FACTORS AFFECTING VOLUNTARY FOOD CONSUMPTION BY CHANNEL CATFISH

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Abstract: Nutritional and physical properties of the diet, management, and environment affect voluntary food consumption by channel catfish (*Ictalurus punctatus*). Laboratory studies in which channel catfish were fed twice daily to satiation with semipurified diets containing various ratios of protein and digestible energy indicated that food intake was directly proportional to calorie density in the diet but independent of protein density until the protein percentage exceeded 45. Protein levels above 45% caused reduced food intake. Pond experiments in which channel catfish were fed to satiation twice daily, once daily, or on alternate days demonstrated that fish fed twice daily consumed the most food when water temperature was 26 C or greater, those fed once daily consumed the most food at 20-26 C, and those fed on alternate days consumed the most food when temperature declined below 20 C. channel catfish fed to satiation once daily in ponds consumed 17% more of an extruded feed that had a mass density of 0.92 g/cm^3 than one having a density of 0.83 g/cm^3 even though the former had a higher calorie density, indicating that stomach fill limited food intake.

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When fast growth with efficient food conversion is an objective of the fish culturist, the fish should be fed at a high level of nutrient intake; however, overfeeding must be minimized. This is more difficult to achieve with fish than with land animals because if fish are offered more food than they will consume in a short time, the uneaten feed cannot be recovered and this reduces feed efficiency and deters water quality. More precise information on the food consumption rate of channel catfish, and factors affecting this, will allow the feeder to feed the fish more effectively for maximum yield without overfeeding.

A series of feeding experiments in a controlled environment and in ponds were conducted at Auburn University to investigate the effects of diet composition, feeding schedule, and period during the growing season on voluntary food consumption and subsequent growth by channel catfish. In experiment 1, channel catfish fingerlings were fed diets containing 3 digestible energy (DE) levels at 3 protein percentages (a 3 X 3 factorial design) in a controlled environment. In experiment 2, channel catfish were fed from fingerling to marketable size in ponds according to 3 feeding schedules (twice daily, once daily, or on alternate days) or on diets containing different energy concentrations and mass densities. In all experiments the amounts of food offered and refused were carefully measured.

METHODS

Experiment I

Nine purified diets containing 3 DE levels (230, 290 and 350 kcal/100g) at 3 protein percentages (23, 29 and 35%) were fed for 4 weeks to channel catfish in 60-liter glass aquaria through which constant temperature (29 ± 1C) water flowed at a rate of 1 liter/min. The fish were fed to satiation twice daily and uneaten food was removed by siphon tube and measured within 30 minutes after feeding.

Ingredient composition of the diets is shown in Table 1. DE levels of the diets were controlled by varying the ingredients on a digestible calorie basis, on the basis of previous digestibility trials conducted in this laboratory (Lovell 1977) which indicated that DE from carbohydrate decreased as level of carbohydrate in the diet increased. Ratio of DE from carbohydrate to DE from lipid was maintained constant in each diet. The diets were

TABLE 1. The ingredient composition and protein and energy content of experimental diets 1-9 fed to channel catfish in experiment 1.

Ingredient	Diets 1	2	3	4	5	6	7	8	9
	%	%	%	%	%	%	%	%	%
Casein	19.32	19.32	19.32	24.36	24.36	24.36	29.40	29.40	29.40
Gelatin	4.83	4.83	4.83	6.09	6.09	6.09	7.35	7.35	7.35
Soybean oil	3.29	6.62	9.96	1.60	4.93	8.26	0.00	3.24	6.57
Cooked starch	16.65	27.06	38.87	12.17	21.63	32.70	7.69	16.51	26.92
Alphacel	44.40	30.66	15.51	44.27	31.48	17.08	44.15	31.99	18.25
Carboxymethyl celluslose	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
Vitamin mix[a]	1.40	1.40	1.40	1.40	1.40	1.40	1.40	1.40	1.40
Vitamin C	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05
Mineral mix[b]	4..00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00
$CaHPO_4$	0.66	0.66	0.66	0.66	0.66	0.66	0.66	0.66	0.66
Fish flavor	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40
Fish oil	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
Crude protein	23.00	23.00	23.00	29.00	29.00	29.00	35.00	35.00	35.00
Digestible energy (Kcal/ 100 g)	230.00	290.00	350.00	230.00	290.00	350.00	230.00	290.00	350.00
DE/P ratio	10.00	12.61	15.22	7.93	10.00	12.07	6.57	8.29	10.00

