

## The Role of Density Dependence in Growth Patterns of Ceded Territory Walleye Populations of Northern Wisconsin: Effects of Changing Management Regimes

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*Abstract.*—We assessed density-related changes in growth of walleye *Sander vitreus* in the ceded territory of northern Wisconsin from 1977 to 1999. We used asymptotic length ( $L_{\infty}$ ), growth rate near  $t_0$  ( $\omega$ ), and body condition as measures of walleye growth to determine the relationship between growth and density. Among lakes, there was weak evidence of density-dependent growth: adult density explained only 0–6% of the variability in the growth metrics. Within lakes, growth was density dependent,  $L_{\infty}$ ,  $\omega$ , and body condition of walleyes changing with density for 69, 28, and 62% of the populations examined, respectively. Our results suggest that walleye growth was density dependent within individual lakes. However, growth was not coherently density dependent among lakes, which was possibly due to inherent differences in the productivity, surface area, forage base, landscape position, species composition, and management regime of lakes in the ceded territory. Densities of adult walleyes averaged 8.3 fish/ha and did not change significantly during 1990–1999. Mean  $L_{\infty}$  and body condition of walleyes were significantly higher before 1990 than after 1990, which may indicate an increase in density due to changes in management regimes. The observed growth changes do not appear to be a consequence of the statewide 15-in minimum size limit adopted in 1990 but rather a response to the treaty rights management regime. We conclude that walleye growth has the potential to predict regional-scale adult walleye densities if lake-specific variables are included in a model to account for regional-scale differences among walleye populations and lakes.

Because the goal of most fisheries management is to ensure sustainable production over time from fish stocks and to avoid overexploitation, the understanding of density-dependent relationships in fish populations is paramount (Hilborn and Walters 1992). The importance of considering density-dependent processes in fisheries management is apparent in stock–recruitment relationships (Ricker 1975; Walters and Kitchell 2001), growth (Kempinger and Carline 1977; Shuter and Koonce 1977), intraspecific and interspecific competitive interactions (Forney 1974; Walters and Juanes

1993), and natural mortality (Everhart et al. 1953) within fish populations. Although fisheries managers are able to regulate fishing mortality through bag limits, size limits, and seasonal closures, little control can be administered over density-independent processes, such as temperature or storms. Therefore, fisheries managers are better able to control the population dynamics and densities of fish stocks where density-dependent processes dominate. Moreover, managers must consider the tradeoff between producing large numbers or large sizes of fish when harvest is regulated to control fish densities (Walters and Post 1993).

Fish growth dynamics are a strong indicator of ecological conditions within and among aquatic ecosystems. In addition to density-independent (extrinsic) factors, the inverse relationship between fish growth and density is a major density-dependent (intrinsic) process regulating fish

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growth. For example, Diana et al. (1991) showed that growth rate of stocked Nile tilapia *Oreochromis niloticus* decreased linearly with increases in density. In general, competition for limiting resources (e.g., food or space) are, in fish populations, common mechanisms leading to observations of density-dependent growth (Post et al. 1999). Furthermore, density-dependent growth is common for size-structured fish populations in which competition for food is influenced by differences in size among individuals (Mittelbach and Osenberg 1993; Post et al. 1999). In most cases, changes in fish growth dynamics can be attributed directly or by correlation to changes in varying intrinsic and extrinsic ecological conditions.

Our objectives in this study were to determine whether growth of walleyes *Sander vitreus* was density dependent in ceded territory lakes of northern Wisconsin and to assess the effects of the tribal fishery management program on walleye growth. We examined asymptotic length, initial growth rate, and body condition in relation to adult walleye density within and among lakes to determine if walleye growth was density dependent and used these relationships to evaluate the effect of changing management programs in northern Wisconsin.

The recreational fishery for walleyes in northern Wisconsin was historically and is currently extremely popular. Beginning in the spring of 1985, an off-reservation Chippewa Indian spear fishery for walleyes began in the ceded territory of northern Wisconsin (Hansen et al. 1991). In addition to an extensive recreational fishery, walleye stocks in northern Wisconsin were now exposed to an additional source of fishing mortality. To avoid overexploitation of walleye stocks, the Wisconsin Department of Natural Resources (WDNR) adopted a conservative management strategy in 1990 and enacted an extensive stock assessment program to monitor the ceded territory walleye populations. The current management system for ceded territory lakes places a harvest quota on individual lakes, based upon adult population estimates (Hansen et al. 1991). For up to 2 years after a population estimate is conducted, the annual total allowable catch in individual lakes is 35% of the adult population, minus error margins to account for variability in population estimates (Hansen et al. 1991); after 2 years, walleye abundance is estimated by a model based on population size and lake area. Following tribal harvest declaration of catch, a sliding angler bag limit is implemented on individual lakes based on the total allowable catch. This management practice reduces the

chances of overexploiting a walleye stock to 1 in 40 (Hansen et al. 1991). Because of the conservative nature of the harvest regulations, we expected that walleye densities increased after 1990 in ceded territory lakes. Because no walleye density estimates were conducted before 1990, we used density-dependent growth relationships to suggest densities before 1990.

### Methods

We examined data collected by the Great Lakes Indian Fish and Wildlife Commission (GLIFWC) and WDNR during 1977–1999 to assess growth dynamics of walleyes in the ceded territory of Wisconsin. The ceded territory of Wisconsin encompasses approximately the northern third of the state (Hansen et al. 1991; Beard et al. 1997) and contains most of the lakes in Wisconsin; 859 of the ceded lakes support populations of walleyes (Nate et al. 2000). Since 1990, an extensive walleye monitoring program has been conducted on ceded territory lakes; this includes annual creel surveys; adult and age-0 walleye population estimates; and data on length, weight, and age (Hansen et al. 1991; Beard et al. 1997). Although samples of walleye lengths, weights, and ages were collected for a number of lakes in the ceded territory before 1990, walleye population estimates were not conducted.

*Walleye abundance.*—Beginning in 1990, walleye abundance was estimated in approximately 25–30 randomly selected lakes per year in the ceded territory. During the spring of each year, density of adult (sexually mature) and total (immature + mature) walleyes were estimated using the Chapman modification of the Petersen mark–recapture population estimation technique (Ricker 1975). Mature walleyes, captured via fyke nets, were marked and released shortly after ice-out in each year. The target marking goal was 10% of the mature (i.e., if the sex could be determined or if the total length was longer than 15 in) walleye population. One or 2 d after marking, the entire shoreline was electrofished to recapture mature walleyes for the adult population estimate. In addition, all mature and immature walleyes not previously marked were marked. To estimate total walleye abundance, the entire shoreline was electrofished 2–3 weeks after the second marking to estimate the proportion of marked walleyes in the population. In addition to the population estimates, lengths, weights, and ages were subsampled from most populations from 1990 to 1999.

*Data analyses.*—We examined density-dependen-

dent growth of walleyes within and among ceded territory lakes. First, we looked for patterns in walleye growth among all available lakes from 1990 to 1999. Second, we examined walleye growth within lakes over multiple years to look for evidence of density-dependent growth within individual populations. We used the growth characteristics of asymptotic length ( $L_\infty$ ), growth rate near  $t_0$  ( $\omega$ ; where  $t_0$  = age when length is 0), and body condition to address these questions.

