Effect of Feeding Frequency on Growth, Food Conversion Efficiency, and Meal Size of Juvenile Atlantic Sturgeon and Shortnose Sturgeon

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Effect of Feeding Frequency on Growth, Food Conversion Efficiency, and Meal Size of Juvenile Atlantic Sturgeon and Shortnose Sturgeon

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Abstract.—We examined the importance of feeding frequency on the growth, conversion efficiency, and meal size of juvenile Atlantic sturgeon *Acipenser oxyrinchus* and shortnose sturgeon *A. brevirostrum*. Trials by species were completed consecutively after the fish reached 8 months of age. For both trials, 12 tanks were each stocked with five fish. The feed ration was set at 3% of the tank biomass per day and was adjusted weekly according to increases in tank total biomass. Tanks were randomly chosen to be fed one, four, or eight times during each 24-h period. We found differences in specific growth rate (SGR), corrected food conversion efficiencies (CFCE), and meal size among species. Overall, Atlantic sturgeon grew better, ate more, and exhibited greater feeding efficiencies than shortnose sturgeon, regardless of feeding frequency. Atlantic sturgeon exhibited SGRs of 2.3%/d and conversion efficiencies of 100%. Shortnose sturgeon exhibited growth rates of 0.7–1.6%/d and conversion efficiencies of 42–93%. Only shortnose sturgeon fed four times per day (SGR, 1.6%/d; CFCE, 93%) exhibited results similar to those of Atlantic sturgeon. Atlantic sturgeon had similar growth and feeding efficiencies in all feeding frequency regimes. Shortnose sturgeon fed once per day had significantly lower growth rates (0.7%/d) and feeding efficiencies (42%) than those fed four and eight times per day.

Populations of Atlantic sturgeon *Acipenser oxyrinchus* in North America once supported major commercial harvesting (Smith and Dingley 1984). Currently, the U.S. Atlantic sturgeon fishery is under a moratorium. In Canada, however, Atlantic sturgeon populations continue to support a small fishery. In both Canada and the USA, shortnose sturgeon *A. brevirostrum* are protected and are no longer harvested commercially. These conditions have led to a worldwide decrease in availability of products, particularly caviar, and have created an interest in sturgeon aquaculture (Smith and Dingley 1984; Logan et al. 1995). Although both Atlantic and shortnose sturgeon are potential candidates for aquaculture in North America, little work has been conducted to develop rearing protocols. Food delivery strategies for juveniles are key to their successful culture,either as a food fish or for enhancement programs.

Feeding frequency is an important factor affecting the growth of cultured fish. The effects of feeding frequency on fish growth and food conversion efficiency have been studied for several species (e.g., Andrews and Page 1975; Jarboe and Grant 1997; Whalen et al. 1998; Lee et al. 2000). Results of feeding frequency studies are highly variable among and within species because regimes are age and size dependent. No single conclusion can be drawn on the effects of increasing feeding frequency.

For example, juvenile Japanese flounder (also known as olive flounder) *Paralichthys olivaceus* (3.5 g) that are fed to satiation two or three times per day exhibit better growth and feed efficiency than those fed once daily or once every 2 days (Lee et al. 2000). Juvenile yellowtail flounder *Pleuronectes ferrugineus* (6.8 g) also exhibited increased growth rates and food conversion ratios as frequency of feeding was increased (Whalen et al. 1998). Channel catfish *Ictalurus punctatus* (53 g) grew more slowly when fed to satiation once per day then when fed two or four times per day; however, there were no differences in food conversion (Andrews and Page 1975). No differences in overall growth or feed conversion were exhibited by small channel catfish (26 g) fed a 3% ration in one or two feedings per day (Jarboe and Grant 1997). However, larger channel catfish (219 g) fed twice per day had greater weight gain, specific growth rates (SGRs), and feed conversion than those fed once per day.