[a]Vitamin mix (mg/kg diet): Thiamine, 10; Riboflavin, 20; Pyridoxine, 10; Folic acid, 5; Pantothenate, 40; Choline chloride, 3000; Niacin, 150; Vitmin B-12, 0.06; Vitamin A, 12; Vitamin D, 6; vitamin E, 45.50; Menadione-Na-bisulfite, 80; Inositol, 400; Biotin, 2; Ethoxyquin, 200.

[b]Mineral mix = Williams and Briggs (Biolgical diets manual) salt mixture with 0.2981 g of $Cacl_2 .6H_2O$ and 0.1328 g of $ALK (SO_4)_2 . 12H_2O$ added per kg of salt mixture.

prepared as moist, 2 mm-diameter pellets. The gelatin and carboxy-methyl cellulose in the diets provided for satisfactory binding quality and water stability. The diets were stored frozen until a short time prior to feeding.

Inasmuch as the protein percentages in the diets previously described did not influence food consumption, a subsequent 4-week feeding trial was conducted in which diets covering a wider range of protein percentages were fed. the diets in the second feeding trail were isocaloric (348 kcal/ 100g) and contained from 15 to 65% protein (Table 2).

Average daily weight gains and average daily intakes of diet, protein and DE were determined for fish in both feeding trials. Near the end of the feeding trials, 5 fish from each aquarium were sampled just prior to the morning meal time. Measurements were made of stomach fill and blood serum levels of glucose, nonprotein nitrogen and lipids. Methods of analysis are described by Boonyaratpalin (1978).

Experiment 2

A pond study was conducted in which channel catfish were fed from fingerlings to a harvestable size of 400-500 g to determine effects of energy or mass density of the diet and feeding frequency on voluntary food consumption and growth of the fish.

Channel catfish fingerlings of the Auburn strain averaging 83 g in size were stocked at a density of 5,000 fish/ha into 12 0.04-ha earthen ponds at the Auburn University Fisheries Research Unit. A 1.8 m diameter feeding ring of 8 cm (diameter) flexible plastic pipe, with a 15 cm depth skirt made from 5 mm mesh hardward cloth, was placed in each pond to contain the floating diet until consumed by the fish or collected for measurement

TABLE 2. The ingredient composition and protein and energy content of experimental diets 10-15 fed to channel catfish in experiment 1.

Ingredients(%)	Diets 10	11	12	13	14	15
Casein	16.13	26.88	37.63	48.38	59.14	69.89
Dextrin	51.94	39.94	30.04	20.52	13.56	6.60
Soybean oil	13.15	10.52	7.89	5.26	2.63	0.00
Alphacel	8.17	12.05	13.83	15.23	14.06	12.90
Fish oil[a]	2.50	2.50	2.50	2.50	2.50	2.50
Vitamin mix[a]	1.40	1.40	1.40	1.40	1.40	1.40
Vitamin C	0.05	0.05	0.05	0.05	0.05	0.05
Mineral mix[a]	4.00	4.00	4.00	4.00	4.00	4.00
Carboxymethyl cellulose	2.00	2.00	2.00	2.00	2.00	2.00
$CaHPO_4$	0.66	0.66	0.66	0.66	0.66	0.66
Crude protein(%)	15.00	25.00	35.00	45.00	55.00	65.00
Digestible energy (Kcal/100 g)	348.00	348.00	348.00	348.00	348.00	348.00
DE/P ratio	23.20	13.92	9.94	7.73	6.33	5.35