We estimated  $L_\infty$  via the von Bertalanffy growth equation (von Bertalanffy 1938):

$$l_t = L_\infty[1 - e^{-K(t-t_0)}], \quad (1)$$

where  $l_t$  = length at age  $t$ ,  $K$  = Brody growth coefficient. Asymptotic total length was estimated for 254 walleye populations from 1990 to 1999 (Table 1). Asymptotic length and  $t_0$  are often poorly determined because of lack of data for very young or very old fish (Hilborn and Walters 1992). Therefore, we used an ad hoc procedure of initially estimating asymptotic length based on visual inspection of the plot of mean length at age as a function of age for each lake-year. We then solved for  $K$  and  $t_0$  using nonlinear estimation procedures. Our estimated asymptotic length was then varied, and  $K$  and  $t_0$  were reestimated until a specific combination of the three parameters resulted in the highest  $r^2$  value. Once the best model was found, the three growth parameters were recorded to describe the walleye population growth in each particular lake-year. In all cases, both male and female length-at-age data were used. We excluded any lake where the growth data for the corresponding adult density estimate was insufficient to provide reasonable growth estimates. Populations with low sample sizes or poor representations of each age-class were excluded from growth data when the sample size was less than three; a minimum of three individuals is necessary to calculate a reasonable variance. For low sample sizes, the von Bertalanffy growth equation does not accurately estimate  $L_\infty$ ,  $K$ , and  $t_0$ . We used  $L_\infty$  to represent the asymptotic length of walleyes in a given population.

We used  $\omega$ , as proposed by Gallucci and Quinn (1979), to assess growth of younger fish in a population. This parameter corresponds to the growth rate near  $t_0$  and is given by

$$\omega = K \cdot L_\infty. \quad (2)$$

Because of the lack of independence between  $K$  and  $L_\infty$ ,  $\omega$  provides a suitable measure for com-

parison because it is statistically more robust than  $K$  or  $L_\infty$  alone (Gallucci and Quinn 1979). Growth rate ( $\omega$ ) of 254 juvenile walleye populations was estimated from 1990 to 1999 (Table 1).

We assessed body condition by developing a single linear relationship for weight versus total length for 228 individual walleye populations in ceded territory lakes from 1977 to 1999. Both total length and weight were  $\log_{10}$  transformed to establish linearity between the variables, and all outliers were removed to achieve homoscedasticity. An outlier was removed when the Studentized residual was greater than or equal to three (Draper and Smith 1998). Length and weight for more than 48,000 individual fish collected by the WDNR during 1977–1999 were used to establish this relationship. Body condition of a given population in a given year was determined as the mean residual error relative to the ceded territory length–weight relationship (Hrabik et al. 1998). Residuals for individual fish were represented as the difference between the observed weight and the predicted weight per given length from the standard line. The mean residual was the average of all individual residuals from a given population in a specific lake and year. Body condition was estimated for 258 walleye populations from 1990 to 1999 (Table 1).

Pooling data from all lakes during the post-1990 period, we applied regression analysis to each of the growth characteristics (asymptotic length,  $\omega$ , body condition) as a function of adult walleye density. We considered numerous models and transformations of the independent and dependent variables in our analysis. We chose simple linear regression and a  $\log_e$  transformation of adult walleye densities because the data were lognormally distributed. The natural log transformation also normalized the residual variability of the regressions (Draper and Smith 1998). For all tests, statistical significance was determined by an  $F$ -test at  $\alpha = 0.05$ .

To look for density-dependent growth within individual walleye populations, we examined the growth characteristics in relation to density for all lakes that had two or more population estimates and corresponding length, weight, and age data during 1990–1999 ( $N = 29$ ). We expected that density-dependent growth would be expressed by an inverse relationship between the growth characteristics and adult walleye density between the years of the population estimates. For example, an increase in adult density between population estimates with a decrease in the growth variables or

TABLE 1.—Ceded territory lakes of northern Wisconsin used for walleye growth analysis, with year (1977–1999), adult walleye density estimates (fish/ha) and three estimated population growth parameters: asymptotic length ( $L_{\infty}$ ), growth rate ( $\omega$ ) near the age when length is zero, and body condition.

Lake	County	Adult density	$L_{\infty}$ (cm)	$\omega$ (cm/year)	Body condition
<b>Year: 1977</b>					
Shell	Washburn		102	8.772	0.014
<b>Year: 1978</b>					
Long	Washburn		102	11.118	0.014
<b>Year: 1986</b>					
Big McKenzie	Burnett		76	9.804	0.017
Grindstone	Sawyer		69	21.045	0.104
Yellow Lake	Burnett		74	11.47	0.005
<b>Year: 1987</b>					
Big McKenzie	Burnett		71	13.632	00.018
Chippewa Flowage	Sawyer		94	12.878	-0.004
Grindstone	Sawyer		N/A		-0.04
Round	Sawyer		N/A		-0.011
Sand	Sawyer		76	8.664	0.028
Whitefish	Douglas		89	7.743	0.008
<b>Year: 1988</b>					
Balsam	Polk		84	9.996	0.012
Big Carr	Oneida		76	13.832	0.05
Buffalo	Oneida				0.025
Clear	Oneida		102	7.854	-0.006
Half Moon	Polk		69	11.592	0.009
Hasbrook	Oneida		76	9.348	-0.013
Lac Courte Oreilles	Sawyer		86	7.912	0.024
Minong Flowage	Douglas		76	10.488	-0.007
North Sand	Washburn		N/A		-0.033
Owen	Bayfield		91	10.465	0.007
Pike	Price		74	7.4	0.016
Round	Price		97	9.312	0.026
Sweeney	Price				0.018
Trout	Vilas		89	9.612	-0.004
Two Sisters	Oneida		N/A		-0.003
Willow Flowage	Oneida		81	9.72	0.03
<b>Year: 1989</b>					
Ballard	Vilas				-0.197
Balsam	Polk		84	7.98	0.067
Beaver Dam	Barron				0.041
Big Butternut	Polk				0.026
Big Round	Sawyer				0.026
Butternut	Forest		56	16.016	-0.04
Franklin	Forest		97	7.081	-0.039
Harris	Vilas				0.035
Kentuck	Vilas				0.017
Laura	Vilas				-0.122
Magnor	Polk				-0.019
Pipe	Polk				-0.018
Round	Polk				-0.044
Trude	Iron		64	9.728	0.018
Turtle Flambeau Flowage	Iron		86	7.654	0.028
<b>Year: 1990</b>					
Bearskin	Oneida	16.6478	99	6.633	0.006
Big Butternut	Polk	11.58	60	13.14	0.049
Big McKenzie	Burnett	8.0769	61	13.176	0.035
Birch	Vilas	2.7417	76.2	12.192	-0.082
Boulder	Vilas	7.6817	69	9.591	
Butternut	Price	4.9153	69	9.453	0.005
Chain	Oneida	11.9548	81	9.477	0.035
Chippewa Flowage	Sawyer	12.9428	74	8.584	0.009
Clear	Oneida	5.7551	91	7.007	-0.058

TABLE 1.—Continued.

