The relationship between individual consumption and growth in juvenile turbot, *Scophthalmus maximus*

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Abstract

The development of feeding hierarchies was investigated in juvenile turbot, *Scophthalmus maximus* (Rafinesque) held at two rearing densities for 82 days. Individual biometrics were measured on five occasions and a diet labelled with ballotini glass beads was used in combination with a noninvasive radiographic technique to estimate consumption rates. The results demonstrate that the inclusion of the radio-opaque glass beads in the diet did not significantly reduce consumption by turbot. A significant relationship was found between individual consumption and growth of juvenile turbot. A weight differential within groups increased with time and was largely explained by inter-individual variation in food consumption. This differential was driven by an uneven distribution of food within groups, where individuals of a higher weight than the group average consistently consumed a greater than average share of the group meal, and showed less day to day variation in consumption than their smaller counterparts. The results demonstrate that in captive turbot groups, size hierarchies are mediated, at least in part, through inter-individual differences in food consumption. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Differential food consumption; Growth; Growth variation; Turbot; *Scophthalmus maximus*; Radiography

1. Introduction

Differential growth rates in captive fish groups have been reported in recent years for fish of several species (Koebele, 1985; Jobling and Baardvik, 1994; Carter et al., 1996),

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including turbot (*Scophthalmus maximus*, Rafinesque) (Howell, 1998; Irwin et al., 1999). Many investigations into the causative effects of such intraspecific variation in growth have been undertaken, particularly with commercially important species in aquaculture, where uniform sized fish groups are desirable (Irwin et al., 1999). Commercial rearing practises such as manipulation of rearing density and size grading are known to effect the emergence of size variability in captive turbot groups (Sunde et al., 1998; Irwin et al., 1999). Some variations in growth can be attributed to genetic differences in growth potential between individuals (Volpato and Fernandes, 1994; Imsland et al., 1997) but social interactions, particularly intraspecific competition for food, and physiological differences between individuals are believed to be a major contributor to differential growth (Jobling, 1985; Koebele, 1985).

In many species, differential growth arises where food is limiting and there is monopolisation of food resources by a small number of dominant individuals (Carter et al., 1996), with the relationship between consumption and growth being well documented (Tuene and Nortvedt, 1995). Dominant individuals within feeding hierarchies consume a disproportionate share of a group meal either by acquiring a larger portion of the ration first, or by behaviourally inhibiting a subordinate's feeding behaviour (Koebele, 1985). In other cases, however, differences in individual growth persist even where food supply does not appear limiting (Abbott and Dill, 1989), and physiological differences between individuals, based on their social rank or the stress associated with subordinance, lead to differential growth regardless of food availability.

The development of a noninvasive X-radiographic technique (Talbot and Higgins, 1983; McCarthy et al., 1993) for measuring food consumption by fish has greatly facilitated the investigation of meal apportionment among individual fish within groups. This method involves the use of a specially formulated diet labelled with a radio-opaque marker being fed to the fish in the same way as the normal food. Subsequent radiography allows for calculation of individual consumption rates. This noninvasive technique permits repeated measures of food consumption rates of individual fish, and measures of food distribution patterns within groups, without any alteration in feeding regimen, and has been put into practise in several investigations (McCarthy et al., 1992; Jobling et al., 1995a; Carter et al., 1996). It is a particularly useful tool in investigations of food distribution within groups and the determination of the relationship between food intake and individual growth rates (Jobling et al., 1995b).

Here, we adapt and use this radiographic technique to describe the development of size hierarchies within groups of juvenile turbot. Additionally, we set out to describe the consumption–growth relationship for juvenile turbot, and to evaluate the importance of disproportional food consumption in mediating growth depensation.

2. Materials and methods

Individual consumption rates were measured in this study using an adapted version of the X-radiographic method first described by Talbot and Higgins (1983) and further refined by McCarthy et al. (1993). Preliminary trials were carried out to validate the use of this method with juvenile turbot. Radiographs were taken of the gastro-intestinal

tracts of 10 juvenile turbot that had been fed labelled food. These fish were then fed a nonlabelled commercial diet for a further 6 days when second radiographs were taken. It was established that all ballotini beads were evacuated from the gastro-intestinal tract of juvenile turbot within this period. The effect of ballotini incorporation and repelleting of the food was investigated in a 6-day long trial designed to assess differences, if any, in consumption of the labelled feed compared to the commercial diet. The first treatment group was fed the commercial feed and a second was fed the labelled feed throughout the trial. A third group was fed the commercial feed for 2 days, then switched to the labelled feed for 2 days and then returned to the commercial feed for the final 2 days. In this preparatory phase three replicate tanks were used for each of the three treatments, and each tank held eight fish.