[a]Mineral mix and vitamin mix compositions presented in Table 1.

as refused food. The fish were conditioned to feeding inside the feeding rings for approximately 3 weeks, and on 30 June, fish in 9 of the ponds were fed diet 1 (Table 3) and randomly assigned to 1 of 3 feeding schedules: once daily (1700), twice daily (0800 and 1700), and on alternate days (1700). Fish in the other 3 ponds were fed diet 2, once daily. The fish were fed as much as they would consume during a 45-minute period at each feeding. To insure that the fish were fed to satiation, they were always offered more of the diet than they would consume and the uneaten food particles were removed from the

TABLE 3. Ingredient composition of experimental diets fed in experiment 2.

Ingredient	High energy	Low energy
Fish meal	10.3	8.3
Ground corn	22.2	28.0
Ground wheat	5.0	0.0
Soybean mean (49% protein)	51.2	32.2
Distiller's dired solubles	7.5	5.8
Wheat midds	0.0	22.6
Alfalfa meal	0.0	2.0
Animal fat	2.5	0.0
Dicalcium phosphate	1.0	0.8
Vitamin premix[a]	0.1	0.1
Trace mineral premix	0.08	0.08
Ascorbic acid	0.05	0.05
Protein %	36	30
energy, kcal DE/100 g	280	250
Density, g/cm^3	0.91	0.83

[a]Same as the premix presented in Table 1.

feeding ring with a swimming pool net and counted after each 45-minute feeding period. the diets were processed by extrusion into floating type pellets approximately 0.8 mm in diameter. Diet 1 had a density of 0.91 g/cm^3 and contained 36% protein and 280 kcal/g of DE, and diet 2 had a density of 0.83 g/cm^3 and contained 30% protein and 250 kcal/100 g of DE. Tests showed that 96% of the extruded particles remained afloat in water for 45 minutes. Water temperature and dissolved oxygen were measured in each pond daily in the morning and afternoon. Fish from each treatment were sampled at 5-week intervals for weight measurement. On 15 October, 16 weeks after initiation, the experiment terminated and weight gain, food consumption, surviving fish and size variation for each pond was determined.

RESULTS

Experiment 1

Daily food consumption was significantly (P>0.01) influenced by the DE level of the diet; as DE content of the diet increased, amount of food consumed per day decreased at each protein level (Table 4). As the protein percentage of the diet changed from 23 to 35 (in the first trial), amount of food consumed by the fish did not change as long as calorie density of the diet remained constant (N.S. at $P > 0.05$). These results indicate that digestible calorie density of the diet influenced the quantity of food consumed by channel catfish, but protein percentage, between 23 and 35% (normal dietary range), did not. Channel catfish, like chickens (Hill and Dansky 1954) and rats (Hegsted et al. 1949) will apparently consume larger quantities of a low energy diet than of a higher energy diet in order to satisfy their metabolic energy requirement.

Although food consumption at the 3 energy levels was significantly different, there were no significant differences (P>0.05) in De consumption among fish fed the 9 experimental diets (Table 4). Portein consumption was directly related to dietary protein level and inversely related to dietary energy level. As calorie density increased in diets at a given protein percentage, protein consumption was significantly reduced (P>0.01).

Growth was significantly affected by both protein (P>0.01) and energy (P>0.01) levels of the diet. At each protein percentage, an increase in dietary energy level caused a decrease in weight gain. This obviously resulted from the reduction in food (thus protein) consumption caused by the increase in energy level in the diets.

TABLE 4. Average consumption of food, protein and digestible energy, weight gain, protein gain and efficiency ratios for food, protein and energy for channel catfish fed diets 1-9 in experiment 1.