Lake	County	Adult density	$L_{\infty}$ (cm)	$\omega$ (cm/year)	Body condition
Dam	Oneida	8.7191	102	7.752	0.001
Kentuck	Vilas	20.3775	81	7.371	-0.011
Lac Vieux Desert	Vilas	7.2618	84	8.736	0.0004
Little Arbor Vitae	Vilas	11.115	94	9.776	0.038
Lost Land	Sawyer	1.5067	84	6.888	-0.006
Middle McKenzie	Washburn	5.1623	58	14.732	0.02
Pelican	Oneida	7.3606	81	10.692	0.061
Plum	Vilas	4.6189	89	8.544	-0.028
Rainbow Flowage	Oneida	10.621	97	8.536	0.037
Sand	Oneida	8.2498	84	7.56	-0.033
Squaw	Vilas	13.2392	91	5.46	-0.024
Squirrel	Oneida	12.2759	91	8.008	-0.033
Teal	Sawyer	10.9421	76.2	6.7056	-0.011
<b>Year: 1991</b>					
Amik	Price	4.00	99	6.93	0.044
Anvil	Vilas	28.95	71	8.804	-0.143
Ballard	Vilas	12.77	81	10.287	-0.054
Big	Vilas	36.61	91	8.372	-0.041
Big Round	Polk	4.89	74	13.098	0.035
Bridge	Oneida	14.82	71	11.289	0.036
Buckskin	Oneida	7.76	86	8.428	0.007
Busky Bay	Bayfield	16.35	66	7.788	
Butternut	Forest	4.08	66	9.702	-0.095
Clam River	Burnett	3.21	66	12.408	-0.002
Deer	Lincoln	2.25	76	12.464	0.003
Dowling	Douglas	17.88	70	6.23	0.02
Eagle	Bayfield	0.69	66	6.534	
Enterprise	Langlade	12.40	71	9.443	0.044
Half Moon	Polk	4.10	69	12.489	-0.018
Hart	Bayfield	21.19	71	8.165	
Irving	Vilas	0.77	71	13.135	-0.044
Lac Courte Orielles	Sawyer	3.24	66	12.606	0.041
Lac Vieux Desert	Vilas	5.93	61	10.004	0.055
Long	Washburn	7.24	84	10.752	-0.041
Long	Washburn	4.35	69	9.039	0.021
Lynx	Vilas	6.50	91	7.371	-0.051
Nokomis	Lincoln	8.79	86	8.944	-0.0002
North Twin	Vilas	5.58	94	8.648	-0.013
Pike	Price	9.61	89	7.387	0.03
Pine	Forest	1.88	71	12.212	0.027
Rock	Vilas	4.50	69	8.832	-0.071
Round	Sawyer	7.78	66	8.844	0.011
Round	Price	10.45	66	8.184	0.012
Sand	Sawyer	7.34	58	16.356	0.014
Shell	Washburn	3.73	56	8.512	-0.024
Sissabagama	Sawyer	22.38	86	8.084	0.049
South Turtle	Vilas	4.45	61	11.956	-0.094
Sparkling	Vilas	17.98	69	15.042	-0.007
Squaw	Vilas	14.60	48	13.008	0.031
Squirrel	Oneida	13.68	69	9.039	0.002
Turner	Price	30.83	76	7.6	0.028
Twin Bear	Bayfield	10.45	71	17.04	
Whitefish	Douglas	5.85	60	12.66	-0.035
White Birch	Vilas	6.64	69	14.076	0.058
<b>Year: 1992</b>					
Big Portage	Vilas	8.15	61	9.27	-0.052
Big St Germaine	Vilas	5.34	89	6.319	
Buckskin	Oneida	14.35	71	11.928	
Butternut	Forest	12.84	89	6.141	-0.087
Crescent	Oneida	9.73	74	11.544	-0.043
Kawaguesaga	Oneida	10.97	94	10.528	-0.009
Kentuck	Vilas	10.37	69	11.178	
Little St Germaine	Vilas	1.65	81	9.558	0.025

TABLE 1.—Continued.

Lake	County	Adult density	$L_{\infty}$ (cm)	$\omega$ (cm/year)	Body condition
Lynx	Vilas	8.84	86	6.536	
Metonga	Forest	5.71	91	7.553	0.028
Minocqua	Oneida	13.88	102	7.548	-0.042
Nancy	Washburn	11.14	71	6.532	
Nelson	Sawyer	35.91	71	9.372	0.061
Palmer	Vilas	1.61	79	10.823	0.021
Pine	Iron	17.39	74	9.768	
Presque Isle Chain	Vilas	7.11	91	8.645	-0.033
Seven Mile	Oneida	12.00	81	8.991	0.012
Shell	Washburn	3.95	48	12.816	
Squaw	Vilas	14.13	64	7.36	
Squirrel	Oneida	14.05	84	7.14	
Tenderfoot	Vilas	57.35	66	8.91	
Tomahawk	Oneida	6.15	84	12.012	-0.024
Trude	Iron	12.40	56	9.24	-0.014
Turtle Flambeau Flowage	Iron	10.52	58	10.962	0.008
Two Sisters	Oneida	7.85	86	9.288	0.012
Upper St Croix	Douglas	8.42	56	11.368	0.004
Yellow	Burnett	9.95	69	11.04	0.056
Yellow River	Burnett	N/A	69	8.763	-0.006
<b>Year: 1993</b>					
Bass Patterson	Washburn	14.50	74	8.362	
Beaver Dam	Barron	1.56	91	7.462	0.037
Big Arbor Vitae	Vilas	22.35	91	9.555	0.002
Big Eau Pleine	Marathon	4.62	89	11.214	0.036
Butternut	Forest	11.46	66	7.92	N/A
Clear	Vilas	8.84	71	8.875	-0.04
Crab	Vilas	4.74	97	7.857	-0.022
Fishtrap	Vilas	13.91	69	8.142	-0.029
High	Vilas	8.92	74	12.802	-0.037
Jackson	Bayfield	3.75	64	9.088	0.111
Katherine	Oneida	9.88	74	10.286	-0.01
Kentuck	Vilas	5.88	66	10.23	
Manitowish	Vilas	2.52	89	8.811	-0.023
Namekagon	Bayfield	12.40	71	7.952	0.017
Nancy	Washburn	1.73	64	12.48	0.018
Rest	Vilas	9.46	64	11.008	-0.018
Sand	Barron	4.15	84	10.584	N/A
Spider	Vilas	7.36	79	10.349	0.002
Squaw	Vilas	8.35	91	5.005	-0.026
Squirrel	Oneida	11.51	86	6.02	
Star	Vilas	16.28	86	7.138	-0.029
Whitefish	Sawyer	5.06	66	13.992	0.051
Yellow Birch	Vilas	31.25	71	10.366	-0.088
<b>Year: 1994</b>					
Balsam	Polk	4.08	79	10.349	0.031
Big St Germaine	Vilas	6.97	84	10.164	0.019
Dog/Deer	Oneida	3.24	102	7.752	0.01
Franklin	Forest	5.83	81	9.072	-0.01
Gilmore	Oneida	2.91	84	11.676	0.034
Grindstone	Sawyer	3.11	89	8.544	
Kentuck	Vilas	8.52	76	13.528	
Lipsett	Burnett	0.96	58	17.052	0.013
Long	Washburn	7.68	71	15.052	0.025
Lynx	Vilas	3.46	97	9.118	-0.019
Nancy	Washburn	N/A	53	18.497	
Nebagamon	Douglas	6.37	79	8.532	-0.006
Papoose	Vilas	7.53	102	9.384	-0.035
Shell	Washburn	2.59	66	8.382	-0.005
Squaw	Vilas	9.29	64	8.32	
Squirrel	Oneida	14.18	84	7.56	
Trout	Vilas	6.25	74	11.174	-0.001
Willow Flowage	Oneida	6.40	79	8.848	-0.014

TABLE 1.—Continued.