In this study, we examined the effects of feeding frequency on the growth and food conversion ef-

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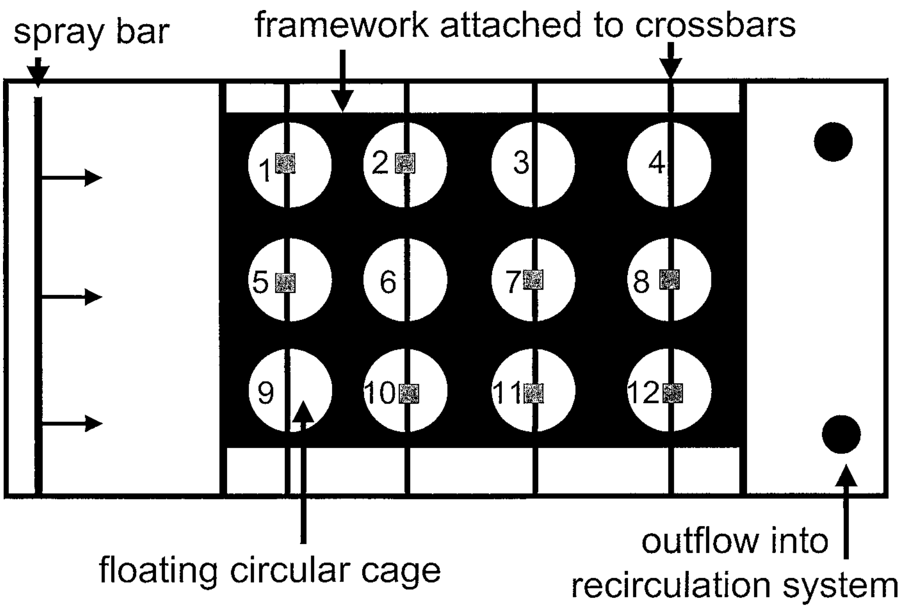

FIGURE 1.—Schematic of experimental design. Floating cages (diameter, 30 cm) were suspended from crossbars in a larger fiberglass lobster tank (240 × 120 × 40 cm). Fish in tanks 3, 4, 6, and 9 were fed once per day, fish in tanks 1, 8, 10, and 11 four times per day, and fish in tanks 2, 5, 7, and 12 eight times per day. Sweeny F7 vibratory feeders (gray squares) were hung above the tanks in which feeding took place four or eight times per day.

ficiency of juvenile Atlantic and shortnose sturgeon. By examining two closely related sturgeon species, we were able to gain an interesting perspective on species-dependent requirements for feeding frequencies. Identification of feeding frequencies that lead to good growth performance and food conversion efficiency should provide much needed information for culture and conservation programs.

Methods

The sturgeons used in these experiments were reared at the University of New Brunswick, Saint John. Twelve circular floating cages (diameter = 30 cm, height of water = 15 cm, volume = 3.4 L/cage, mesh size = 0.64 cm square) were held in a framework placed in a larger lobster tank (Legay fiberglass lobster tank measuring 240 × 120 × 40 cm; Figure 1). The lobster tank was a component of a larger recirculation system (1,850 L of water) and had 2.3 total system turnovers of new water every 24 h. Temperature (°C) and dissolved oxygen levels (mg/L) were monitored and recorded daily for the duration of the experiment. Water temperature was maintained at 14.5 ± 0.08°C (average ± SE). Dissolved oxygen levels were 85.4% ± 5.3% (average ± SE). The floating cages and lobster tank were cleaned by siphoning before feeding each morning. Although undigested food did not collect inside the floating cages, small amounts would collect outside them within the framework and in the lobster tank. Daily siphoning helped maintain water quality.

Each floating cage was randomly assigned to one of three feeding frequency regimes that were implemented at equal intervals over a 24-h period: one, four, or eight feedings (Figure 1). There were four replicates per feeding regime. Five 8-month-old sturgeon were placed into randomly chosen tanks (shortnose sturgeon, 28.3 ± 0.25 g; Atlantic sturgeon, 28.2 ± 0.42 g). We ran the experiment on the two species consecutively. The experiment was first run on shortnose sturgeon (11 February–20 March 2000) then on Atlantic sturgeon (24 March–1 May 2000). This order was chosen so we could compare fish of similar size and age. These species spawn at different times of the year, shortnose sturgeon in May and Atlantic sturgeon in July.