Diet				Daily consumption/100 g of fish			Percentage gain		Efficiency ratio		
No.	DE (Kcal/100 g)	Protein (%)	DE/P ratio	Food (g)	DE (Kcal)	Protein (g)	Weight	Protein	Food g gain/100 g food fed	Protein g gain/g protein fed	Energy g gain/Kcal fed
1	230	23	10.00	3.06^a	7.05^a	0.70^d	67.48^c	65.64^e	58.46^a	2.54^{bc}	0.25^{de}
2	290	23	12.16	2.32^b	6.74^a	0.54^e	49.32^{ab}	44.12^b	60.99^{bc}	2.66^{ab}	0.21^{bc}
3	350	23	15.22	2.00^c	7.02^a	0.46^f	42.94^a	35.94^a	63.32^c	2.76^a	0.18^a
4	230	29	7.93	2.99^a	6.88^a	0.86^b	76.73^d	74.17^f	62.33^{bc}	2.15^c	0.27^f
5	290	29	10.00	2.42^b	7.02^a	0.70^d	62.70^c	58.04^d	70.41^d	2.42^d	0.24^d
6	350	29	12.07	1.93^c	6.76^a	0.56^e	48.72^{ab}	42.98^b	72.94^{def}	2.52^{cd}	0.21^{bc}
7	230	35	6.57	2.95^a	6.78^a	1.03^a	93.48^e	100.06^g	77.24^g	2.20^e	0.34^g
8	290	35	8.29	2.32^b	6.74^a	0.81^c	65.06^c	63.16^e	75.39^{fg}	2.16^e	0.26^{ef}
9	350	35	10.00	1.97^c	6.89^a	0.69^d	52.36^b	50.94^c	75.14^{efg}	2.14^e	0.22^c
Probability level[1]:											
Protein (P)				NS	NS	.01	.01	.01	.01	.01	.01
L[2]				NS	NS	.01	.01	.01	.01	.01	.01
Q[2]				NS	NS	NS	NS	NS	NS	N3	NS
Digestible energy (DE)				.01	NS	.01	.01	.01	.01	.01	.01
L[2]				.01	NS	.01	.01	.01	.01	.01	.01
Q[2]				.05	NS	.05	.05	.01	NS	NS	NS
P X DE				NS	NS	.01	.05	.01	.01	.01	.01

1 Probability level at which treatments are statistically different. NS is not significant at P<.05. Means in columns with a common superscript (a, b, c, d, e, f or g) are not statistically different.
2 L = linear effects; Q = curvelinear effects.

The best weight gain and protein gain were from fish fed the diet with the lowest DE level 230 kcal/100g) and the highest protein level (35%). Possibly an even smaller DE/protein ratio, effected by reducing energy or increasing protein, would have resulted in a further increase in weight gain. The available energy requirement of channel catfish, as indicated by these data, appears to be less than that previously reported (Garling and Wilson, 1976). The lowest energy diet in this ecperiment (230 kcal/100 g) was adequate to meet the fish's energy needs, as evidenced by the linear increase in weight gain as protein increased in this diet. Perhaps this disagreement on energy requirement of channel catfish is caused by differences in evaluating available energy in the experimental diets.

In the second feeding trial, where dietary DE was constant and protein percentage varied from 15-65%, there was no significant effect ($P>0.05$) of dietary protein level on food consumption up to 45% protein; however, above this level food intake declined significantly ($P>0.05$) as protein increased (Table 5). The results of the second feeding trail substantiate those of the first trial in that the amount of protein in the diet does not affect food consumption by channel catfish over a normal range of dietary protein levels in isocaloric diets, but indicate that unusually high percentages of dietary protein will reduce food consumption.

TABLE 5. Average consumption of food, protein and digestible energy; weight gain, protein gain; efficiency ratios for food, protein and energy for channel catfish fed diets 10-15 in experiment 1.

