamogeton zosteriformis*, and northern milfoil *Myriophyllum sibiricum* occurred more frequently ($r$ = -0.33 and $r$ = -0.30, respectively). Bluefill relative stock density (RSDP) had significant negative correlation with coontail and northern milfoil. Bluegill relative abundance increased with coontail, northern milfoil, and large-leaf pondweed *Potamogeton amplifolius*. HPI increased with the occurrence of coontail, floating-leaf pondweed *Potamogeton natans*, northern milfoil, and sago pondweed (Table 5). Some plant species, such as muskgrass, northern milfoil, and various pondweeds, floating-leaf, large-leaf, flatstem, and Richard's pondweed *Potamogeton richardsonii*, were correlated with bluegill population dynamics while others, such as water celery *Vallisneria americana*, and water lilies *Nymphaea odorata* and *Nuphar variegata*, were correlated with none. Eurasian milfoil and curly-leaf pondweed were not considered because of their infrequent occurrence.

Submerged vegetation explained variation in bluegill growth (increment at age 2 and back calculated length at age 6), mortality, maturity and production, but not recruitment or population size structure (Table 6; models used for comparison are in Appendix 2, Tables 2-1 to 2-5). FQI was an independent variable in the best models of growth, mortality, and maturity with the exception of those fit for MEI (Table 6), which included Spp. However, several alternative MEI models had delta BIC values that were less than two, including the model that included only FQI (Appendix Table 2-5). The year class strength of 6-year-old bluegill and water clarity affected the growth of both juvenile and adult bluegill. Mean annual air temperature and latitude did not explain enough variation in bluegill growth, mortality, maturity, and production to be included in the models with the best fit.

We were able to validate the age-at-maturity estimates using bluegill samples separated by sex. The maturity estimate using bluegill of known maturity was positively correlated with the median of the maturity estimates made using the von Bertalanffy curve for males and with mean $t_R$ for females (Table 7).

## Discussion

Bluegill population dynamics were related to submerged aquatic vegetation. Juvenile bluegill growth, the proportion of large bluegill, total mortality, and MEI were inversely correlated with submerged aquatic vegetation species diversity, susceptibility to disturbance, and the value index. Adult bluegill growth, bluegill relative abundance, and HPI were directly correlated with submerged aquatic vegetation species diversity, susceptibility to disturbance, and the value index. Submerged aquatic vegetation was an important source of variation in juvenile and adult bluegill growth, mortality, and production. Therefore, alterations in submerged aquatic vegetation could be expected to affect bluegill population dynamics, but the nature of these impacts may be dependent on bluegill size.

Bluegill growth was negatively related to VI, consistent with most previous research. Bluegill growth was negatively related to vegetation abundance and coverage (Theiling 1990) and percent vegetation cover (Cheruvelil et al. 2005). Pothoven et al. (1999) reported increased bluegill growth in two Minnesota lakes after whole lake herbicide treatments removed most of the vegetation. Crowder and Cooper (1979) also found bluegill grew poorly in dense vegetation, but found bluegill grew best in intermediate density vegetation. Though we found a negative relationship consistent with most research, VI did not explain sufficient variation to be included in models of either juvenile or adult bluegill growth. Rather, FQI explained significant variation in bluegill growth, a result not described previously. No previous research has evaluated the relationship between bluegill growth and aquatic plant diversity.

Table 4. Pairwise correlation coefficients and number of surveys (*N*) of bluegill population dynamics and percent frequency of occurrence of plant species. The population dynamics used in the correlations were increment at age 2 (Incr2), backcalculated length at age 2 (XL2), backcalculated length at age 6 (XL6), natural mortality (M), and age at first reproduction ($t_R$) and the $\log_e$ transformed values of year class strength at age 6 (YCS6), relative stock density for 200 mm bluegill (RSDP), and morphoedaphic index (MEI) and relative abundance of bluegill taken in trapnets (CPU). The plant species used in the correlations were *Scirpus acutus* (Bulrush), *Najas flexilis* (Bushy), *Ceratophyllum demersum* (Coontail), *Elodea canadensis* (Elodea), *Potamogeton zosteriformis* (FlatStem), *Potamogeton natans* (FloatP), *Myriophyllum sibiricum* (NMilfoil), *Chara* spp. (MuskGr), *Potamogeton amplifolius* (P Ampli), *Potamogeton richardsonii* (P Richa), *Potamogeton pectinatus* (Sago), *Vallisneria americana* (Vallis), *Nymphaea odorata* (WhitLily), and *Nuphar variegata* (YelLily). Significant correlations are designated by an asterisk (Bonferroni adjustment for 14 comparisons; *P* < 0.004).

