

STATE OF MICHIGAN DEPARTMENT OF NATURAL RESOURCES

April 1, 2003

Growth and Appetite of Juvenile Lake sturgeon Acipenser fulvescens James S. Diana Paul W. Webb and **Timothy Essington**

FISHERIES DIVISION

www.michigan.gov/dnr/

MICHIGAN DEPARTMENT OF NATURAL RESOURCES FISHERIES DIVISION

Fisheries Research Report 2063 April 2003

Growth and Appetite of Juvenile Lake sturgeon Acipenser fulvescens

James S. Diana Paul W. Webb and Timothy Essington

The Michigan Department of Natural Resources (MDNR), provides equal opportunities for employment and access to Michigan's natural resources. Both State and Federal laws prohibit discrimination on the basis of race, color, national origin, religion, disability, age, sex, height, weight or marital status under the Civil Rights Acts of 1964, as amended, (1976 MI P.A. 453 and 1976 MI P.A. 220, Title V of the Rehabilitation Act of 1973, as amended, and the Americans with Disabilities Act). If you believe that you have been discriminated against in any program, activity or facility, or if you desire additional information, please write the MDNR Office of Legal Services, P.O. Box 30028, Lansing, MI 48909; or the Michigan Department of Civil Rights, State of Michigan, Plaza Building, 1200 6th Ave., Detroit, MI 48226 or the Office of Human Resources, U. S. Fish and Wildlife Service, Office for Diversity and Civil Rights Programs, 4040 North Fairfax Drive, Arlington, VA. 22203.

For information or assistance on this publication, contact the Michigan Department of Natural Resources, Fisheries Division, Box 30446, Lansing, MI 48909, or call 517-373-1280.

This publication is available in alternative formats.



Printed under authority of Michigan Department of Natural Resources Total number of copies printed 200 — Total cost \$311.74 — Cost per copy \$1.56 Michigan Department of Natural Resources Fisheries Research Report 2063, 2003

Growth and Appetite of Juvenile Lake sturgeon Acipenser fulvescens

James S. Diana and Paul W. Webb

School of Natural Resources and Environment University of Michigan Ann Arbor, Michigan 48109-1115

Timothy Essington

Center for Limnology University of Wisconsin Madison, Wisconsin 53706

Abstract.–Growth rates of juvenile lake sturgeon (initial weight 8 to 9 g, temperature 17.5° C), fed twice a day on brown worms for 56 days increased from -1.5% BW/d (% body wet weight/day) at zero ration to 2.6% BW/d at a ration of 13.2% BW/d. Maintenance ration was 1.6% BW/d. Fish fed larger rations had higher energy densities and lower water content. Appetite (average volitional daily food consumption) was compared for lake sturgeon initially weighing 6.3 g fed once and twice a day. Appetite was $12.8\pm1.6\%$ BW/d (n=36) for fish fed twice daily compared to $7.4\pm0.8\%$ BW/d (n=36) of fish fed once a day. Growth rates and food consumption in single feedings per day averaged $1.8\pm0.2\%$ BW/d and $9.4\pm2.2\%$ BW/d respectively, and were independent of weight for lake sturgeon weighing from 10 to 1322 g. These growth patterns are similar to other fish species. The most prominent feature of lake sturgeon growth was variation in daily food consumption, by as much as 15-fold for fish fed twice a day. Daily food consumption was correlated with previous consumption history, but mechanisms causing the effect could not be determined. The ability to gorge may be important for a species feeding on patchy prey. Management of lake sturgeon would be facilitated by selecting larger fish for stocking.

The lake sturgeon *Acipenser fulvescens* is a unique freshwater fish because of its longevity, slow growth, late maturity, large adult size, and relative rareness (Probst and Cooper 1954). This combination also makes the lake sturgeon extremely sensitive to exploitation, resulting in the historical decline of the lake sturgeon fishery (Houston 1987; Fortin et al. 1993). Only in recent years has management of lake sturgeon stocks, primarily by stocking and closure of fishing, begun to rebuild populations severely reduced by past human activities (Brousseau 1987; Fortin et al. 1993). As lake sturgeon populations rebuild, it is important to evaluate the carrying capacity and population size supportable by available habitat. Such information cannot be obtained from a census of existing populations because these are depressed.

An alternative for evaluating carrying capacity is to compare food resources and their use by lake sturgeon populations using information on growth and production energetics. This may be especially important for management of lake sturgeon because their slow growth could derive either from genetically determined life-history traits or from naturally occurring food limitations (Power and McKinley 1997). Thus, in estimating carrying capacity, it is important to distinguish between physiological and food resource limitations to growth.

The basis for determining the physiological potential for growth is the relationship between growth rate and food consumption called the growth-ration response curve (Brett and Groves 1979). In addition to describing growth rates at various ration levels, this relationship defines maintenance and maximum rations, as well as maximum and optimum growth rates (Brett and Groves 1979). Complete determination of the growth-ration response for a poikilotherm over a range of body sizes and temperatures is a difficult task, rarely performed due to its expense in time and resources. However, the general shape of the growth-ration curve is similar among species, among individuals of various sizes, and at different temperatures. The curve rises unimodally through maintenance ration, which is close to but somewhat lower than energy expenditure in routine metabolism, and asymptotes at maximum growth rate at maximum food consumption (see Brett and Groves 1979; Diana 1995). Thus, maintenance ration, maximum growth rate, and maximum food consumption are key variables describing growth patterns. These can be measured for a wide range of conditions more readily than detailed evaluation based on complete determination of growth-ration curves for all situations.