Ninety juvenile turbot (mean weight ± s.d., 26.72 ± 0.29 g) were used in this study and all of these were individually marked with a unique colour code on the ventral surface using a subcutaneous injection of alcian blue dye (Sigma). The turbot were divided between four 500-l tanks at two densities; density A comprised 14 and 16 individuals per tank, and density B, 30 individuals per tank. These were equivalent to initial biomass stocking densities (mean ± s.d.) of 0.39 (0.02) and 0.77 (0.01) kg/m^2 of the tank bottom, respectively. The mean seawater temperature was 20.1 (2.3)°C and photoperiod was 12 h light:12 h dark. The fish were fed at a rate of 1.5% body weight per day spread over three meals, initially with 3.5-mm pellets and later, as fish grew, with 5.0-mm pellets.

Labelled food for use with X-radiography was prepared by reconstituting the standard feed with 4% by weight ballotini glass beads (size 8, 400–520 µm, Jencon's Scientific). Two batches were prepared, one of 3.5-mm pellets and one of 5.0-mm pellets. A calibration curve was plotted for each size batch by taking radiographs of known quantities of labelled food and correlating the number of glass beads recovered with the weight of the food. On test days (16, 44, 67 and 82), labelled feed was presented to the fish in the same manner as the standard diet was presented on all other feeding occasions. One hundred minutes after feeding, the fish were anaesthetised in 20% Benzocaine and placed on an X-ray plate (Kodak ultra speed film, ds-50, 57 × 76 mm). X-radiographs were taken at a film focal distance of 80 mm using a Premadent Mark 2 X-ray unit (60 KVp, 1.4 mA). This length of time was deemed appropriate during preliminary investigations, with turbot of this size (Irwin, 1998) being short enough to preclude defecation of the ballotini beads, but long enough to prevent regurgitation during handling. Weights and lengths of individual fish were then measured. Following the development of X-ray plates, two independent observers counted the number of radio-opaque beads in the gastrointestinal tract of each fish.

Data analysis was carried out using only data for fish where a complete record of food consumption and growth were available. The increase in variability in fish weight was estimated using the coefficient of variation for weight (CV_w), and in food consumption using the coefficient of variation for the share of meal consumed (CV_{sm}), using the formula $CV = 100 \times$ standard deviation/mean. Specific growth rate (SGR, %/day) was calculated according to the formula $SGR = 100 \times (\ln w_t - \ln w_i)/t$, where t is the time interval in days, w_i is the initial weight and w_t is the weight at time t (g). Food consumption was expressed as weight-specific food intake (C) (mg/g/day), and

was calculated by first subtracting the weight of food consumed from the wet weight of each individual fish. The share of the meal (SM) (%) consumed by each individual fish on each radiographic occasion was calculated as a proportion of the total amount eaten by the group and following repeated measurements of food consumption the mean share of group meal (MSM) was calculated (McCarthy et al., 1992). Differences between the regressions of rank (assigned using MSM) and growth (SGR) were tested using analysis of covariance (ANCOVA). The relationship between the weight of an individual and the share of meal consumed was investigated using Spearman's rank correlation coefficient. A one-way ANOVA, following a normality test and Levene's F-test for homogeneity of variance, was used to identify significant differences between groups. Percentage data was transformed using an arcsine transformation before analysis. All analyses were carried out using SPSS for Windows (Release 7.0, SPSS, 1989–1995).

3. Results

Each of the 90 experimental turbot was X-radiographed four times. A total of 27 X-radiographs of ballotini-labelled food were also taken for use in construction of calibration curves. The calibration curves revealed that for the 3.5-mm pellets,

$$W = 0.02\,P\,(R = 0.86,\ df = 13,\ P < 0.01)$$

and for the 5.0-mm pellets,

$$W = 0.02\,P\,(R = 0.96,\ df = 9,\ P < 0.01),$$

where W = weight of food (g) and P = number of pellets. The mean number of ballotini beads per pellet was 2.2 (0.1) in the 3.5-mm feed and 5.1 (0.2) in the 5.0-mm feed. During the preliminary trial, daily consumption, measured as the percent fish biomass per tank, was similar for labelled and nonlabelled food. No significant differences were found in the food consumption (%body weight/day) between any of the treatment groups ($F_{2,24} = 1.00$, NS). There was a positive correlation between the amount of food delivered to each tank (Fd) and the amount recovered using X-radiography (Fr) (Fr = 0.76Fd + 0.69; $r = 0.95$, $df = 13$, $P < 0.01$) and the proportion of food fed to each tank recovered on each radiographic occasion was $88.8 \pm 18.2\%$.

