

ANALYSIS OF FACTORS AFFECTING GROWTH OF NORTHERN PIKE IN MINNESOTA¹

Peter C. Jacobson

Minnesota Department of Natural Resources
Section of Fisheries
500 Lafayette Road
St. Paul, MN 55155

Abstract--Age and growth data from 3,713 fish sampled during 112 lake surveys conducted in 1990 were analyzed to identify factors that affected growth rates of northern pike *Esox lucius*. Small, young northern pike grew fastest in shallow, fertile lakes with long growing seasons. Data from a fishing contest in the Park Rapids area indicated that most large northern pike were caught in lakes with deep water and cisco *Coregonus artedii*. Bioenergetic modeling indicated that summer water temperature and population density affect growth rates of northern pike. Reduced growth rates at high population densities result in poor size structures. Statewide quartiles of northern pike growth as functions of age and size were calculated and presented as a method for comparing growth rates.

Introduction

Northern pike *Esox lucius* exhibit a wide range of growth rates in Minnesota. Slow growth, in combination with high mortality rates, result in size structures dominated by small northern pike in many lakes (Goeman and Spencer 1992). In other lakes, faster growth rates, in combination with low mortality rates, result in better quality size structures with greater numbers of large fish. Wide variations in growth rates in combination with fishing mortality present a challenge to fisheries managers.

Management strategies that improve poor size structures and maintain quality size structures would be useful. Identification of factors that affect growth rates of northern pike, and a quantitative description of how growth rates are interrelated with mortality rates in determining size structure would assist in developing these strategies.

Several environmental and biological factors that affect growth rates of northern pike have been identified. Diana (1987) concluded that northern pike growth can be significantly slowed by intraspecific competition, lack of large prey

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items, and warm temperatures. Casselman (1978a) noted the importance of a cool water thermal habitat for growth of northern pike. Kempinger and Carline (1978) suggested that density dependent changes in growth were responsible for a reduction of growth rates observed after a northern pike population increased in Escanaba Lake, Wisconsin following implementation of a minimum size limit. Eddy and Carlander (1940), in an earlier study of Minnesota lakes, found northern pike growth rates to be correlated with total dissolved solids, total alkalinity, and length of growing season.

This study investigates effects of these and other factors on growth of northern pike in Minnesota. Three separate approaches were used. The first approach identified factors affecting northern pike growth rates using data collected during standard lake surveys conducted by management areas throughout the state. The second approach identified factors affecting production of large northern pike from historical fishing contest records. The third approach investigated actual mechanisms that control northern pike growth using a bioenergetics model.

Methods

Lake Survey Growth Rates

Growth rates were estimated from 3,713 northern pike collected during 112 lake surveys conducted in 1990 by 15 management areas (Detroit Lakes, Bemidji, Walker, Glenwood, French River, Grand Marais, Grand Rapids, International Falls, West Metro, Brainerd, Little Falls, Montrose, Windom, Ortonville, and Hutchinson). Northern pike were sampled with 76 m experimental gill nets (mesh sizes 19, 25, 38, 50, 64 mm bar measure). Ageing and digitizing of annular marks (radii measurements for scales and anterior radii for cleithra (Casselman 1979)) were performed by each management area (except for 10 lakes in the Grand Marais and Windom area aged and digitized by the author). Age and growth information was obtained from each area in the form of DISBCAL .ANU computer files, which contained actual

bony part measurements (Frie 1982). The analysis was limited to lake surveys where cleithra or scales in combination with cleithra were collected. Annular growth increments were calculated using the Lee direct proportion method (Carlander 1981). A body-scale constant of 53.3 mm and a body-cleithra constant of 23.8 mm were used. Only the most recent annual length increments (1989 increments) were used in the analysis (see Gutreuter 1987). The 1989 increments were the best available measures of annual growth that were most likely influenced by conditions (biological, chemical, and physical) present in 1990 when the lake surveys were conducted.

The body-cleithra constant of 23.8 mm was estimated during this study. Data from 2,383 northern pike cleithra collected during 78 lake surveys from four management areas (Detroit Lakes, French River, Grand Marais, and Windom) in 1988, 1989, and 1990 were used to calculate the body-cleithra relationship. Also included were 81 yearling northern pike cleithra sampled during winter rescue operations in Gourd Lake, Otter Tail County and Rice Lake, Aitkin County. The relationship between anterior cleithral radii and total body length was estimated by linear regression (body length = $10.111 \text{ anterior cleithra length} + 23.8$, $r^2=0.976$, $P<0.001$).

Physical, chemical, and biological variables were measured during the lake surveys (Table 1). Physical characteristics included surface area, percent littoral area (surface area less than 4.6 m deep), maximum depth, and shoreline development factor. Chemical and water transparency characteristics included total alkalinity, total phosphorous, and secchi depth. As a measure of availability of oxygenated cool water, the approximate temperature at 3.0 ppm of dissolved oxygen (DO) in the water column was calculated from lake survey temperature and dissolved oxygen profiles. Headrick (1985) noted that northern pike would generally not move into water with less than 3.0 ppm DO during summer stratification in Ohio reservoirs. Only August temperature and dissolved oxygen profiles were used because gradual depletion of oxygen in the hypolimnion results in an increase of the temperature at 3.0 ppm DO throughout

Table 1. Minimum, maximum, median, and sample size of lake characteristic variables used in the lake survey growth rate analysis.

Variable	Units	N	Min	Max	Median
Degree days >50°C	degree days	112	1,300	2,700	1,800
Area	ha	112	6	89,392	101
Maximum depth	m	112	1.5	61.6	11.1
Percent littoral	%	109	10	100	59.0
Shoreline dev. factor	none	101	1.06	7.26	1.72
Secchi depth	m	108	0.24	8.67	1.83
Temp @ 3 ppm DO	°C	30	5	23	19
Total alkalinity	ppm	100	5	305	107
Total phosphorus	µg/l	75	5	550	25
Percent emergents	%	106	0	50	4.5
Submergent index	none	95	0	5	5.0
Potamogeton index	none	95	0	5	3.0
Pike spawning index	none	94	0	4	3.0
White sucker biomass	kg/net	112	0	26.51	0.55
Yellow perch biomass	kg/net	112	0	24.44	0.35
Cisco biomass	kg/net	112	0	15.14	0
Walleye biomass	kg/net	112	0	26.81	1.37
Northern pike biomass	kg/net	112	0	37.80	5.08
Largemouth bass biomass	kg/net	99	0	2.53	0.01
Bluegill biomass	kg/net	99	0	19.46	0.94
Pumpkinseed biomass	kg/net	99	0	4.39	0.16
Rock bass biomass	kg/net	99	0	1.64	0
Black crappie biomass	kg/net	99	0	4.46	0.25
Black bullhead biomass	kg/net	99	0	43.08	0.10
Brown bullhead biomass	kg/net	99	0	5.90	0.08
Yellow bullhead biomass	kg/net	99	0	12.71	0.53

the summer (August was chosen as a standard month). Air temperature degree days greater than 10°C were estimated for the location of each lake from data presented in Baker et al. (1985), and were used as a measure of length of growing season.

Biological variables included measures of vegetation characteristics of the lakes: percent of lake surface covered by emergent aquatic vegetation, relative abundance of submergent aquatic vegetation (scale of 1 to 5: 1=rare, 2=present, 3=occasional, 4=common, 5=abundant), and relative abundance of large-leaf pondweed *Potamogeton* spp. (same 1 to 5 scale). Quality of northern pike spawning habitat estimated during the survey (scale of 1 to 4: 1=poor, 2=fair, 3=good, 4=excellent) was used in the analysis. Indices of fish abundance (biomass) were calculated as mean catch (kg) per net from the lake surveys. These catch per effort values were based on a standard gear for each species (experimental gill nets for northern pike, walleye *Stizostedion vitreum vitreum*, yellow perch *Perca flavescens*, white sucker *Catostomus commersoni*, and cisco *Coregonus artedii*, and 19 mm inch bar measure trap nets for black bullhead *Ictalurus meles*, brown bullhead *Ictalurus nebulosus*, yellow bullhead *Ictalurus natalis*, bluegill *Lepomis machrochirus*, pumpkinseed sunfish *Lepomis gibbosus*, black crappie *Pomoxis nigromaculatus*, rock bass *Ambloplites rupestris*, and largemouth bass *Micropterus salmoides*). Winterkill histories were also recorded from lake survey files.

Pearson correlation coefficients were calculated for the 1989 length increment for individual fish, and the physical, chemical, and biological variables for the lake from where each fish was sampled. Transformations suggested by Schupp (1992) were used to normalize distributions of variables. Logarithmic transformations normalized distributions of area, maximum depth, percent emergents, and fish abundance indices. Square root transformations normalized shoreline development factor, and the chemical and water transparency variables (total alkalinity, total phosphorus, secchi depth, and temperature @ 3 ppm DO). The Bonferoni technique (Trippel and

Hubert 1990) was used for determining an appropriate level of significance for multiple comparisons.

Fishing Contest Analysis

Fuller's Tackle Shop of Park Rapids, Minnesota, has sponsored an annual fishing contest since 1915, for fish caught within a 695 square kilometer area in northwestern Minnesota. Contest entries are weighed to the nearest 29 grams at Fuller's Tackle Shop or at other certified weighing stations located throughout the area. No entry fee is required. Fish must be caught from lakes and streams within the contest area and from the opening of the walleye angling season in May to a contest closing date in September or October. Weekly and seasonal prizes are awarded from the tackle shop, area businesses, and resort owners for larger entries of 10 fish species. Records of fish entered are published annually in *Fuller's Golden Book and Fishing Directory*, and include date of each contest entry, species, weight in pounds and ounces, lake or stream where the fish was caught, angler's name and address and hosting summer resort. Olson and Cunningham (1989) provide further details of the contest and analysis of trends throughout the period.

Numbers of trophy (greater than 6.8 kg) northern pike entered and recorded in Fuller's Golden Book Fishing Contest between 1924 and 1989 (records for years 1925, 1926, 1928-1930, 1932, 1943, 1944, 1966 were missing) were tabulated for each lake for the entire period. Lakes with names common to more than one lake (e.g., Bass, Stocking) and chemically reclaimed trout lakes were omitted from the analysis. Numbers of northern pike entries were standardized on a lake area basis by dividing by surface area.

