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Variation in individual food consumption rates of fish and its implications for the study of fish nutrition and physiology

BY IAN D. McCARTHY, DOMINIC F. HOULIHAN, CHRIS G. CARTER AND KATERINA MOUTOU

Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen AB9 2TN

The aim of the present paper is to review recent information on food consumption rates of individual fish and to explore the ways in which values for individual food consumption can be used in studies of fish behaviour, nutrition and physiology. There are two main ways of carrying out nutritional studies in fish in which the aim is to investigate how the amount or the composition of the diet influences growth rate. One involves feeding tanks of animals and measuring the growth rates of the groups. This method stresses the importance of the group response to dietary manipulation and the ground rules for carrying out such studies have recently been clearly expounded (Cho, 1992; Cowey, 1992). An alternative method is to measure the food consumption of the individual fish and to construct from the data on individual animals food consumption–growth rate relationships for the species. In some species of fish which can be held and fed individually, e.g. cod (*Gadus morhua* L.; Houlihan *et al.* 1989) or minnow (*Phoxinus phoxinus* L.; Cui & Wootton, 1989), there is not a problem in determining food consumption and growth rate relationships. However, in fish feeding in groups a major problem has been to develop a reliable method to make repeated measurements of an individual's food consumption. Early attempts involved direct observations of feeding activity or the examination of gut contents in order to estimate consumption. These techniques have proved unsatisfactory, as the methodologies involved are time-consuming, stressful or invasive and periods of pre- or postprandial starvation were necessary (for review, see Talbot, 1985). In the 1980s, two non-invasive methods were developed to measure consumption rates of individual fish, held in groups, which employed either feed labelled with the radioisotope ^{131}I (Storebakken *et al.* 1981) or with an X-ray opaque particulate marker (Talbot & Higgins, 1983). These techniques permitted repeated measurements of food consumption rates of fish held in groups without any alteration to the feeding regimen. However, for health and safety reasons X-radiography has been the preferred technique (for review, see Talbot, 1985).

THE USE OF RADIOGRAPHY TO MEASURE INDIVIDUAL CONSUMPTION RATES OF FISH

A number of studies have reported on food consumption rates of individual fish in groups using X-radiography (Jobling *et al.* 1989; Jørgensen & Jobling, 1989, 1990, 1992; Christiansen & Jobling, 1990; Carter *et al.* 1992*a*,*b*, 1993, 1994; Christiansen *et al.* 1992; McCarthy *et al.* 1992, 1993; McCarthy, 1993). However, up to now there has not been an agreed set of procedures aimed at generating accurate food consumption rates. In an attempt to advance work in this area we have assembled in Table 1 an outline of the steps that we have found useful when using radiography to measure food consumption rates of individual fish. Two particulate markers have been used in radiographic studies, ballotini

Table 1. *Outline of protocol for the successful use of X-radiography to measure individual consumption rates of fish*

1. Ideally the labelled diet should be prepared in the same way and have the same nutritional composition and physical texture as the normal diet. This is easily achieved if experimental diets are being prepared but is more problematic if commercial diets have to be repelleted. In the latter case the unlabelled food should be treated in the same way as the ballotini-labelled food and also repelleted
2. A calibration curve must be provided for each batch of labelled diet. This is obtained by X-raying known dry weights of food and counting the number of glass beads contained in the diet. A regression line can then be constructed relating number of ballotini to an estimated dry weight of food. The range of food weights X-rayed must be sufficient to cover the range of anticipated meal sizes taken by the fish
3. On the day selected for the radiographic measurement of consumption, the labelled diet should be supplied at the same time, for the same duration and in exactly the same way as the normal diet. X-ray measurements of consumption should be made at regular intervals during the course of the experiment
4. Once consumed, the glass ballotini must be retained in the gut until the fish are X-rayed, since any loss of the marker will result in an underestimation of consumption; therefore, the time-interval between the initiation of feeding and X-raying must be short enough to prevent defecation of ballotini but long enough to allow the food to settle in the stomach to avoid regurgitation of the stomach contents by the fish during anaesthesia. A period of 60 min is usually long enough to avoid the latter problem. The time taken for glass beads to be evacuated from the gastrointestinal tract should be determined for each species under the experimental conditions
5. After the feeding period, the fish are removed from the tank, anaesthetized and placed in a Perspex tray with compartments for individual fish. The fish are X-rayed and individual fish identified, weighed and returned to a recovery tank. The number of fish removed from the tank and X-rayed in each batch will be dependent on the size of fish, the size of film used and the cone of illumination of the X-ray. Whilst exposed to the X-ray, an adequate level of anaesthesia is necessary to ensure the fish remain still during the X-ray and prevent a blurred image
6. After development of the radiographs the number of ballotini present in the gastrointestinal tract of the fish are counted and the amount of food eaten by the individual estimated from the calibration curve. The moist weight of food consumed by each fish is then subtracted from the measured wet weight of the fish and the weight-specific consumption rate calculated (mg dry food/g wet weight per d)