Lake	County	Adult density	$L_{\infty}$ (cm)	$\omega$ (cm/year)	Body condition
<b>Year: 1995</b>					
Allequash	Vilas	2.42	71	10.366	-0.025
Annabelle	Vilas	4.20	89	5.607	
Bass Patterson	Washburn	30.13	99	6.435	
Beauregard	Douglas	9.51	53	9.911	0.018
Big	Vilas	9.95	79	9.638	-0.024
Boulder	Vilas	10.74	69	8.832	-0.022
Buckskin	Oneida	23.17	89	6.319	
Butternut	Forest	6.97	53	9.752	
Cisco	Bayfield	4.79	74	10.582	0.05
Connors	Sawyer	14.52	81	9.963	0.009
Devils	Burnett	2.32	76	7.524	0.027
George	Oneida	6.50	79	8.453	0.029
Kentuck	Vilas	2.35	81	12.312	
Laura	Vilas	14.55	86	7.052	-0.031
Long	Bayfield	15.36	64	9.536	-0.041
Mohawkson	Lincoln	6.64	74	9.176	0.049
Nelson	Sawyer	5.09	94	6.58	
Pelican	Oneida	3.06	84	5.208	
Pipe	Polk	5.83	64	11.008	0.03
Plum	Vilas	9.48	91	8.463	-0.023
Sherman	Vilas	16.06	64	10.624	
Siskiwit	Bayfield	6.77	51	13.209	
Snipe	Vilas	4.03	76	13.984	-0.005
Squirrel	Oneida	15.66	86	6.708	
Tenderfoot	Vilas	15.36	74	8.51	
<b>Year: 1996</b>					
Annabelle	Vilas	3.58	91	8.645	
Bass Patterson	Washburn	26.45	89	5.874	
Bearskin	Oneida	19.59	74	9.472	-0.037
Big McKenzie	Burnett	4.84	91	7.644	0.002
Buckskin	Oneida	29.94	71	8.804	-0.017
Butternut	Forest	6.52	53	12.402	
Butternut	Price	10.23	69	8.832	0.027
Clear	Oneida	9.04	86	8.858	-0.035
Diamond	Bayfield	8.08	64	17.984	0.073
Kentuck	Vilas	1.51	69	24.357	
Little Arbor Vitae	Vilas	18.62	84	8.568	-0.003
Lyman	Douglas	2.79	74	7.992	-0.002
North Twin	Vilas	10.18	79	11.139	-0.014
Seven Island	Lincoln	10.70	74	10.656	0.01
Sherman	Vilas	10.79	61	8.113	
Siskiwit	Bayfield	9.53	53	11.342	
Squaw	Vilas	9.86	58	7.54	
Squirrel	Oneida	16.15	84	9.072	
Wissota	Chippewa	4.30	71	8.094	0.004
<b>Year: 1997</b>					
Annabelle	Vilas	9.44	94	5.922	
Big Round	Polk	9.24	56	16.18	0.06
Butternut	Forest	12.47	69	12.282	-0.053
Chain	Oneida	3.48	86	7.568	0.005
Chetac	Sawyer	4.30	71	13.703	0.092
Clam River	Burnett	5.11	56	18.816	0.013
Dam	Oneida	8.50	81	11.745	-0.01
Franklin	Forest	5.09	71	10.721	0.009
Half Moon	Polk	2.59	71	9.585	
Harris	Vilas	9.31	74	9.324	-0.006
Kentuck	Vilas	2.59	69	36.777	
Lac Courte Oreilles	Sawyer	N/A	66	8.844	
Lac Vieux Desert	Vilas	3.58	69	12.834	
Lipsett	Burnett	2.64	58	13.514	0.007
Little St Germaine	Vilas	5.58	86	9.976	0.006
Lower Nine Mile	Oneida	0.59	81	7.614	
Metonga	Forest	9.14	71	9.017	
Nebagamon	Douglas	4.35	56	11.144	

TABLE 1.—Continued.

Lake	County	Adult density	$L_{\infty}$ (cm)	$\omega$ (cm/year)	Body condition
Sand	Oneida	5.34	81	8.181	0.022
Seven Mile	Oneida	6.59	84	7.812	0.02
Sherman	Vilas	10.77	51	12.699	
Siskiwit	Bayfield	10.79	46	14.996	
Sissabagama	Sawyer	15.86	91	7.098	-0.005
Squaw	Vilas	3.66	56	8.4	
Squirrel	Oneida	15.91	71	7.668	
Star	Vilas	11.21	97	6.596	-0.043
Stone	Oneida	0.67	71	9.372	0.028
Trout	Vilas	5.29	74	9.102	
Trude	Iron	11.07	64	9.024	0.007
Turtle Flambeau Flowage	Iron	9.98	71	6.532	0.005
Upper St Croix	Douglas	7.14	53	11.289	0.022
Yellow	Burnett	5.11	76	10.564	
<b>Year: 1998</b>					
Bass Patterson	Washburn	11.98	81	3.321	
Bearskin	Oneida	22.13	58	8.294	
Big Arbor Vitae	Vilas	12.08	86	8.858	-0.001
Booth	Oneida	2.64	76	8.588	0.02
Butternut	Forest	9.83	61	10.004	
Kawaguesaga	Oneida	12.89	86	10.578	0.013
Kentuck	Vilas	1.88	74	17.834	0.053
Lac Courte Oreilles	Sawyer	4.20	64	16.192	
Laura	Vilas	9.98	99	6.93	-0.006
Long	Washburn	3.31	76	10.716	
Lynx	Vilas	4.35	89	7.209	-0.044
Minocqua	Oneida	11.39	86	11.008	-0.013
Nelson	Sawyer	11.76	74	11.026	
North Nokomis	Oneida	6.50	94	6.768	0.019
North Twin	Vilas	3.61	71	10.295	
Pelican	Oneida	7.04	74	9.546	
Rainbow Flowage	Oneida	9.86	76	8.588	0.024
Rangeline	Forest	5.36	86	9.976	0.042
Sherman	Vilas	12.89	64	9.152	
Siskiwit	Bayfield	26.70	48	12.384	
Squaw	Vilas	10.70	61	8.967	
Squirrel	Oneida	13.44	81	7.857	
Tomahawk	Oneida	6.20	89	10.502	-0.003
Trump	Forest	2.00	74	10.952	-0.007
Two Sisters	Oneida	4.69	94	7.708	-0.003
Upper Post	Langlade	4.67	89	7.387	0.038
<b>Year: 1999</b>					
Amnicon	Douglas	10.25	68	9.59	-0.024
Arbutus	Forest	1.88	67	11.12	-0.007
Bass Patterson	Washburn	8.35	81	5.589	
Bear	Oneida	1.43	76	11.48	0.006
Black Oak	Vilas	8.30	94	7.238	0.044
Buckskin	Oneida	16.55	66	9.57	
Clear	Vilas	7.19	74	10.138	0.013
English	Ashland	4.03	86	6.192	0.002
George	Oneida	11.24	89	7.12	0.03
Island	Iron	9.24	91	7.371	0.021
Kentuck	Vilas	4.69	71	38.766	
Little Arbor Vitae	Vilas	12.67	69	11.523	
Little Star	Vilas	5.01	81	8.424	-0.173
Middle McKenzie	Washburn	3.78	58	12.876	0.027
Rest	Vilas	7.58	81	7.614	-0.018
Sand	Barron	5.56	84	9.828	
Shell	Washburn	2.00	71	6.745	0.021
Sherman	Vilas	13.49	71	6.177	
Siskiwit	Bayfield	12.79	48	10.848	
Squaw	Vilas	10.40	66	7.788	
Squirrel	Oneida	13.29	66	7.788	
Stevens	Forest	13.81	79	9.559	0.043
Thompson	Oneida	3.33	76	7.98	0.039
Wild Rice	Vilas	1.63	99	8.217	0.004

vice versa over the same period would be indicative of density-dependent growth. For individual populations with three or more estimates from 1990 to 1999, the earliest estimates were always used as initial density and growth, and all later density and growth estimates were compared with the initial conditions. Density dependence was concluded if the change in density corresponded to an inverse change in growth in the later year or years. We used a chi-square test to determine whether the proportion of walleye populations exhibiting density-dependent growth were significantly different than the expected proportions of half density dependent and half density independent ( $\alpha = 0.05$ ; Sokal and Rohlf 1981).