Diet				Daily consumption/100 g of fish			Percentage gain		Efficiency ratio		
No.	DE (Kcal/100 g)	Protein (%)	DE/P ratio	Food (g)	DE (Kcal)	Protein (g)	Weight	Protein	Food g gain/100 g food fed	Protein g gain/g protein fed	Energy g gain/Kcal fed
10	348	15	23.20	3.52^{a}	12.24^{a}	0.53^{a}	41.85^{a}	4.42^{a}	38.05^{a}	2.54^{a}	0.11^{a}
11	348	25	13.92	3.46^{ab}	12.03^{ab}	0.87^{b}	70.79^{b}	40.83^{b}	62.48^{b}	2.50^{ab}	0.18^{b}
12	348	35	9.94	3.45^{ab}	12.01^{ab}	1.21^{c}	92.48^{c}	66.78^{c}	79.54^{c}	2.27^{abc}	0.23^{c}
13	348	45	7.73	3.19^{ab}	11.12^{ab}	1.44^{d}	97.93^{c}	81.75^{d}	90.63^{d}	2.01^{cd}	0.26^{de}
14	348	55	6.33	2.98^{b}	10.37^{bc}	1.64^{e}	97.33^{c}	97.19^{e}	96.47^{d}	1.75^{d}	0.29^{e}
15	348	65	5.35	2.62^{c}	9.12^{c}	1.70^{e}	83.36^{c}	93.54^{e}	95.82^{d}	1.47^{e}	0.28^{de}
Probability level[1],				.05	.01	.01	.01	.01	.01	.01	.01

[1] Probability level at which treatments are statistically different. Means in columns with a common superscript (a, b, c, d or e) are not statistically different.

Protein consumption was directly related to dietary protein percentage even though food consumption was less at the 2 highest protein levels (Table 5). Rate of weight gain increased with dietary protein level up to 45%, then decreased. This result indicates that too high protein levels in catfish diets can have deleterious metabolic effects when the fish are fed to satiation.

Neither stomach fill nor serum levels of glucose, nonprotein nitrogen (mainly free amino acids and ammonia) and lipids at meal time, were significantly correlated with amount of food consumed by the fish.

Results of experiment I indicate that when catfish are allowed to feed to satiation, high levels of available energy in the diet can limit food consumption and prevent catfish from consuming enough pritein for maximum rate of weight gain.

Experiment 2

Weight gained was closely related to amount of food consumed for fish fed twice daily, once daily or on alternate days (Table 6). The fish fed once daily consumed almost

TABLE 6. Average food consumption, weight gain, food conversion, and harvest size variation for channel catfish fed by three schedules for 16 weeks in ponds[a].

Feeding Schedule	Times fed	Food consumed per pond kg	Weight gained Per pond kg	Weight gained Per fish kg	Food Conversion kg food/kg gain	Harvest size variation ≤30 cm %	Harvest size variation 30-38 cm %	Harvest size variation ≥38 cm %
Alternate days	54	72.0 a	49.0 a	0.255	1.47 a	38 a	56 a	6 a
Once daily	92	99.6 b	64.1 b	0.332	1.55 b	19 b	62 b	19 b
Twice daily	184	102.9 b	65.7 b	0.329	1.57 b	18 b	66 b	16 b

[a]Values in the table represent averages of data from 3 ponds.
Averages in columns followed by common letter are not statistically different at $P > 0.05$.

the same amount of food and gained nearly the same amount of weight as those fed twice daily for the overall 16-wk growing period. The fish fed on alternate days consumed 27% less food and gained 23% less than those fed daily.

The effect of feeding frequency on food consumption was not the same during all phases of the experimental period (Fig. 1). From the third through the tenth week the fish fed twice daily consumed 18% more food than those fed once daily. After the tenth week, when water temperature decreased below 26 C, the fish fed twice daily consumed less food than those fed once daily, and after the twelfth week their food consumption per 2-wk period was less than that of fish fed on alternate days. From the tenth through the fourteenth week the fish fed once daily consumed the most food per 2-wk period, and during the last 2 weeks the fish fed on alternate days consumed the most food.