glass beads and Fe particles. In the present paper we focus on the use of ballotini glass beads, although the protocol discussed here will also apply to the use of Fe particles. The construction of a nutritional experiment which includes the use of radiography will be similar to a standard nutritional trial. Groups of individually numbered fish acclimatized to the conditions are set up and maintained on a constant feeding regimen for the course of the experiment. Fish can be fed one meal daily (e.g. Carter *et al.* 1992*a*; McCarthy *et al.* 1992) or continuously over 24 h (e.g. Jobling *et al.* 1989; Jørgensen & Jobling, 1992) provided point 4 in Table 1 is met.

The inclusion of the radio-opaque marker in the diet and the pelleting process must not reduce the palatability of the diet to the degree that pellets are rejected or the results will underestimate the feeding rates of the fish on the normal diet (Table 1, point 1). Studies in our laboratory have indicated that for rainbow trout (*Oncorhynchus mykiss* (Walbaum)) the inclusion of ballotini beads in the diet does not alter the palatability of the diet (McCarthy *et al.* 1992; McCarthy, 1993, unpublished results; K. Moutou, unpublished results). Changes in palatability can be assessed by recording the weights of labelled and unlabelled food eaten by a group of fish on consecutive days. This can be achieved by noting that each pellet dropped into the tank is eaten before the next is

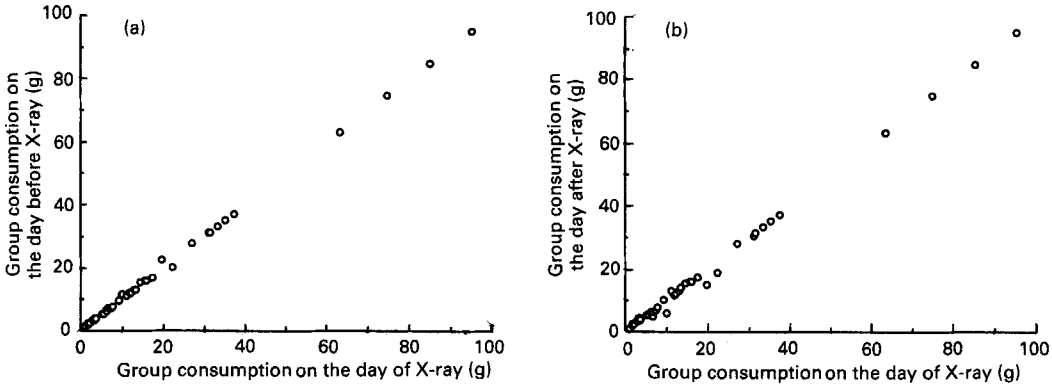

Fig. 1. The relationship between the total amount of ballotini-labelled diet eaten by groups of rainbow trout (*Oncorhynchus mykiss* (Walbaum)) on the days that consumption was measured using radiography and the amount of food eaten by each group on (a) the day before and (b) the day after X-raying. Linear regression coefficients are given as means with their standard errors: (a) $Y = 0{\cdot}999$ (SE $0{\cdot}004)X + 0{\cdot}176$ (SE $0{\cdot}108$), R^2 $0{\cdot}999$, n 53, $P<0{\cdot}001$, (b) $Y = 0{\cdot}999$ (SE $0{\cdot}007)X - 0{\cdot}171$ (SE $0{\cdot}176$), R^2 $0{\cdot}998$, n 53, $P<0{\cdot}001$.

added. The results from many such experiments are shown in Fig. 1. The intercepts for both regression lines were not significantly different from zero (t test) and the slopes were not significantly different from one (analysis of covariance). No difference was found in the total ration consumed by each group on any of the 3 d, indicating that there is no difference in the palatability of the labelled diet compared with the normal experimental food.