| | Bluegill population dynamics | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Plant sp. | Incr2 | *N* | XL2 | *N* | XL6 | *N* | YCS6 | *N* | RSDP | *N* | M | *N* | $t_R$ | *N* | MEI | *N* | CPU | N |
| Bulrush | -0.17* | 322 | -0.18 | 212 | 0.09 | 274 | 0.02 | 271 | -0.04 | 220 | -0.20* | 316 | 0.13 | 276 | -0.11 | 191 | 0.03 | 330 |
| Bushy | -0.26* | 336 | -0.17 | 228 | -0.20* | 306 | 0.21* | 302 | -0.16 | 227 | -0.22* | 329 | 0.19* | 289 | -0.13 | 197 | 0.15 | 339 |
| Coontail | -0.12 | 413 | -0.12 | 293 | 0.09 | 352 | 0.03 | 347 | -0.26* | 272 | -0.05 | 406 | 0.07 | 359 | -0.03 | 229 | 0.24* | 418 |
| Elodea | 0.13 | 319 | 0.19 | 224 | 0.02 | 282 | 0.03 | 278 | 0.10 | 203 | 0.12 | 316 | -0.10 | 279 | 0.04 | 180 | 0.01 | 324 |
| FlatStem | -0.20* | 345 | -0.33* | 232 | -0.10 | 313 | 0.08 | 309 | -0.13 | 234 | -0.10 | 340 | 0.09 | 293 | -0.14 | 196 | 0.15* | 350 |
| FloatP | -0.21* | 235 | -0.28* | 144 | -0.09 | 221 | 0.21* | 219 | -0.10 | 168 | -0.15 | 233 | 0.13 | 202 | 0.03 | 135 | 0.15 | 240 |
| MuskGr | -0.33* | 325 | -0.27* | 211 | -0.18* | 296 | 0.16 | 293 | -0.12 | 219 | -0.34* | 322 | 0.27* | 276 | -0.06 | 194 | 0.14 | 330 |
| NMilfoil | -0.24* | 312 | -0.30* | 209 | -0.19* | 282 | 0.20* | 279 | -0.27* | 207 | -0.14 | 307 | 0.09 | 268 | 0.10 | 184 | 0.25* | 316 |
| P Ampli | -0.27* | 225 | -0.19 | 135 | -0.29* | 219 | 0.26* | 217 | -0.12 | 152 | 0.01 | 225 | 0.04 | 196 | -0.05 | 144 | 0.24* | 229 |
| P Richa | -0.26* | 314 | -0.26* | 202 | -0.20* | 288 | 0.15 | 285 | -0.10 | 212 | -0.17* | 313 | 0.21* | 269 | -0.08 | 185 | 0.18* | 316 |
| Sago | -0.06 | 347 | -0.04 | 248 | 0.02 | 281 | 0.09 | 276 | -0.11 | 226 | -0.10 | 338 | 0.03 | 300 | 0.22* | 208 | 0.16* | 349 |
| Vallis | -0.09 | 249 | -0.12 | 148 | -0.11 | 237 | 0.03 | 234 | 0.08 | 174 | -0.05 | 248 | 0.10 | 213 | 0.13 | 154 | 0.02 | 253 |
| WhitLily | -0.06 | 288 | -0.01 | 198 | -0.11 | 262 | 0.14 | 259 | 0.03 | 192 | -0.05 | 284 | 0.05 | 256 | 0.06 | 176 | 0.07 | 292 |
| YelLily | -0.06 | 324 | -0.15 | 218 | 0.07 | 290 | -0.01 | 289 | 0.15 | 221 | -0.08 | 315 | 0.01 | 276 | 0.12 | 192 | 0.02 | 331 |

Table 5. Correlation coefficients (*r*), number of lakes (*N*), and probability (*P*) of the log$_e$ transformed values of the habitat productivity index versus of the frequency of occurrence (FreqOccur) of aquatic species, *Scirpus acutus* (Bulrush), *Najas flexilis* (Bushy), *Ceratophyllum demersum* (Coontail), *Elodea canadensis* (Elodea), *Potamogeton zosteriformis* (FlatStem), *Potamogeton natans* (FloatP), *Myriophyllum sibiricum* (NMilfoil), *Chara* spp. (MuskGr), *Potamogeton amplifolius* (P Ampli), *Potamogeton richardsonii* (P Richa), *Potamogeton pectinatus* (Sago), *Vallisneria americana* (Vallis), *Nymphaea odorata* (WhitLily), and *Nuphar variegata* (YelLily). Significant correlations are designated by an asterisk (Bonferroni adjustment for 14 comparisons; $P < 0.004$).

| FreqOccur | *r* | *N* | *P* |
|---|---|---|---|
| Bulrush | 0.00 | 213 | 0.982 |
| Bushy | 0.12 | 207 | 0.088 |
| Coontail | 0.32* | 254 | 0.000 |
| Elodea | 0.02 | 187 | 0.743 |
| FlatStem | 0.17 | 216 | 0.015 |
| FloatP | 0.27* | 144 | 0.001 |
| MuskGr | 0.17 | 201 | 0.014 |
| N.Milfoil | 0.23* | 203 | 0.001 |
| PAmpi | 0.24 | 132 | 0.006 |
| PRicha | 0.16 | 199 | 0.026 |
| Sago | 0.19* | 217 | 0.004 |
| Vallis | -0.03 | 153 | 0.698 |
| WhitLily | 0.08 | 162 | 0.298 |
| YelLily | 0.02 | 188 | 0.810 |

Table 6. Best-fit models of growth, estimated as mean increment at age 2 (Incr2), mean back calculated length at age 6 (XL6), total mortality estimated using maximum age (Z), age of first reproduction ($t_R$) of bluegill sampled, and the morphoedaphic index (MEI) estimated for 1477 Minnesota lakes, 1982-1997, the number of parameters (P), and sample size (*N*) of the model. Models were compared using Akaike Information Criterion (AIC), Bayes Information Criterion (BIC), the weight of evidence supporting a model (w), and the adjusted $R^2$ (Adj$R^2$) of the model. The independent variables in the models are the floristic quality index (FQI), the habitat productivity index (HPI), maturity estimated from piecewise linear models (MatPiece), mean back calculated length at age 6 (XL6), mean back calculated length at age 3 (XL3), plant species richness (Spp), the square-root transformed values of Secchi depth (Secc), and the log$_e$ transformed values of year class strength at age 6 (YCS6), relative stock density for 200 mm bluegill (RSDP), total mortality estimated using maximum age (Z), and the morphoedaphic index (MEI). Signs for the coefficients are listed in parenthesis following each independent variable.