*Effect of ceded territory management regime.*—We tested for changes in walleye growth and density as a result of the current ceded territory management regime using a one-way analysis of variance (ANOVA) with each year serving as an individual treatment. All available adult densities and measured growth characteristics during the 1990–1999 period were used in this analysis. All adult density estimates were  $\log_e$  transformed before conducting the ANOVA to increase the power to detect differences among years and to satisfy the normality assumption of ANOVA. The null hypothesis that density,  $L_\infty$ ,  $\omega$ , and body condition were equal over time was tested at the  $\alpha = 0.05$  level. If significant differences were observed among years, a sequential Bonferroni test was used on all 95% confidence intervals because of the high number of comparisons ( $N = 45$ ; Holm 1979). We also used a one-way ANOVA with unequal sample sizes to compare the effects of past and current management systems on walleye growth. Two treatments, pre-1990 ( $N = 63$ ) and post-1990 ( $N = 258$ ), were used to test the null hypothesis that growth was equal between the two periods. All available length, weight, and age data from 1977 to 1999 was used in this analysis, and statistical significance was determined at  $\alpha = 0.05$ . Pre-1990 growth included data from 1990 because the walleye data were collected in the spring of 1990, which preceded the current management system.

## Results

### *Growth Dynamics among Lakes*

Total lengths (TL; mm) and weights ( $W$ ; g) from more than 48,000 walleyes from 228 individual populations from 1977 to 1999 provided the weight–length relationship in ceded territory lakes:

$$\log_{10}W = -5.637 + 3.231 \log_{10}TL. \quad (3)$$

The developed length–weight relationship was used to calculate average body condition for each walleye population examined.

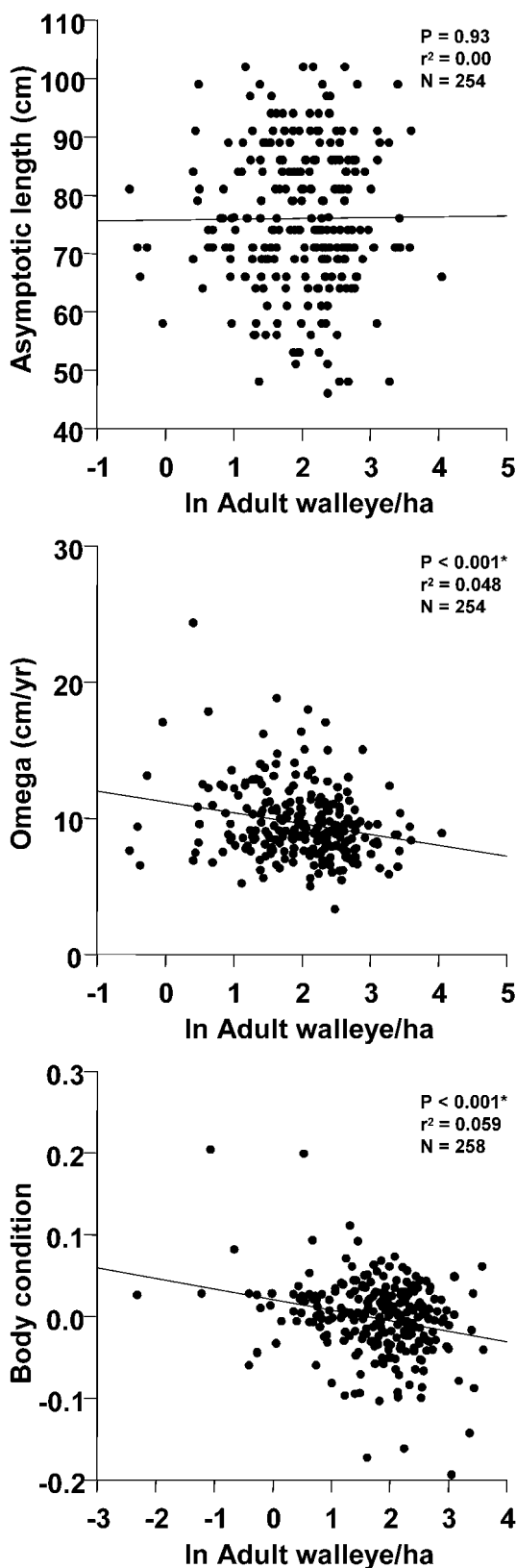
Asymptotic length was unrelated to density, whereas body condition and juvenile growth rate decreased as density increased (Figure 1). Juvenile growth rate,  $\omega$ , ( $F_{1,252} = 13.1$ ,  $P < 0.001$ ) and body condition ( $F_{1,256} = 16.02$ ,  $P < 0.001$ ) were inversely related to density, whereas  $L_\infty$  was unrelated to density ( $F_{1,252} = 0.007$ ,  $P = 0.93$ ). In each case, the  $r^2$  values were very low and  $\log_e$  adult walleye density explained less than 6% of the variability in the growth variables during 1990–1999 (Figure 1). Predicted  $L_\infty$ ,  $\omega$ , and body condition averaged 75.2 cm, 9.96 cm/year, and  $-0.003$ , respectively, for data from 1990 to 1999.

### *Growth Dynamics within Lakes*

Walleye growth in 29 individual lakes with population estimates in multiple years suggested growth was density dependent in many lakes (Table 2). In most lakes,  $L_\infty$  and body condition decreased as walleye density increased. Contrary to our expectations,  $\omega$  increased as adult abundance increased. Walleyes exhibited density dependence in body condition,  $L_\infty$ , and  $\omega$  in 62% (16 of 26), 69% (20 of 29), and 28% (8 of 29), respectively, of the comparisons examined (Figure 2). Observed frequencies of lakes in which walleyes exhibited density-dependent growth were significantly different than expected frequencies for  $L_\infty$  ( $\chi^2 = 4.21$ ,  $df = 1$ ,  $P < 0.05$ ) but not for juvenile growth rate ( $\chi^2 = 0.84$ ,  $df = 1$ ,  $P > 0.05$ ) or body condition ( $\chi^2 = 1.37$ ,  $df = 1$ ,  $P > 0.05$ ; Figure 2).

### *Management Effects on Walleye Growth and Density*

Adult walleye density and growth in ceded territory lakes did not change substantially after 1990. Adult walleye density during 1990–1999, which averaged 8.3 walleyes/ha (range  $<1$  to 60 walleyes/ha) for all lakes sampled (Figure 3), did not change significantly among years ( $F_{9,482} = 1.59$ ,  $P = 0.116$ ; Figure 4). Similarly,  $L_\infty$  ( $F_{9,239} = 1.657$ ,  $P = 0.10$ ) and  $\omega$  ( $F_{9,239} = 0.904$ ,  $P = 0.523$ ) did not change significantly. In contrast, body condition changed significantly among years during 1990–1999 ( $F_{9,267} = 2.55$ ,  $P = 0.008$ ; post-hoc Bonferroni comparisons,  $P > 0.05$ ). After the sequential Bonferroni procedure was used, no individual year comparisons of body condition were



found to be statistically significant at the tablewide alpha level ( $0.05/45 = 0.0011$ ).

Asymptotic length and body condition decreased significantly after 1990, whereas early growth rate did not change significantly. Average asymptotic length decreased from 82 cm before 1990 to 75 cm after 1990 ( $F_{1,281} = 13.02$ ,  $P < 0.001$ ). Early growth rate did not change significantly and averaged 9.9 cm/year before and after 1990. ( $F_{1,281} = 0.092$ ,  $P = 0.762$ ). Average body condition decreased significantly from 0.008 before 1990 to  $-0.005$  after 1990 ( $F_{1,317} = 4.55$ ,  $P = 0.034$ ; Figure 5).