Before each batch of ballotini-labelled diet is used in a nutritional study, a calibration line must be determined (Fig. 2(a) and Table 1, point 2). The concentration of glass beads incorporated into the diet and the size of ballotini used will be governed by the size of fish and the expected consumption rates, and will also be influenced by factors such as the tank ration and water temperature. Ideally each pellet should be labelled with several ballotini in order to give confidence in the consumption estimates. However, if the meal sizes taken by the fish are large or the level of incorporation of ballotini is high there will be large numbers of ballotini in the gastrointestinal tract. This may result in errors in the calculation of consumption due to ballotini superimposed on each other on the radiograph or due to human error in counting the number of ballotini present. We suggest that fish should have no more than 100–150 ballotini present in the gastrointestinal tract when measuring consumption. The advantage in using glass ballotini is that beads are available in a variety of sizes with an average bead diameter ranging from 30 μm (size 20) to 1280 μm (size 3). There is no size grading of Fe particles and samples need to be sieved before use. Increasing the bead size allows the level of incorporation to be kept constant when larger pellets are produced and also allows control over the number of ballotini that will be present in the gastrointestinal tract. The advantage in preparing a calibration line such as that shown in Fig. 2(a) in advance of feeding the diet to the fish is that it enables verification of concentration and homogeneity of distribution of the ballotini. It is important that the number of pellets containing no ballotini is low or zero. In the diet shown in Fig. 2(a), only nine pellets of the 398 X-rayed were unlabelled, i.e. 2·3% of the diet (Fig. 2(b)) and on average four ballotini were found in each pellet. In their original work, Talbot & Higgins (1983) found that the apparent gut contents,

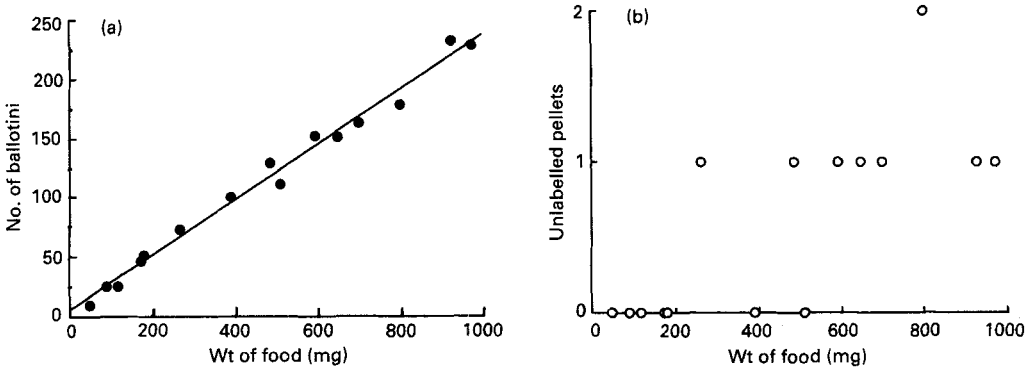

Fig. 2. (a) A calibration line showing the relationship between known dry weights of food labelled with size 9 ballotini glass beads (290–420 μm) at an incorporation level of 20 g/kg and the number of ballotini glass beads contained within each sample. Linear regression coefficients are given as means with their standard errors: $Y = 0{\cdot}232$ (SE $0{\cdot}007)X + 4{\cdot}981$ (SE $3{\cdot}952$), R^2 $0{\cdot}988$, n 15, $P<0{\cdot}001$. (b) Scatter plot showing the number of unlabelled food pellets in each of the food samples used to obtain the calibration line.