| Model | P | *N* | AIC | BIC | w | Adj$R^2$ |
|---|---|---|---|---|---|---|
| Incr2 ~ YCSI6 (-) + Secc (-) + FQI (-) | 4 | 54 | 356.23 | 364.18 | 0.97 | 0.71 |
| XL6 ~ YCS6 (-) + RSDP (+) + Secc (-) + FQI (-) + HPI (+) | 6 | 83 | 716.27 | 730.78 | 0.99 | 0.63 |
| Z ~ MatPiece (-) + FQI (-) + XL6 (+) | 4 | 83 | -75.20 | -65.52 | 0.46 | 0.33 |
| $t_R$ ~ XL3 (-) + FQI (+) | 3 | 83 | -15.68 | -8.42 | 0.41 | 0.36 |
| MEI ~ Spp (-) | 2 | 54 | 154.36 | 158.34 | 0.18 | 0.36 |

Table 7. The correlation coefficients for mean and median (Med) maturity estimates made using von Bertalanffy curves (vonBert), age of first reproduction ($t_R$), and estimates made using piecewise linear models (Piecewise) vs. maturity estimated from probit fit of age at maturity curves (ProbitMat) for all bluegill sampled from 18 Minnesota lakes (All), for females (Female) and for males (Male). Significant correlations are designated by an asterisk (Bonferroni adjustment for 3 comparisons; $P < 0.02$).

| | Maturity Estimates | | | | | |
|---|---|---|---|---|---|---|
| | vonBert | | $t_R$ | | Piecewise | |
| ProbitMat | Mean | Med | Mean | Med | Mean | Med |
| All | -0.33 | -0.40 | 0.06 | 0.03 | -0.06 | -0.09 |
| Female | 0.30 | 0.35 | 0.42* | 0.32 | 0.31 | 0.33 |
| Male | 0.12 | 0.47* | 0.09 | 0.02 | 0.01 | -0.02 |

Bluegill growth was correlated with submerged vegetation, but the sign of this correlation depended on bluegill age. Growth of age 2 and age 3 bluegill was strongly, negatively correlated to submerged vegetation estimates whereas growth of older bluegill was positively but weakly correlated to vegetation, suggesting adult bluegill were less dependent on a vegetation. We note that the effect of FQI on increment at age 2 appears considerably stronger than the effect on back calculated length at age 6, based on visual comparison of leverage plots. Growth of young bluegill slowed in diverse vegetation with high biovolume. Dense vegetation hindered bluegill consumption of macroinvertebrate prey (Crowder and Cooper 1979). Bass predation efficiency was also reduced in dense vegetation (Savino and Stein 1982). Intraspecific competition for food resources is high in submerged vegetation (Osenberg et al. 1994). Juvenile bluegill, confined to submerged aquatic vegetation to avoid predation (Werner and Hall 1988), were not free to consume more profitable zooplankton, as were adult bluegill (Werner et al. 1983). Based on our results, we conclude that submerged aquatic vegetation is crucial habitat for juvenile bluegill, though biovolume or plant density appears important.

Our results indicate a negative relationship between juvenile bluegill growth and high plant species richness. More detailed information is required to allow meaningful interpretation of this relationship. For example, in highly fertile, turbid lakes with low plant diversity, bluegill may grow faster because of lower abundance and relaxed density dependence. Thus, the effect may not be directly related to plant species diversity or species richness. FQI does estimate susceptibility to disturbance, in addition to incorporating species richness. Thus, faster juvenile growth occurred in plant communities that had low species richness and were resilient to disturbance. Some plants resilient to disturbance are sago, elodea and coontail (Nichols 1999), and these three species are the most common in the plant surveys reported here with low FQI scores (Table 3).

Juvenile bluegill grew fastest in low diversity plant communities. Low diversity plant communities occurred in warm temperatures and at southern latitudes in Minnesota. Because temperature and latitude are correlated, we hypothesize that the apparent relationship with temperature is actually from the human disturbance gradient that increases towards southern and western Minnesota. In comparison to plant community diversity, the relationship between the plant value index and both latitude and temperature was more complex, with a higher value index at moderate latitudes and temperature. We conjecture that the decline in the value index at higher latitudes may be related to restricted growing season or less fertile systems, and suggest that this particular relationship warrants further investigation. Though juvenile bluegill grew faster in southern latitudes and warm temperatures, neither temperature nor latitude explained enough variation to be included in the model of juvenile bluegill growth. FQI may incorporate aspects of temperature and latitude, thereby explaining more variation in juvenile bluegill growth than the other variables do separately. The effects of temperature could be potentially isolated with the application of bioenergetics analysis.

The negative correlation of bluegill growth and plant variables, and the positive relation of bluegill relative abundance and vegetation suggests that bluegill populations may experience a density-dependent reduction in growth in diverse vegetation that fills the water column. The positive relationship between bluegill relative abundance and vegetation was consistent with previous research, which reported a positive correlation between bluegill relative abundance and vegetation density, the frequency of occurrence of fineleaf plants, and other estimates of submerged vegetation (Cross et al. 1992; Cross and McInerny 2001, 2005). Bluegill relative abundance increased with all the plant variables but was most strongly correlated with VI. When VI increased, some combination of the components (frequency of occurrence, relative abundance and presence of plant species that fill the water column) increased, as well as plant species richness. We are uncertain of the components that had the greatest effect on bluegill relative abundance.