Growth and feeding potential of fish vary dramatically, usually as a power function of body weight with an exponent varying from 0.5 to 1 (Brett and Groves 1979; Diana 1995). Therefore, it is necessary to correct for fish weight in setting consumption rates or measuring growth. Most scientists, therefore, measure growth and feeding rates at frequent Short-term weight changes are intervals. considered sufficiently small that scale effects are approximately linear. As a result, weight effects are usually reported as weight specific values (% BW/d, that is percent body weight per day, or kJ/g·d) to compare ration and growth for fish of different sizes (Hung and Lutes 1987).

This assumes that dividing by weight directly corrects for differences in body size.

The purpose of this study was to determine growth patterns for juvenile lake sturgeon by measuring the growth-ration curve for small fish, and food consumption and maximum growth rates of fish weighing up to 1300 g at 17.5°C, typical of summer temperatures (Hay-Chmielewski 1987). Lake sturgeon growth is compared with data for other species to test the hypothesis that lake sturgeon have a low physiological capacity for growth.

Methods

Lake sturgeon were obtained from the Wolf Lake State Fish Hatchery in Michigan, which raised the fish from eggs collected by the Wisconsin Department of Natural Resources from the Menominee River. Fish were kept in the laboratory from several weeks to several months at the test temperature of 17.5°C, and fed *ad libitum* on live brown worms (immature individuals of family Lumbriculidae: order Oligochaeta.). This food source averaged 84.33% water and 22.53 kJ/g dry weight. Three sets of experiments were performed to determine effects of ration and fish size on food consumption and growth.

Effects of Ration on Growth

Growth was measured for six groups of lake sturgeon using standard batch methods (Brett et al. 1969; Brett 1979). Fish were held in 110liter tanks, with a bottom surface area of 0.5 m^2 . Tanks were continuously aerated and flushed with water with a replacement rate of 200%/d. Lake sturgeon (average wet weight 8 to 9 g) were individually weighed and assigned at random to one of six treatment groups, with 35 fish in each group. Groups were randomly assigned to one of six treatment levels with initial rations of 0, 5, 10, 15, 20, or 25% body wet weight per day (% BW/d). Ration levels were based on a preliminary measurement of maximum food consumption of 24% BW/d for lake sturgeon averaging 6.3 g fed twice each day over a 12-d period. Individual fish in each treatment were weighed every 14 d during the 56-d duration of the experiment. Food application rates were recalculated immediately after each sampling period.

Fish were fed pre-weighed amounts of brown worms twice a day over a period of 30 min to 1 h. Any food remaining in the tank at the next feeding was removed and the original amount of food given corrected for the weight of the uneaten portion. Lake sturgeon grew so rapidly at higher rations that the number of fish in each treatment was reduced to 20 after 42 d by removing individuals at random during the scheduled weighing.

We found that maximum food consumption over a long period was substantially lower than that measured over 12 d. As a result, fish ate similar amounts of food at the nominal rations of 15, 20, and 25% BW/d. Therefore, after 28 d, the group initially fed 20% BW/d was converted to 2% BW/d and followed for a further 28 d. Such fine-tuning is appropriate when the size range is relatively small, as in the present situation (see Webb and Brett 1973; Brett 1979).

Mortalities occurred in all treatments during the first 28 d among apparently healthy fish. All fish were feeding prior to the experiments, but some did not recommence feeding after introduction to the experimental tanks. These fish eventually became immobile and nonresponsive. They were removed, and length and weight were recorded. Growth and ration were corrected for mortalities. Reasons for failure to feed could not be ascertained. Mortalities also occurred throughout the 56-d period for the starved fish.

Dry weight and energy content were measured for the food and fish. A subsample of every shipment of brown worms was dried at 80° C and combusted in a Phillipson microbomb calorimeter. A subsample of eight fish was similarly treated at the start of the experiment. Final dry weight and energy content were determined for five fish in each treatment at the end of the experiment.

Growth trajectories for wet weight over time were determined using least squares regression methods. Wet weights measured after each 14-d period were compared using ANOVA. Changes in dry weight and energy content were averaged for the 56-d period (28 d for the nominal ration of 2% BW/d), assuming that average values for the fish subsampled applied to all fish in a treatment. Food consumption was totaled and converted to dry weight and energy content using means from subsamples. Growth-ration curves were curvilinear, and the best-fit curve was obtained by relating growth to the logarithm of ration (to which one was added to accommodate the zero ration level). Statistical tests were performed using SYSTAT (Wilkinson 1990) and differences were judged significant at the 5% level.

Effect of Single and Twice-Daily Feeding on Food Consumption

Six groups of 37 fish averaging 6.3 g were fed for 12 d. Of the six groups, three were fed once a day and three were fed twice a day. Food was offered over a 30- min to 1-h period. Fish were held in 110-1 tanks (bottom area 0.5 m^2). Tanks were continuously aerated and flushed with water.

As with the 56-d experiment, food consumption was determined from the difference between food offered to the fish and uneaten food siphoned from tanks at the next feeding.

Effects of Size on Maximum Growth Rate and Food Consumption

Fourteen fish weighing from 10 to 1322 g were placed in separate tanks. Small fish (<44 g) were placed in 40 l tanks (bottom area 0.2 m²), medium-sized fish (107 to 500 g) in 110-l tanks (bottom area 0.5 m²), and the largest fish (>836 g) in 220 l wading pools (bottom area 1.2 m²). Tanks were continuously aerated and flushed with water.

Each fish was fed once a day for 28 d. Fish were offered food over a period of 30 min to 1 h until they no longer ate. Fish were fed from a pre-weighed sample of brown worms. Uneaten food was weighed at the end of a feeding period. Residual uneaten food in the fish tanks was removed at the next feeding period and total food consumption corrected for this uneaten portion. Fish were weighed at 0, 14, and 28 d. Growth rates were determined from average changes in wet weight over the observation period.