Correlations between numbers of trophy northern pike entries per hectare, and physical, chemical, and biological lake characteristics were investigated. The Bonferoni technique (Trippel and Hubert 1990) was used for determining an appropriate level of significance for multiple comparisons. Physical, chemical, and biological characteristics of 98 lakes within the study area were measured during standard lake

surveys conducted by the Area Fisheries Headquarters in Park Rapids and Detroit Lakes from 1962 through 1989 (Table 2). Lake characteristic variables were the same as described in the Lake Survey Growth Rates section with the exception of not using degree days (where there was little variation within the relatively small contest area). All lakes within the study area that had fisheries lake surveys (98 lakes) were included in the analysis, including lakes without any trophy northern pike entries. Nine hundred twenty-four northern pike larger than 6.8 kg were entered in the contest from these lakes during the study period (1924 through 1989).

The effect of variable fishing pressure could not be included in the analysis. Although relatively lighter fishing pressure could allow some lakes to produce more large northern pike, all of the major lakes in the area had public accesses which should have evened out some of the fishing pressure variability.

Bioenergetics Modeling

A bioenergetics model was developed to investigate actual mechanisms of northern pike growth. Energetic components of respiration, egestion, excretion, and consumption were described as functions of fish weight and temperature (Kitchell 1983; Hewett and Johnson 1987). Growth was the result of energy remaining after metabolic, reproductive, and waste material energy requirements were met.

Although bioenergetic parameters for an Ohio stock of northern pike have been estimated by Bevelhimer et al. (1985), parameter values may not be applicable to Minnesota stocks. For example, Casselman (1978a) documented cessation of growth at 27.5°C for northern pike from an Ontario stock and death occurred at 29.4°C, whereas, the Ohio fish of Bevelhimer et al. (1985) were still growing at 30°C. Also, Casselman (1978a) reported that optimum temperature for growth was 19°C, whereas, Bevelhimer et al. (1985) found 25°C to be optimal for growth. Stocks of northern pike studied by Casselman (1978a) were at a latitude of 45° 54' N (approximately the same latitude as Alexandria, Minnesota), whereas, stocks studied by Bevelhimer et al. (1985) were at approximately 39° N.

Table 2. Minimum, maximum, median, and sample size of variables used in the fishing contest analysis.

Variable	Units	N	Min	Max	Median
Trophy entries	#	98	0	89	2
Trophy entries/hectare	#/ha	98	0	0.0478	0.0032
Area	ha	98	7	3140	392
Maximum depth	m	98	2.7	41.1	10.7
Percent littoral	%	98	10	100	62.0
Shoreline development factor	none	98	1.08	5.57	1.73
Secchi depth	m	98	0.8	7.2	3.2
Temp @ 3 ppm DO	°C	39	6	24	19
Total alkalinity	ppm	97	18	208	129
Total phosphorus	µg/l	23	5	58	20
Percent emergents	%	96	1	80	5
Submergent index	none	98	2	5	4
Potamogeton index	none	98	1	5	3
Pike spawning index	none	98	1	4	2
White sucker biomass	kg/net	94	0	12.22	1.36
Yellow perch biomass	kg/net	94	0	6.88	1.13
Cisco biomass	kg/net	94	0	3.95	0
Walleye biomass	kg/net	94	0	7.75	1.41
Northern pike biomass	kg/net	94	0	42.0	6.0
Largemouth bass biomass	kg/net	98	0	2.18	0.28
Bluegill biomass	kg/net	98	0	40.34	2.63
Pumpkinseed biomass	kg/net	98	0	6.58	0.86
Rock bass biomass	kg/net	98	0	1.50	0.08
Black crappie biomass	kg/net	98	0	4.65	0.31
Black bullhead biomass	kg/net	90	0	21.79	0.03
Brown bullhead biomass	kg/net	90	0	19.38	0.16
Yellow bullhead biomass	kg/net	90	0	3.94	0.39

Bevelhimer et al. (1985) noted these differences and suggested that the northern pike they studied may have adapted to the relatively warmer waters of Ohio. Therefore, a new set of parameters was developed for this study. Details of the model and estimation of parameter values are presented in Appendix 1.

Results

Lake Survey Growth Rates

Pearson correlation coefficients for lake characteristic variables and 1989 length increments were computed (Table 3). Length at the start of the most recent annual increment (1989) was used to categorize fish into three size groups. Age at the start of the 1989 increment was the most influential variable of the data set for all length groups. Length at the start of the 1989 increment was also correlated with magnitude of the increment (even after the grouping of increments by length). Remaining variables had lower correlation coefficients.

Of the remaining variables, degree-days $>10^{\circ}\text{C}$ was most strongly associated with growth of the smallest size group of northern pike. Significant negative correlations were observed between maximum depth and northern pike growth for 0 to 304 mm and 305 to 609 mm fish. Smaller size groups of northern pike were generally correlated with higher productivity lakes, in terms of total alkalinity, total phosphorus and secchi depth. Total phosphorus was also correlated with growth of northern pike 609 mm and larger. Growth rates of smaller northern pike were negatively correlated with submerged vegetation variables, northern pike abundance, and yellow and brown bullhead abundance, and positively correlated with black crappie abundance.

Many lake characteristic variables were highly correlated with each other (Table 4), making identification of specific variables important in determining northern pike growth rates difficult. For example, degree-days $>10^{\circ}\text{C}$ was strongly correlated with secchi depth, total alkalinity, total phosphorus and black bullhead abundance, and all were correlated with growth

Table 3. Pearson correlation coefficients (r) for individual 1989 length increments and lake characteristic variables for three size groups (based on initial lengths at start of the increment) of northern pike. Significant correlations are designated by * (initial $\alpha=0.05$, with Bonferoni adjustment for 26 comparisons; $P<0.0019$).

Variable	0-304 mm		305-609 mm		>609 mm	
	r	N	r	N	r	N
Age at annulus formation	-0.597*	1326	-0.565*	2064	-0.306*	323
Length at annulus formation	-0.555*	1326	-0.495*	2064	-0.258*	323
Degree days >50C	0.287*	1326	0.033	2064	0.039	323
Area	-0.012	1326	-0.012	2064	-0.089	323
Maximum depth	-0.126*	1326	-0.109*	2064	-0.093	323
Percent littoral	-0.006	1286	0.108*	1903	0.063	298
SDF	-0.035	1205	0.045	1736	0.030	251
Secchi depth	-0.260*	1285	-0.138*	2021	-0.004	303
Temp @ 3 ppm DO	-0.099	346	-0.168*	628	-0.138	101
Total alkalinity	0.124*	1241	0.026	1975	0.132	300
Total phosphorus	0.173*	1060	0.166*	1660	0.207*	244
Percent emergents	0.108*	1326	-0.021	2064	-0.129	323
Submergent index	-0.200*	1137	-0.111*	1673	0.035	247
Potamogeton index	-0.234*	1137	-0.114*	1673	0.076	247
Pike spawning index	-0.156*	1115	-0.045	1647	-0.038	241
White sucker biomass	-0.081	1326	0.011	2064	-0.087	323
Yellow perch biomass	0.055	1326	0.010	2064	0.015	323
Cisco biomass	-0.007	1326	0.033	2064	0.029	323
Walleye biomass	0.027	1326	0.013	2064	0.059	323
Northern pike biomass	-0.088*	1326	-0.014	2064	0.124	323
Largemouth bass biomass	-0.072	1174	-0.048	1707	-0.017	241
Bluegill biomass	-0.057	1174	-0.086*	1707	-0.024	241
Pumpkinseed biomass	0.050	1174	0.015	1707	-0.012	241
Rock bass biomass	-0.090	1174	-0.093*	1707	0.043	241
Black crappie biomass	0.154*	1174	0.104*	1707	0.103	241
Black bullhead biomass	0.126*	1174	0.062	1707	-0.034	241
Brown bullhead biomass	-0.175*	1174	-0.139*	1707	0.022	241
Yellow bullhead biomass	-0.250*	1174	-0.117*	1707	-0.015	241

rates of 0 to 304 mm northern pike. Multiple regressions were attempted to separate out important variables, but no stable subset of variables could be found (different variable selection techniques such as forward and backward stepwise regressions produced very different variable subsets - with each subset model performing similarly in terms of explaining variance). Snedecor and Cochran (1967) note the difficulty of defining relative importance of independent variables highly correlated with each other.

Partial correlations (Snedecor and Cochran 1967) between highly correlated variables and length increments were calculated. The use of partial correlations allowed for the direct examination of manually selected sets of highly correlated variables. They suggested that degree days >10°C and secchi depth were the important variables of the set of highly correlated variables described above. Partial correlation coefficient between degree-days >10°C and 1989 length increment for fish 0 to 304 mm, given total

phosphorus, total alkalinity, maximum depth, secchi depth and black bullhead biomass, was 0.233 ($P<0.05$, $N=936$), whereas the partial correlation coefficient between maximum depth and 1989 length increments given the other variables in the subset, including degree-days >10°C, was only -0.020 ($P>0.05$) and between black bullhead biomass and 1989 length increments, given the other variables, was -0.026 ($P>0.05$). Other partial correlation coefficients were -0.096 ($P<0.05$) for total phosphorus and -0.065 ($P>0.05$) for total alkalinity, given the other variables.

For all size groups of northern pike, significantly larger length increments were measured in lakes that had a history of winterkill (t-tests; $P<0.05$).

Fishing Contest Analysis

More trophy northern pike were entered in the contest on a per hectare basis from larger,

Table 4. Pearson correlation coefficient matrix for lake characteristic variables (abbreviation definitions below table) for 112 lakes in the lake survey growth rate segment of the study.

