

Notes

Variation in the food intake of grass carp, *Ctenopharyngodon idella* (Val.), fed singly or in groups

Chris G. Carter⁽¹⁾, Dominic F. Houlihan⁽¹⁾, Ian D. McCarthy⁽¹⁾ and Alan E. Brafield⁽²⁾

⁽¹⁾ Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen AB9 2TX, U.K.

⁽²⁾ Division of Biosphere Sciences, King's College London, Campden Hill Road, London W8 7AH, U.K.

Received June 1, 1992; accepted July 30, 1992.

Carter C. G., D. F. Houlihan, I. D. McCarthy, A. E. Brafield, *Aquat. Living Resour.*, 1992, 5, 225-228.

Variation de la prise de nourriture chez la carpe Ctenopharyngodon idella (Val.), nourrie individuellement ou en groupes.

INTRODUCTION

Each animal may be assumed to possess a unique combination of physiological traits (Bennett, 1987). However, there is little information on the effects of interindividual variation in fish (Cui and Liu, 1990). Individual differences in competitive ability, aggressiveness and or size can lead to the establishment of dominance hierarchies within groups of fish (Metcalf, 1989; Metcalfe *et al.*, 1989). The variation in growth rates in groups of fish are related to dominance hierarchies and preferential access to food resources by dominant individuals (Jenkins, 1969; Fausch, 1984; Koebele, 1985). Recently, radiography has been used to measure individual consumption rates for groups of salmonids and has demonstrated considerable inter-individual variation in food intake (Jobling *et al.*, 1989; Carter *et al.*, 1992a; McCarthy *et al.*, 1992). Two aims of this study were to use radiography to examine the variation in the food consumption rate of grass carp, *Ctenopharyngodon idella* (Val.), held together and to assess whether variation in growth rates could be explained by variation in consumption rates. A final aim of this study was to compare the day to day variation in consumption

rates of grass carp held in a group to those held individually, in terms of the individual meal share, in order to examine the effect of endogenous influences on appetite.

MATERIALS AND METHODS

The maintenance of the fish and the experimental procedures have been described previously (Carter *et al.*, 1992b). Briefly, 15 grass carp were anaesthetized, weighed (17.3 ± 2.4 g; mean \pm SD), individually numbered with alcian blue applied using a Panjet and placed in a 5 dm³ glass tank of well-aerated, filtered recirculating fresh water. The temperature was maintained at 22°C and the photoperiod at 12L:12D. Fish were fed to satiation two times each day at 09:00 and 11:00. The diet was prepared as 2.4 mm diameter pellets with a California pellet mill and was the same composition as used in a previous study (Carter and Brafield, 1991). In order to construct food consumption growth curves a further 6 (19.6 ± 1.8 g) fish were placed in a second aquarium and starved for 28 days.

During the 28 day experiment the daily food intake of individual fish was determined on three occasions

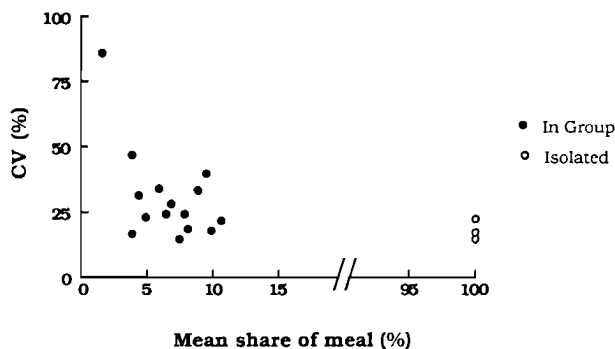


Figure 1. – The relationship between the mean share of meal (MSM) and the coefficient of variation for consumption (CV_c) for 15 grass carp held together and for 3 grass carp held separately. Correlation between grouped grass carp: $n=15$; $r=-0.561$; $p<0.05$.