Table 2. *Consumption of ballotini-labelled food, estimated from radiographic data expressed as a percentage of the food hand-fed to fish*

(Mean values with their standard errors)

Species	Mean	SE	*n*	Range	Diet	Reference
Atlantic salmon (*Salmo salar* L.)	93·0	1·45	8	91–99	P	Carter *et al.* (1992*a*)
Rainbow trout (*Oncorhynchus mykiss* (Walbaum))	94·2	0·85	9	91–98	R	McCarthy *et al.* (1992)
Rainbow trout	94·3	1·67	9	88–101	R	McCarthy (1993)
Rainbow trout	95·2	2·29	6	89–105	R	I. D. McCarthy (unpublished results)
Rainbow trout	96·1	1·47	16	87–106	R	K. Moutou (unpublished results)
Rainbow trout	96·2	0·52	26	90–100	P	W. M. K. Perera (unpublished results)
Rainbow trout	98·6	0·36	19	95–100	P	W. M. K. Perera (unpublished results)

P, pelleted once; R, repelleted commercial diet.

calculated from the X-ray estimates, and the actual gut contents, calculated from the dry weight of food in the stomach, were virtually identical. In radiographic studies where fish are hand-fed and the amount of food consumed by a group of fish on the day of X-ray is known, it is possible to assess the accuracy of the technique by comparing this with the total group ration calculated from the radiographs. The results for several studies on salmonid fish are shown in Table 2 and indicate that on average 95% of the food fed to each group could be accounted for from the radiographic data.

When repeated measurements of consumption are to be made during an experiment, the time interval between X-rays must be sufficient to ensure that the fish recover from the handling stress and resume their normal feeding patterns. This also allows all the ballotini to be evacuated from the gut to avoid overestimation of consumption on

Table 3. *Consumption (mg feed/d) by Atlantic salmon (*Salmo salar *L.) on consecutive days (days 1 and 2) measured using X-radiography; the second day's consumption expressed as a percentage of the previous day's consumption (Per) and the correlation (r) between the meal size of individual fish on subsequent days*

(Mean values with their standard errors)

	Feed consumption							
	Day 1		Day 2		Per			
Tank	Mean	SE	Mean	SE	Mean	SE	*n*	*r*
1	255·1	13·6	178·3	10·1	74·0	4·2	40	0·534*
2	220·6	13·0	167·7	7·9	82·7	4·6	45	0·512*
3	190·2	11·2	135·3	8·8	77·2	5·6	44	0·433*
All	221·3	7·6	160·5	5·5	78·0	2·8	129	0·469*

* $P<0·001$.

subsequent occasions. In rainbow trout, the handling stress from the X-ray procedure does not affect the total amount of food eaten by the group on the day following radiography (Fig. 1(b)). However, it appears that this response to handling may be species-specific. In a recent study on the feeding behaviour of Atlantic salmon, (*Salmo salar* L.) radiographic measurements of consumption were made for three groups on consecutive days using diets labelled with different size ballotini (C. G. Carter, unpublished results). The results indicated a general suppression of appetite on the second day and average consumption rates were 22% lower following handling than the amount of food eaten on the first day (Table 3). However, the amount of food eaten by an individual fish on the 2 d was significantly correlated, indicating that the reduced consumption was not attributable to a change in the feeding rank of an individual within the group (Table 3). In order to minimize the disturbance to the fish due to handling and yet obtain several estimates of consumption during a growth trial, X-rays have been taken at intervals of between 1 and 4 weeks depending on the species under examination (Jobling *et al.* 1989; Carter *et al.* 1992*a*,*b*; McCarthy *et al.* 1992). X-radiography is unlikely to be any more stressful than routine anaesthesia and weighing of fish and in previous studies in our laboratory there have been no mortalities associated with the radiographic procedure (Carter *et al.* 1992*a*,*b*; McCarthy *et al.* 1992). The advantage of this technique is that it can be easily incorporated into the routine weighing of fish carried out to obtain growth rates during nutritional experiments.