GDD	AREA	MAXD	PLIT	SDF	SCCH	TMP3	TALK	TOTP	PEME	SUBN	POTN	SPNN	WTS	YEP	TLC	WAE	NOP
GDD	1.000																
AREA	-0.198	1.000															
MAXD	-0.287	0.366	1.000														
PLIT	0.224	-0.232	-0.666	1.000													
SDF	-0.169	0.428	0.077	0.021	1.000												
SCCH	-0.545	-0.007	0.533	-0.436	-0.005	1.000											
TMP3	0.532	-0.270	-0.688	0.617	-0.240	-0.576	1.000										
TALK	0.635	0.033	-0.304	0.254	-0.096	-0.368	0.400	1.000									
TOTP	0.626	-0.098	-0.255	0.254	0.172	-0.597	0.377	0.457	1.000								
PEME	-0.191	0.580	0.343	-0.214	0.146	-0.002	-0.151	-0.224	-0.129	1.000							
SUBN	-0.054	0.016	0.323	-0.231	-0.090	0.073	0.240	0.195	0.185	0.181	1.000						
POTN	-0.409	0.168	0.332	-0.213	-0.049	0.445	-0.023	-0.179	-0.372	-0.106	0.328	1.000					
SPNN	-0.183	0.075	0.090	0.150	0.038	-0.037	0.219	-0.013	-0.020	0.288	0.120	0.095	1.000				
WTS	-0.093	-0.040	-0.201	0.103	0.114	-0.071	-0.224	0.093	0.104	-0.293	-0.108	-0.044	-0.207	1.000			
YEP	0.114	0.093	-0.122	0.041	0.054	-0.155	0.065	0.335	0.249	-0.254	0.109	0.088	-0.009	0.432	1.000		
TLC	-0.226	0.202	0.317	-0.296	0.022	0.219	-0.392	-0.028	-0.197	-0.107	0.121	0.210	-0.076	0.175	0.088	1.000	
WAE	0.112	0.129	-0.160	0.051	-0.021	-0.078	0.062	0.363	0.087	-0.331	-0.161	0.156	-0.135	0.369	0.355	0.087	1.000
NOP	0.242	-0.430	-0.147	0.127	-0.338	0.058	0.358	0.236	0.123	-0.553	0.116	0.072	0.044	-0.024	0.244	-0.027	0.114
LMB	0.030	0.011	0.149	-0.051	-0.062	0.145	0.124	0.095	0.011	-0.056	0.109	0.133	0.109	-0.031	0.026	-0.101	0.212
BLG	-0.112	0.044	0.032	0.037	-0.170	0.216	0.200	-0.163	-0.245	0.078	0.087	0.311	0.168	-0.268	0.126	-0.176	-0.122
PKB	-0.309	0.338	0.334	-0.363	0.171	0.459	-0.461	-0.166	-0.301	-0.033	0.062	0.299	-0.175	0.042	0.259	-0.045	-0.045
RKB	-0.400	0.028	-0.068	0.159	-0.006	-0.295	0.193	0.193	0.569	-0.017	0.098	0.018	-0.025	-0.093	0.191	-0.198	0.086
BLB	0.504	-0.049	-0.455	0.283	-0.164	-0.497	0.311	0.406	0.372	-0.070	-0.165	-0.361	-0.157	0.008	0.044	-0.203	0.124
BRB	-0.171	0.230	-0.062	0.036	0.138	-0.103	0.311	0.129	0.033	0.169	0.190	0.027	0.127	0.025	0.171	-0.047	-0.135
YEB	-0.008	0.100	0.252	-0.048	-0.190	0.205	0.183	0.033	0.052	0.091	0.235	0.157	0.307	0.001	0.087	-0.138	-0.090

LMB	BLG	PKB	RKB	BLB	BRB	YEB
LMB	1.000					
BLG	0.314	1.000				
PKB	0.233	0.365	1.000			
RKB	-0.081	-0.151	0.075	1.000		
BLB	-0.106	0.330	0.175	-0.078	1.000	
BRB	-0.033	-0.055	-0.161	-0.274	0.135	1.000
YEB	0.149	0.023	0.050	-0.052	-0.137	0.287
	0.301	0.472	0.297	-0.002	0.085	-0.174
					0.062	1.000

Variable name abbreviation definitions:

GDD - degree days >50C
 AREA - lake surface area
 MAXD - maximum depth

Table 4 cont.

PLIT	- percent littoral
SDF	- shoreline development factor
SCCH	- secchi depth
TMP3	- temperature @ 3 ppm of dissolved oxygen
TALK	- total alkalinity
TOTP	- total phosphorus
PEME	- percent of the surface area covered by emergent vegetation
SUBN	- index of submerged vegetation abundance
POTN	- index of largeleaf Potamogeton abundance
SPNN	- northern pike spawning habitat index
WTS	- index of white sucker biomass
YEP	- index of yellow perch biomass
TLC	- index of cisco biomass
WAE	- index of walleye biomass
NOP	- index of northern pike biomass
LMB	- index of largemouth bass biomass
BLG	- index of bluegill biomass
PMK	- index of pumpkinseed biomass
RKB	- index of rock bass biomass
BLC	- index of black crappie biomass
BLB	- index of black bullhead biomass
BRB	- index of brown bullhead biomass
YEB	- index of yellow bullhead biomass

deeper lakes, with small littoral zones (Table 5). Correlation coefficients were significantly positive for surface area and maximum depth, and significantly negative for percent littoral area. The correlation coefficient for shoreline development factor was positive but not statistically significant. Maximum depth and percent littoral were highly correlated with each other (Table 6). Partial correlations suggested that percent littoral may have been the most important variable of the two (partial correlation coefficient between trophy entries per hectare and percent littoral given maximum depth was -0.324; $P < 0.05$ and maximum depth given percent littoral was -0.023; $P > 0.05$). Maximum depth was also correlated with area and partial correlations suggested that area may be more important (partial correlation coefficient between trophy entries per hectare and area, given maximum depth, was 0.378; $P < 0.05$ and maximum depth given area was 0.188; $P > 0.05$).

Total alkalinity was positively correlated with trophy entries of northern pike. No relationships could be identified for total phosphorus and secchi depth. The correlation coefficient for temperature at 3 ppm of dissolved oxygen, was negative but not statistically significant (sample size was small because only the August temperature and dissolved oxygen profiles were used). None of the correlations with aquatic vegetation variables were significant.

Table 5. Pearson correlation coefficients (r) between numbers of trophy northern pike fishing contest entries per hectare and lake characteristic variables. Significant correlations are designated by * (initial $\alpha = 0.05$, with Bonferoni adjustment for 25 comparisons; $P < 0.002$).

Variable	r	N
Area	0.443*	98
Maximum depth	0.309*	98
Percent littoral	-0.436*	98
Shoreline development factor	0.153	98
Total alkalinity	0.394*	97
Total phosphorus	-0.196	23
Secchi depth	-0.052	98
Temp. @ 3 ppm DO (August)	-0.163	39
Percent emergent	0.157	96
Submergent index	-0.029	98
Potamogeton index	0.025	98
Pike spawning index	0.208	98
White sucker biomass	0.544*	94
Yellow perch biomass	0.379*	94
Cisco biomass	0.342*	94
Walleye biomass	0.556*	94
Northern pike biomass	0.217	94
Largemouth bass biomass	-0.100	98
Bluegill biomass	0.092	98
Pumpkinseed biomass	0.139	98
Rock bass biomass	0.466*	98
Black crappie biomass	0.160	98
Black bullhead biomass	-0.033	90
Brown bullhead biomass	0.076	90
Yellow bullhead biomass	0.274	90

Potential prey fish (white sucker, yellow perch, and cisco) biomasses were significantly, positively correlated with trophy northern pike entries per hectare. Walleye and rock bass

Table 6. Pearson correlation coefficient matrix for lake characteristic variables (abbreviation definitions on next page) for 98 lakes in the fishing contest analysis.

AREA	MAXD	PLIT	SDF	SCCH	TMP3	TALK	TOTP	PENE	SUBN	POTN	SPNN	WTS	YEP	TLC	WAE	NOP
AREA	1.000															
MAXD	0.339	1.000														
PLIT	-0.401	-0.740	1.000													
SDF	0.327	0.209	-0.040	1.000												
SCCH	-0.186	0.399	-0.306	0.176	1.000											
TMP3	-0.148	-0.689	0.581	0.089	-0.456	1.000										
TALK	0.458	0.218	-0.356	0.149	-0.302	0.054	1.000									
TOTP	-0.006	-0.463	0.492	-0.068	-0.634	0.009	0.357	1.000								
PENE	0.201	-0.288	0.092	-0.038	-0.255	0.009	0.104	0.249	1.000							
SUBN	0.007	-0.296	0.191	-0.058	-0.137	0.307	0.249	0.173	0.086	1.000						
POTN	-0.108	-0.046	0.077	-0.013	0.205	-0.038	0.337	-0.212	-0.197	0.324	1.000					
SPNN	0.287	-0.175	0.108	0.145	-0.305	0.095	0.383	0.337	0.428	0.164	-0.081	1.000				
WTS	0.476	0.000	-0.136	0.073	-0.236	-0.108	0.389	-0.045	0.216	0.024	-0.073	0.160	1.000			
YEP	0.425	-0.011	-0.199	0.143	-0.076	-0.037	0.274	-0.115	0.146	0.099	0.065	0.400	0.599	1.000		
TLC	0.301	0.379	-0.483	-0.131	-0.106	0.373	0.280	0.149	0.024	0.046	0.055	0.120	0.196	0.208	1.000	
WAE	0.632	0.304	-0.373	0.069	-0.004	-0.167	0.300	-0.335	0.085	-0.029	0.052	0.143	0.570	0.463	0.275	1.000
NOP	0.324	0.052	-0.134	-0.162	-0.036	0.052	0.189	0.265	0.194	0.080	0.001	0.437	0.200	0.360	0.135	0.207
LMB	-0.065	0.012	-0.028	-0.105	-0.239	-0.115	-0.291	-0.291	-0.122	0.056	0.251	-0.078	-0.134	-0.066	0.022	0.080
BLG	-0.069	0.107	-0.139	-0.077	0.399	-0.134	-0.185	-0.359	-0.098	0.054	0.190	-0.031	-0.180	-0.035	0.035	0.083
PMK	0.042	-0.166	0.117	0.023	0.037	0.164	-0.071	-0.045	-0.070	0.119	0.044	0.325	-0.050	0.196	0.124	0.012
RKB	0.502	0.559	-0.580	-0.066	0.098	-0.590	0.350	-0.403	-0.038	-0.222	-0.043	-0.028	0.326	0.198	0.376	0.515
BLC	0.145	-0.100	0.084	0.023	-0.034	0.123	0.015	0.049	0.130	0.048	-0.009	0.199	0.139	0.150	-0.055	0.070
BLB	0.339	-0.205	0.029	-0.110	-0.349	0.027	0.277	0.324	0.487	0.148	-0.201	0.174	0.157	0.065	-0.004	0.092
BRB	0.344	-0.150	0.059	-0.078	-0.392	0.262	0.157	0.518	0.211	0.224	-0.349	0.254	0.100	-0.009	0.086	0.111
YEB	0.304	0.117	-0.183	-0.044	-0.121	-0.297	0.405	0.261	0.164	0.023	-0.087	0.348	0.155	0.014	0.200	0.263

LMB	BLG	PMK	RKB	BLC	BLB	BRB	YEB
LMB	1.000						
BLG	0.591	1.000					
PMK	0.319	0.415	1.000				
RKB	-0.023	-0.055	-0.029	1.000			
BLC	0.118	0.093	0.246	-0.036	1.000		
BLB	-0.223	-0.283	-0.220	0.055	0.136	1.000	
BRB	-0.180	-0.276	0.086	0.035	0.369	0.559	1.000
YEB	0.098	0.297	0.362	0.162	0.295	0.174	0.177

Table 6 cont.