## Discussion

### Growth Dynamics among Lakes

Our results suggest that density dependence is a weak driver of regional walleye growth in the ceded territory. Asymptotic length of individual walleye populations showed no relationship with adult density (Figure 1). Contrary to our findings, Walters and Post (1993) found evidence that  $L_{\infty}$  decreased exponentially with increased kokanee *Oncorhynchus nerka* density in Montana and Idaho lakes. Our results indicated that walleyes in some lakes at very low adult densities had higher than average asymptotic lengths and at very high densities had lower asymptotic lengths; however only a small sample of lakes were available at these extremes of density. Body condition and juvenile growth rate decreased significantly with increasing density; however, little of the variability was explained (Figure 1). Growth increment and mean size-at-age analysis of walleye populations in the ceded territory also revealed an apparent lack of density dependence on a regional scale from 1990 to 1999 (Sass 2001). The weak relationships and high variability observed between the growth variables and adult density suggests that walleye populations behave individually and that no regionally coherent density-dependent relationship exists for ceded territory populations. Our inability to detect a stronger regional signal of density-dependent

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FIGURE 1.—Linear regressions of three estimated population growth parameters— asymptotic length ( $L_{\infty}$ ), growth rate ( $\omega$ ) near the age when length is 0, and body condition—versus  $\log_e$  ( $\ln$ ) adult walleye density for ceded territory lakes in northern Wisconsin, 1990–1999. Each data point represents the growth estimate for the corresponding individual adult walleye density estimate.  $P$ -values with asterisks denote significance at  $\alpha = 0.05$ .

TABLE 2.—Ceded territory lakes of northern Wisconsin used for within-lake comparisons and the corresponding year, adult density estimate, and the three estimated population growth parameters: asymptotic growth ( $L_{\infty}$ ), growth rate ( $\omega$ ) near age when length is zero, and body condition. Asterisks next to growth estimates signify density-dependent growth.

Lake	Year	Adult density (fish/ha)	Body condition	$L_{\infty}$ (cm)	$\omega$ (cm/year)
Laura	1995	14.55	-0.031*	86*	7.05
Laura	1998	9.98	-0.006	99	6.93
Buckskin	1991	7.76	0.007*	86*	8.43
Buckskin	1996	29.94	-0.017	71	8.8
North Twin	1991	5.58	-0.014	94*	8.65
North Twin	1996	10.18	-0.013	79	11.14
Clam River	1991	3.21	-0.002	66*	12.41
Clam River	1997	5.11	0.013	56	18.82
Lipsett	1994	0.96	0.013*	58	17.05*
Lipsett	1997	2.64	0.007	58	8.57
Little St. Germaine	1992	1.65	0.025*	81	9.56
Little St. Germaine	1997	5.58	0.006	86	9.98
Seven Mile	1992	12	0.012*	81*	8.99
Seven Mile	1997	6.59	0.02	84	7.81
Sissabagama	1991	22.38	N/A	86*	8.08
Sissabagama	1997	15.86	N/A	91	7.1
Star	1993	16.28	-0.029	86*	7.14
Star	1997	11.21	-0.043	97	6.6
Trude	1992	12.4	-0.014*	56*	9.24
Trude	1997	11.07	0.007	64	9.03
Trutle Flambeau Flowage	1992	10.52	0.008	58*	10.96
Trutle Flambeau Flowage	1997	9.98	0.005	71	6.53
Upper St. Croix	1992	8.42	0.004*	56	11.37
Upper St. Croix	1997	7.14	0.022	53	11.29
Kawaguesaga	1992	10.97	-0.009	94*	10.53
Kawaguesaga	1998	12.89	0.013	86	10.58
Minocqua	1992	13.88	-0.042*	102	7.55*
Minocqua	1998	11.39	-0.013	86	11.01
Two Sisters	1992	7.85	0.012	86*	9.29
Two Sisters	1998	4.69	-0.003	94	7.71
Lynx	1991	6.5	-0.051*	91*	7.37*
Lynx	1992	8.84	N/A	86	6.54
Lynx	1994	3.46	-0.019	97	9.12
Lynx	1998	4.35	-0.044	89	7.21
Shell	1991	3.73	-0.024*	56*	8.51
Shell	1994	2.59	-0.005	66	8.38
Shell	1999	2	0.021	71	6.75
Sand	1990	8.25	-0.033*	84	7.56*
Sand	1997	5.34	0.022	81	8.18
Middle McKenzie	1990	5.16	0.02*	58	14.73
Middle McKenzie	1999	3.78	0.027	58	12.88
Big McKenzie	1990	8.08	0.035	61*	13.18
Big McKenzie	1996	4.84	0.002	91	7.64
Chain	1990	11.95	0.035	81*	9.48
Chain	1997	3.48	0.005	86	7.57
Clear	1990	5.76	-0.058	91*	7.01
Clear	1996	9.04	-0.035	86	8.86
Bearskin	1990	16.65	0.006*	99*	6.63*
Bearskin	1996	19.59	-0.037	74	9.47
Big Arbor Vitae	1993	22.35	0.002	91	9.56*
Big Arbor Vitae	1998	12.08	-0.001	86	8.86
Franklin	1994	5.83	-0.01*	81	9.07*
Franklin	1997	5.09	0.009	71	10.72
Butternut	1990	4.92		69	9.45*
Butternut	1996	10.23		69	8.83

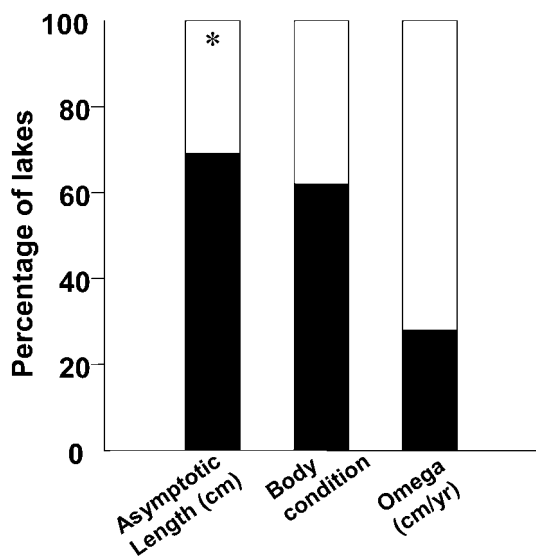


FIGURE 2.—Percentage of within-lake comparisons for northern Wisconsin ceded territory lakes, 1990–1999, showing density-dependent walleye growth estimates of asymptotic length, body condition, and growth rate ( $\omega$ ) near the age when length is 0. Dark bars denote density-dependent growth and light bars represent density-independent growth. Asterisks within columns denote significant differences ( $\alpha = 0.05$ ) between the observed frequencies of lakes exhibiting density-dependent growth and the expected frequencies (half density dependent and half density independent).

growth among walleye populations is probably due to inherent differences among the lakes of the ceded territory and measurement error in the population estimates of individual walleye populations.