Results

Effects of Ration on Growth

Lake sturgeon (8 g initial wet weight) grew steadily at all rations greater than approximately 2.2% BW/d, with a maximum growth rate of 2.6% BW/d at an average daily food consumption of 13.2% BW/d (Figure 1). Fish lost a little weight on a ration of 2.2% BW/d (nominal ration 2% BW/d) which was, therefore, close to maintenance. Individuals in the starved group lost weight and the smallest fish died. Consequently, the frequency distribution of weights of surviving fish shifted towards larger sizes (Figure 2). As a result, mean weight of surviving fish increased! However, the maximum size of the fish in this treatment declined at successive sample dates. We chose to estimate weight loss during starvation from the rate of decrease at the upper boundary of the weight-frequency distribution using weight changes of the three largest fish that survived for the entire 56 d. On this basis, starved fish lost weight at a rate of 1.5% BW/d.

The relationship between wet weight and time (Figure 1) for each treatment was best described by linear regression (Table 1). Coefficients of determination using all data ranged from 0.15 to 0.81. This reflects relatively large coefficients of variation, averaging 42%, for weight within each treatment. This variation was unaffected by ration level or time. Stronger linear trends were found using mean weights at each sampling time (r^2 >0.97).

Energy content and water content of lake sturgeon were affected by ration level (Table 2). Initial values were 17.8 ± 1.4 kJ/g dry weight and $86.5\pm1.0\%$ water (mean ± 2 SE). Energy density increased with ration level to approximately 22 kJ/g dry weight at rations above 10% BW/d. Water content decreased with increasing ration to approximately 80% at similar ration levels.

Growth rates increased with ration level (Figure 3a) and were best described by a logarithmic function. For energy content, growth rate (Q_{GE} , kJ/d), increased from -0.77 kJ/d for starved fish to 2.87 kJ/d for fish fed to excess according to:

$$\begin{split} Q_{GE} &= -0.772(\pm 0.86) + 3.36(\pm 1.10) \cdot \log{(Q_{RE}+1)} \eqno(1) \\ r^2 &= 0.889; \, p{<}0.001 \end{split}$$

where Q_{RE} is the ration level in kJ/d.

In terms of body weight changes (Figure 3b), growth rate (Q_{GW} , % BW/d) was related to food intake (Q_{RW} , kJ/d) by:

$$\begin{split} Q_{GW} &= -1.49(\pm 0.48) + 3.54(\pm 0.46) \cdot \log{(Q_{RW}+1)} \eqno(2) \\ r^2 &= 0.979; \, p{<}0.001. \end{split}$$

For this relationship, starved fish lost weight at 1.49% BW/d, similar to that estimated from the upper weight change boundary among fasting lake sturgeon, and fish fed to excess gained 2.59% BW/d at 13.2% BW/d ration. Maintenance ration was 1.64% BW/d (0.69 kJ/g·d).

Gross conversion efficiency was calculated from wet weight-specific growth rates and food consumption. It increased from a negative value (-2%) for fish fed the smallest ration, just below maintenance, to about 25% for fish fed 8% BW/d, thereafter decreasing slightly at higher ration levels (Figure 3c).

Variation in Food Consumption with Time

We also found substantial variation in daily food consumption, as monitored for the group fed to excess (nominal ration 25% BW/d). In 56 d, these fish grew from 9.32±1.04 g to 41.31±5.98 g (mean±2SE). They consumed large amounts of food for the first two days with a mean per capita consumption of approximately 3 g/d (approximately 32% BW/d). On the third day, food consumption decreased to approximately a half of that eaten on the first Absolute food consumption then two days. increased with time as fish grew, but appeared to plateau at about 3.5 g/d (Figure 4). This represented approximately 10% BW/d. The average consumption for the entire 56-d period was 13.2% BW/d.

Food consumption varied by a factor of about 2 during the first 25 d, but differences became larger with time. Between days 40 and 50, minimum and maximum food consumption

varied by a factor of about 14. Tests for autocorrelation were significant (Bartlett's test; p=0.02) for lags of three to four days, suggesting that food consumption was influenced by preceding meal history.

Effect of Single and Twice-Daily Feeding on Food Consumption and Growth

The average daily food consumption of fish fed twice a day for 12 d ranged from 5.1 to 24.0% BW/d, averaging $12.8\pm1.6\%$ BW/d (n=36). Fish fed once a day consumed from 5.0 to 12.9% BW/d, averaging $7.4\pm0.8\%$ BW/d (n=36). Although fish fed once per day consumed 57% of the amount of food eaten in two meals a day, the variability in daily consumption was large enough that fish essentially ate the same amount of food at each feeding, irrespective of whether fish were fed once or twice per day. The average growth rate of fish fed twice a day was 2.4% BW/d compared to 1.6% BW/d for fish fed once a day.

Effects of Size on Maximum Growth Rate

Absolute growth rate (g/d) was significantly and positively correlated with fish weight (p<0.001, $r^2=0.58$). However, in spite of a high relative growth rate for one small fish and a low relative growth rate for one large fish, relative growth rate (% BW/d) of lake sturgeon was not correlated with fish weight (Figure 5; regression, p=0.84). The average weight specific growth rate for these fish fed once per day was $1.8\pm0.2\%$ BW/d.