Variable name abbreviation definitions:

AREA	- lake surface area
MAXD	- maximum depth
PLIT	- percent littoral
SDF	- shoreline development factor
SCCH	- secchi depth
TMP3	- temperature @ 3 ppm of dissolved oxygen
TALK	- total alkalinity
TOTP	- total phosphorus
PEME	- percent of the surface area covered by emergent vegetation
SUBN	- index of submerged vegetation abundance
POTN	- index of largeleaf Potamogeton abundance
SPNN	- northern pike spawning habitat index
WTS	- index of white sucker biomass
YEP	- index of yellow perch biomass
TLC	- index of cisco biomass
WAE	- index of walleye biomass
NOP	- index of northern pike biomass
LMB	- index of largemouth bass biomass
BLG	- index of bluegill biomass
PMK	- index of pumpkinseed biomass
RKB	- index of rock bass biomass
BLC	- index of black crappie biomass
BLB	- index of black bullhead biomass
BRB	- index of brown bullhead biomass
YEB	- index of yellow bullhead biomass

biomasses were also significantly, positively correlated with trophy entries. No relation between abundance of northern pike and number of trophy entries was measured. Lakes with a history of winterkill produced significantly fewer trophy entries (19 lakes, mean trophy entries per hectare = 0.0013) than lakes without a record of winterkill (79 lakes, mean trophy entries per hectare = 0.0097, t-test, $P < 0.01$).

Bioenergetic Modeling

The bioenergetic model as a function of temperature is illustrated in Figure 1. Areas in the figure represent the magnitude of each energetic component as a function of temperature, for a 100 g northern pike, fed at maximum rates of consumption. Consumption rate (the sum of all areas - defined by the upper line in the figure) reaches a maximum at 21.9°C, whereas, standard and active metabolism increase continuously and exponentially as temperature increases. Resulting energy remaining for somatic and gonadal growth (represented as surplus in the figure) increases as temperature increases to approximately 21°C and then decreases as temperature increases further. This

surplus, defined as scope for growth (the amount of energy available for growth after metabolic, feeding, and waste costs have been met) by Warren and Davis (1967) is plotted in Figure 2. Optimum temperature for growth of northern pike in this model, at maximum consumption, is approximately 21°C. Growth ceases at 26°C.

The model was validated by predicting growth from data calculated in a series of laboratory feeding experiments of northern pike (Casselman 1978b) with varying temperatures (Figure 18 in Casselman (1978b)) and rations (Figure 20 in Casselman (1978b)). Although data from these experiments was used to compute the maximum consumption component of the model, use of the reported, fixed rations eliminates the consumption component and allows for independent validation of metabolic and waste material components. Figure 3 compares actual growth measured during the temperature experiments with model predictions. Predicted growth closely tracked observed growth through early periods of the experiment, but underestimated growth at low temperatures ($< 10^{\circ}\text{C}$) and at high temperatures ($> 23^{\circ}\text{C}$). Figure 4 illustrates results of validation of the model under varying ration experiments. Model

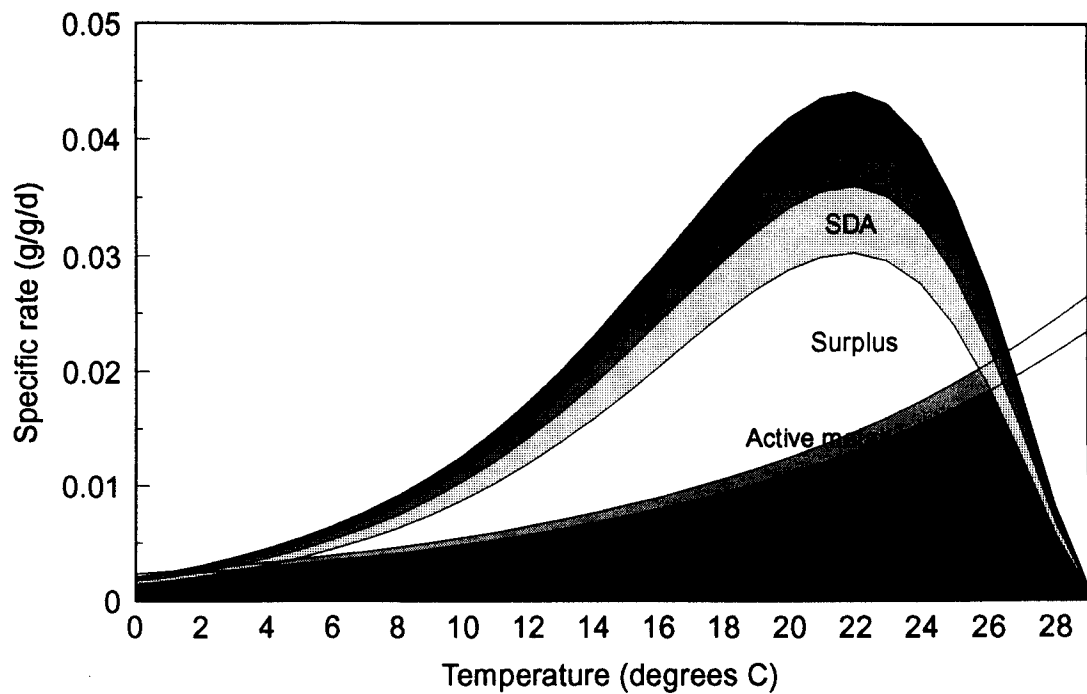


Figure 1. Components of the bioenergetic model for a 100 g northern pike as a function of temperature. The magnitude of each component is represented by the area between lines. SDA is specific dynamic action.

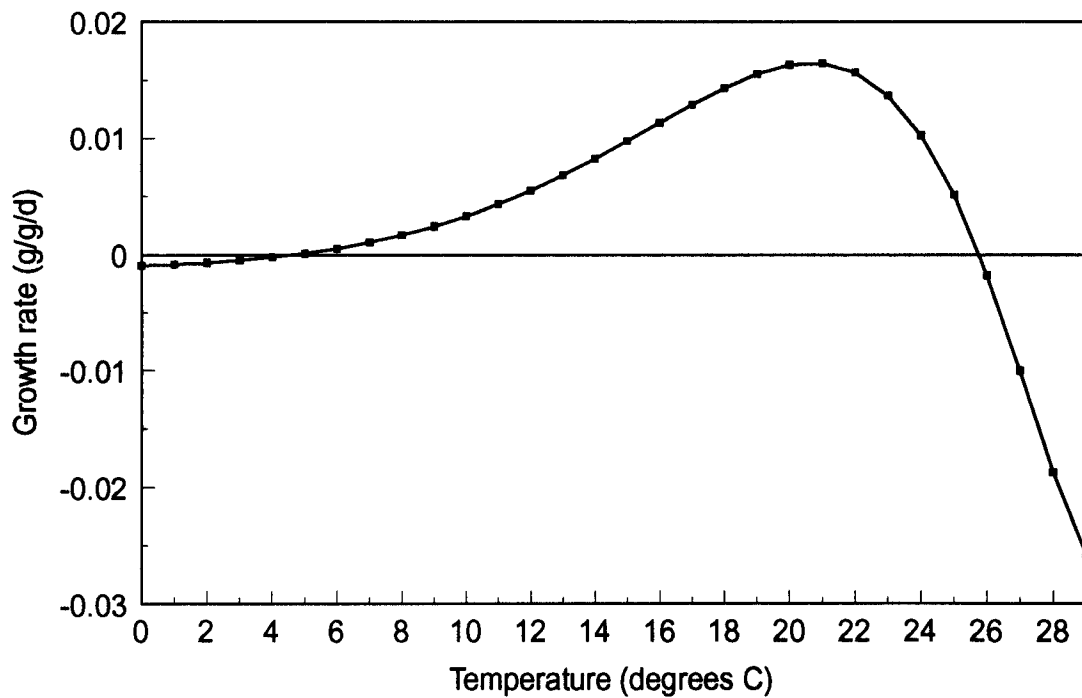


Figure 2. Scope for growth of a 100 g northern pike as a function of temperature.

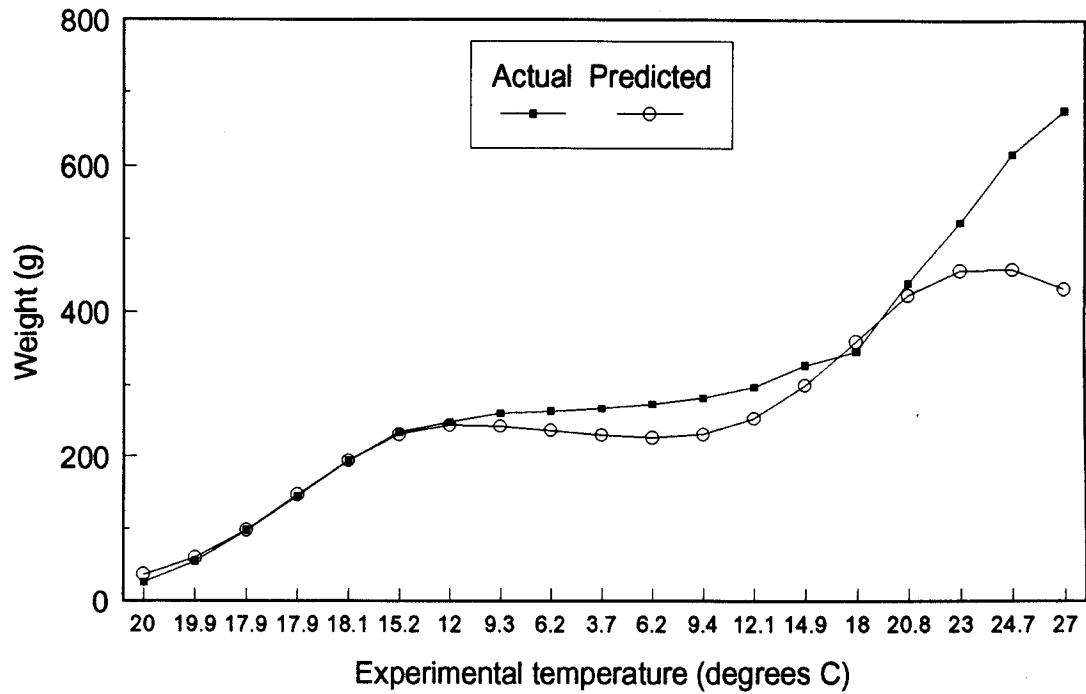


Figure 3. Comparisons of northern pike weights measured at different temperatures in laboratory feeding experiments conducted by Casselman 1978b (Figure 18) with growth predicted by the bioenergetics model.