APPLICATIONS OF THE RADIOGRAPHIC TECHNIQUE

The measurement of food consumption of individual fish in a group has enabled the feeding behaviour of both individual fish and groups of fish to be studied in the laboratory. Field measurements are also possible and portable X-ray machines have enabled feeding studies to be carried out on Atlantic salmon in cages at sea (Thorpe *et al.* 1990). When individual consumption rates are known it is possible to examine the feeding behaviour of fish and to compare the nutritional status of an individual fish with its physiological performance.

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FEEDING BEHAVIOUR

Radiography has been used over the last 10 years to examine the feeding behaviour and consumption rates of fish exposed to a variety of conditions. Diurnal and seasonal variation in consumption rates of salmonid fish have been measured (Talbot & Higgins, 1983; Higgins & Talbot, 1985; Jørgensen & Jobling, 1989, 1992; Pálsson *et al.* 1992). Feeding modes have been studied in Atlantic salmon and Arctic charr (*Salvelinus alpinus* L.) and differences between the proportion of food eaten in the water column and that foraged from the bottom has been reported for these two species (Jørgensen & Jobling, 1990, 1992). Atlantic salmon feed predominantly from the water column while Arctic charr take a substantial proportion of food from the bottom. These results have important implications for the culture of both species. Commercial salmonid culture is predominantly carried out using sea cages and it has been suggested that differences in feeding behaviour and food acquisition between Atlantic salmon and Arctic charr may partly explain the inferior growth performance of charr reared in floating pens compared with those reared in on-shore tanks (Jørgensen & Jobling, 1990). Radiography has been used to measure food consumption of Atlantic salmon in a sea cage over 24 h and to compare the efficiency of two feeding systems (Thorpe *et al.* 1990). Food was distributed to the cage using both sources: (a) automatic feeders that drop food into a localized part of the cage every 15 min during the hours of daylight and (b) hand-feeding of the fish three times daily, to apparent satiation, defined as the time when no more fish rose to the surface when food was offered. The results indicated that approximately 67% of food eaten by the fish was from hand-feeding and 33% from the automatic feeders. The amount of food wastage from hand-feeding was 1·4% compared with 40·5% from the automatic feeders. Hand-feeding resulted in the food being distributed over the whole cage surface and enabled a greater proportion of the fish to feed and a more even distribution of food between fish. Therefore, radiography has valuable applications in devising effective feeding strategies for commercial aquaculture.

Behavioural work on salmonids have shown that dominant individuals within a group gain preferential access to food and maintain higher feeding rates compared with subordinate fish (Metcalfe *et al.* 1989). This will result in a disproportionate distribution of meal sizes, expressed as share of the group meal (McCarthy *et al.* 1992), between individual fish within a group on any given day (Fig. 3). It is important that this share of the group meal is calculated as a proportion of the total amount of food eaten by the group calculated from the radiographic data. When repeated radiographic measurements of consumption are made, the mean share of the group meal (MSM) of each fish over the course of the experiment can be calculated. This average meal size has been used as a measure of dominance to assign social rank to individual fish in several studies (Carter *et al.* 1992*b*; McCarthy *et al.* 1992). MSM has recently been found to correlate with brain serotonergic activity (Winberg *et al.* 1993), another indicator of social rank in fish (Winberg *et al.* 1991). The advantage of using feeding behaviour to assign dominance is that it enables the assessment of social hierarchies in larger groups of fish than is possible using the standard approach of observing aggressive interactions between individuals. The distribution of food between individuals within a group and the strength of the social hierarchy will be dependent on the availability of food (Symons, 1968; McCarthy *et al.* 1992; Olla *et al.* 1992). This is demonstrated in Fig. 3; as ration size increased, the range of meal sizes taken by individual fish within the group decreased. The values for the