The relationships between bluegill year class strength, relative stock density, mortality, and production and submerged aquatic vegetation as expressed here have not been described elsewhere. We found little correlation between estimates of year class strength and submerged vegetation. Relative stock density for 200 mm bluegill was negatively correlated to submerged vegetation estimates indicating that large bluegill were scarce in populations living in diverse vegetation with high biovolume. Both Z, estimated using maximum age, and M were negatively correlated with vegetation, thus bluegill mortality declined in diverse vegetation that filled the water column. The correlation between M and vegetation is likely due to the inclusion of K in the formulation of M. K characterizes the slope at the origin of the von Bertalanffy age-length curve and was correlated with juvenile bluegill growth. MEI was negatively correlated with submerged vegetation estimates, particularly plant species richness. Potential production was highest in lakes with low diversity plant communities that were more common in southern Minnesota in warm water temperatures; however, neither latitude nor temperature were included in the model that explained the most variation in MEI. HPI, an estimate of bluegill production, was positively correlated with the value index, i.e., bluegill production increased in vegetation that filled the water column. Randall et al. (1996) community-based HPI also increased with percent cover. Randall et al. (1996) reported that mean $log_{10}$ community HPI in the Great Lakes varied between 2.04-2.57 in a range of vegetation densities from absent to dense. We found $log_e$ of the mean bluegill HPI was 5.28 and $log_e$ of the median was 4.44, within the range of community production in the Great Lakes. Of the maturity estimates, $t_R$ was most strongly correlated to vegetation estimates. The relationship likely reflected the inclusion of K in the maturity formulation, rather than correlation of maturity with submerged vegetation. However, we suggest caution in interpretation of analysis of maturity estimates because $t_R$ was only confirmed for female bluegill (Table 7), and our complete data set did not include information on sex of fish.

The constructed models indicated that submerged aquatic vegetation was important relative to two other factors found previously to be important, water clarity and bluegill year class strength. The model for early bluegill growth (mean increment at age 2) included Secchi depth, year class strength at age 6, and FQI. Tomcko and Pierce (2005) reported that Secchi depth and relative stock density for 200 mm bluegill (RSDP) were important explanatory variables for a model with a similar estimate of juvenile bluegill growth, mean backcal culated length at age 3. Compared to FQI, RSDP did not explain enough variation to be included in the model of early bluegill growth. A model of an estimate of adult bluegill growth, mean backcalculated length at age 6, included year class strength at age 6, FQI, RSDP, Secchi depth, and HPI. Tomcko and Pierce (2005) also reported that Secchi depth and RSDP were important explanatory variables for mean backcalculated length at age 6.

The results indicated that specific plant species were related to bluegill relative abundance and growth. Bluegill relative abundance increased with the frequency of occurrence of coontail and northern milfoil, consistent with Cross and McInerny's (2001) finding that bluegill relative abundance increased with frequency of occurrence of fine-leaf plants, including coontail and milfoil. We found bluegill growth declined with increasing frequency of Chara, flatstem pondweed, and northern milfoil. Cheruvelil et al. (2005) expected a negative relationship between bluegill growth and occurrence of Eurasian milfoil, a fine-leaf plant, but found no relationship.

The close correlation of plant species richness, FQI, and VI reflected the effect of plant species richness in the formulations of FQI and VI. Reformulating VI did not substantially improve correlation coefficients. The reformulation suggested that plant species richness and adding species to produce VI, had a greater effect on the end value of VI than did the relative abundance plant value scores. The models we found for juvenile and adult bluegill growth suggests that plant value scores need to be calculated separately for juvenile and adult bluegill. For example, we assumed the plant species that fill the water column would have greater value to bluegill than plants with low growth forms, such as *Chara* spp. However, juvenile bluegill growth was strongly correlated with aquatic vegetation estimates, and low growth form plants are important to small-bodied, juvenile bluegill. The models we found for juvenile and adult bluegill growth, plus the direction of correlations of frequency of occurrence for common plant species and bluegill population dynamics, could be instrumental in formulating a better index of the value of aquatic plants to bluegill.

A potential shortcoming of working with data collected by many people is the large amount of variation in the data due to measurement error. Measurement error in independent variables decreases our ability to detect significant relationships (Fuller 1987). However, an advantage is the large sample size. If two variables have a bivariate normal relationship, a large dataset ensures that the direction and pattern of the association between the variables is known with some confidence, assuming the variables adequately represent the quantities we attempt to estimate. Evaluating large databases cannot take the place of long-term experiments that track changes in fish population dynamics when vegetation is altered, but the logistical problems inherent in such experiments make evaluation of large databases a useful first step.

## Management Implications

We found juvenile bluegill grew faster in low diversity, submerged aquatic vegetation, but have no previous research on plant diversity to compare this result. The negative correlation between juvenile bluegill growth and VI suggests that bluegill also grow slowly in dense vegetation. Managers interested in producing harvestable-sized bluegill should work to reduce nutrient inputs to lakes that fuel the production of overly dense aquatic vegetation.

More detailed assessment of vegetation in lakes would allow more detailed analysis of the effect of submerged aquatic vegetation on bluegill population dynamics. In particular, the subjective coding of relative abundance by multiple assessors is suspect.

We recommend following the point intercept method of surveying aquatic vegetation (Madsen 1999), which would remove the subjective coding of relative abundance, but does not estimate vegetation density. VI, the estimate of biovolume we used, should be compared to biovolume estimates from hydroacoustic surveys. Hydroacoustic surveys estimate vegetation biomass and can be used to estimate total vegetation density in a lake, yet avoid the labor-intensive work of estimating stem densities (Valley et al. 2005). Better estimates of both plant density and diversity are necessary to examine in more detail the relationship between bluegill growth and these ecological features of aquatic plant communities.

We recommend maintaining restrictions on submerged aquatic vegetation removal in Minnesota. We need more information on bluegill populations in lakes devoid of vegetation. Though bluegill grew best in lakes with low diversity plant communities, we suspect that lakes devoid of vegetation will not produce quality bluegill populations. Assessing bluegill populations in enriched shallow lakes without rooted aquatic plants would clarify if very low or zero density aquatic vegetation harms bluegill populations. We need information on how fragmentation of vegetation beds affects bluegill. We did not map aquatic vegetation in lakes to evaluate the potentially negative effect of vegetation bed fragmentation on bluegill populations. Fragmentation could potentially negatively affect bluegill populations. Finally, our recommendations apply only to bluegill. Bluegill have flexible habitat requirements compared to other fish species (Keast et al. 1978). We recommend study of the relationship of submerged vegetation and the population dynamics of other fish species that may be more susceptible to altered aquatic vegetation.