Evidence for density-dependent growth in fish populations has generally been shown in pond experiments (e.g., Diana et al. 1991) or whole-lake experiments (e.g., Walters and Post 1993; Post et al. 1999) where density and the size-structure of the fish populations have been manipulated. Under these protocols, differences between populations and conditions are controlled. The ceded territory of Wisconsin represents an uncontrolled test of density-dependent walleye growth, where population density, size-structure, and lake characteristics are highly variable. Our lack of ability to detect a strong density-dependent signal among ceded territory walleye populations may be representative of the inherent differences of the lakes across the region or because of measurement error in the adult population estimates. For example, lake productivity varies widely among ceded territory lakes and is positively correlated with fish growth (Trippel and Beamish 1989; Deegan and

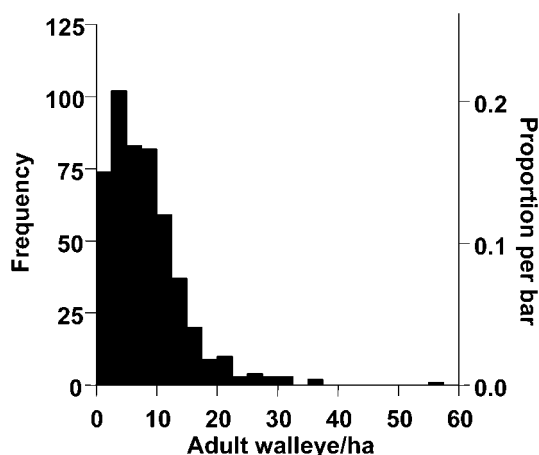


FIGURE 3.—Frequency distribution of adult walleye density estimates from ceded territory lakes of northern Wisconsin during 1990–1999 and the proportions for each density category.

Peterson 1992; Hubert and Chamberlain 1996; Budy et al. 1998; Gross et al. 1998). In addition, the confidence intervals for each individual population estimate are variable and high for many lakes (mean coefficient of variation = 13%). Further, the estimated percentage of male walleyes in each population (mean = 76%) is much greater than the percentage of females (mean = 24%), which may suggest unequal catchability of the sexes during the spawning season and an underesti-

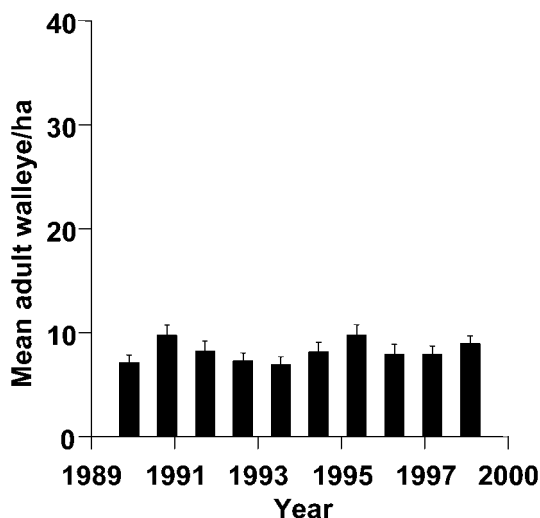


FIGURE 4.—Mean adult walleye densities by year from ceded territory lakes of northern Wisconsin during 1990–1999. Error bars represent the standard errors of the means.

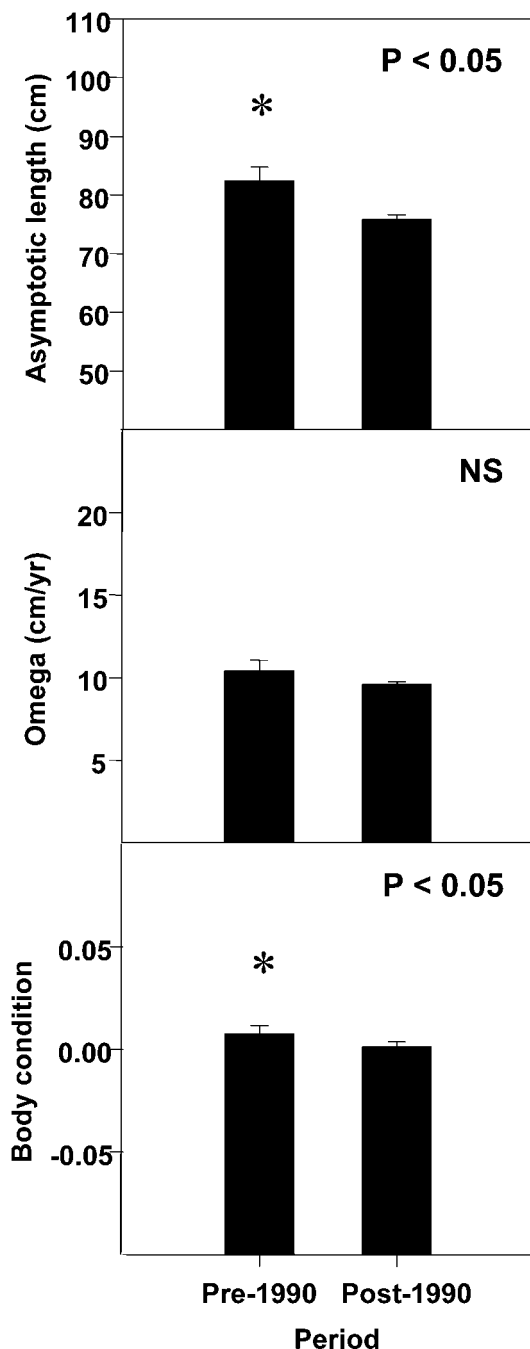


FIGURE 5.—Mean asymptotic length, growth rate ( $\omega$ ) near the age when length is 0, and body condition of walleyes under the pre-1990 and post-1990 management strategies used for ceded territory lakes of northern Wisconsin. Asterisks above the pre-1990 period denote a significant difference from the post-1990 period (one-way ANOVA with unequal sample sizes,  $\alpha = 0.05$ ). Error bars represent the standard errors of the means.

mated adult population (Ricker 1975). Although error associated with the population estimates may have influenced our results, we feel that the data still provide a reasonable measure of abundance because the same protocol was used among lakes and years. Further, this protocol must be used in order to sample enough lakes each spring to set future harvest quotas for walleyes.

#### *Growth Dynamics within Lakes*

Our results suggest that density plays a role in shaping walleye growth patterns within lakes, as evidenced by asymptotic length and body condition (Figure 2). Growth of most walleye populations was density dependent in the ceded territory for asymptotic length and body condition because these growth measures remained consistent with density-dependent theory within lakes. Our results for individual lakes suggest that density-dependence in growth is more likely to be detected in individual populations, where lake characteristics remain similar (Diana et al. 1991; Walters and Post 1993; Post et al. 1999). For example, patterns in  $L_{\infty}$  were not consistent across scales, suggesting decreased sensitivity for this growth character to detect density related effects among lakes (Figures 1, 2, 5).

Most walleye populations in the ceded territory showed a significant increase in  $\omega$  with increasing adult walleye densities, which is contrary to our expectations. According to Gallucci and Quinn (1979),  $\omega$  provides a measure of growth rate for younger walleyes in a given population (near  $t_0$ ). According to Hansen et al. (1998), highest age-0 recruitment of walleyes in Escanaba Lake, Wisconsin, occurred at intermediate densities of adult spawners. A similar stock–recruitment relationship was also found for Lake Erie walleyes (Madenjian et al. 1996). Because cannibalism is commonly the mechanism underlying the Ricker stock–recruitment model, higher adult densities may increase juvenile mortality through cannibalism (but see Madenjian et al. 1996) and subsequently decrease competition and increase growth among juveniles (Ricker 1975). However, cannibalism appears to be population-specific for walleyes because it has been noted in some populations (Oneida Lake, Forney 1974) but not in others (Lake Erie, Madenjian et al. 1996). Due to this stock–recruitment relationship and size-structured interaction, our expectations for the relationship between  $\omega$  and adult density for walleyes may not be in agreement with the observed patterns. Further, the negative correlation that exists between

$L_{\infty}$  and  $\omega$  suggests an increase in juvenile growth rate with decreases in asymptotic length. If this were the case, 72% of the walleye populations exhibited density-dependent  $\omega$  within lakes. However, a typical density-dependent pattern in  $\omega$  was noted in the regional-scale analysis and management periods. The lack of consistent pattern in  $\omega$  across scales may suggest that the  $\omega$  parameter proposed by Gallucci and Quinn (1979) is not suitable for measuring growth changes in juvenile fishes among populations.