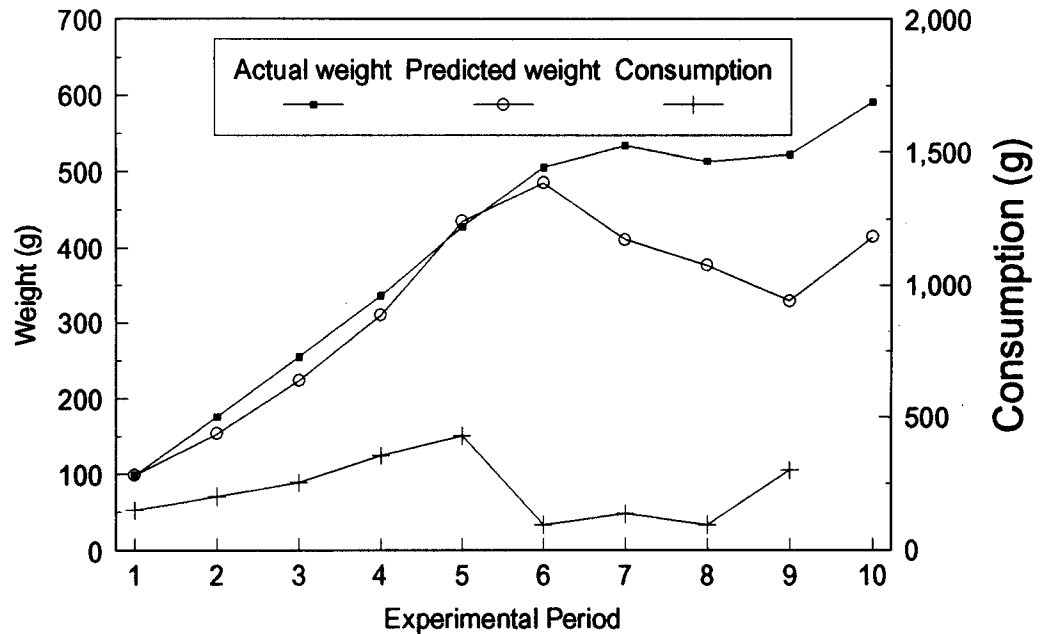


Figure 4. Comparison of northern pike weights measured by varying rations in laboratory experiments conducted by Casselman 1978b (Figure 20) with weights predicted by the bioenergetics model.

predictions tracked observed growth well under initial *ad libitum* feeding conditions, underestimated growth under very low ration levels, and eventually underestimated final weight for the entire experimental period by 40%. The model appears to simulate laboratory conditions well for temperatures between 10 and 23°C and for small northern pike. Further simulations with the population energetics model set consumption rate at maintenance levels for temperatures under 10°C. This technique helps reduce the effects of poor predictive capabilities of many bioenergetic models at low temperatures (Hewett and Johnson 1987; Kitchell et al. 1977).

Effects of summer temperature on simulated growth of northern pike are illustrated in Figure 5. Simulations were made at several summer temperatures. Specifically, the temperature on June 1 was set at the x-axis values in Figure 5 and maintained through September 1. Annual population consumption and production (total annual elaboration of fish tissue minus gonadal production (Chapman 1967)) were summed and plotted for each temperature. Annual population consumption was at a maximum at 22°C and

annual population production at 21°C (as expected from Figure 2). Predicted individual weight at the start of age 5 also was at a maximum at 21°C. The smaller weights at higher summer water temperatures were due to slow or negative growth in the summer. Negative population productions and weights at age 5 occurred when summer temperatures exceeded 26°C.

Effects of density were investigated by simulating populations at various rates of recruitment. Annual recruitments of 250, 500, 750, 1,000, 1,250, 1,500, and 2,000 three year old fish were simulated (Figure 6). Total annual population consumption increases as recruitment increases until reaching the asymptote of the constant population consumption model (as described in Methods). Amount of energy remaining for production decreases at higher recruitments because much of the energy consumed is required for maintenance. Maximum population production occurs at the point where the constant consumption "cap" becomes limiting.

Effects of population density on individual fish are illustrated in Figure 7. Population

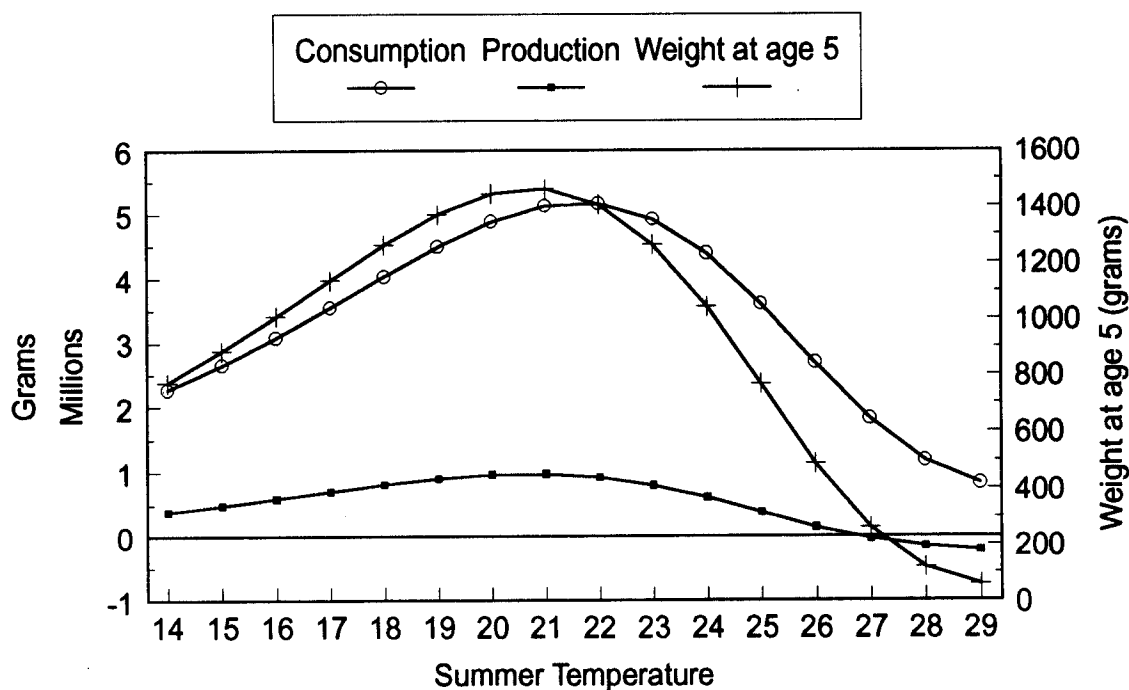


Figure 5. Total annual consumption and production of a simulated population of northern pike at various summer water temperatures. Also included is the predicted weight at age 5.

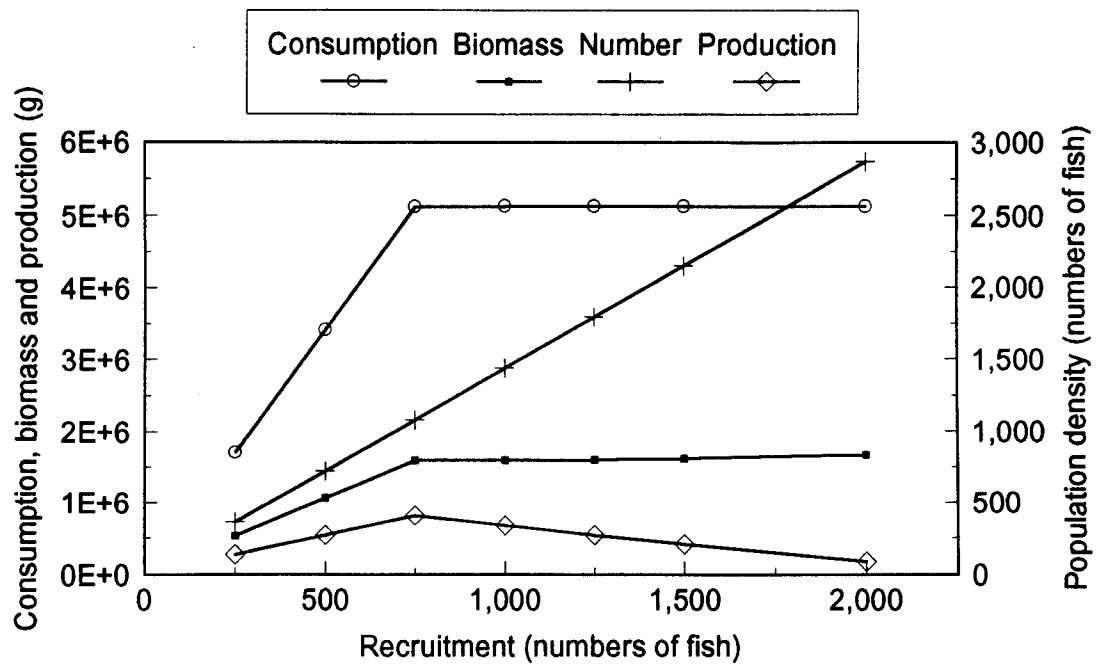


Figure 6. Total annual population consumption, production, biomass and density of a simulated population of northern pike at various levels of recruitment.

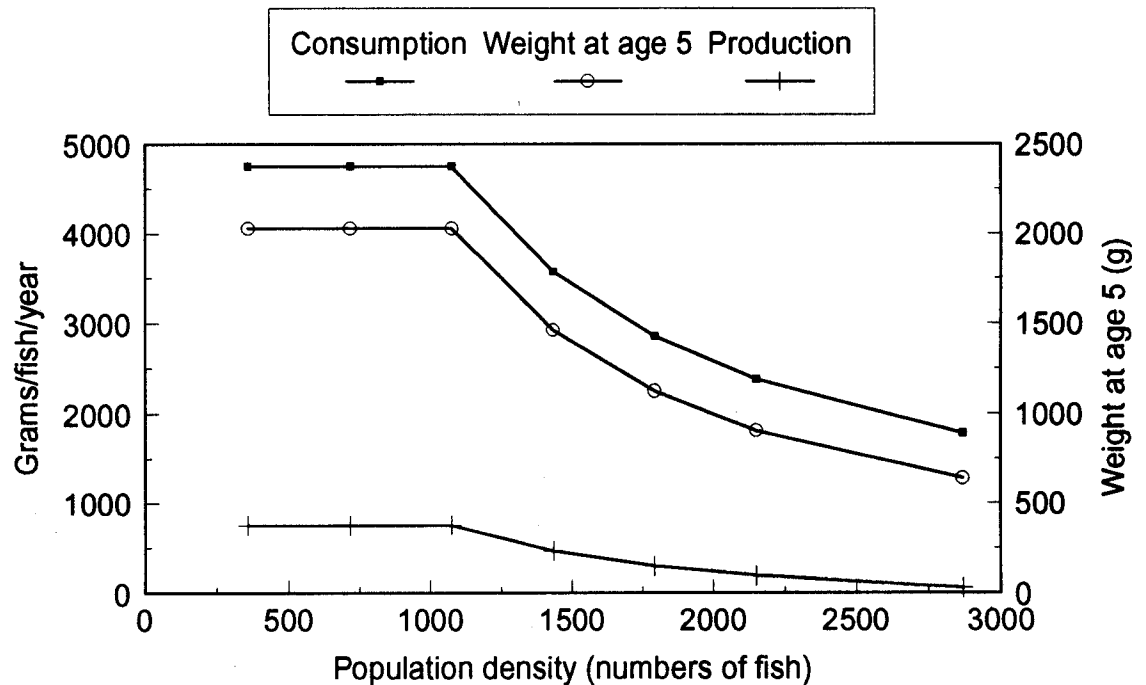


Figure 7. Mean annual individual consumption and production rates of northern pike at various simulated population densities. Also, included are simulated weights at age 5.

densities of fish along the x-axis represent population sizes that resulted from each level of recruitment. Mean annual individual consumption rates are at a maximum until population densities become high enough to reach the consumption "cap" and population consumption must be divided among a larger number of fish. Individual consumptions and productions then decline exponentially as population densities increase. Weights at age 5 decrease at higher population densities as individuals obtain "smaller slices of the pie" (reduced individual consumption), which reduces energy available for somatic production (after constantly required maintenance energy costs are met). In other words, individual growth is strongly density dependent at higher fish densities.