(days 6, 14 and 28) using radiography. The fish were fed to satiation as normal, but with diets containing radio-opaque glass beads. The fish were removed from the aquarium after the second meal, anaesthetized, radiographs taken, weighed and returned (Carter *et al.* 1992a,b). This allowed a mean weight specific food intake (C_m : mg dry food per gram wet weight of fish per day: $\text{mg}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) to be calculated for each fish. The intra-individual variation in the food intake was assessed using the coefficient of variation for consumption (CV_c):

$$CV_c (\%) = 100 (\text{SD}/C_m)$$

(McCarthy *et al.*, 1992) where C_m and SD are the mean intakes ($\text{mg}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) and their standard deviations, respectively, for each fish. The proportions of the “group meal” eaten by each fish on each occasion were averaged to obtain an estimate for the mean share of meal (MSM: %) eaten by each individual fish. The feeding data obtained from the group fish were compared with feeding data obtained from 3 grass carp (13.5 ± 1.7 g) held individually under similar conditions of 22°C , a 12L:12D photoperiod and being fed to satiation twice per day for 28 days (Carter and Brafield, 1991).

Specific growth rates (SGR) for individual fish were calculated as:

$$\text{SGR} (\% \text{d}^{-1}) = 100 (\text{Log}_e W_2 - \text{Log}_e W_1)/t$$

where W_1 and W_2 were the initial and final wet weights (g) of the fish, respectively, after t days (28). The relationships between the rates of food intake and growth were investigated using the data for both the fed and starved grass carp which had been held in groups. The relationship was described using a simple power function of the form

$$\text{Log}_e (\text{SGR} + 1) = a + b \text{Log}_e (C_m + 1)$$

(i.e. $\text{SGR} + 1 = a' (C_m + 1)^b$) where SGR is the specific growth rate and C_m the mean weight-specific

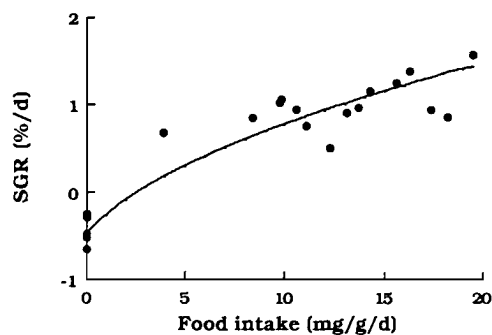


Figure 2. The relationship between mean weight specific food intake (C_m) of a pelleted diet and growth (SGR) of grass carp. The relationship is described by $\text{Log}_e (\text{SGR} + 1) = -0.662 + 0.514 \text{Log}_e (C_m + 1)$ ($n=21$; $R^2 = 0.888$; $p < 0.001$).

food intake for each fish (Christiansen and Jobling, 1990; Carter *et al.*, 1992a). The relative success of the model in describing the data was evaluated by calculating the size of the coefficient of determination (R^2). Further statistical treatment of the data was as described by McCarthy *et al.* (1992).

RESULTS AND DISCUSSION

There was both inter-and intra-individual variation in the daily weight-specific food intake of the grouped grass carp. Inter-individual variation was demonstrated by the MSM having a range between 1.7 and 10.5% (fig. 1). Intra-individual variation was demonstrated by the CV_c , which highlighted individual differences in the consistency of the daily meal size, which varied between 14.4 and 86.2%. A low CV_c indicated that the meal size of an individual fish was similar from day to day whilst a high CV_c indicated a more varied intake. The CV_c decreased as MSM increased ($n=15$; $r=-0.561$; $p<0.05$) indicating that the grass carp which were more successful in obtaining food ate consistently larger meals (fig. 1). A similar situation was observed in a group of rainbow trout, *Oncorhynchus mykiss*, which displayed a strong feeding hierarchy. The CV_c for individual rainbow trout varied between 13.9 and 139.5% and CV_c showed a strong negative correlation with MSM (McCarthy *et al.*, 1992). Under constant environmental conditions a major exogenous factor which causes inter-individual variation in food intake of fish in a group is the existence of feeding hierarchies. Disproportional food acquisition has been demonstrated between individuals in group of fish (e.g. Yamagishi *et al.*, 1974; Christiansen and Jobling, 1990; Carter *et al.*, 1992a; McCarthy *et al.*, 1992) and dominance hierarchies play a key role in mediating these differences in food intake (Metcalfe *et al.*, 1989; Gotceitas and Godin, 1991). Endogenous factors also influence daily variation in food intake as can be seen from the CV_c

values of 15.6, 16.8 and 22.2% obtained from the food intake data of the three isolated grass carp fed to satiation. Similar day to day variation in food intake was found in isolated minnows, *Phoxinus phoxinus*, for which CV_c varied between 21 and 27% (Cui and Wootton, 1988). Thus, day to day variation in an individual's food intake may be due to a combination of endogenous and exogenous influences on appetite, and day to day variation in food intake appears to be a natural feature of feeding fish (Smagula and Adelman, 1982; Cui and Wootton, 1988).