We chose a daily fixed ration of 3% of body weight per day (bw/d), based on feeding practices used in the sturgeon aquaculture facility at the University of New Brunswick, Saint John. Those tanks being fed once per day received the entire 3% bw/d ration at one feeding, whereas for those fed four and eight times per day the 3% bw/d ration was divided among the feedings. At this ration, the majority of feed offered was consumed and substantial growth rates were maintained. Fish were fed Moore–Clark Nutra Plus Number 3 crumble. All fish in each tank were weighed weekly, and the ration levels were adjusted as necessary. Daytime feedings were presented by hand. Regimes (four and eight times) that required night feedings were completed with automated feeders (Sweeny F7 vibratory feeder).

All statistical analyses were completed by using SAS for Windows (SAS Institute 1990). We tested all data for normality by using PROC UNIVARIATE (SAS Institute 1990) and tested the homogeneity of variances by using an F_{max} test (Sokal and Rohlf 1981).

Before any further analyses were completed, a two-way analysis of variance (ANOVA) was run on the mean weight (g) per tank to confirm that there were no significant differences between species or feeding frequency regimes at the start of each experiment. This ensured that between-experiment comparisons were appropriate. Two-way ANOVAs were completed on tank means to determine the effects of feeding frequency regime (one, four, or eight times per day) and species (shortnose or Atlantic sturgeon) on SGR, corrected food conversion efficiency (CFCE), meal size, and relative coefficient of variation (CV) of weight. If a significant first-order interaction was detected, a one-way ANOVA was completed on cell means (e.g., shortnose sturgeon fed once per day constituted a cell mean or experimental group) to examine differences across all experimental treatment groups (Zar 1996). By taking this approach of completing one-way ANOVAs on cell means, we compared all experimental treatment groups: Atlantic sturgeon fed once per day (A1), Atlantic sturgeon fed four times per day (A4), Atlantic sturgeon fed eight times per day (A8), shortnose sturgeon fed once per day (S1), shortnose sturgeon fed four times per day (S4), and shortnose sturgeon fed eight times per day (S8). All effects were tested at an α-level of 0.05. A posteriori comparisons of cell means (experimental treatment groups) were completed by using Tukey's honestly significant difference test.

We calculated SGR (%/d) with the following equation:

$$\mathrm{SGR} = 100 \cdot [(\log_e \mathrm{Wt}_f - \log_e \mathrm{Wt}_i)/\Delta t], \tag{1}$$

where Wt_f is final weight, Wt_i is initial weight, and Δt is the duration of the experiment (Stickney 1994).

Once per week, the amount of food eaten during one feeding was determined for each tank. This was completed at the first feeding of the day because fish in the single daily feeding treatments were fed in the morning. An insert was placed in each tank so that uneaten food was not pushed from the cage by movement of the fish. Fish were allowed to eat for 15 min. This period of time was chosen on the basis of laboratory observations that feeding activity ceased within 15 min after food was offered. Afterward, any uneaten food was siphoned out of the cage and dried for 24 h at 60°C in an oven. Dried food was weighed and the percentage of food offered that was eaten was calculated. This correction factor was used to determine the total amount of food ''eaten'' each week. The corrected feed conversion efficiency (CFCE, %) was calculated for each cage over the entire experiment. Corrected food conversion efficiency was calculated with the following equation:

$$\mathrm{CFCE} = 100 \cdot (1/\mathrm{FCR}), \tag{2}$$

where FCR is the corrected amount of food ingested or the amount of feed eaten divided by the weight gain of the fish in the tank (adapted from Stickney 1994).

The amount of food left uneaten at one feeding per week for each tank was also used to calculate meal size (% consumed per feeding) for each feeding frequency and species. The percentage of food consumed per feeding was calculated for each cage over the entire experiment as 100 × (amount of food offered − amount uneaten)/(amount of food offered).

A two-way ANOVA run on the CVs of the average weight per tank at stocking revealed significant differences from the start of the experiment. The CV of weight (%) was calculated with the following equation:

$$\mathrm{CV} = 100 \cdot (\mathrm{SD}/\text{average weight of tank}), \tag{3}$$

where SD = the standard deviation of the tank's average weight. Because of these initial differences, we followed Wang et al. (1998) in examining the overall change in the CV or relative CV of the average tank weight.