Effects of this strongly density dependent growth on length distributions are even more dramatic. Length distributions were generated for a low density population (recruitment = 500 three year old fish), medium density (recruitment = 1,000 three year old fish), and high density (recruitment = 2,000 three year old fish) (Figure 8). The low density population has the highest mean individual consumption rate, highest growth rate, and best length distribution. The high density population has a low mean individual consumption rate, with little energy remaining for growth after metabolic, feeding and waste requirements are met. The resulting length distribution is very poor. Actual numbers of fish in each graph are important to note. Numbers of fish at small sizes in the high density population are much larger than lower density populations. Fish that grow slower spend more time in smaller length intervals and force the length distribution to "stack up" at small sizes.

Discussion

The set of factors that affected northern pike growth rates changed with body size. Although correlation coefficients were small (possibly due to errors in ageing and measuring annular distances, inability to differentiate sexes in the samples, or due to the existence of a large number of factors that actually affect growth), lake survey data indicated that small, young

northern pike grew fastest in shallow, fertile lakes, with long growing seasons (types of lakes generally found in southern Minnesota). Eddy and Carlander (1940) also found positive correlations between length of growing season (and alkalinity) and northern pike growth. The fishing contest data suggest that conditions favorable for growth of large northern pike are different than for small fish. Production of larger northern pike was greater in lakes with deeper water and cisco (types of lakes more likely to be found in northern Minnesota). These differences could possibly be explained by ontogenetic changes in metabolic processes that control growth in northern pike. Specifically, temperature dependent components of metabolic functions could change with body size, resulting in lower optimum temperatures for growth as the size of northern pike increase. Such changes in optimum temperatures for growth, as a function of body size, have been observed in yellow perch (McCauley and Read 1973). Possibility of ontogenetic changes in metabolic processes could also explain the differences in optimum growth temperatures that Casselman (1978a) and Bevelhimer et al. (1985) found (see previous discussion in Methods). Bevelhimer et al. (1985) used smaller northern pike (9-53 g) and estimated optimum temperature for growth to be 25°C. Casselman (1978a) used larger fish (203-664 g) and estimated optimum temperature for growth to be 19°C. Further evidence of ontogenetic changes comes from Hokanson et al. (1973), who estimated optimum temperature for larval (<55 mm) northern pike growth to be 26°C. Further research is necessary to determine if these possible ontogenetic changes exist or if differences in optimum temperatures in the literature are the result of different genetic stocks of fish from different latitudes. In either case, it appears that large northern pike in Minnesota have relatively cool temperature requirements for optimum growth. Warm summer temperatures may inhibit their growth.

Presence of cisco may be an important indicator of the capability of a lake to produce large northern pike. The majority of trophy contest entries came from lakes where cisco were present (816 entries from 10,150 total hectares) in comparison to lakes where cisco were absent

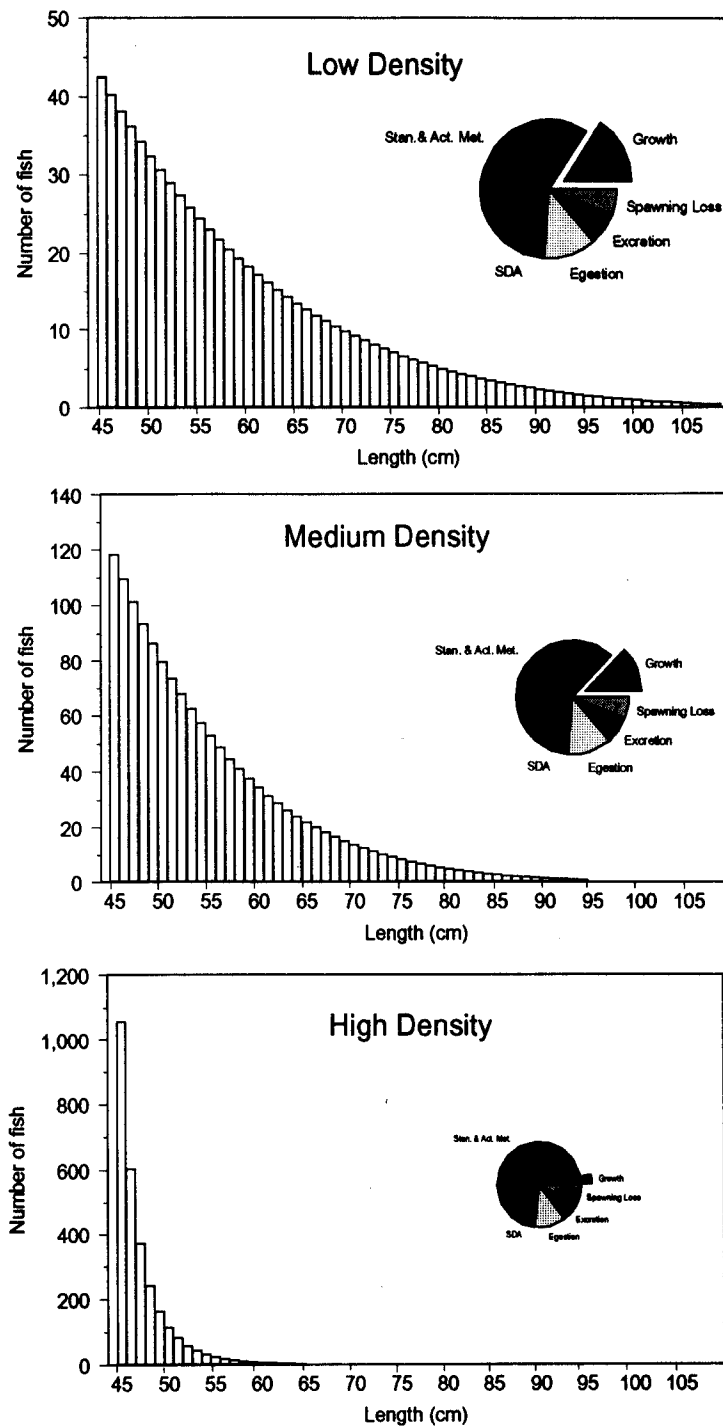


Figure 8. Predicted length frequencies of a population of northern pike simulated at high, medium, and low densities. Also included, are pie charts of the mean annual individual bioenergetic components (size of the total pie is proportional to the mean annual individual consumption).

(108 entries from 5,413 hectares). On a per hectare basis, trophy northern pike were produced from cisco lakes at four times the rate from lakes where cisco were absent. Although it cannot be determined from this data set if large northern pike require cisco as prey or simply need the same cool, well-oxygenated water cisco require, some evidence suggests that cisco may be an important and preferred prey species for large pike. Several laboratory studies have concluded that northern pike select for cylindrical, soft rayed fishes (Beyerle and Williams 1968; Wahl and Stein 1988). Although, Lawler (1965) found yellow perch *Perca flavescens* and trout-perch *Percopsis omiscomaycus* to be the most important prey species of northern pike in Heming Lake, Manitoba, coregonids (cisco and whitefish) were used increasingly as northern pike got larger and from fish that were sampled in deeper water. Colby et al. (1987) suggest that cisco are important prey for northern pike in north-temperate lake fish communities. Colby et al. (1987) describe how removal of larger northern pike from Heming Lake disrupted the *Triaenophorus* spp. parasite life cycle, of which coregonids are an intermediate host. The authors concluded that the remaining small northern pike did not consume cisco (and whitefish) in the same quantities consumed by medium and large pike. Makowecki (1973) described a shift in northern pike diet in Siebert Lake, Alberta from a varied diet for small northern pike of fish and invertebrates to a diet of almost exclusively lake whitefish for northern pike greater than 2.7 kg. Although yellow perch are an important prey species for northern pike in Minnesota (Seaburg and Moyle 1964; Anderson and Schupp 1986; Colby et al. 1987), it is possible that yellow perch provide a suitable prey for small and medium size northern pike, and that cisco become important for growth of large northern pike.

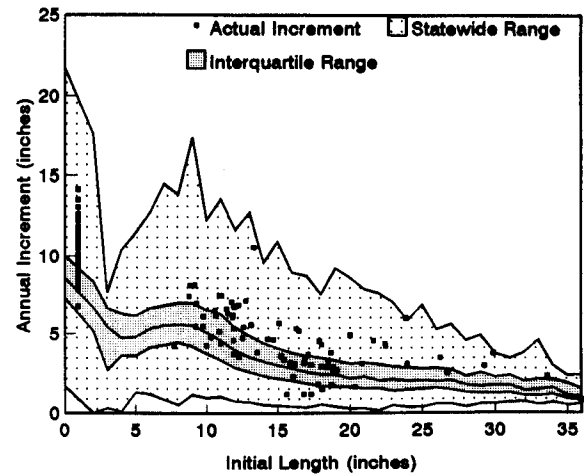
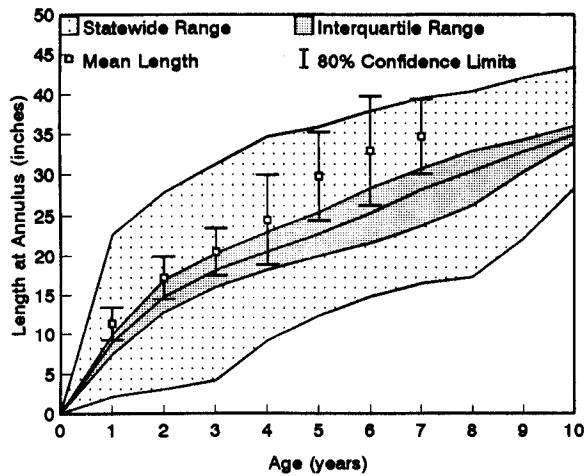
Another important constraint on northern pike growth appears to be population density. The population energetics model illustrated how density dependent growth can have a dramatic influence on size structure of northern pike populations. The constant consumption model placed severe constraints on the population as density increased. Density dependent mortality

rates and changes in fish behavior at high densities were not incorporated into the simulations. How realistically this model simulates actual northern pike populations is unknown, however, northern pike populations with slow growth, high densities, and poor size structures, are common in Minnesota (Goeman and Spencer 1992).