The 15 grass carp fed in a group had a final mean weight 22.9 ± 3.2 g and of a mean specific growth rate of $1.0 \pm 0.3\%$ d⁻¹. A major effect of dominance hierarchies and differential food intake is growth depensation, an increase in variance of a size frequency distribution (Abbott and Dill, 1989). Growth depensation may also be influenced by differences in the activity of dominants and subordinates and by the "physiological stress" of subordination (Koebele, 1985; Jobling and Reinsnes, 1986; Abbott and Dill, 1989). The curvilinear food intake-growth model suggested that the variation in consumption rates explained 89% of the variation in growth rates of grass carp (fig. 2) and it was concluded that the differences in the growth rate of grouped-grass carp were primarily due to differences in food intake. Although growth rates varied between 0.5 and 1.6% d⁻¹ the coefficient of variations for initial and final wet weight were 13.9 and 14.0%, respectively. This suggested a weak dominance hierarchy which was related to the high level of food resource since the fish were fed to satiation. Groups of "stunted" Arctic charr, *Salvelinus alpinus* (L.), showed a small increase in a CV index for wet weight compared with the large

variation between isolated individuals (Jobling and Reinsnes, 1986). The low growth rates of the grouped Arctic charr suggested high levels of social interaction and energy expenditure (Jobling and Reinsnes, 1986) which may have been the result of a weak dominance hierarchy and continued contests for rank (Abbott and Dill, 1985). Physiological variables, other than those related to dominance hierarchies, also influence growth of individual fish and may also explain some of the variation in growth not accounted for by differing rates of consumption. Rates of protein synthesis are correlated with growth rate and account for a large proportion of total energy expenditure in fish (Houlihan, 1991) and there are data which indicate that in grass carp and rainbow trout individual differences in protein turnover contribute to the inter-individual variation in growth (Carter *et al.*, 1991). Additionally individuals may vary in their ability to capture, digest and absorb food (Metcalfe *et al.*, 1989; Cui and Liu, 1990). The influence that the regularity with food is consumed has on growth is not well understood. We have found that grass carp with a larger variability in daily food intake had lower rates of protein synthesis ($n=15$; $r=-0.573$; $p<0.05$) although it should be noted that fish with greater variability in food intake would have had lower growth rates and hence lower rates of synthesis (Carter, unpublished). The costs of growth may be greater for fish on a low plane of nutrition which obtain nutrients surplus to maintenance requirements intermittently. It takes fish several days to become acclimated to new feeding regimes (Weiser and Medgyesy, 1991; Carter and Brafield, 1992) and this may be due in part to the time it takes for the capacity for protein synthesis to increase (Rosenlund *et al.*, 1984).

Acknowledgements

CGC and IDM are grateful to the Science and Engineering Research Council for funding.

REFERENCES

- Abbott J. C., L. M. Dill, 1985. Patterns of aggressive attack in juvenile steelhead trout (*Salmo gairdneri*). *Can J. Fish. Aquat. Sci.*, **42**, 1702-1706.
- Abbott J. C., L. M. Dill, 1989. The relative growth of dominant and subordinate juvenile steelhead trout (*Salmo gairdneri*) fed equal rations. *Behaviour*, **108**, 104-113.
- Bennett A. F., 1987. Interindividual variability: an underutilized resource. In: *New Directions in Ecological Physiology*, M. E. Feder, A. F. Bennett, W. W. Burggren, B. B. Huey Eds., Cambridge University Press, Cambridge, 147-166.
- Carter C. G., A. E. Brafield, 1991. The bioenergetics of grass carp, *Ctenopharyngodon idella* (Val.): energy allocation at different planes of nutrition. *J. Fish Biol.*, **39**, 873-887.
- Carter C. G., A. E. Brafield, 1992. The relationships between specific dynamic action and growth in grass carp, *Ctenopharyngodon idella* (Val.) *J. Fish Biol.*, **40**, 895-907.
- Carter C.G., I. D. McCarthy, H. Heba, D. F. Houlihan, 1991. Why do fish grow at different rates? *Eur. Aquac. Soc. Spec. Publ.*, **14**, 52-53
- Carter C. G., D. F. Houlihan, I. D. McCarthy, 1992a. Feed utilization efficiencies of Atlantic salmon (*Salmo salar* L.) parr: effect of a single supplementary enzyme. *Comp. Biochem. Physiol.*, **101A**, 369-374.