Results

Specific Growth Rate

A significant interaction was detected when the effects of feeding frequency regime and species

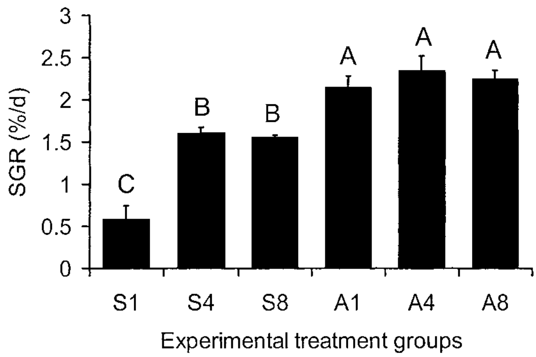

FIGURE 2.—Mean specific growth rate (SGR) of juvenile shortnose and Atlantic sturgeon fed one, four, or eight times per day. Treatment groups are designated according to the species (S = shortnose sturgeon, A = Atlantic sturgeon) and the frequency of feeding. A Tukey's honestly significant difference a posteriori test, which controls for type I errors, was performed across treatment groups. Values with different uppercase letters are significantly different at $\alpha = 0.05$.

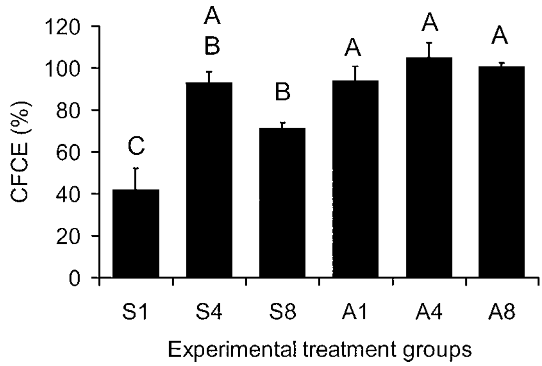

FIGURE 3.—Corrected food conversion efficiency (CFCE) of juvenile shortnose and Atlantic sturgeon fed one, four, or eight times per day. See Figure 2 for additional details.

on SGR were tested (two-way ANOVA; $P = 0.03$, $F = 8.29$, df = 2, 18). Therefore, we completed a one-way ANOVA on all cell means (Figure 2). Experimental treatment groups A1, A4, and A8 had significantly greater SGRs than did S1, S4, and S8. A1, A4, and A8 exhibited SGRs approaching 3%, whereas those for S1, S4, and S8 were 2% or less. Moreover, the SGR for S1 was significantly lower than those for S4 or S8.

Corrected Feed Conversion Efficiency

The effects of feeding frequency regime and species on CFCE also showed a significant interaction (two-way ANOVA; $P = 0.007$, $F = 11.02$, df = 2, 18). We then ran a one-way ANOVA on cell means, which allowed us to compare the six experimental treatment groups. Experimental treatment groups A1, A4, and A8 had similar CFCEs (Figure 3). The greatest CFCE exhibited by shortnose sturgeon treatment groups was 93.0 $\pm$ 5.3%, seen in fish fed four times per day (S4), which was not significantly different from that for other regimes except for S1, which was significantly less than for all other groups.

Meal Size (Percent Consumed per Feeding)

A significant interaction was detected when we tested the effects of feeding frequency regime and species on percent consumed per feeding (two-way ANOVA; $P = 0.004$, $F = 7.47$, df = 2, 18). A one-way ANOVA completed on cell means revealed no significant differences in percent consumed per feeding among treatment groups A1, A4, and A8 (Figure 4). Fish in the S1 treatment, however, ate significantly less per feeding than did all other groups.

Relative Coefficient of Variation

There was no significant effect of feeding frequency and species on relative CV (two-way ANOVA; $P = 0.25$, $F = 1.48$, df = 2, 18).

Discussion

It is important to determine the appropriate feeding schedule and ration to minimize cost of production while maximizing growth (Goddard 1996). This is not a simple problem. Factors such as physical environment also play a role in what feeding schedules are appropriate (Stickney 1994; Goddard 1996). No single feeding regime can