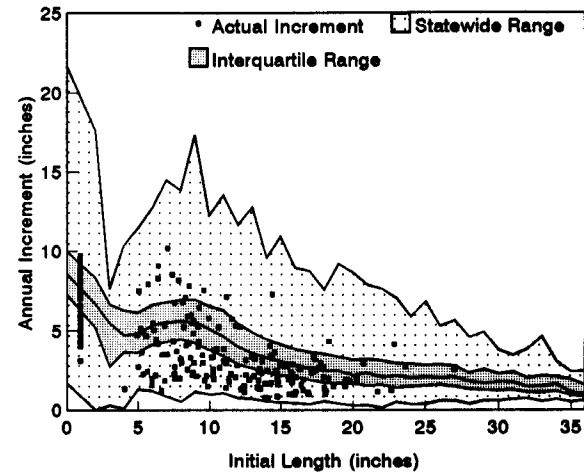
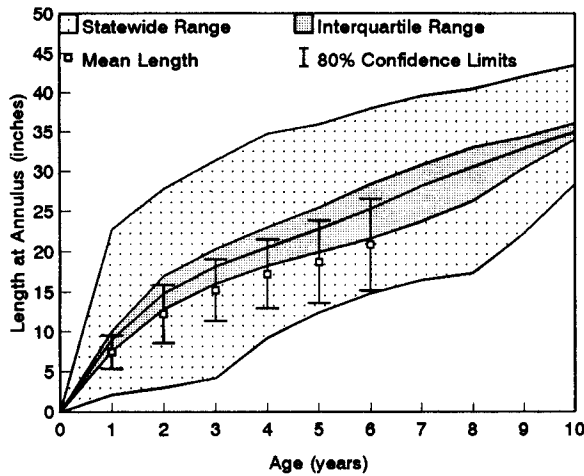
Several parameters of the bioenergetics model need to be refined. Inaccuracy of the model $< 10^{\circ}\text{C}$ was only partially corrected by using the winter maintenance function (no winter weight loss or gain). Diana (1983b) actually measured significant growth of northern pike during winter in three Michigan lakes. The use of P-values greater than one in this study indicate that either the consumption function underestimated the ability of northern pike to feed, or the respiration function overestimated basic metabolic rates. Brett (1979) discusses the difficulty in estimating maximum consumption in the laboratory. Laboratory stresses probably contribute to higher than normal respiration rates. Heart rate telemetry could prove to be a technique for estimating realistic bioenergetic model parameters in the wild (Lucas et al. 1991).

The lake survey data set indicated a wide variation in growth rates of northern pike in Minnesota. A method for comparing growth rates would be valuable. One approach is to compare growth rates of an individual lake to statewide growth rate quartiles, as illustrated in Figure 9. The first panel for each lake consists of mean backcalculated lengths of northern pike as a function of age. The second panel consists of annual increments as a function of initial length (backcalculated length at the start of the increment). Statewide quartiles are displayed in the background of each panel. The line in the middle of the interquartile range represents the statewide median. The stippled area represents the entire range of values observed. Statewide annual increment quartiles were calculated for annual increments grouped by one inch length intervals. Data used to calculate statewide quartiles were from 30,160 individual annual increments measured from 9,181 northern pike collected during lake surveys from 298 lakes in 1988, 1989 and 1990 from 15 management areas (Windom, Ortonville, Glenwood, Detroit Lakes,

Ice Cracking Lake



Detroit Lake



Mountain Lake

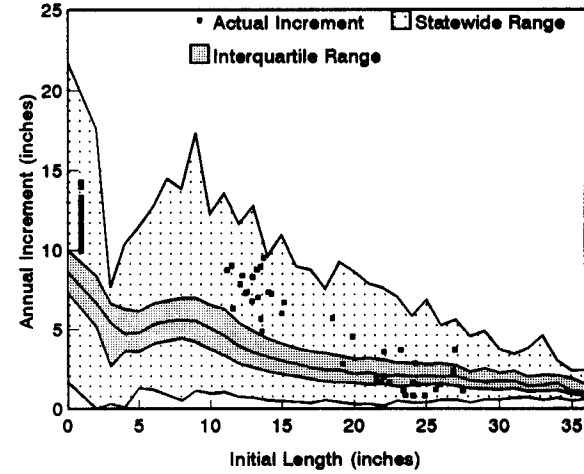
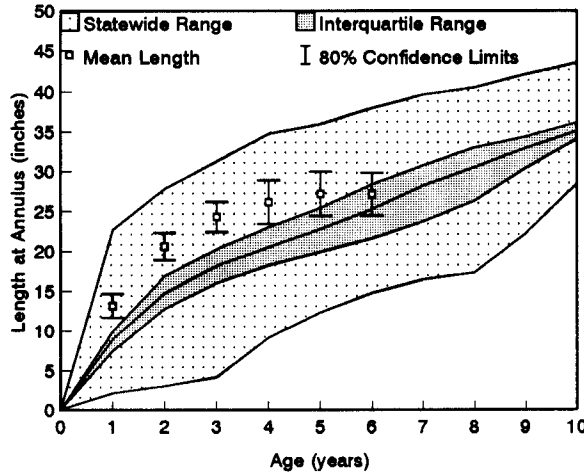


Figure 9. Statewide northern pike growth quartiles, with examples from three lakes (Ice Cracking and Detroit lakes in Becker County and Mountain Lake in Cottonwood County).

Walker, Bemidji, International Falls, Grand Rapids, Grand Marais, Finland, French River, Aitkin, Little Falls, Montrose, and West Metro). Appendices 2 and 3 contain the quartile data in tabular form.

Three lakes were selected to provide examples of the method. Ice Cracking Lake in Becker County is an example of a lake with above average growth for all ages and sizes of northern pike. Mean backcalculated lengths were above the statewide median for all ages. Most annual increments were larger than the statewide median and many were larger than the 3rd quartile for all sizes of fish. Detroit Lake in Becker County is an example of poor northern pike growth. All mean backcalculated lengths were smaller than the statewide median at all ages sampled. Most annual increments were smaller than the statewide median and many were in the 1st quartile for most sizes of fish. Mountain Lake in Cottonwood County provides an example of good growth at small and medium sizes but slower growth at large sizes. Although all of the mean backcalculated lengths are larger than the statewide median, growth rate appears to decrease at age 4. Nearly all annual increments were above the 3rd quartile for lengths less than 22 inches, however, most annual increments for lengths greater than 22 inches were below the statewide median. The figures for Mountain Lake illustrate a distinct change in conditions for growth of northern pike larger than 22 inches. The change could be due to lack of proper size prey or warm summer water temperatures (Mountain Lake is in southern Minnesota). In either case, these figures would allow the lake survey analyst to identify patterns in growth rates and then to investigate potential explanations for the patterns.

Mountain Lake also provides a good example of why the second panel was included in this method. Graphing of annual increments by initial lengths allows for direct examination of growth rates as a function of fish size. Gutreuter (1987) provides an excellent discussion of this subject and suggests that size-related expressions of growth may be more interpretable than age-related expressions. Osenberg et al. (1988) provides an example of how ecological conditions for growth of bluegill were more easily

discerned using size-related functions of growth rather than by more traditional age-based growth functions. Also, note that many metabolic equations used in bioenergetics modeling are functions of size not age. Inclusion of both panels in this method allows the lake survey analyst to examine growth rates in both age and size related forms.

Quartiles for individual lake classes (Schupp 1992) should be developed, rather than for lakes statewide as was used here. Comparisons of growth rates within lake classes are more appropriate than the statewide comparison. Lake class quartiles were not developed during this study because of an insufficient number of lakes in each lake class. However, northern pike age and growth data in DISBCAL .ANU file format from a sufficient number of lakes, should be available in a few more years.

Management Implications

1. Trophy northern pike management probably has the best chance of succeeding in lakes that maintain relatively cool (21°C) water throughout the summer. Larger or deeper lakes with cisco may have the best potential for the production of large northern pike.
2. Management (and research) efforts should be made to reduce abundance of small northern pike in slow growing populations with poor size structure. Although Goeman and Spencer (1992) found direct removal ineffective, other strategies to reduce density could include blocking spawning runs or protecting the larger northern pike that possibly control recruitment of smaller pike through cannibalism (Grimm 1983).
3. Growth rates measured in lake surveys can be compared using a quartile approach. Growth quartiles should be developed for individual lake classes, so that comparisons could be made with lakes that have similar potentials for northern pike growth. This would provide the capability to establish realistic and attainable management goals. Growth "bottlenecks" could be identified (especially with the size-related growth quartiles) and remedial actions could be implemented.

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Appendix 1. Development and parameterization of the bioenergetics model.

Standard metabolism was calculated as an exponential function of temperature and an allometric function of weight (Brett and Groves 1979):

$$M_s = a_s W^{b_s} e^{mT} \quad (1)$$

where,

- M_s = standard metabolic rate (g/g/day)
- a_s = intercept coefficient for standard metabolism (g/g/day)
- b_s = weight dependent coefficient for standard metabolism
- m = temperature dependent exponent for standard metabolism
- T = temperature (degrees Celsius).
- W = individual weight (g)

Diana (1983a) estimated values for these parameters ($a_s=0.00140$, $b_s=-0.18$, $m=0.16$) from a Canadian stock of northern pike. As noted by Bevelhimer et al. (1985), the temperature dependent coefficient (m), calculated by Diana (1983a), is based on only two points and produces a Q_{10} of 5.0, which is larger than expected. Brett and Groves (1979) suggest a general value of $Q_{10}=2.3$. Therefore, the equation was refit, by minimizing the absolute value of residuals at the two points (1°C and 18°C) used by Diana (1983a) and fixing the m parameter at 0.0833 (equivalent to $Q_{10}=2.3$). Resulting parameter values were $a_s=0.00478$, $b_s=-0.18$, $m=0.0833$.