Food consumption varied from meal to meal. The variation tended to be larger for smaller fish, as illustrated by the larger bars representing 2SE (Figure 6). However, there were no significant trends in food consumption with time (regression analysis; p>0.05). In addition, weight-specific food consumption was independent of mass (ANOVA; p = 0.69) averaging 9.4±2.2% BW/d.

Discussion

The growth potential of a species is one piece of information important for its successful management or culture. We determined the general form of the growth response for juvenile lake sturgeon by measuring growth at different ration levels. This curve is scaled by maintenance ration, maximum growth rate, and maximum food consumption. We examined the effect of the latter two factors that determine maximum growth potential (Brett and Groves 1979; Brett 1979).

As with other species, lake sturgeon growth and energy density increased as ration increased, while water content decreased (Brett and Groves 1979). These results were also similar to work on white sturgeon Acipenser transmontanus (Hung and Lutes 1987; Hung et al. 1993). Growth rates and food consumption were also similar for a given feeding schedule among our experiments. These data, as well as maintenance ration, were also comparable to those of other species tested at similar temperatures and of similar sizes (data and scientific names in These similarities include other Table 3). sturgeon, plus top carnivores (bass, catfish), omnivores (stickleback. carp). temperate eurytherms (carp, bass), stenotherms (salmon, trout) and even tropical species. This suggests that compensation, or adaptive convergence in metabolism among species to conditions in their normal habitats, applies to growth as well as to energy catabolism (Brett and Groves 1979; Hochachka and Somero 1984). In addition, lake sturgeon growth in the laboratory, like that of other species (Brett 1979), was very much larger than observed in the field (Probst and Cooper 1954; Beamish et al. 1996). Therefore, realized energetic performance in the field is probably dependent primarily on food availability, as well as temperature (Hung et al. 1993; Fortin et al. 1996; Power and McKinley 1997).

Our results also show growth rate and food consumption (in % BW/d) to be independent of fish weight. This contrasts with results from other species, where the growth (% BW/d) and maximum ration (% BW/d) generally decline with body weight, and optimum and maximum growth occur at lower relative rations as weight increases (Brett and Groves 1979; Hung et al. 1993; Diana 1995). The shift reflects well-known allometric relationships for metabolism. However, maximum food consumption (% BW/d) and hence maximum growth rate, tends to decrease with increasing fish size (Brett and Groves 1979; Peters 1983). Visual inspection of our juvenile lake sturgeon growth data (Figure 6) may suggest a similar trend of reduced growth and food consumption in larger fish. However, as noted above, this impression is due to high growth of one small lake sturgeon and low growth of one large lake sturgeon. The suggestion cannot be supported statistically.

Although we did not quantify movement, larger lake sturgeon clearly spent less time moving around their tanks. In our experiments, tank size increased with fish size. Therefore, we do not attribute differences in locomotor activity to constraints of captivity. Indeed, continuous swimming of small lake sturgeon is in marked contrast to more sedentary behavior of larger juveniles and was apparent in our experimental tanks as well as in the very much larger holding tanks in the hatchery. We suggest the size independence of growth rates we observed may be associated with size-dependent reductions in activity metabolism.

The weight range studied, although large compared to most studies of growth, is still a small portion of total weight changes during lake sturgeon ontogeny. However, it is improbable that food consumption and growth rate remain independent of size throughout life. Larger juveniles and adult lake sturgeon may show expected declines in growth rate and food consumption, as found by Beamish et al. (1996) for natural populations.

The average growth patterns of lake sturgeon proved unremarkable when compared with other species (Table 3). However, the large variability in lake sturgeon food consumption, both within and among experiments, was unexpected and proved to be the most prominent feature of our results. For example, in the ration-growth experiment, fish weighing approximately 5 to 50 g ate up to 30% BW/d but sometimes less than 1% BW/d. A similar range was found in data for fish fed both once and twice a day. Over an extended period, however, average food consumption was about 10%. Variation in daily food consumption and growth has not often been described, but has been noted for white sturgeon (Hung and Lutes 1987), as well as largemouth bass fed large food items (fathead minnows) over a five week period (Smagula and Adelman 1982).

Many factors may contribute to variability of food consumption in fish, such as stomach volume or metabolic scope limiting apparent specific dynamic action. The latter possibility is suggested by the autocorrelation between daily consumption and that 3 to 4 days later. Food consumption has been shown to be affected by previous meal history for winter flounder Pseudopleuronectes americanus (Tyler and Dunn 1976) and cod Gadus morhua (Soofiani and Hawkins 1982). These fish have a small metabolic scope (Priede and Holliday 1980), when average meal size could be limited by the energy demands of apparent specific dynamic action (Tyler and Dunn 1976; Tandler and Beamish 1980; Soofiani and Hawkins 1982; Beamish and Trippel 1990). Hung et al. (1993) found similar variability in white sturgeon diets and growth, which they attributed partly to low dissolved oxygen limiting metabolic scope. However, this probably does not apply to lake sturgeon in our experiments because preliminary observations on swimming metabolism (Jared Cook, unpublished observations) show that metabolic scope is comparable to that of other fishes, such as salmonids (Brett and Glass 1973) and centrarchids (Beamish 1970).

Mechanical limitations are also a plausible limiting factor for food consumption. This possibility is suggested because fish fed once a day ate the same amount of food per feeding as fish fed twice a day. However, a mechanical limitation alone would be expected to result in constant food consumption. Instead, daily food consumption varied widely.

Numerous other factors could affect day-today food consumption, such as liver processing capabilities or buffering in transport systems. Unfortunately, like Smagula and Adelman (1982) we are unable to determine the basis for variation in food consumption.

