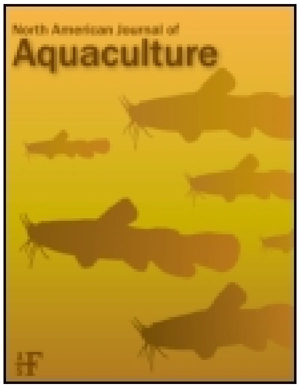

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ARTICLE

Feeding Rate and Frequency Affect Growth of Juvenile Atlantic Spadefish

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Abstract
The Atlantic spadefish *Chaetodipterus faber* is an excellent candidate for aquaculture development, but success will depend on the identification of proper feeds and feeding regimens for this species. Accordingly, we evaluated the growth performance of juvenile Atlantic spadefish (3.60 ± 0.03 g [mean ± SE]) fed at rates of 3, 5, or 7% of body weight (BW) per day, either in a single feeding (1×) or in three equal feedings (3×). Weight gain, specific growth rate, feed conversion ratio, and feed intake were significantly affected by both feeding rate and frequency. Weight gain and the specific growth rate increased significantly with feeding rate, and growth was generally greater and more efficient in the 3× groups than in the 1× groups. Fish fed at higher feeding rates accumulated significantly more lipid within the body and had associated decreases in moisture, protein, and ash content, but carcass composition was unaffected by feeding frequency. We suggest that the growth of juvenile Atlantic spadefish can be optimized when they are fed at 5–7% BW/d in three daily feedings, with 7% BW/d yielding the greatest, albeit slightly less efficient, growth.

The family Ephippidae comprises 20 species of omnivorous, deep-bodied, laterally compressed, marine and brackish fishes (Froese and Pauly 2010), including the Atlantic spadefish *Chaetodipterus faber*, the only ephippid present in waters of the western Atlantic Ocean (Robins and Ray 1986; Walker 1991). The life history and distribution of this species is not

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completely understood (Ditty et al. 1994), but it is known to inhabit coastal waters from the United States to southern Brazil, including the Gulf of Mexico (Hayse 1990) and Caribbean (Burgess 2002). Atlantic spadefish exploit a wide variety of ecosystems depending on life stage, including mangroves and salt marshes, nearshore waters, and offshore reefs (Robins and Ray 1986). Juveniles are generally found in estuaries and protected waters, whereas adults predominate near shore and offshore waters (Hayse 1990). Adult Atlantic spadefish often congregate in large schools in coastal waters, and in the United States they support a popular recreational fishery (Robins and Ray 1986; Bohlke and Chaplin 1993). Wild individuals can reach 91 cm in total length (TL) and 9 kg in weight in tropical waters (Robins and Ray 1986).

The Atlantic spadefish is an excellent candidate for aquaculture development (Tucker and Jory 1991) because of its physical hardiness, ability to adapt well to confinement, good growth rates (Gaspar and Larez 1984), tolerance of low temperatures and salinities, lack of aggressive or cannibalistic behavior during both larviculture and grow out, and excellent flesh quality and consumer appeal (Bohlke and Chaplin 1993; Randall 1996). In addition to food fish culture, young spadefish may have ornamental potential (Gaspar 1995) because of their morphology and striking black and white coloration.

As is the case for any emerging aquaculture species, successful culture of Atlantic spadefish will depend, in part, on the identification of proper feeds and feeding regimens for this species. Among the different management practices that may maximize feeding and growth efficiency, feeding rate and feeding frequency have a crucial function in determining overall feed intake, growth, and waste outputs of fish (Silva et al. 2007). For example, sporadic feeding and low feeding rates may contribute to reduced growth as well as increased hunger, intraspecific aggression, and increased rate of cannibalism (Folkvord and Ottera 1993). Alternatively, frequent feeding and high feeding rates may lead to feed wastage, deteriorating water quality, reduced fish production, and ultimately greater production costs (Booth et al. 2008). Optimizing feeding frequency and feeding rate may minimize feed wastage and lead to improvement in water quality and greater size-class homogeneity (Dwyer et al. 2002; Tucker et al. 2006). Few feeding studies have been conducted with Atlantic spadefish, although cage culture has been investigated in Venezuela (Gaspar and Larez 1984; Robaina and Salaya 1993; Gaspar 2002). However, proper feeds and feeding strategies can vary with fish size, rearing system (Cho et al. 2003), and feed type (Chua and Teng 1978, 1982). Given the interest in developing intensive aquaculture methods for this species, we assessed the influence of feeding rate and feeding frequency on the growth performance of juvenile Atlantic spadefish reared in a land-based recirculation system.