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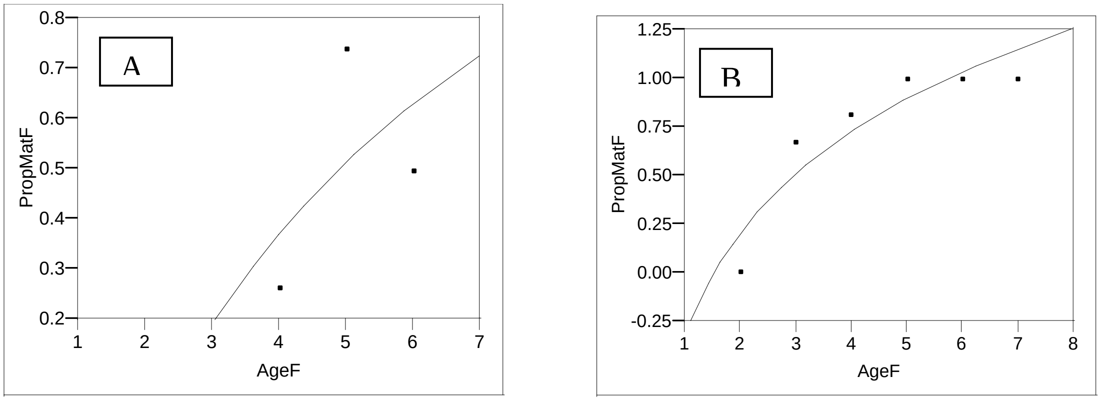
## Appendix 1. Validation of age of maturity estimates using bluegill with known maturities.

We used data from bluegills sampled from 34 lakes in southern or central MN (Drake et al. 1997). Bluegill sex and maturity was determined by dissection and their age was estimated using scales. Of the 34 samples, only 18 had 100 or more bluegill. We used the probit method to estimate the age at which 50% of bluegill were mature for all bluegill separated by sex and for bluegill combined by sex. Separation by sex further reduced sample sizes. The effective degrees of freedom varied from 0 (2 age classes) to 5 (7 age classes) for bluegill separated by sex. Maturity estimates were made using von Bertalanffy curves, piecewise linear models, and age of first reproduction ($t_R$) estimates, for female, male, and combined bluegill in the 18 lakes. We compared the von Bertalanffy estimate, $t_R$, and the piecewise estimate of maturity to maturity estimated from probit curves.

Only two correlations were significant between the three estimates and the known maturity estimates made using the probit function, one between known maturity and the median of the maturity estimates made using the von Bertalanffy curves for males and the other with mean $t_R$ for females. If sexing bluegill is necessary then maturities would be best estimated using the probit function.

Small sample sizes of some ages due to missing year classes made it difficult to fit the probit curve (Appendix Figure 1). SSE for fitting the probit function to the data varied from 0.0002 - 0.17. Only 15 of 34 lakes had SSEs less than 0.05. A particularly egregious example was found in one lake where there were larger numbers of old than young bluegill, resulting in a probit curve with negative slope. We recommend large sample sizes of bluegill for adequate information on ages in lakes where bluegill year class strength is variable.

Appendix Figure 1. Probit curves for female bluegill sampled from two lakes in Minnesota. The effective degrees of freedom is 1 for curve A (*N* = 80) and 4 for curve B (*N* = 54).



PropMatF = -0.51 + 1.46 * $\log_{10}$ (Age); SSE = 0.08 PropMatF = -0.33 + 1.76 * $\log_{10}$ (Age); SSE = 0.1

Appendix 2. The models describing bluegill growth, mortality, maturity, and production, and compared using AIC and BIC statistics.

Table 2-1. Models of growth, estimated as mean increment at age 2 (Incr2), of bluegill sampled from 2571 surveys, 1982-1997, the number of parameters (P), and sample size (*N*) of the model. Models were compared using Bayes Information Criterion (BIC), the difference between the smallest BIC and model BIC (Delta), the weight of evidence supporting a model (w), and the adjusted $R^2$ (Adj$R^2$) of the model. The independent variables in the models are the floristic quality index (FQI), latitude (Lat), mean annual air temperature (Temp), maturity estimated from piecewise linear models (Matur), the square-root transformed values of Secchi depth (Secc), and the log$_e$ transformed values of year class strength at age 6 (YCS6), relative stock density for 200 mm bluegill (RSDP), total mortality estimated using maximum age (Z), and the morphoedaphic index (MEI). The signs of the coefficients for the best fit model based on BIC are as follows: YCSI6 (-); Secc (-); FQI (-).