Irrespective of the cause of variability in food consumption, the ability to take large meals is probably important to the overall energetics of sturgeon in the same way as for deep-sea fish and top carnivores (Sullivan and Smith 1982; Diana 1983). Consumption of occasional large meals is common among these fishes (Diana 1979, 1983; Smagula and Adelman 1982; Sullivan and Smith 1982), where large meals make critical contributions to the overall energy budget (Diana 1983).

Unlike top carnivores, sturgeon eat many small prey items. They typically feed on mucky containing bottom substrates, variable populations of macro-invertebrates, particularly chironomids (Hay-Chmielewski 1987). This food base is not only relatively poor, but very patchy. In addition, food appears to be limiting in natural systems, since laboratory growth rates are very much larger than those of fish in the wild. Thus, sturgeon probably gorge when they can, and the capacity to eat large meals may be essential for lake sturgeon to exploit rich but irregular food patches.

The sort of variation we found for food consumption and growth appears to be typical of sturgeon (Hung and Lute 1987; Hung et al. 1993), differing from patterns in more intensively studied actinopterygian species (Brett and Groves 1979). The variation in size of young fish we used, all spawned from a limited batch of eggs, is also larger than among other commonly studied species. Compare, for example, 95% confidence intervals for weights of sockeye salmon (Brett et al. 1969) and lake sturgeon during ration-growth experiments. In contrast to observations on other species (Brett 1979), increases in variation, indicative of growth depensation (Ricker 1971), did not occur with lake sturgeon in our study.

These observations have implications for the management of lake sturgeon, a threatened species. First, it is apparent that larger fish can store more energy and are more robust. As with other fish, rapid growth to larger sizes is probably essential to build up reserves for overwintering (see Beamish et al. 1996) and to quickly reach a size where predation is reduced.

This suggests that the common practice of stocking fish at 5-12 g, as occurs in the Midwest, is suboptimal. Studies on other species indicate that survival could be increased by stocking larger individuals, and in spite of the high cost of growing fish to a larger size, positive costbenefits may accrue (Seelbach 1987). In view of the large variation in growth patterns of lake sturgeon and the greater energy reserves and robustness of larger fish, early selection for larger fish in hatcheries would focus resources on those fish most likely to survive at planting.

Second, because lake sturgeon have the capacity for rapid growth, food is probably limiting in their natural habitat. Therefore, protection of suitable feeding habitat, as well as abundance and diversity of benthic prey, is essential if lake sturgeon are to persist (Hay-Chmielewski 1987).

Acknowledgments

This project grew out of the interest in lake sturgeon rehabilitation of the Michigan Department of Natural Resources. It was jointly supported by the Michigan Department of Natural Resources Fishery Division, the University of Michigan School of Natural Resources and Environment, and the Saltonstall-Kennedy Fishery Development Project, grant number NA-90AA-H-SK035 from the National Marine Fisheries Service, National Oceanic and Atmospheric Administration, U.S. Department of Commerce. The provision of hatchery facilities, hatchery personnel, and logistic support by Michigan Department of Natural Resources Fishery Division was critical to the completion of these studies.

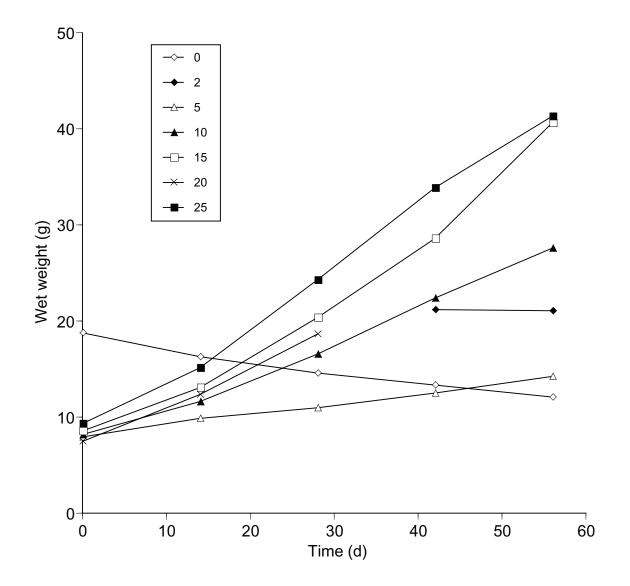


Figure 1.–Changes in the average wet body weight of juvenile lake sturgeon fed twice a day on rations from 0% BW/d to excess. The group initially fed 20% BW/d was reduced to 2% BW/d at day 28.

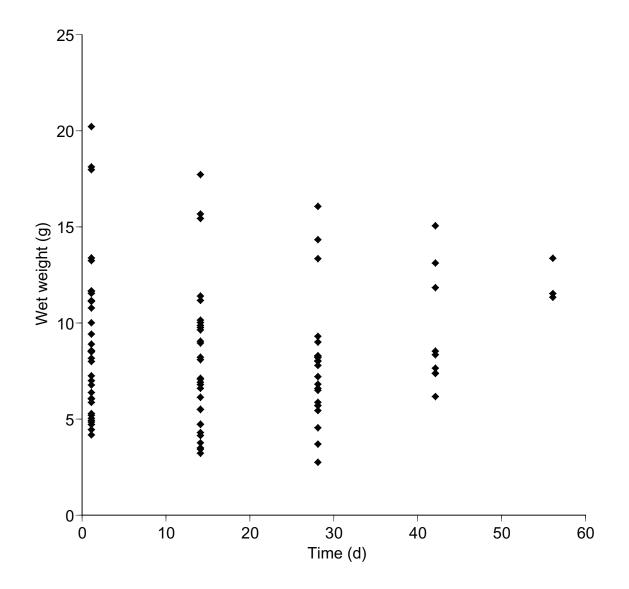


Figure 2.–Changes in the size composition of juvenile lake sturgeon at zero ration.