METHODS

Juvenile Atlantic spadefish (3.60 ± 0.03 g [mean ± SE]; 7 fish/tank), obtained from the aquaculture program at the Virginia Seafood Agricultural Research and Extension Center (VSAREC), Hampton, were stocked into a recirculation system at the VSAREC, which consisted of twenty-four 10-L tanks, a fluidized KMT biofilter, 50-μm particle filter, and 50-W ultraviolet light unit (stand-alone Aquatic Habitats system, Aquatic Eco-Systems, Apopka, Florida). Fish were cultured under conditions presumed optimal for Atlantic spadefish (see water quality information below) and fed a commercially available feed (Otohime S2, Reed Mariculture, Campbell, California; guaranteed analysis: crude protein = 50% minimum, crude fat = 10% minimum, crude fiber = 3% maximum, crude ash = 16% maximum; average pellet size = 1.4 mm; floating feed) at 3, 5, or 7% of body weight (BW) per day, either in a single feeding (1×) or divided equally among three feedings (3×). The feeding frequencies were selected based on our estimation of minimal (1×) and maximal (3×) feeding effort likely to be expended in culturing juvenile Atlantic spadefish. Each feeding rate–feeding frequency treatment combination was randomly assigned to four replicate tanks ($n = 4$). Feeding rates were adjusted for growth every 10 d after group-weighing the fish by tank. Fish in the 1× treatments were fed at 1300 hours, whereas fish in the 3× treatments were fed at 0700, 1300, and 1900 hours. Uneaten pellets were not generally observed, but no attempts were made to remove or quantify uneaten feed.

Water temperature and dissolved oxygen (DO) were monitored daily with a YSI-85 Series dissolved oxygen meter (YSI, Yellow Springs, Ohio). Total ammonia-, nitrite-, and nitrate-nitrogen (spectrophotometric analysis, Hach, Loveland, Colorado), pH (YSI-pH100, YSI), and alkalinity (bromocresol green–methyl red titration method, Hach) were also measured once daily. Throughout the experiment, photoperiod was kept at a 12 h light :12 h dark cycle, tank inflow rates were maintained at 0.6 L/min, and water quality conditions were maintained as follows (mean ± SD): temperature = 28.9 ± 0.9°C, salinity = 27.1 ± 0.2 g/L, DO = 6.1 ± 0.6 mg/L, total ammonia nitrogen = 0.34 ± 0.08 mg/L, nitrite-nitrogen = 0.35 ± 0.13 mg/L, nitrate-nitrogen = 27.0 ± 3.6 mg/L, alkalinity = 140 ± 6 mg/L, and pH = 7.51 ± 0.02. Although the water quality optima for Atlantic spadefish culture are not known, the aforementioned ranges are consistent with environmental conditions in natural habitats where Atlantic spadefish occur in abundance (Robins and Ray 1986; Burgess 2002).

After 39 d of culture, the experiment was terminated and production performance was assessed. Standard metrics of production performance were calculated as follows:

$$\text{Weight gain (\%)} = 100 \times \frac{\text{average final weight} - \text{average initial weight}}{\text{average initial weight}}$$

$$\text{Feed conversion ratio (FCR)} = \frac{\text{average individual dry matter feed intake}}{\text{average individual weight gain}}$$

$$\text{Specific growth rate (SGR; \%BW/d)} = 100 \times \frac{\log_e(\text{average final weight}) - \log_e(\text{average initial weight})}{\text{days of feeding}}$$

$$\text{Feed intake (\%BW/d)} = 100 \times \frac{\text{average individual dry matter feed intake}}{(\text{initial individual weight} \times \text{final initial weight})^{0.5}/\text{days of feeding}}$$

Three fish per tank were randomly selected, euthanized with an overdose of tricaine methanesulfonate (MS-222; Finquel, Argent Chemical Laboratories, Redmond, Washington; immersion in a solution containing an excess of 200 mg/L until cessation of opercular movement), and frozen (−80°C).