The mean weight of all experimental fish at the beginning of this study (day 0) was 26.7(0.3) g and at the conclusion, on day 82, was 85.4(3.0) g. The mean specific growth rate over the experimental period was 1.42%/day. Final stocking densities were 1.5 (0.3) and 2.8 (0.3) kg/m². The coefficient of variation for weight (CV_w, %) increased in all turbot groups over the 82 days of the experiment (Fig. 1).

The relationship between food intake and growth was investigated using the specific growth rate (%/day) and individual consumption rate (mg/g/day) (an average of four measurements). There was an extremely significant positive correlation between these two variables ($r = 0.59$, $df = 82$, $P < 0.01$).
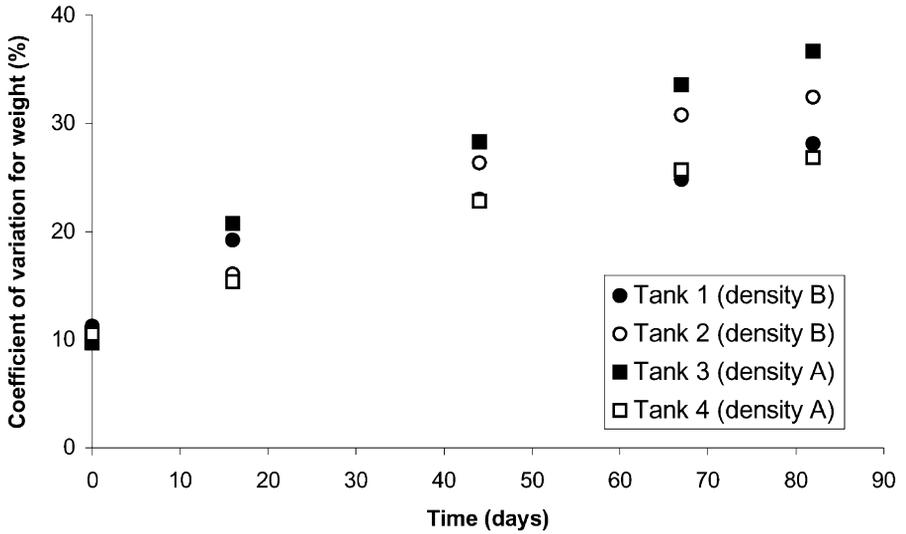
Fig. 1. The increase in the coefficient of variation for weight (CV_w, %) in tanks of juvenile turbot at two different densities (density A = low density, density B = high density).

The distribution of food among individuals within tanks was assessed by examining the range of meal sizes consumed by the individual fish within tanks on each radio-
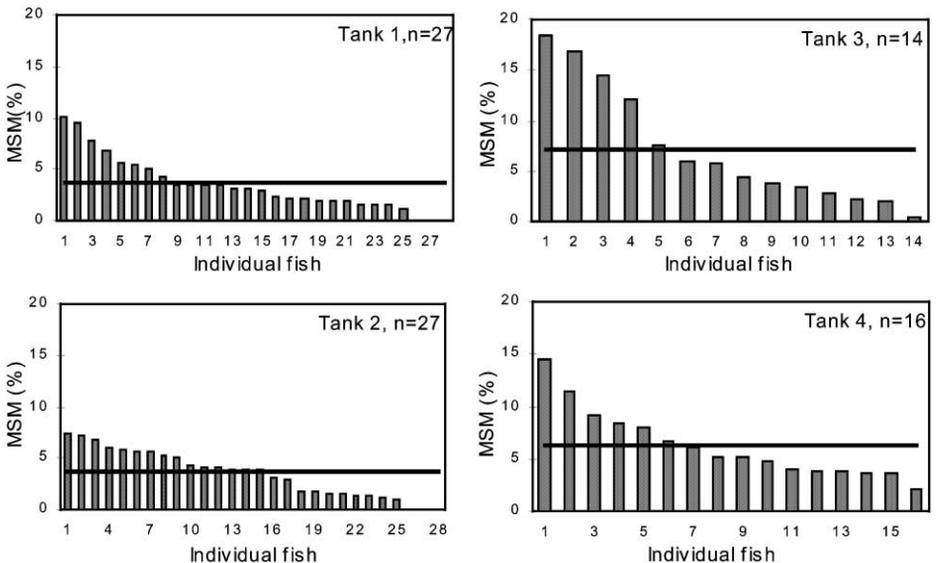

Fig. 2. The distribution of group meals between individual turbot in four different tanks on the final radiographic occasion (day 82). The horizontal lines represent the mean meal sizes of separate tanks of fish. (MSM = mean share of group meal).

Table 1
Relationships between individual fish weight (g) and the share of group meal consumed (%) by juvenile turbot.
Spearman's rank correlation coefficient values with corresponding significance levels (NS = not significant).