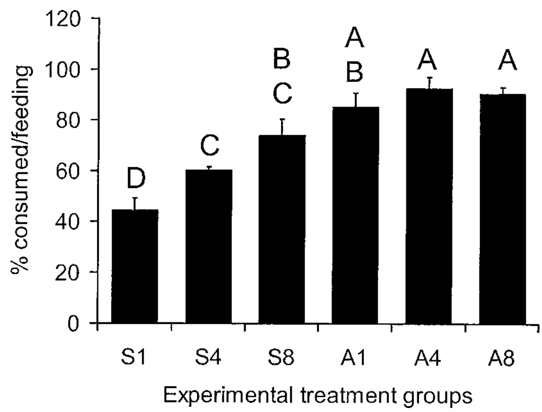

FIGURE 4.—Mean percentage of food consumed per meal by juvenile shortnose and Atlantic sturgeon fed one, four, or eight times per day.

maintain maximal growth and minimal food wastage throughout the life cycle of a fish. Our results suggest that a 3% ration for shortnose and Atlantic sturgeon should be fed four to eight times per day at equal intervals over 24 h.

Because of its effects on growth, feeding frequency has been examined for many different fish species (Andrews and Page 1975; Grayton and Beamish 1977; Marian et al. 1981; Buurma and Diana 1994; Lee et al. 2000). Results of these studies are widely variable because different feeding frequency regimes were applied among fish species, within a fish species over time, at different temperatures, different water qualities, and in different culture systems. Andrews and Page (1975) found that growth of channel catfish (mean weight, 53 g) was not different in fish hand-fed to satiation four times per day instead of two times per day, but a single feeding per day did negatively affect growth. When walking catfish *Clarias fuscus* (mean weight, 37.4 g) were fed at a fixed ration of 3% bw/d, three feedings per day produced significantly more growth than feeding once per day (Buurma and Diana 1994). Channel catfish on a 2% ration grew faster as feeding frequency increased (Greenland and Gill 1979). Juvenile fossil catfish (also known as stinging catfish) *Heteropneustes fossilis* showed significantly greater growth when fed once or twice a day to satiation than when fed once in 2 or 3 days (Marian et al. 1981).

The results of this study suggest that both shortnose and Atlantic sturgeon could be fed four times per day to minimize labor while maximizing growth. However, we anticipate that sturgeon cultured in temperate zones of North America will have to be grown in recirculating systems to maintain growth rates year round. To reduce the ammonia burden on recirculating systems, we may need to feed at a greater frequency (e.g., eight times per day). In this study, however, increasing the frequency from four to eight times per day did not significantlyaffect growth rates for either species. Other studies have found that general increases in growth with increasing frequency of feeding have an upper limit, above which increasing feeding frequency no longer improves growth (Andrews and Page 1975; Grayton and Beamish 1977; Thia-Eng and Seng-Keh 1978; Charles et al. 1984; Wang et al. 1998; Liu and Liao 1999; Lee et al. 2000). Nonetheless, unlike shortnose sturgeon, Atlantic sturgeon growth was comparable in all feeding frequency regimes. Walking catfish fed at fixed ration of 3% showed responses similar to those of shortnose sturgeon when feeding frequency was reduced to once per day (Buurma and Diana 1994).

In comparing the two species, we found that Atlantic sturgeon responded somewhat better to all feeding regimes, their growth rates being significantly greater than those of shortnose sturgeon. Feeding frequency has been suggested to be both species- and size-specific (Windell 1978; Goddard 1996). The results of these experiments suggest that Atlantic sturgeon have the ability to maintain high growth rates over a much wider range of feeding frequencies than do shortnose sturgeon. The differences in performance of these closely related species provide further evidence that we should examine the effects of feeding frequency on a species by species basis.

Atlantic sturgeon were more efficient than shortnose sturgeon at food conversion in all feeding frequency regimes. Atlantic sturgeon had CFCEs approaching or exceeding100% in all feeding frequencies, whereas only the shortnose sturgeon fed four times daily approached this level. This indicates that Atlantic sturgeon have greater conversion efficiency and are able to use the food consumed with equal efficiency regardless of feeding frequency. This ability has also been exhibited by walleye *Sitzostedion vitreum* (Phillips et al. 1998), 26-g channel catfish (Jarboe and Grant 1997), and hybrid sunfish (male green sunfish *Lepomis cyanellus* and female bluegill *L. macrochirus*; Wang et al. 1998).