Frozen carcass samples were packed in ice and transported (∼36 h in transit) to the Fisheries and Illinois Aquaculture Center (FIAC) in Carbondale, Illinois, where the samples were transferred to a −80°C freezer for storage before analysis for composition. Carcass samples were sectioned (∼1 cm thickness) and lyophilized (Freezone 6, Labconco, Kansas City, Missouri) to determine moisture content. Lyophilized samples were pulverized and pooled according to tank before determination of protein, ash, and lipid. Total lipid was determined gravimetrically following a chloroform–methanol extraction method modified from Folch et al. (1957). Ash content was determined gravimetrically after incineration in a muffle furnace for 4 h at 650°C. A LECO protein analyzer (FP-528, LECO, St. Joseph, Michigan) was used to determine protein content.

Although multiple fish were sampled from each tank, replicate tanks served as the experimental units for all statistical analyses ($n = 4$). As multiple weight measurements were taken from each experimental unit (i.e., tank) through time, it was determined that a repeated measures statistical analysis would be most appropriate for the fish weight data in order to reduce error variability arising from within-subject ("within-tank") effects. These data were analyzed by one-way, repeated measures two-way analysis of variance (ANOVA) within the mixed model framework of the Statistical Analysis System, version 9.1 (SAS Institute, Cary, North Carolina) to determine significance of differences among treatment means at each time point as well as whether the stress treatments differed in their overall effect on the response variables. All other data were analyzed by two-way ANOVA within the mixed model framework to determine the significance of feeding rate and feeding frequency as main effects, as well as to test for a significant interaction effect. When two-way ANOVA revealed significant main or interactive effects, Tukey's honestly significance difference (HSD) tests were used for pairwise comparison of means. In all cases, differences were considered significant at $P < 0.05$.

RESULTS

Juvenile Atlantic spadefish weight gain (feeding rate, $P < 0.001$; feeding frequency, $P < 0.001$; interaction, $P = 0.002$), SGR (feeding rate, $P < 0.001$; feeding frequency, $P < 0.001$; interaction, $P = 0.072$), FCR (feeding rate, $P = 0.004$; feeding frequency, $P < 0.001$; interaction $P = 0.288$), and feed intake (feeding rate, $P < 0.001$; feeding frequency, $P = 0.024$; interaction, $P = 0.036$) were significantly affected by both feeding rate and frequency. Fish weight increased significantly over the course of the 39-d experiment, with treatment groups becoming significantly distinct from one another by 20 d (Figure 1). Weight gain and SGR increased significantly with feeding rate (Figure 2). Regardless of feeding rate, growth was generally greater and more efficient in the 3× groups than in the 1× groups. The growth-enhancing effect of greater feeding frequency was particularly evident within the 7% BW treatment. Feeds were offered at specific levels, and feed intake varied expectedly with feeding rate (Figure 2). Although feeding rates were constant within individual rate treatments, feed intake expressed as a percent of body weight was elevated among fish in the 3× group fed at 7% BW relative to the 1× group. Carcass proximate composition was affected by feeding rate, but not by feeding frequency (Table 1). Spadefish fed at higher feeding rates accumulated significantly more lipid within the body and had an associated decrease in moisture, protein, and ash content. No mortalities or moribund fish were observed over the course of the study.