| Model | P | *N* | AIC | BIC | Delta | w | Adj$R^2$ |
|---|---|---|---|---|---|---|---|
| Incr2 ~ Secc | 2 | 54 | 388.16 | 392.14 | 27.96 | <0.01 | 0.46 |
| Incr2 ~ YCSI6 | 2 | 54 | 392.18 | 396.16 | 31.98 | <0.01 | 0.42 |
| Incr2 ~ FQI | 2 | 54 | 398.87 | 402.85 | 38.66 | <0.01 | 0.34 |
| Incr2 ~ Lat | 2 | 54 | 407.70 | 411.67 | 47.49 | <0.01 | 0.23 |
| Incr2 ~ RSDP | 2 | 54 | 410.73 | 414.71 | 50.53 | <0.01 | 0.18 |
| Incr2 ~ Temp | 2 | 54 | 414.36 | 418.33 | 54.15 | <0.01 | 0.12 |
| Incr2 ~ YCSI6 + Secc | 3 | 54 | 366.14 | 372.11 | 7.93 | 0.02 | 0.65 |
| Incr2 ~ YCSI6 + FQI | 3 | 54 | 367.87 | 373.83 | 9.65 | 0.01 | 0.64 |
| Incr2 ~ YCSI6 + Lat | 3 | 54 | 376.51 | 382.48 | 18.29 | <0.01 | 0.57 |
| Incr2 ~ YCSI6 + Secc + FQI | 4 | 54 | 356.23 | 364.18 | 0 | 0.97 | 0.71 |
| Incr2 ~ YCSI6 + Z + FQI | 4 | 54 | 369.68 | 377.64 | 13.45 | <0.01 | 0.63 |
| Incr2 ~ YCSI6 + MEI + FQI | 4 | 54 | 368.14 | 376.09 | 11.91 | <0.01 | 0.64 |
| Incr2 ~ YCSI6 + RSDP + FQI | 4 | 54 | 369.15 | 377.10 | 12.92 | <0.01 | 0.63 |
| Incr2 ~ YCSI6 + RSDP + MEI | 4 | 54 | 382.47 | 390.42 | 26.24 | <0.01 | 0.53 |
| Incr2 ~ YCSI6 + RSDP + MEI + FQI | 5 | 54 | 369.88 | 379.83 | 15.65 | <0.01 | 0.63 |
| Incr2 ~ YCSI6 + RSDP + Z + MEI | 5 | 54 | 382.42 | 392.37 | 28.19 | <0.01 | 0.54 |
| Incr2 ~ YCSI6 + RSDP + Z + FQI | 5 | 54 | 370.83 | 380.77 | 16.59 | <0.01 | 0.63 |
| Incr2 ~ YCSI6 + RSDP + Z + Matur | 5 | 54 | 390.92 | 400.86 | 36.68 | <0.01 | 0.46 |
| Incr2 ~ YCSI6 + RSDP + Z + Lat | 5 | 54 | 373.48 | 383.42 | 19.24 | <0.01 | 0.61 |
| Incr2 ~ YCSI6 + RSDP + Z + FQI + MEI | 6 | 54 | 371.51 | 383.44 | 19.26 | <0.01 | 0.63 |

Table 2-2. Models of growth, estimated as mean backcalculated length at age 6 (XL6), of bluegill sampled from 2571 surveys, 1982-1997, the number of parameters (P), and sample size (*N*) of the model. Models were compared using Bayes Information Criterion (BIC), the difference between the smallest BIC and model BIC (Delta), the weight of evidence supporting a model (w), and the adjusted $R^2$ (Adj$R^2$) of the model. The independent variables in the models were the floristic quality index (FQI), latitude (Latit), age at first reproduction (Matur), the $\log_e$ transformed values of year class strength at age 6 (YCS6), relative stock density for 200 mm bluegill (RSDP), maximum depth (mxD), and the habitat productivity index (HPI), and the square-root transformed values of Secchi depth (Secc). The signs of the coefficients for the best fit model based on BIC are as follows: YCS6 (-); RSDP (+); Secc (-); FQI (-); HPI (+).

| Model | P | *N* | AIC | BIC | Delta | w | Adj$R^2$ |
|---|---|---|---|---|---|---|---|
| XL6 ~ Secc | 2 | 83 | 759.47 | 764.30 | 33.52 | <0.01 | 0.36 |
| XL6 ~ YCS6 | 2 | 83 | 761.98 | 766.82 | 36.03 | <0.01 | 0.34 |
| XL6 ~ RSDP | 2 | 83 | 772.04 | 776.88 | 46.10 | <0.01 | 0.25 |
| XL6 ~ mxD | 2 | 83 | 773.07 | 777.90 | 47.12 | <0.01 | 0.24 |
| XL6 ~ FQI | 2 | 83 | 780.04 | 784.87 | 54.09 | <0.01 | 0.17 |
| XL6 ~ YCS6 + Secc | 3 | 83 | 742.28 | 749.53 | 18.75 | <0.01 | 0.48 |
| XL6 ~ YCS6 + FQI | 3 | 83 | 751.36 | 758.62 | 27.84 | <0.01 | 0.42 |
| XL6 ~ Secc + FQI | 3 | 83 | 757.26 | 764.52 | 33.74 | <0.01 | 0.38 |
| XL6 ~ YCS6 + RSDP + Secc | 4 | 83 | 737.84 | 747.51 | 16.73 | <0.01 | 0.52 |
| XL6 ~ YCS6 + Secc + mxD | 4 | 83 | 739.68 | 749.35 | 18.57 | <0.01 | 0.50 |
| XL6 ~ YCS6 + Secc + FQI | 4 | 83 | 739.84 | 749.51 | 18.73 | <0.01 | 0.50 |
| XL6 ~ YCS6 + Secc + Latit | 4 | 83 | 743.41 | 753.08 | 22.30 | <0.01 | 0.48 |
| XL6 ~ YCS6 + RSDP + FQI | 4 | 83 | 747.25 | 756.92 | 26.14 | <0.01 | 0.46 |
| XL6 ~ YCS6 + Secc + HPI + FQI | 5 | 83 | 727.40 | 739.50 | 8.71 | 0.01 | 0.58 |
| XL6 ~ YCS6 + RSDP + Secc + FQI | 5 | 83 | 735.80 | 747.89 | 17.11 | <0.01 | 0.53 |
| XL6 ~ YCS6 + RSDP + Secc + Latit | 5 | 83 | 736.87 | 748.96 | 18.17 | <0.01 | 0.53 |
| XL6 ~ YCS6 + RSDP + Secc + mxD | 5 | 83 | 737.98 | 750.07 | 19.29 | <0.01 | 0.52 |
| XL6 ~ YCS6 + RSDP + Secc + FQI + HPI | 6 | 83 | 716.27 | 730.78 | 0 | 0.99 | 0.63 |
| XL6 ~ YCS6 + RSDP + Secc + FQI + Matur | 6 | 83 | 731.02 | 745.54 | 14.75 | <0.01 | 0.56 |
| XL6 ~ YCS6 + RSDP + Secc + FQI + mxD | 6 | 83 | 736.44 | 750.96 | 20.17 | <0.01 | 0.53 |