The 3% ration used in this study was higher than those used in other Atlantic sturgeon experiments. Kelly and Arnold (1999) found when rearing Atlantic sturgeon (60 g) at a temperature of 15°C that growth was best at their highest ration of 1.5%. However, the upward trend in growth as ration increased led them to hypothesize that maximum growth would occur at some ration greater than 1.5%. Jodun et al. (2002), feeding Atlantic sturgeon a ration of 2.5% to examine effects of density on growth, survival, and feed conversion, found conversion efficiencies ranging from 38% to 52%. Atlantic sturgeon fed a ration of 3% in our experiment consumed a majority of the food offered and maintained high growth rates (2.3%/d) and conversion efficiencies (100%). Differences in conversion efficiencies observed by Jodun et al. (2002) and in the current study may reflect differences in initial fish size—368.7 g in the study of Jodun et al. (2002) compared with 28.2 g in this study.

The ability of Atlantic sturgeon to efficiently utilize food despite differences in feeding frequency indicates that a still greater ration may increase their growth and conversion efficiency. Shortnose sturgeon fed a 3% ration once per day exhibited poor growth and conversion efficiencies because they were not able to consume most of the feed offered to them.

The small effect of reducing the feeding frequency on the growth and food conversion efficiency of Atlantic sturgeon indicates they can consume and efficiently utilize more of their entire daily ration at a single feeding than can shortnose sturgeon. The appetite of a fish species dictates the amount of food that will be eaten before a fish ceases to feed voluntarily (Wootton 1990). When shortnose sturgeon were presented with the entire 3% ration in one feeding, food was well in excess of their appetite. Atlantic sturgeon had a greater appetite than shortnose sturgeon and consequently ate larger amounts in all feeding frequencies. Only shortnose sturgeon fed eight times daily were able to consume amounts comparable to that by any Atlantic sturgeon groups. Consequently, our results suggest the need for further investigation into ration size and its effect on feeding frequency for these species.

In some fish, decreases in CV have been observed as the frequency of feedings increased (Jobling 1983; Wang et al. 1998). When fish are reared together under hatchery conditions, dominance hierarchies may be formed (Thomassen and Fjaera 1996). In studies where increasing feeding frequency decreased the CV, this effect was suggested to be a result of decreased competition. When food is abundant, effects of size hierarchies can be minimized (Slaney and Northcoate 1974). Walleye fingerlings (28.2 g) fed a fixed ration over 3 or 30 feedings per day exhibited similar CVs of weight and length (Phillips et al. 1998). Our results suggest that a 3% ration provided sufficient food for the juvenile sturgeon because no differences in relative CV were observed.

Conclusions

Our study indicates that feeding regimes of even closely related species are species specific. We found significant differences in mean SGR, CFCE, and meal size between these two sturgeon species. Feeding frequency did not significantly affect Atlantic sturgeon, whereas shortnose sturgeon fed once per day grew very little and had lower CFCEs than did those fed more frequently. Overall, Atlantic sturgeon fed at all regimes exhibited better growth than even the best results exhibited by shortnose sturgeon. The 3% ration provided sufficient food for the fish in this study; however, further investigation on the relationship between feeding frequency and different rations should be explored. This study provides much needed information pertaining to the culture of juveniles of these two species. Development of feeding strategies for these two species are key to their successful culture. Culture of these protected sturgeon species will be necessary to provide products that are in worldwide demand and, if necessary, fish for stocking programs.

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References

Andrews, J. W., and J. W. Page. 1975. The effects of frequency of feeding on culture of catfish. Transactions of the American Fisheries Society 2:317–321.

Buurma, B. J., and J. S. Diana. 1994. Effects of feeding frequency and handling on growth and mortality of cultured walking catfish *Clarias fuscus*. Journal of the World Aquaculture Society 25:175–182.

Charles, P. M., S. M. Sebastian, M. C. V. Raj, and M. P. Marian. 1984. Effects of feeding frequency on growth and food conversion of *Cyprinus carpio* fry. Aquaculture 40:293–300.

Goddard, S. 1996. Feed management in intensive aquaculture. Chapman and Hall, New York.

Grayton, B. D., and F. W. H. Beamish. 1977. Effects of feeding frequency on food intake, growth and body composition of rainbow trout (*Salmo gairdneri*). Aquaculture 11:159–172.

Greenland, D. C., and R. L. Gill. 1979. Multiple daily feedings with automatic feeders improve growth and feed conversion rates of channel catfish. Progressive Fish-Culturist 41:151–153.