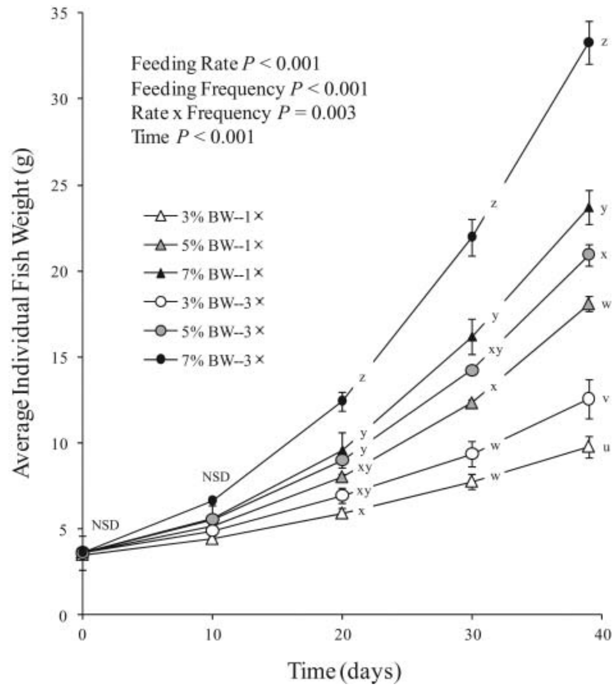

FIGURE 1. Average individual weight gain of juvenile Atlantic spadefish fed at 3, 5, or 7% of body weight (BW) per day in single (1×) or multiple (3×) feedings. Each data point represents the treatment combination mean ± SE. Data points at a given time point with common letters are not significantly different ($P > 0.05$). P-values generated by a two-way repeated measures ANOVA that assessed feeding rate and frequency as main effects are also provided; NSD indicates no significant difference between means at a time point.

DISCUSSION

Naturally, feeding rate affects the growth of fishes: increasing feeding rate increases the availability of resources (e.g., amino acids, structural lipids, energy) for growth, and weight gain is

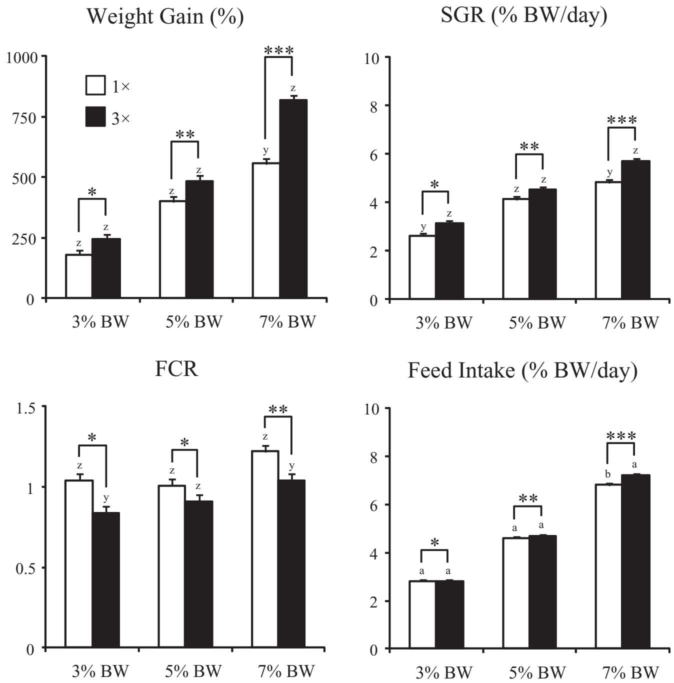

FIGURE 2. Growth performance of juvenile Atlantic spadefish fed at 3, 5, or 7% of body weight (BW) per day in single (1×) or multiple (3×) feedings. Bars represent least-squares means; error bars represent pooled SE. Significant differences between feeding frequencies within a feeding rate are indicated by different letters; significant differences among feeding rates are indicated by different numbers of asterisks ($P < 0.05$).