The increase in metabolic rate due to activity (swimming) was assumed to be constant proportion of M_s and was estimated by Bevelhimer et al. (1985) to be 0.13 (activity multiplier of 1.13, increases M_s by 13%). Specific Dynamic Action (SDA), the costs of processing, digesting and assimilating food, was assumed to be a constant proportion of consumption and estimated by Diana (1983a) at 0.1042. Therefore, total metabolism (M_t) was described as,

$$M_t = 1.13M_s + 0.1042C \quad (2)$$

Consumption rates were modeled by multiplying a constant proportion (P) by a maximum consumption rate determined by a function of temperature and weight (Kitchell et al. 1977):

$$C = a_c W^{b_c} f(T) P \quad (3)$$

where,

$$f(T) = V^X e^{(X(1-V))}$$

and,

$$V = (T_m - T) / (T_m - T_o)$$

$$X = (U^2 (1 + (1 + 40/Y)^{0.5})^2) / 400$$

$$U = \ln(Q)(T_m - T_o)$$

$$Y = \ln(Q)(T_m - T_o + 2)$$

with,

C = rate of consumption (g/g/day)

a_c = intercept coefficient for maximum consumption (g/g/day)

b_c = weight dependent coefficient for maximum consumption

Q = temperature dependent coefficient for maximum consumption

T_o = optimum temperature for maximum consumption

T_m = maximum temperature for consumption ($C=0$).

Parameters for this equation were estimated from *ad libitum* food consumption data on northern pike in the laboratory, measured by Casselman (1978b: Figures 18,19,20). An attempt to fit the entire equation by nonlinear least squares was unsuccessful when the procedure would not converge on a realistic set of parameters. By fixing $T_m=29.4$ (lethal maximum temperature estimated by Casselman (1978a)), a realistic set of parameters could then be obtained by nonlinear least squares: $a_c=0.322$, $b_c=-0.431$, $Q=3.30$, $T_o=21.9$, $T_m=29.4$.

Waste losses (egestion= F and excretion= U) were assumed to be constant proportions of consumption and were estimated by Diana (1983a) at 0.13 for egestion and from Brett and Groves (1979) at 0.079 for excretion.

Growth was calculated by subtracting energetic costs from consumption:

$$G = C - (M_e + F + U) \quad (4)$$

where, G = specific growth rate (g/g/day) and absolute growth was calculated by multiplying G by W .

The bioenergetics model was extended to the population level to explore the effects of energetic growth constraints on the population dynamics of northern pike stocks. The population energetics model consisted of dividing a constant rate of annual population consumption (the sum of individual annual consumptions) across various simulated population densities of northern pike. This model assumes that a relatively constant amount of food will be available to a predator population from the prey base. Although, predator-prey dynamics are certainly far more complex than this, parameterizing a more complex predator-prey model was beyond the scope of this study. The constant population consumption function has been observed in yearling cutthroat trout in natural and laboratory streams (Warren and Davis 1967) and does provide a useful starting point for understanding mechanisms of density dependent growth rates of northern pike.

Specifically, the population energetics model was developed by establishing a baseline population of northern pike that had a growth rate equal to statewide northern pike mean lengths at age (Scidmore 1970: ages 3-10: 450, 537, 616, 682, 738, 791, 847, 893 mm), an annual natural mortality rate of 30%, an exploitation rate of 20% (R. Pierce, personal communication) and an annual recruitment of 1000 fish. P-values for the consumption function were calculated for each age (ages 3-10: 1.149, 1.261, 1.333, 1.394, 1.469, 1.563, 1.602, 1.715) using the P-fit module of Hewett and Johnson (1987). The thermal regime was simulated by maintaining a winter temperature of 4°C through April 5, then rising linearly to 21°C on June 1 and maintained at 21°C through September 1, then falling linearly to 4°C again on November 15. A GW-BASIC program was developed to run the simulations. Simulations started with 1000 three year old northern pike on January 1, each with an initial weight of 559 g. Energetic components and resulting growth increments of individuals and mortality of the cohort were simulated for one life span, with a maximum age of 11 years and time steps of one day. Only the female component of the baseline population was simulated. Spawning occurred on April 5 of each year and resulted in a loss of 24.7% of the total weight of each fish (Diana and MacKay 1979).

Consumption for the entire life span of the cohort was equal to annual consumption of the entire population for this model. Consumption for the baseline population was used as the limit for further simulations that examined effects of population density on growth. A multiplier, PA , was used to increase or decrease the value of the baseline P-value array and resulting population consumption. Fish growth at low population densities is unrealistic, with this type of model, if not constrained (a large value of population consumption spread across a small population results in unrealistic individual consumption rates). Therefore, growth was constrained by setting a limit of $PA_{max}=1.147$, which resulted in a

maximum weight at 11 years of 8,491 g. The value of PA was iterated for each simulation until either population consumption converged to the baseline population consumption limit or PA was equal to PA_{max} .

Length frequency distributions were generated by integrating the mortality rate function for each length interval:

$$n_i = \int_{t_1}^{t_2} R e^{-Z(t-t_r)} dt \quad (5)$$

that solves to:

$$n_i = \frac{R}{Z} (e^{-Z(t_1-t_r)} - e^{-Z(t_2-t_r)}) \quad (6)$$

where,

- n_i = number of fish in length interval i (e.g., 10 mm intervals)
- t_1 = age at start of length interval i
- t_2 = age at end of length interval i
- t_r = age at recruitment
- R = recruitment (number of fish at t_r)
- Z = total instantaneous mortality rate.

Ages for Equation 6 were calculated as whole numbers (e.g., 3.12 years) from a smoothed growth trajectory of the full life span of the cohort. Smoothed growth trajectories resulted in smoothed length frequency distributions that were easily compared. Lengths at age on January 1 were fitted with a second-order polynomial (parabola). The parabolic fit was chosen for simplicity and good fit and not because of any underlying growth function (Rafail 1972; Roff 1980).

$$l_t = c_0 + c_1 t + c_2 t^2 \quad (7)$$

where,

- l_t = length at age t
- c_0, c_1, c_2 = polynomial coefficients

Age, t for equation 6, was calculated from roots of equation 7 (both roots were calculated and the root between 0 and maximum age was selected):

$$t = \pm \left(-\frac{c_1}{2c_2} + \sqrt{\frac{l_t - c_0}{c_2} + \frac{c_1^2}{4c_2^2}} \right) \quad (8)$$

Appendix 2. Minimum, 25th percentile, median, 75th percentile, and maximum backcalculated lengths at age for northern pike from 298 Minnesota lakes with sample size (N).

Age	Min	25%	Median	75%	Max	N
1	2.10	7.51	8.99	10.01	22.68	9181
2	3.00	12.80	14.76	16.92	27.80	8464
3	4.18	15.99	18.15	20.29	31.31	6186
4	9.17	18.22	20.50	22.97	34.75	3417
5	12.34	19.92	22.75	25.43	35.96	1622
6	14.75	21.57	25.28	28.39	37.97	749
7	16.45	23.71	28.21	30.77	39.62	340
8	17.30	26.28	30.54	33.02	40.49	133
9	22.22	30.42	32.95	34.48	42.17	52
10	28.42	34.08	35.08	36.17	43.53	13

Appendix 3. Minimum, 25th percentile, median, 75th percentile, and maximum backcalculated annual increments as a function of initial length for northern pike from 298 Minnesota lakes with sample sizes (N).

Initial Length (Inches)	Min	25%	Median	75%	Max	N
0.0- 1.9 ^a	1.68	7.29	8.58	9.98	21.74	2305
2.0- 2.9 ^b	0.41	5.18	6.70	8.36	17.63	6882
3.0- 3.9	0.30	2.71	5.45	6.65	7.65	12
4.0- 4.9	0.09	3.64	4.72	6.29	10.37	141
5.0- 5.9	1.30	3.61	4.80	6.17	11.45	499
6.0- 6.9	1.20	4.12	5.33	6.64	12.72	937
7.0- 7.9	0.85	4.29	5.56	6.82	14.47	1305
8.0- 8.9	0.52	4.45	5.59	6.97	13.83	1687
9.0- 9.9	1.15	4.20	5.56	6.97	17.35	1594
10.0-10.9	0.96	3.77	5.10	6.57	12.24	1545
11.0-11.9	1.03	3.36	4.60	6.28	13.54	1299
12.0-12.9	0.74	2.86	3.97	5.45	11.63	1147
13.0-13.9	0.70	2.60	3.56	4.89	12.75	1230
14.0-14.9	0.53	2.35	3.27	4.46	9.59	1188
15.0-15.9	0.47	2.18	3.03	4.11	10.93	1228
16.0-16.9	0.41	2.04	2.82	3.80	8.97	1149
17.0-17.9	0.36	1.89	2.59	3.63	8.74	1081
18.0-18.9	0.54	1.70	2.45	3.51	7.57	924
19.0-19.9	0.40	1.66	2.45	3.33	9.21	805
20.0-20.9	0.27	1.63	2.19	3.12	8.65	672
21.0-21.9	0.29	1.53	2.30	3.19	7.88	521
22.0-22.9	0.15	1.56	2.06	3.09	7.62	447
23.0-23.9	0.49	1.40	2.12	2.92	7.04	341
24.0-24.9	0.36	1.47	2.03	2.89	5.87	259
25.0-25.9	0.38	1.53	2.07	2.80	6.85	209
26.0-26.9	0.57	1.58	2.02	2.84	5.28	175
27.0-27.9	0.57	1.45	2.07	2.75	5.63	147
28.0-28.9	0.39	1.29	1.79	2.33	4.57	106
29.0-29.9	0.58	1.25	1.69	2.54	4.89	86
30.0-30.9	0.59	1.21	1.77	2.26	3.76	57
31.0-31.9	0.68	1.26	1.74	2.39	3.44	54
32.0-32.9	0.72	1.09	1.44	2.02	3.83	40
33.0-33.9	0.54	1.10	1.48	2.13	4.61	31
34.0-34.9	0.68	1.17	1.61	2.11	3.02	18
35.0-35.9	0.50	0.92	1.11	1.92	2.41	16
36.0-36.9	0.61	0.81	1.04	1.55	2.42	12

^a - all initial lengths in this length group are initial lengths for the first annulus of cleithra-aged fish equal to the body-cleithra constant of 0.94 inches (23.8 mm)

^b - all initial lengths in this length group are initial lengths for the first annulus of scale-aged fish equal to the body-scale constant of 2.10 inches (53.3 mm)