Jarboe, H. H., and W. J. Grant. 1997. The influence of feeding time and frequency on the growth, survival, feed conversion, and body composition of channel catfish, *Ictalurus punctatus*, cultured in a three-tier, closed, recirculating raceway system. Journal of Applied Aquaculture 7:43–52.

Jobling, M. 1983. Effect of feeding frequency on food intake and growth of Arctic charr, *Salvelinus alpinus* (L.). Journal of Fish Biology 23:177–185.

Jodun, W. A., M. J. Millard, and J. Mohler. 2002. The effect of rearing density on growth, survival, and feed conversion of juvenile Atlantic sturgeon. North American Journal of Aquaculture 64:10–15.

Kelly, J. L., and D. E. Arnold. 1999. Effects of ration and temperature on growth of age-0 Atlantic sturgeon. North American Journal of Aquaculture 61: 51–57.

Lee, S-M., S. H. Cho, and D-J. Kim. 2000. Effects of feeding frequency and dietary energy level on growth and body composition of juvenile flounder, *Paralichthys olivaceus* (Temminck & Schlegel). Aquaculture Research 31:917–921.

Liu, F-G., and I. C. Liao. 1999. Effect of feeding regime on the food consumption, growth, and body composition in hybrid striped bass *Morone saxatilis* × *M.chrysops*. Fisheries Science 65:513–519.

Logan, S. H., W. E. Johnston, and S. I. Doroshov. 1995. Economics of joint production of sturgeon (*Acipenser transmontanus* Richardson) and roe for caviar. Aquaculture 130:299–316.

Marian, M. P., and A. G. Ponniah, R. Pitchairaj, and M. Narayanan. 1981. Effect of feeding frequency on surfacing activity and growth in the air-breathing fish, *Heteropneustes fossilis*. Aquaculture 26:237–244.

Phillips, T. A., R. C. Summerfelt, and R. D. Clayton. 1998. Feeding frequency effects on water quality and growth of walleye fingerlings in intensive culture. Progressive Fish-Culturist 60:1–8.

SAS Institute. 1990. SAS/STAT user's guide, version 6, edition 4, volume 2. SAS Institute, Cary, North Carolina.

Slaney, P. A., and T. G. Northcoate. 1974. Effects of prey abundance on density and territorial behaviour of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. Journal of the Fisheries Research Board of Canada 31:1201–1209.

Smith, T. I. J., and E. K. Dingley. 1984. Review of biology and culture of Atlantic sturgeon (*Acipenser oxyrhynchus*) and shortnose sturgeon (*A. brevirostrum*). Journal of the World Mariculture Society 15: 210–218.

Sokal, R. R., and F. J. Rohlf. 1981. Pages 403–405 *in* S. Cotter, editor. Biometry. Freeman, New York.

Stickney, R. R. 1994. Principles of aquaculture. Wiley, New York.

Thia-Eng, C., and T. Seng-Keh. 1978. Effects of feeding frequency on the growth of young estuary grouper, *Epinephlus tauvina* (Forskal), cultured in floating net-cages. Aquaculture 14:31–47.

Thomassen, J. M., and S. O. Fjaera. 1996. Studies of feeding frequency for Atlantic salmon (*Salmo salar*). Aquacultural Engineering 15:149–157.

Wang, N., R. S. Hayward, and N. B. Noltie. 1998. Effect of feeding frequency on food consumption, growth, size variation, and feeding pattern of age-0 hybrid sunfish. Aquaculture 165:261–267.

Whalen, K. S., J. A. Brown, C. C. Parish, S. P. Lall, and J. S. Goddard. 1998. Frequency of feeding in juvenile yellowtail flounder (*Pleuronectes ferruginus*): possible regimes for grow-out. Bulletin of the Aquaculture Association of Canada 2:25–26.

Windell, J. T. 1978. Digestion and daily rations of fishes. Pages 151–173 *in* S. D. Gerking, editor. Ecology of freshwater fish production. Blackwell Scientific Publications, London.

Wootton, R. J. 1990. Ecology of teleost fishes. Chapman and Hall, London.

Zar, J. H. 1996. Biostatistical analysis, 3rd edition. Prentice-Hall, Englewood Cliffs, New Jersey.