typically greater among fish at higher feeding rates. However, if any of the required elements for somatic growth (e.g., certain amino acids or phospholipids) become limiting or if nutrient intake simply exceeds that which can be used according to the maximum intrinsic growth rate of the fish, surplus resources will be lost via increased fecal losses or stored as glycogen or neutral lipid deposits within the hepatic, muscular, and adipose tissues (Jobling 1994). In turn, carcass levels of energy storage products and FCR will increase over time. Our data illustrate this pattern quite clearly: regardless of feeding frequency, Atlantic spadefish fed at higher rates gain more weight, but growth efficiency is reduced at 7% BW/d and the composition of the gain is increasingly skewed towards greater adiposity. Similarly, cuneate drum *Nibea miichthioides* fed 1–6% BW/d grew more at the highest feeding rates, but grew less efficiently, had a reduced nitrogen retention efficiency, and accumulated higher carcass lipid levels (Wang et al. 2007). Comparable results have also been reported for gilthead seabream *Sparus aurata* (Mihelakakis et al. 2002), Chinese sucker *Myxocyprinus asiaticus* (Yuan et al. 2010), rainbow trout *Oncorhynchus mykiss* (Reinitz 1983; Storebakken et al. 1991), white sturgeon *Acipenser transmontanus* (Hung et al. 1993), grass carp *Ctenopharyngodon idella* (Du et al. 2006), and olive flounder *Paralichthys olivaceus* (Kim et al. 2007). Given the wide range of taxa for which this phenomenon is reported, perhaps this pattern is exhibited by all fishes. If we focus on the effect of feeding rate exclusively, our data suggest Atlantic spadefish should be fed at 5–7% BW/d to maximize growth, but lean growth may be more efficient at the lower end of this range.

Feeding rate has a strong effect on the growth performance of fishes, but feeding frequency can independently and interactively influence the growth and growth efficiency as well. When fish are fed to apparent satiety, increasing the frequency of feeding events tends to increase total feed intake up to a threshold determined, perhaps in part, by gastrointestinal evacuation rate (Jobling 1994). As a result, feeding rate is effectively increased and growth is enhanced, though as previously mentioned,

TABLE 1. Proximate composition of juvenile Atlantic spadefish carcasses at the end of the feeding trial. Except for moisture, all variables are reported as percentages of dry matter. Least-squares means ± SEs are shown for each treatment factor combination in normal text; means across diets and stress exposure replacement factors are shown in italics. *P*-values for each response parameter and their interaction are also provided. For response parameters exhibiting significant factor effects, means without common letters are significantly different ($P < 0.05$).

Variable	Feeding frequency (times per day)	Feeding rate (%BW/d)			Mean value	*P*-values		
		3	5	7		Rate	Frequency	Interaction
Moisture	1×	76.4 ± 0.9	73.2 ± 0.9	70.5 ± 0.9	*73.4*			
	3×	73.9 ± 0.9	73.6 ± 0.9	68.9 ± 0.9	*72.2*	0.001	0.104	0.222
	Mean values	*75.1* z	*73.4* z	*69.7* y				
Lipid	1×	10.6 ± 1.1	19.9 ± 1.1	25.7 ± 1.1	*18.7*	<0.001	0.066	0.061
	3×	12.9 ± 1.1	18.6 ± 1.1	29.2 ± 1.1	*20.2*			
	Mean values	*11.7* x	*19.3* y	*27.4* z				
Protein	1×	69.0 ± 1.1	63.2 ± 1.1	56.6 ± 1.1	*62.9*			
	3×	65.7 ± 1.1	63.1 ± 1.1	54.7 ± 1.1	*63.1*	<0.001	0.074	0.385
	Mean values	*67.3* z	*63.1* y	*55.7* x				
Ash	1×	17.8 ± 0.5	14.0 ± 0.5	12.0 ± 0.5	*14.6*			
	3×	16.7 ± 0.5	14.3 ± 0.5	10.5 ± 0.5	*13.8*	<0.001	0.076	0.217
	Mean values	*17.2* z	*14.1* y	*11.2* x				