Table 2-3. Models of total mortality, estimated using maximum age (Z), $\log_e$ transformed, of bluegill sampled from 2571 surveys, 1982-1997, the number of parameters (P), and sample size (*N*) of the model. Models were compared using Bayes Information Criterion (BIC), the difference between the smallest BIC and model BIC (Delta), the weight of evidence supporting a model (w), and the adjusted $R^2$ of the model (Adj$R^2$). The independent variables in the models are mean backcalculated length at age 6 (XL6), maturity estimated from piecewise linear models (Matur), the floristic quality index (FQI), percent littoral area (Litt), mean annual air temperature (Temp), latitude (Lat), and the $\log_e$ transformed values of maximum depth (mxD), relative stock density for 200 mm bluegill (RSDP), year class strength at age 6 (YCS6), and the habitat productivity index (HPI). The signs of the coefficients for the best-fit model based on BIC are as follows: Matur (-); FQI (-); XL6 (+).

| Model | P | *N* | AIC | BIC | Delta | w | Adj$R^2$ |
|---|---|---|---|---|---|---|---|
| Z ~ XL6 | 2 | 83 | -68.82 | -63.98 | 1.54 | 0.21 | 0.26 |
| Z ~ Matur | 2 | 83 | -60.57 | -55.74 | 9.78 | <0.01 | 0.18 |
| Z ~ FQI | 2 | 83 | -55.22 | -50.38 | 15.14 | <0.01 | 0.12 |
| Z ~ Litt | 2 | 83 | -47.44 | -42.61 | 22.91 | <0.01 | 0.04 |
| Z ~ mxD | 2 | 83 | -46.46 | -41.62 | 23.90 | <0.01 | 0.03 |
| Z ~ RSDP | 2 | 83 | -45.74 | -40.90 | 24.62 | <0.01 | 0.02 |
| Z ~ XL6 + YCS6 | 3 | 83 | -68.33 | -61.08 | 4.44 | 0.05 | 0.26 |
| Z ~ XL6 + RSDP | 3 | 83 | -68.02 | -60.77 | 4.75 | 0.04 | 0.26 |
| Z ~ Matur + FQI | 3 | 83 | -65.33 | -58.07 | 7.45 | 0.01 | 0.23 |
| Z ~ Matur + FQI + XL6 | 4 | 83 | -75.20 | -65.52 | 0 | 0.46 | 0.33 |
| Z ~ XL6 + Temp + HPI | 4 | 83 | -69.05 | -59.37 | 6.15 | 0.02 | 0.28 |
| Z ~ XL6 + RSDP + YCS6 | 4 | 83 | -69.02 | -59.35 | 6.17 | 0.02 | 0.28 |
| Z ~ XL6 + RSDP + FQI | 4 | 83 | -69.00 | -59.33 | 6.19 | 0.02 | 0.28 |
| Z ~ XL6 + Temp + FQI | 4 | 83 | -68.83 | -59.16 | 6.36 | 0.02 | 0.27 |
| Z ~ Matur + FQI + Lat | 4 | 83 | -63.97 | -54.30 | 11.22 | <0.01 | 0.23 |
| Z ~ Matur + FQI + XL6 + Lat | 5 | 83 | -74.00 | -61.90 | 3.62 | 0.08 | 0.33 |
| Z ~ Matur + FQI + XL6 + mxD | 5 | 83 | -73.58 | -61.48 | 4.04 | 0.06 | 0.32 |
| Z ~ XL6 + Temp + RSDP + HPI | 5 | 83 | -68.55 | -56.46 | 9.06 | <0.01 | 0.28 |
| Z ~ XL6 + RSDP + YCS6 + FQI + mxD | 6 | 83 | -68.80 | -54.28 | 11.24 | <0.01 | 0.29 |
| Z ~ XL6 + RSDP + YCS6 + FQI + Lat | 6 | 83 | -68.63 | -54.11 | 11.41 | <0.01 | 0.29 |

Table 2-4. Models of the age of first reproduction, $t_R$ (Matur), of bluegill sampled from 2571 surveys, 1982-1997, the number of parameters (P), and sample size (*N*) of the model. Models were compared using Bayes Information Criterion (BIC), the difference between the smallest BIC and model BIC (Delta), the weight of evidence supporting a model (w), and the adjusted $R^2$ of the model (Adj$R^2$). The independent variables in the models are mean backcalculated length at age 3 (XL3), the floristic quality index (FQI), latitude (Lat), mean annual air temperature (Temp), the $\log_e$ transformed values of year class strength at age 6 (YCS6), relative stock density for 200 mm bluegill (RSDP), total mortality estimated using maximum age (Z), and the habitat productivity index (HPI), and the square-root transformed values of Secchi depth (Secc). The signs of the coefficients for the best fit model based on BIC are as follows: XL3 (-); FQI (+).