The high variability found in the relationship between the growth characters examined and density on a regional scale highlight differences in walleye growth in different lakes within the same region and under the same management. Growth parameters in lakes containing similar densities of adult walleyes behaved differently. This may be attributed to differences in the physical, chemical, and biological characteristics of individual lakes, such as in productivity, species composition, forage base, landscape position, and lake size. For example, Nate et al. (2000) found that lake surface area explained 59% of the variability in adult walleye abundance in ceded territory lakes. Further, the presence of rainbow smelt *Osmerus mordax* as a forage base can lead to rapid increases in walleye growth (Jones et al. 1994; Johnson and Goettl 1999). The substantial differences between lakes in these physical, chemical, and biological characteristics were probably one reason that density-dependent growth was not evident across the region.

Differential angling and spearing pressure among lakes is probably another mechanism leading to the high variability observed in ceded territory walleye growth. Angling fisheries for walleyes have been considered self-regulating, whereas spearing has been considered to be a high-efficiency method of harvest that is not self-regulating (Staggs et al. 1990; Beard et al. 1997; Hansen et al. 2000). In either fishery, walleye harvest and natural mortality combine to decrease adult density; however, fishing pressure is not distributed randomly across the region. Therefore, walleye densities may change rapidly, and certain populations are better able than others to sustain changes in adult density without changes in growth. In this study, 3 of 29 comparisons showed no change in  $L_{\infty}$  with variable changes in adult density between years. For example,  $L_{\infty}$  of the walleye populations remained unchanged when adult densities increased from 4.92 to 10.23 fish/ha in Butternut Lake and from 5.16 to 3.78 fish/ha in Middle McKenzie Lake (Table

2). Overall, change in the walleye growth characters (e.g.,  $L_{\infty t} - L_{t+1}$ ) is independent of change in adult density ( $N/A_t - N/A_{t+1}$ ) in the same 29 lake comparisons (Sass 2001). That is, a certain amount of change in adult density does not correspond to a certain amount of change in the growth characters among all populations examined (Sass 2001). We predict that more productive lakes with an abundant forage base will be better able to sustain changes in adult density without altering walleye growth than other lakes with low productivity and limited forage bases. High variability in walleye growth among ceded territory lakes probably reflects such differences in productivity and forage abundance.

#### *Management Effects on Walleye Growth and Density*

Adult walleye densities did not change significantly during 1990–1999. Adult densities most frequently ranged between 4 and 10 walleye/ha and averaged 8.3 walleye/ha (Figure 4). Similarly, the current management system did not significantly change growth parameters of  $L_{\infty}$ ,  $\omega$ , and body condition on a broad regional and temporal scale. Therefore, the current management strategy has had little effect on walleye growth and density following its implementation in 1990.

Before 1990, no walleye population estimates exist for ceded territory lakes; however, some length, weight, and age data were collected during 1977–1989 for a number of lakes. Comparisons of growth characters before and after 1990 indicate significantly higher asymptotic lengths and body condition for walleye before 1990 (Figure 5). Further, paired lake comparisons before and after 1990 also show a significant decrease in walleye growth in  $L_{\infty}$ , body condition, and the mean size of males and females ages 4–10 (Sass 2001). If the patterns observed in  $L_{\infty}$ , body condition, and mean size can be used as indicators of adult walleye densities, as suggested by individual lake comparisons, adult walleye abundance may have increased, but remained stable, after 1990.

Our analyses suggested that increases in walleye density produced the decrease in walleye growth in ceded territory lakes between the pre-1990 and post-1990 periods. Further, the increases in walleye density were most likely attributable to the treaty rights management, rather than the imposition of the 15-in minimum size limit beginning in 1990. Although minimum length limits for walleyes and sauger *Sander canadensis* have resulted in reduction of growth rates, body condition, num-

bers of large fish, and total harvest (Schneider 1978; Serns 1978; Munger and Kraai 1997), our data suggests that the conservative treaty rights management could be responsible for increased densities of adults and subsequent decreases in growth. According to Fayram et al. (2001) and Sass (2001), the 15-in minimum length limit probably did not lead to an increase in walleye density because walleye growth decreased in both lakes with and without this regulation after 1990. Thus, the size limit apparently had no effect on walleye growth.

However unlikely, decreases in lake productivity or loss of forage across ceded territory lakes could be responsible for the decreases observed in walleye growth after 1990. A positive correlation exists between lake productivity and fish growth (Trippel and Beamish 1989; Deegan and Peterson 1992; Hubert and Chamberlain 1996; Budy et al. 1998; Gross et al. 1998), and increased forage increases walleye growth rates (Jones et al. 1994; Johnson and Goettl 1999). We believe that decreases in lake productivity and forage are not responsible for the observed growth change because (1) lakes generally become more productive over time (Wetzel 1983; Horne and Goldman 1994), and (2) the most common losses of native forage bases in the ceded territory (i.e., cisco *Coregonus artedii* and whitefish *C. clupeaformis*) are caused by displacements by rainbow smelt. We further believe that decreases in productivity and forage are not the mechanisms effecting walleye growth declines because rapid development of lakeshore properties in the ceded territory would increase productivity via increase of septic tanks, nutrient loading, and fishing (Goedde and Coble 1981; Hanson and Leggett 1982; NRC 1992, WDNR 1996) and only a small number of lakes can maintain populations of cisco and whitefish (thermal habitat).

#### *Implications for Fishery Management*

The goals of the current treaty rights management program in the ceded territory of Wisconsin are to maintain a minimum of 7.5 adult walleyes/ha, increase walleye densities, and provide angler catch rates of 1 walleye/h. Our results indicate that adult walleye densities changed little during 1990–1999, remaining at about 8.3 walleyes/ha, an estimate that is perhaps higher than before 1990. Furthermore, angler catch rates in the ceded territory have been much greater than 1 fish/h (Beard et al. 1997; Hansen et al. 2000). Despite indications of slower walleye growth after 1990, the current system appears to be achieving the goals of

the Wisconsin Department of Natural Resources to maintain a sustainable walleye fishery in the ceded territory.

We found that walleye growth exhibited density-dependent changes on a lake-specific basis for most ceded territory lakes. Thus, the growth parameters examined in this study have the potential to serve as a surrogate for adult population estimates. This pattern was not observed on a regional scale because of intrinsic differences among lakes. Therefore, we suggest further research to develop a predictive model that includes physical, chemical, and biological characters of lakes to expand these results to a regional scale. Because walleye growth is not affected equally in all lakes by changes in density, incorporating these lake-specific characteristics may help to explain more variability in the model. Because growth is easier to quantify than population abundance, a regular program of growth rate surveys could identify lakes needing additional research. For example, current protocol for walleye population estimation requires three nights of sampling per lake. Growth rate surveys could be conducted in one or two nights with the same associated laboratory time for age analysis, which would allow the WDNR the opportunity to sample more lakes in a given year. Further, if sexual dimorphism is unimportant in the ceded territory's walleye populations, growth rate surveys could be conducted at any time throughout the year. Under this protocol, large changes in growth rate or condition could reveal a drastic change in walleye density within a lake.

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