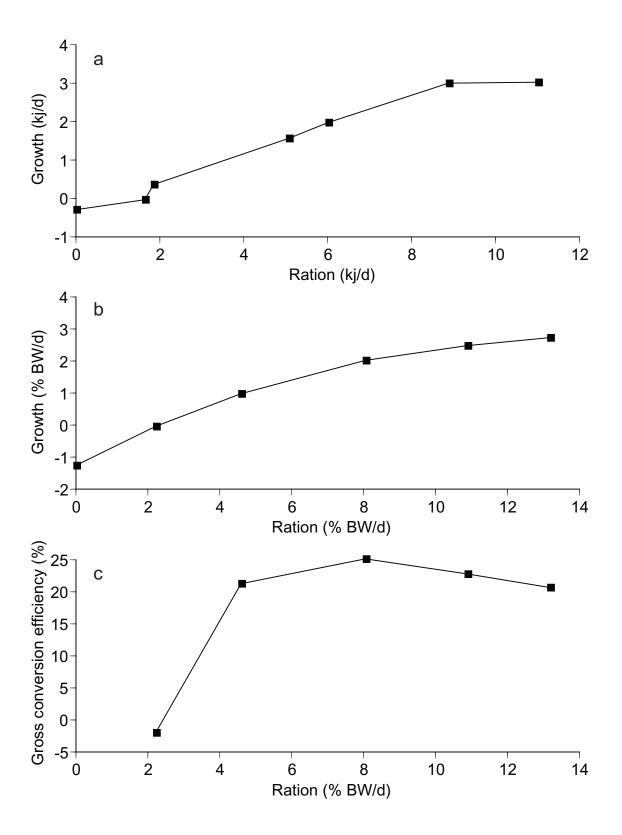


Figure 3.–The relationship between; (a) growth rate and ration in terms of energy content, (b) growth rate and ration in terms of body (wet) weight, and (c) gross conversion efficiency and ration in terms of body (wet) weight for juvenile lake sturgeon fed for 56 days.

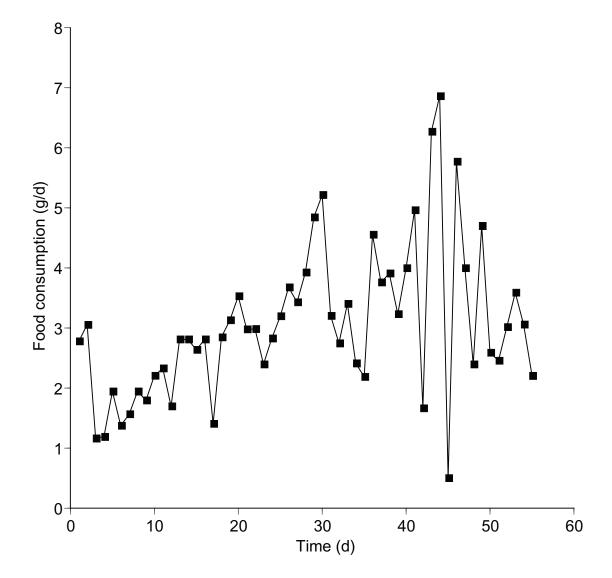


Figure 4.–Daily average food consumption per fish for a group of lake sturgeon fed twice daily over a 56-day period.

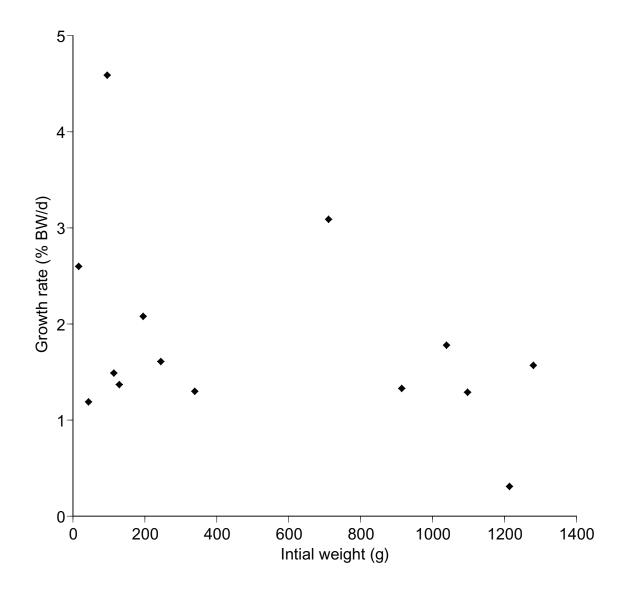


Figure 5.–Growth rates of juvenile lake sturgeon of various weights fed to excess once per day.