| Model | P | *N* | AIC | BIC | Delta | w | Adj$R^2$ |
|---|---|---|---|---|---|---|---|
| Matur ~ XL3 | 2 | 83 | -12.01 | 7.17 | 1.25 | 0.22 | 0.33 |
| Matur ~ FQI | 2 | 83 | -0.22 | 4.62 | 13.04 | <0.01 | 0.22 |
| Matur ~ YCS6 | 2 | 83 | 4.32 | 9.16 | 17.58 | <0.01 | 0.18 |
| Matur ~ Secc | 2 | 83 | 7.44 | 12.27 | 20.70 | <0.01 | 0.15 |
| Matur ~ Lat | 2 | 83 | 7.67 | 12.51 | 20.93 | <0.01 | 0.15 |
| Matur ~ Z | 2 | 83 | 10.72 | 15.56 | 23.98 | <0.01 | 0.11 |
| Matur ~ RSDP | 2 | 83 | 17.23 | 22.07 | 30.49 | <0.01 | 0.04 |
| Matur ~ XL3 + FQI | 3 | 83 | -15.68 | -8.42 | 0 | 0.41 | 0.36 |
| Matur ~ Z + XL3 | 3 | 83 | -12.45 | -5.20 | 3.22 | 0.08 | 0.34 |
| Matur ~ Z + FQI | 3 | 83 | -2.14 | 5.12 | 13.54 | <0.01 | 0.25 |
| Matur ~ FQI + Lat | 3 | 83 | 1.59 | 8.84 | 17.27 | <0.01 | 0.21 |
| Matur ~ YCS6 + RSDP | 3 | 83 | 6.32 | 13.57 | 21.99 | <0.01 | 0.17 |
| Matur ~ Z + FQI + XL3 | 4 | 83 | -14.95 | -5.28 | 3.15 | 0.09 | 0.36 |
| Matur ~ XL3 + YCS6 + FQI | 4 | 83 | -16.36 | -6.69 | 1.73 | 0.17 | 0.37 |
| Matur ~ XL3 + Temp + HPI | 4 | 83 | -8.50 | 1.18 | 9.60 | <0.01 | 0.31 |
| Matur ~ YCS6 + RSDP + Secc | 4 | 83 | 2.48 | 12.15 | 20.57 | <0.01 | 0.22 |
| Matur ~ XL3 + YCS6 + Secc + FQI | 5 | 83 | -14.39 | -2.30 | 6.13 | 0.02 | 0.37 |
| Matur ~ XL3 + Temp + RSDP + HPI | 5 | 83 | -7.40 | 4.69 | 13.11 | <0.01 | 0.31 |
| Matur ~ YCS6 + RSDP + Secc + Lat | 5 | 83 | -1.84 | 10.25 | 18.67 | <0.01 | 0.26 |
| Matur ~ YCS6 + RSDP + Secc + FQI + Lat | 6 | 83 | -6.47 | 8.04 | 16.46 | <0.01 | 0.31 |

Table 2-5. Models of production, estimated as the morphoedaphic index (MEI), $\log_e$ transformed, of bluegill sampled from 2571 surveys, 1982-1997, the number of parameters (P), and sample size (*N*) of the model. Models were compared using Bayes Information Criterion (BIC), the difference between the smallest BIC and model BIC (Delta), the weight of evidence supporting a model (w), and the adjusted $R^2$ (Adj$R^2$) of the model. The independent variables in the models were plant species richness (Spp), the floristic quality index (FQI), the fish value index (FVI), mean backcalculated length at age 3 (XL3), latitude (Lat), percent littoral area (Litt), mean air temperature in June and July (Temp), and maturity estimated from piecewise linear models (Matur). The signs of the coefficients for the best fit model based on BIC are as follows: Spp (-).

| Model | P | *N* | AIC | BIC | Delta | w | Adj$R^2$ |
|---|---|---|---|---|---|---|---|
| MEI ~ Spp | 2 | 54 | 154.36 | 158.34 | 0 | 0.18 | 0.36 |
| MEI ~ FQI | 2 | 54 | 156.07 | 160.05 | 1.71 | 0.08 | 0.34 |
| MEI ~ FVI | 2 | 54 | 164.63 | 168.61 | 10.27 | <0.01 | 0.23 |
| MEI ~ XL3 | 2 | 54 | 165.49 | 169.46 | 11.12 | <0.01 | 0.21 |
| MEI ~ Lat | 2 | 54 | 169.50 | 173.48 | 15.14 | <0.01 | 0.15 |
| MEI ~ Litt | 2 | 54 | 169.58 | 173.56 | 15.22 | <0.01 | 0.15 |
| MEI ~ Spp + XL3 | 3 | 54 | 152.84 | 158.80 | 0.46 | 0.14 | 0.39 |
| MEI ~ Spp + Secc | 3 | 54 | 154.23 | 160.20 | 1.86 | 0.07 | 0.37 |
| MEI ~ Spp + Temp | 3 | 54 | 154.43 | 160.40 | 2.06 | 0.06 | 0.37 |
| MEI ~ Matur + Spp | 3 | 54 | 156.11 | 162.07 | 3.73 | 0.03 | 0.35 |
| MEI ~ Spp + Lat | 3 | 54 | 156.35 | 162.32 | 3.98 | 0.02 | 0.35 |
| MEI ~ Spp + XL3 + Litt | 4 | 54 | 150.77 | 158.73 | 0.39 | 0.15 | 0.42 |
| MEI ~ Spp + XL3 + Temp | 4 | 54 | 151.50 | 159.45 | 1.11 | 0.10 | 0.41 |
| MEI ~ Spp + XL3 + Secc | 4 | 54 | 154.56 | 162.51 | 4.17 | 0.02 | 0.38 |
| MEI ~ Spp + XL3 + Lat | 4 | 54 | 154.82 | 162.78 | 4.44 | 0.02 | 0.38 |
| MEI ~ Matur + Spp + Lat | 4 | 54 | 158.01 | 165.96 | 7.62 | <0.01 | 0.34 |
| MEI ~ Spp + XL3 + Litt + Lat | 5 | 54 | 152.76 | 162.71 | 4.37 | 0.02 | 0.41 |
| MEI ~ Spp + XL3 + Litt + Lat + Secc | 6 | 54 | 154.63 | 166.56 | 8.22 | <0.01 | 0.40 |
| MEI ~ XL3 + Litt + Lat + Secc + Temp | 6 | 54 | 154.74 | 166.67 | 8.33 | <0.01 | 0.40 |
| MEI ~ Spp + XL3 + Litt + Lat + Secc + Temp | 7 | 54 | 145.45 | 159.37 | 1.03 | 0.11 | 0.50 |

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Edited by:
Rodney Pierce, Fisheries Research Scientist
Donald L. Pereira, Fisheries Research Supervisor
Paul J. Wingate, Fisheries Research and Policy Manager