growth efficiency may be somewhat reduced at excessively high feed intake rates. This phenomenon has been demonstrated in yellowtail flounder *Limanda ferruginea* (Dwyer et al. 2002), channel catfish *Ictalurus punctatus* (Peterson and Small 2006), black sea trout *Salmo trutta labrax* (Başçınar et al. 2007), Korean rockfish *Sebastes schlegeli* (Lee et al. 2000), great sturgeon *Huso huso* (Mohseni et al. 2006), hybrid sunfish (female green sunfish *Lepomis cyanellus* × male bluegill *L. macrochirus*; Wang et al. 1998), cuneate drum (Wang et al. 2007), and pikeperch *Sander lucioperca* (Wang et al. 2009). When fish are fed at a fixed feeding rate, increasing the feeding frequency still tends to improve growth to a point, but the magnitude of the effect is diminished and is probably the result of moderate improvements in conversion efficiency associated with gastrointestinal adaptation to more consistent, but lower instantaneous "gut fill" (Jobling 1982; Peterson and Small 2006). For example, Asian seabass *Lates calcarifer* gained more weight and grew more efficiently when fed the same ration in three daily feedings compared with one or two feedings, but feeding four times daily failed to increase growth further and resulted in an elevated FCR (Biswas et al. 2010); largely consistent results were also reported for this species by Salama (2008). Similar responses to increasing feeding frequencies have been reported for ayu *Plecoglossus altivelis* (Cho et al. 2003), Australian snapper *Pagrus auratus* (Tucker et al. 2006), and red-spotted grouper *Epinephelus akaara* (Kayano et al. 1992). Our results are broadly consistent with those in published literature, although differences were not significant in all cases, Atlantic spadefish fed three times daily grew more and more efficiently than those fed once daily regardless of feeding rate. Although a significant difference in feed intake was observed within the 7% BW treatment, the magnitude of the difference was relatively small, and was probably an artifact arising from the differences in body weight observed for these two treatments, which grew more marked over time. Based on our data, it would seem that a 3× daily feeding rate would be advantageous for Atlantic spadefish, regardless of feeding rate.

We observed significant interaction between feeding rate and frequency in terms of weight gain, which suggests that the performance-enhancing effects of higher feeding frequencies are more pronounced among fish fed higher rates (a significant interaction effect was also observed for feed intake, but as previously mentioned, this is probably an artifact of the differences in weight gain). Fewer studies have simultaneously evaluated the effects of different feeding rates and frequencies, and among species the literature is somewhat divided. Similar to what we observed in Atlantic spadefish, tambaqui *Colossoma macropomum* performed better when they were fed more frequently at 10% BW/d, but these effects were not observed when fed at 5% BW/d (Silva et al. 2007). Conversely, increasing the feeding frequency in ayu to more than once daily did not improve performance of fish fed 3% or 6% BW/d (Cho et al. 2003). Despite these conflicting results, given the negative effect of excessively high feed intake on growth efficiency via greater fecal losses (in the absence of adequate gastrointestinal adaptation to compensate for larger meal sizes), it is logical to hypothesize that dividing high feed intake into multiple feeding events would improve digestive and absorptive efficiencies and yield greater weight gain. Increasing feeding frequency for fish fed at high feeding rates may also be beneficial in the sense that it would decrease the duration of each feeding event, and thus the possibility of producing feeding inefficiencies owing to pellets sinking or being flushed from the system before they could be consumed. Certainly, behavioral interactions such as social dominance play a role in feeding efficiency and feed intake in fishes (Jobling 1994), but for species such as Atlantic spadefish that do not appear to exhibit strong social hierarchies and competitive feeding behaviors in intensive culture, increasing feeding frequencies may be beneficial in terms of digestive and absorptive efficiencies and growth performance, particularly at high feeding rates. Furthermore, increased feeding frequencies may have the added benefit of dispersing associated negative short-term effects of reduced water quality over multiple time periods during the day, especially in recirculation aquaculture systems. Taking this and the rest of our results into consideration, we suggest that the growth performance of Atlantic spadefish is optimized when fish are fed at 5–7% BW/d in three daily feedings, and 7% BW/d yields the greatest, albeit slightly less efficient, growth.

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