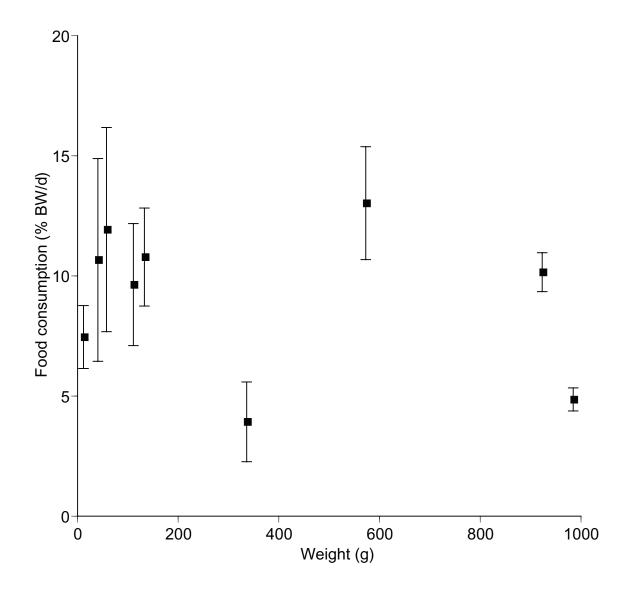


Figure 6.–Food consumption of juvenile lake sturgeon of various weights fed to excess once per day.

		r^2		
Nominal ration (% BW/d)	Actual ration (% BW/d)	Regression using weights of individual fishes at each sample date	Regression using average weights of fish at each sample date	Slope
0	0	0.81	0.98	-0.12
5	4.59	0.15	0.99	0.11
10	8.05	0.48	0.99	0.35
15	10.88	0.56	0.97	0.55
20	12.43	0.44	n/a	0.35
25	13.16	0.66	0.99	0.59

Table 1.–Regression statistics for wet weight changes over time during the measurement of growth of lake sturgeon fed various rations.

Table 2.–Composition of lake sturgeon fed different rations. Data are mean \pm 2SE for a random sample of five fish at the end of the experiment measuring effects of ration on growth.

Nominal ration (% BW/d)	Actual ration (% BW/d)	Percent water	Energy density (kJ/g dry weight)
Initial sample		86.5±1.0	17.8±1.4
0	0	86.1±1.3	16.3±0.2
5	4.59	85.0±0.6	18.1±0.5
10	8.05	81.7±2.1	21.1±0.6
15	10.88	79.0±0.9	21.7±1.2
20	12.43	81.7±1.5	21.3±0.4
25	13.16	78.5±2.0	21.7±0.6

Table 3.-Comparison of juvenile lake sturgeon growth with other fish species.

Species	Temperature °C	Initial weight	Maintenance ration % BW/d	Maximum food consumption % BW/d	Growth rate at maximum ration % BW/d	Reference
Salmo trutta	15	12	3.4	10.3	1	Elliott (1975)
Gasterosteus aculeatus	19	<10	2.5	14.0		Allen and Wootton (1982)
Clarias lazera	20	5	1.0	6.0	2.5	Hogendoorn (1983)
Cyprinus carpio	18	9	0.8	7.0	2.3	Goolish and Adelman (1984)
Parophrys vetulus	15	5	4.0	16.0	0.8	Williams and Caldwell (1978)
Morone sp.	20	28	1.9	8.3	1.0	Woiwoode and Adelman (1991)
Micropterus salmoides	18	8	0.8	10	3.0	Niimi and Beamish (1974)
Oncorhynchus nerka	20	13	2.8	8.0	1.1	Brett et al. (1969)
Acipenser transmontanus	20	30	3.0^{1}	14.9^{1}	3.8^{1}	Hung and Lute (1987)
Acipenser fulvescens						
Growth-ration experiment	17.5	8	1.6	13.2	2.6	
56-day food consumption	17.5	9		13.2	2.6	
maximum				32		
average				10		
12-day food consumption	17.5	6				
feeding once per day				7.4 ± 0.8	2.4	
feeding twice per day				12.8±1.6	1.6	
28-day maximum growth rate,						
food consumption and size						
(1 feeding/d)	17.5	10-1322		9.4 ± 2.2	1.8 ± 0.2	

¹Values corrected by caloric ratios of feeds for use of prepared feeds in that study.

References

- Allen, R. J., and R. J. Wootton. 1982. The effect of ration and temperature on the growth of the three-spined stickleback, *Gasterosteus aculeatus*. Journal of Fish Biology 20:409-522.
- Beamish, F. W. H. 1970. Oxygen consumption of largemouth bass, *Micropterus salmoides*, in relation to swimming speed and temperature. Canadian Journal of Zoology 48:1221-1228.
- Beamish, F. W. H., and E. A. Trippel. 1990. Heat increment: A static or dynamic dimension in bioenergetic models. Transactions of the American Fisheries Society 119:649-661.
- Beamish, F. W. H., J. Jebbink, A. Rossiter, and D. L. G. Noakes. 1996. Growth strategy of juvenile lake sturgeon (*Acipenser fulvescens*) in a northern river. Canadian Journal of Fisheries and Aquatic Sciences 53:481-489.
- Brett, J. R. 1979. Environmental factors and growth. Pages 599-675 *in* W. S. Hoar, D. J. Randall, and J.R Brett, editors. Fish physiology, Volume 8: Bioenergetics and growth. Academic Press, New York, New York.
- Brett, J. R., and N. R. Glass. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. Journal of the Fisheries Research Board of Canada 30:379-387.
- Brett, J. R., and T. D. D. Groves. 1979.
 Physiological energetics. Pages 280-352 in
 W. S. Hoar, D. J. Randall, and J. R. Brett, editors. Fish physiology, Volume 8: Bioenergetics and growth. Academic Press, New York, New York.