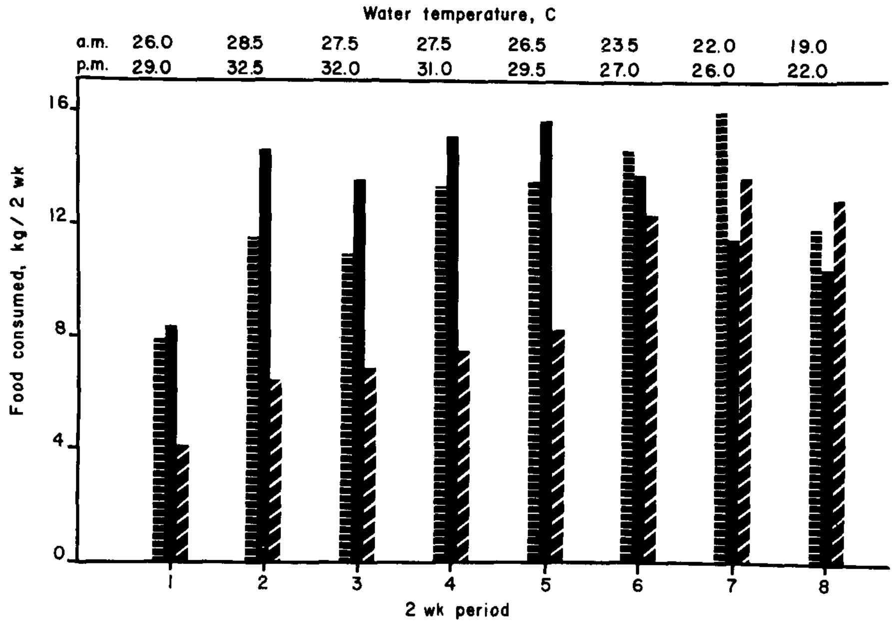

Fig. 1. Food consumed per 2-week period by channel catfish fed by three feeding schedules (horizonal bars, once daily; soldi line, twice daily; diagonal bars, alternate days) for 16 weeks in earthen ponds.

The increased rate of food consumption by the fish fed twice daily during the first part of the feeding period agrees closely with a study by Page and Andrews (1973) who reported than channel catfish fed twice daily, in constant temperature (27.6 C) raceways, gained 20% more than fish fed once daily. they found that more frequent feeding than twice daily offered no benefit.

The inverse relationship between feeding frequency and food consumption during the latter part of the feeding period is assumed to be related largely to the effect of decrease in water temperature on digestion and metabolism rates by the fish. Possibly other factors which reduce food consumption by fish, such as increase in water temperature on digestion and metabolism rates by the fish. Possibly other factors which reduce food consumption by fish, such as increase in size, may have come into play. It is assumed that during the latter part of the growing season when temperature decreased, rate of stomach evacuation decreased and the fish which were fed more frequently actually consumed less food because of the continuous presence of food in their gut. During the early part of the feeding period, when water temperature was highest, stomach fill seemed to be the major factor regulating amount of food consumed by channel catfish. Under these conditions twice daily feeding was beneficial. During the latter phase of the feeding period when the energy requirement and digestion rate of the fish decreased, less frequent feeding was advantageous.

These results indicate that feeding channel catfish in ponds twice daily will increase food consumption and growth rate when the minimum daily water temperature is 26 C or above. As water temperature decreased, a change to once daily feeding and subsequently, when the water temperture descends to 20 C, to alternate day feeding will be more productive.