- Carter C. G., D. F. Houlihan, J. Brechin, I. D. McCarthy, I. Davidson, 1992b. Protein synthesis in grass carp, *Ctenopharyngodon idella* (Val.), and its relationship to diet quality. In: Fish Nutrition In Patrice, *Proc. IVth. Symp. Fish Nutrition and Feeding*, S. J. Kaushik, P. Luquet Eds., INRA, Paris (in press).
- Christiansen J. S., M. Jobling, 1990. The behaviour and the relationship between food intake and growth of juvenile Arctic charr *Salvelinus alpinus* L., subjected to sustained exercise. *Can J. Zool.*, **68**, 2185-2191.
- Cui Y., J. Liu, 1990. Comparison of energy budget among six teleosts-IV. Individual differences in growth and energy budget. *Comp. Biochem. Physiol.*, **97A**, 551-554.
- Cui Y., R. J. Wootton, 1988. Effects of ration, temperature and body size on the body composition, energy content and condition of the minnow, *Phoxinus phoxinus* (L.). *J. Fish Biol.*, **32**, 749-764.
- Fausch K. D., 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Can J. Zool.*, **62**, 441-451.
- Gotceitas V., J. G. J. Godin, 1991. Foraging under the risk of predation in juvenile Atlantic salmon (*Salmo salar* L.): effects of social status and hunger. *Behav. Ecol. Sociobiol.*, **29**, 255-261.
- Houlihan D. F., 1991. Protein turnover in ectotherms and its relationship to energetics. In: *Advances in Comparative and Environmental Physiology*, R. Gilles Ed., Springer International, Berlin, **7**, 1-43.
- Jenkins T. M., 1969. Social structure, position choice and micro-distribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. *Anim. Behav. Monogr.*, **2**, 57-123.
- Jobling M., T. G. Reinsnes. Physiological and social constraints on growth of Arctic charr, *Salvelinus alpinus*: and investigation of factors leading to stunting. *J. Fish Biol.*, **28**, 379-384.
- Jobling M., B. M. Baardvik, E. H. Jørgensen, 1989. Investigations of food-growth relationships of Arctic charr.. *Salvelinus alpinus* L., using radiography. *Aquaculture*, **81**, 367-372.
- Koebele B. P., 1985. Growth and the size hierarchy effect: an experimental assessment of three proposed mechanisms; activity differences, disproportional food acquisition, physiological stress. *Env. Biol. Fish.*, **12**, 181-188.
- McCarthy I. D., C. G. Carter, D. F. Houlihan, 1992. Disproportional food acquisition and feeding hierarchy in individual rainbow trout, *Oncorhynchus mykiss* (Walbaum). *J. Fish Biol.*, **41**, 257-263.
- Metcalf N. B., 1989. Differential response to a competitor by Atlantic salmon adopting alternative life-history strategies. *Proc. R. Soc. Lond.*, **B236**, 21-27.
- Metcalf N. B., F. A. Huntingford, W. D. Graham, J. E. Thorpe, 1989. Early social status and the development of life-history strategies in Atlantic salmon. *Proc. R. Soc. Lond.*, **B236**, 7-19.
- Rosenlund G., B. Lund, K. Sandres, D. R. Brackkan, A. von der Decken, 1984. Muscle protein synthesis *in vitro* of saithe (*Pollachius virens*) correlated to growth and daily energy intake. *Comp. Biochem. Physiol.*, **77B**, 7-13.
- Smagula C., C. B. Adelman, 1982. Day-to-day variation in food consumption by largemouth bass. *Trans. Am. Fish. Soc.*, **111**, 543-548.
- Weiser W., N. Medgyesy, 1991. Aerobic maximum for growth in the larvae and juveniles of a cyprinid fish, *Rutilus rutilus* (L.): implications for energy budgeting in small poikilotherms. *Funct. Ecol.*, **4**, 233-242.
- Yamagishi H., T. Maruyama, K. Mashiko, 1974. Social relation in a small experimental population of *Odontobutis obscurus* (Temminck et Schelgel) as related to individual growth and food intake. *Oecologia (Berlin)*, **17**, 187-202.