- Brett, J. R., J. E. Shelbourn, and C. T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. Journal of the Fisheries Research Board of Canada 26:2363-2394.
- Brousseau, C. D. 1987. The lake sturgeon (Acipenser fulvescens) in Ontario.
 Proceedings of a workshop on the lake sturgeon (Acipenser fulvescens). Ontario Ministry of Natural Resources, Fisheries Technical Report 23, Toronto.
- Diana, J. S. 1979. The feeding patterns and daily ration of a top carnivore, the northern pike (*Esox lucius*). Canadian Journal of Zoology 57:2121-2127.
- Diana, J. S. 1983. An energy budget for northern pike. Canadian Journal of Zoology 61:1968-1975.
- Diana, J.S. 1995. Biology and ecology of fishes. Biological Sciences Press, Carmel, Indiana.
- Elliott, J. M. 1975. The growth rate of brown trout (*Salmo trutta* L.) fed on reduced rations. Journal of Animal Ecology 44:823-842.
- Fortin, R., J. R., Mongeau, G. Desjardins, and P. Dumont. 1993. Movements and biological statistics of lake sturgeon (*Acipenser fulvescens*) populations from the St. Lawrence and Ottawa River system, Quebec. Canadian Journal of Zoology 71:638-650.
- Fortin, R., P. Dumont, and S. Guenette. 1996. Determinants of growth and body condition of lake sturgeon (*Acipenser fulvescens*). Canadian Journal of Fisheries and Aquatic Sciences 53:1150-1156.
- Goolish, E. M., and I. R. Adelman. 1984. Effects of ration size and temperature on the growth of juvenile common carp (*Cyprinus carpio L.*). Aquaculture 36:27-35.

- Hay-Chmielewski, E. M. 1987. Habitat preference and movement patterns of the lake sturgeon (*Acipenser fulvescens*) in Black Lake, Michigan. Michigan Department of Natural Resources, Fisheries Research Report 1949, Ann Arbor.
- Hochachka, P. W., and G. N. Somero. 1984. Biochemical adaptation. Princeton University Press, Princeton, New Jersey.
- Hogendoorn, H. 1983. Growth and production of the African catfish, *Clarias lazera* (C and V.). III. Bioenergetic relations of body weight and feeding level. Aquaculture 35:1-17.
- Houston, J. J. 1987. Status of the lake sturgeon, *Acipenser fulvescens*, in Canada. Canadian Field Naturalist 101:171-185.
- Hung, S. S. O., and P. B. Lutes. 1987. Optimum feeding rate of hatchery-produced juvenile white sturgeon (*Acipenser transmontanus*) at 20° C. Aquaculture 65:307-317.
- Hung, S. S. O., P. B. Lutes, A. A. Shqueir, and F. S. Conte. 1993. Effect of feeding rate and water temperature on growth of juvenile white sturgeon (*Acipenser transmontanus*). Aquaculture 115:297-303.
- Niimi, A. J., and F. W. H. Beamish. 1974. Bioenergetics and growth of largemouth bass (*Micropterus salmoides*) in relation to body weight and temperature. Canadian Journal of Zoology 52:447-456.
- Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, England.
- Power, M., and R. S. McKinley. 1997. Latitudinal variation in lake sturgeon size as related to the thermal opportunity for growth. Transactions of the American Fisheries Society 126: 549-558.

- Priede, I. G., and F. G. T. Holliday. 1980. The use of a new tilting respirometer to investigate some aspects of metabolism and swimming activity of the plaice (*Pleuronectes platessa L.*). Journal of Experimental Biology 85:295-309.
- Probst, R. T., and E. L. Cooper. 1954. Age, growth, and production of lake sturgeon (*Acipenser fulvescens*) in Lake Winnebago, Wisconsin. Transactions of the American Fisheries Society 84:989-1000.
- Ricker, W. E. 1971. Methods of assessment of fish production in fresh waters. IBP Handbook No. 3. Blackwell Scientific Publications, Oxford, England.
- Seelbach, P. W. 1987. Smolting success of hatchery-raised steelhead planted in a Michigan tributary of Lake Michigan. North American Journal of Fisheries Management 7:232-237.
- Smagula, C. M., and I. R. Adelman. 1982. Day-to-day variation in food consumption by largemouth bass. Transactions of the American Fisheries Society 111:543-548.
- Soofiani, N. M., and A. D. Hawkins. 1982. Energetic costs at different levels of feeding in juvenile cod, *Gadus morhua L*. Journal of Fish Biology 21:577-592.
- Sullivan, K. M., and K. L. Smith. 1982. Energetics of sablefish, Anoplopoma fimbria, under laboratory conditions. Canadian Journal of Fisheries and Aquatic Sciences 39:1012-1020.
- Tandler, A., and F. W. H. Beamish. 1980. Specific dynamic action and diet in largemouth bass, *Micropterus salmoides* (Lacépède). Journal of Nutrition 110:750-764.

- Tyler, A. V., and R. S. Dunn. 1976. Ration, growth, and measures of somatic and organ condition in relation to meal frequency in winter flounder, *Pseudopleuronectes americanus*, with hypotheses regarding population homeostasis. Journal of the Fisheries Research Board of Canada 33:63-75.
- Webb, P. W., and J. R. Brett. 1973. Effects of sublethal concentrations of sodium pentachlorophenate on growth rate, food conversion efficiency and swimming performance in underyearling sockeye salmon (*Oncorhynchus nerka*). Journal of the Fisheries Research Board of Canada 30:499-507.

- Wilkinson, L. 1990. SYSTAT: the System for Statistics. SYSTAT Inc., Evanston, Illinois.
- Williams, S. F., and R. S. Caldwell. 1978. Growth, food conversion, and survival of the English sole (*Parophyrs vetulus Gerard*) at five temperatures and rations. Aquaculture 15:129-139.
- Woiwoode, J. G., and I. R. Adelman. 1991. Effects of temperature, photoperiod, and ration size on growth of hybrid striped bass x white bass. Transactions of the American Fisheries Society 120:217-229.

Richard D. Clark, Jr., Reviewer Alan D. Sutton, Graphics Deborah L. MacConnell, Desktop Publishing Ellen S. Grove, Word Processor

Approved by Paul W. Seelbach