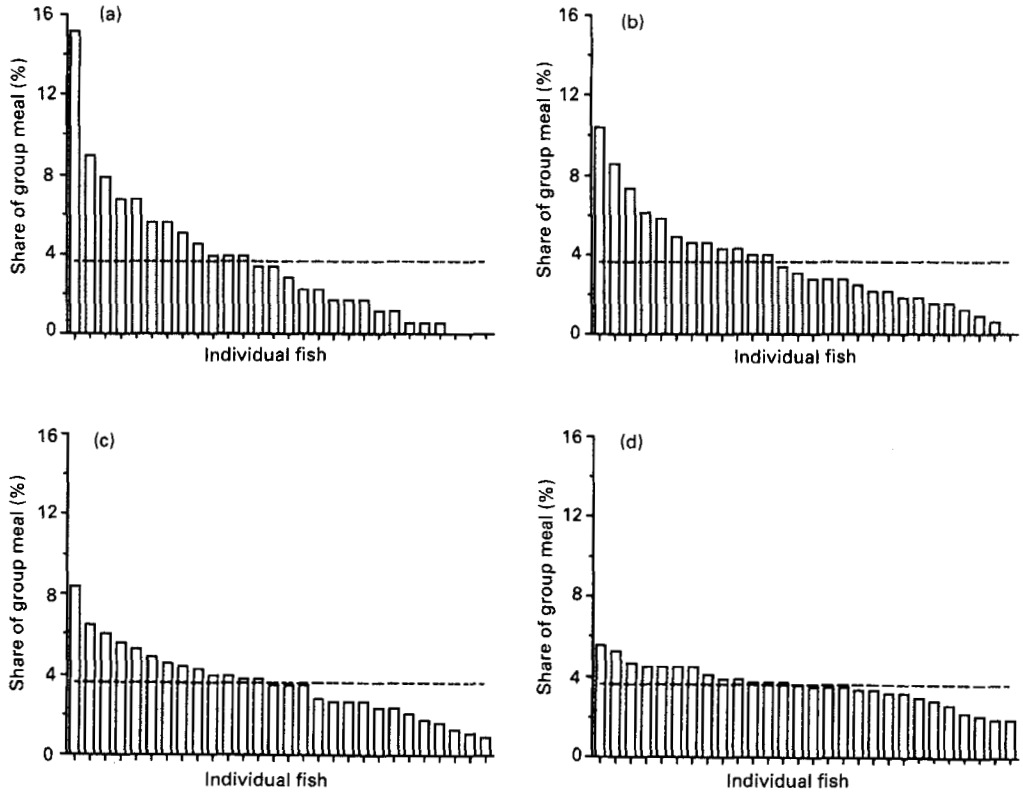

Fig. 3. The effect of ration size on the distribution of meal sizes eaten by individual fish in four groups of rainbow trout (*Oncorhynchus mykiss* (Walbaum)). The values presented in (a)–(d) are for groups receiving 2·5, 5, 10 and 15 g/100 g body weight per d rations respectively fed in a single daily meal. (– – – –) An equal distribution of food between individuals within the group. The coefficients of skewness for each ration group were: (a) 1·55, (b) 1·05, (c) 0·67, (d) 0·01. (Data from K. Moutou, unpublished results.)

coefficients of skewness provide a quantitative demonstration that as ration size increased, the distribution of meal sizes between individual fish became more even.

Repeated radiographic measurements have also been used to examine the day-to-day variation in consumption by individual fish within a group (McCarthy *et al.* 1993). This variability has been quantified using the coefficient of variation for consumption (CV_c) (McCarthy *et al.* 1992). This is calculated from the weight-specific consumption data (mg dry food/g wet body weight per d) using the equation CV_c = (standard deviation × 100)/mean. A high CV_c indicates that an individual fish has a highly variable daily consumption. A significant negative correlation between MSM and CV_c has been reported for groups of fish (McCarthy *et al.* 1992) with dominant fish showing less day-to-day variation in feeding rates. Subordinate fish appeared to be more erratic and opportunistic in their daily feeding. The relationship between MSM and CV_c for two groups of Atlantic salmon is shown in Fig. 4. Although the fish in both groups were of a similar size and under the same feeding regimen, both the range of meal sizes and the