The fish fed the higher nutrient diet (36% protein, 280 kcal DE/100 g) consumed 9.5% more food and gained 9.4% more weight than fish fed the lower energy diet (30% protein, 250 kcal DE/100 g) (Table 7). The explaination for the higher consumption of the higher energy diet was that the higher energy diet was more compact (0.91 g/cm^3) than the lower energy diet (0.83 g/cm^3) and the fish's stomach could hold more of the higher energy diet. Evidence of this is that the volume of food consumed by the fish fed the 2 diets was almost the same (Table 7). One important disadvantage of expanded (floating) fish diets is that some formulations may expand so much during processing that the capacity of the stomach will not allow the fish to consume enough of the bulky diet to meet its nutrient requirement for maximum rate of growth.

Table 8 shows the food consumption rates of channel catfish in ponds over the growing season when fed the 2 extruded diets to satiation. During the first 6 weeks fish fed the diet of high nutrient and mass density consumed 18% more food (by weight) than the fish fed the diet of lower nutrien and mass density. This was apparently due to the greater bulkiness of the latter. During the middle of the feeding period food consumption was about equal for the 2 groups. During the latter part of the growing period the fish fed the diet of lower energy and mass density consumed more food. This interaction effect between diet and period on food consumption is assumed to be due primarily to decrease in water temperature, and to some degree to increase in fish size, during the feeding period which would reduce the fish's energy requirement. During the early part of the growing period both groups of fish were apparently eating to stomach capacity and the fish fed the denser diet consumed more food. During the later stages of the feeding period the fish were not eating to stomach capacity but to calorie satiation, thus those fed the lower energy diet were consuming more.

TABLE 7. Average weight and volume of food consumed, weight gained, and food conversion ratio for channel catfish fed two diets to satiation in ponds[a].

Diet		Food consumed/fish			
DE (kcal/100g)	Protein (%)	Weight (kg)	Volume ($cm^3 X 10^2$)	Weight gain/fish (kg)	Food conversion
280	36	0.51 a	5.58 a	0.33 a	1.54 a
250	30	0.45 b	5.58 a	0.29 b	1.55 a

[a]Values in columns followed by the same letter are not statistically different at $P > 0.05$.

TABLE 8. Weight (G) and volume (Cm^3) of food consumed per 100 grams of body weight by channel catfish fed diets of 2 nutrient densities to satiation.

Date	6/30-7/13		7/14-7/27		7/28-8/11		8/12-8/25		8/26-9/8		9/9-9/22		9/23-10/6		10/7-10/17	
Temp. °C[a]	29.2		31.1		30.5		29.8		28.1		24.7		23.6		19.6	
Diet[b]	G	Cm^3	G	Cm^3	G	Cm^3	G	Cm^3	G	Cm^3	G	Cm^3	G	Cm^3	G	Cm^3
High energy	3.3	3.7	3.0	3.2	2.4	2.6	2.1	2.3	1.9	2.1	1.7	1.9	1.8	1.9	0.9	1.0
Low energy	3.3	3.9	2.8	3.4	2.1	2.5	2.1	2.6	2.0	2.4	2.0	2.4	2.0	2.4	1.3	1.5

[a] Average afternoon temperature at 1 meter depth.

[b] Mass density of the diets was 0.91 g/cm^3 for the high energy diet and 0.83 g/cm^3 for the low energy diet.

CONCLUSION

Several factors affect the amount of food that channel catfish, which are "meal eaters" rather than "nibblers", will consume. Calorie concentration of the diet plays a major role, whereas dietary protein level is not important unless excessively high. Period during the growing season is important. In this study daily voluntary food consumption decreased from 3.3% of body weight early during the feedin period to 1.0% at the end of the feeding period. This decline in food consumption is assumed to be due largely to temperature decrease and fish size increase. Feeding schedule affects food consumption during all phases of the growing season. Under conditions when channel catfish have a vigorous appetite, or high metabolic energy requirement, twice daily feeding will allow a marked increase in food intake. Page and Andrews (1973) reported that more frequent feeding than twice daily did not increase consumption. when water temperature decreases, once daily and even alternte day feeding can result in higher food consumption. Bulk or mass density of the diet is important when the fish's food requirement is high, but decreases in significance when appetite decreases.

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