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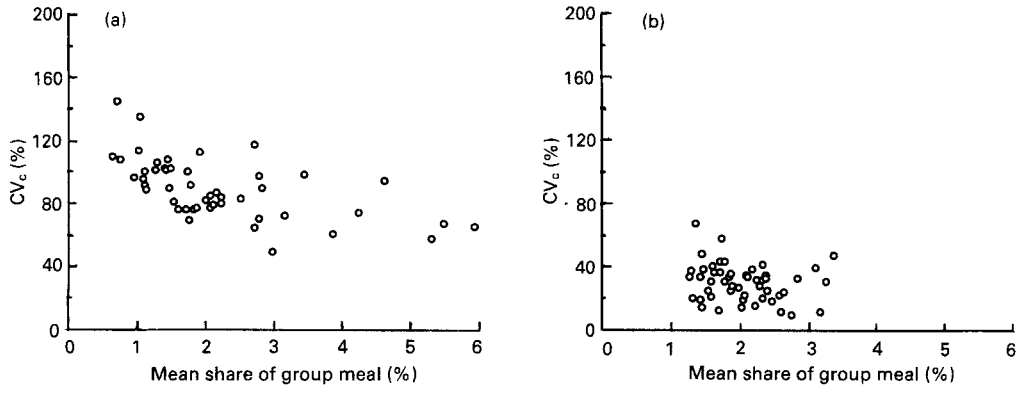

Fig. 4. The relationship between the mean percentage share of group meal and the coefficient of variation for weight-specific consumption (CV_c) for two groups (a, b) of Atlantic salmon (*Salmo salar* L.). Spearman rank correlation coefficients were : (a) −0·600 (*n* 48; $P<0·001$), (b) −0·181 (*n* 50; not significant). (Data from C. G. Carter, unpublished results.)

range of individual values for CV_c were significantly different for the two groups indicating that the strength of the social hierarchy, inferred from the correlation coefficient, varied between the two groups. Previous studies have shown that the strength of the social hierarchy can vary between groups of fish given the same treatment (Symons, 1968; Winberg *et al.* 1992, 1993). Under these conditions, it appears that the strength of the social hierarchy is dependent on the particular individuals present in the group and the differences in competitive ability and aggression between individuals in each group.

CONSUMPTION–GROWTH RELATIONSHIPS

The construction of consumption–growth relationships using individual fish as the unit of analysis is made possible by radiography. Consumption and growth have been measured as wet (growth only) and dry weight (Christiansen & Jobling, 1990; McCarthy *et al.* 1993; Carter *et al.* 1994) and in terms of C and N (Carter *et al.* 1992*a*) and protein (Carter *et al.* 1993; McCarthy, 1993). Since body composition can vary and 'real' growth is achieved by protein accretion it is preferable to use measures of protein or N. Such relationships can be exploited to investigate differences in, for example, protein turnover (see below) or the effect of experimental variables such as stocking density or feeding regimen on groups of fish (Christiansen *et al.* 1992; Jørgensen & Jobling, 1992; Jørgensen *et al.* 1993). This approach has also been used for nutritional studies in order to compare different diets fed to salmonids (e.g. Carter *et al.* 1992*a*, 1994; W. M. K. Perera, unpublished results). Analysis of variance of the consumption–growth curves of salmonids fed on diets with or without supplementary enzymes has shown that enzyme supplementation elicits increased growth rates (Carter *et al.* 1994). This procedure has also been used to compare the growth rates of Arctic charr swimming at different speeds and a significantly higher elevation for fish swimming at 2·0 body lengths/s compared with at lower speeds demonstrated greater growth for the same food intake at this speed (Christiansen & Jobling, 1990).

PROTEIN TURNOVER AND NITROGEN BUDGETS

Recently radiography has been used to correlate individual differences in protein metabolism with protein consumption rates for fish reared in groups (McCarthy, 1993; Carter *et al.* 1993). The measurement of individual consumption rates allows the protein growth efficiency (g protein deposited/g protein eaten) to be calculated for each fish and compared with rates of protein synthesis and degradation. Recent studies have shown that increased protein growth efficiency in fish is attributable to reduced rates of protein turnover and an increased retention of synthesized protein as growth (Carter *et al.* 1993; McCarthy, 1993). Combined with measurements of digestibility, N budgets for fish receiving different diets have been constructed (Carter *et al.* 1993). These analyses will prove valuable in studying the effect of diet composition on nutrient partitioning in fish. If individual differences in growth efficiency can be shown to have a genetic basis, whether through control of maintenance expenditure or of degradation, they will have important implications for the selection of genotypes that make efficient use of dietary protein.

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