Tank	X-radiographic occasion				Overall
	1	2	3	4	
1	0.225	0.713	0.372	0.402	0.122
$n = 27$	NS	$P < 0.01$	NS	$P < 0.05$	NS
2	0.476	0.585	0.446	0.543	0.336
$n = 27$	$P < 0.05$	$P < 0.01$	$P < 0.05$	$P < 0.01$	$P < 0.01$
3	0.415	0.474	0.407	0.604	0.175
$n = 14$	NS	NS	NS	$P < 0.05$	NS
4	0.349	0.227	0.480	0.345	0.063
$n = 16$	NS	NS	NS	NS	NS

graphic occasion (an example from one radiographic occasion is shown in Fig. 2). The share of the group meal (SM, %) consumed by individual fish ranged from 0.0% to 18.4%. The relationship between the weight of an individual and the share of meal on each measurement occasion are summarized in Table 1. The correlations between these two variables, when significant, were always positive, and the correlation coefficient ranged from 0.063 to 0.713. As the coefficient of variation for fish weight (CV_w) increased, so too did the coefficient of variation for share of the group meal (CV_{sm}), thus
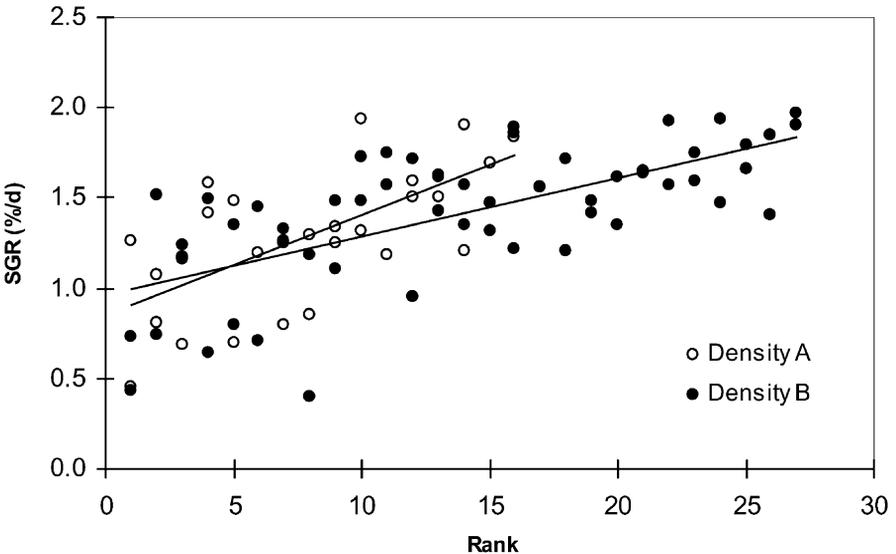

Fig. 3. The relationship between feeding rank, assigned using MSM (%) and specific growth rate (SGR, %/day) of juvenile turbot at two densities (density A = low density, density B = high density).
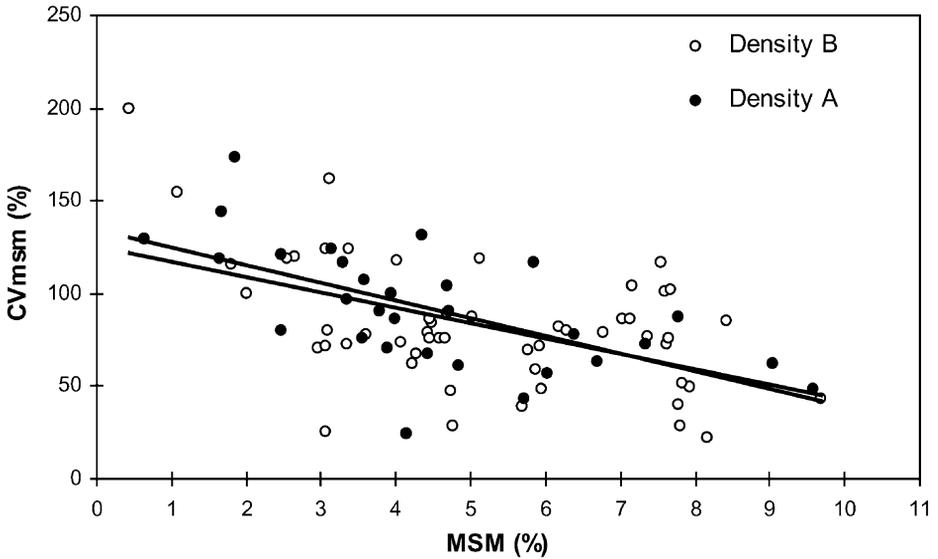
Fig. 4. Plot of the relationship between inter-individual (MSM, %) and intra-individual (CV$_{sm}$, %) variability in food consumption in juvenile turbot reared at two different densities (density A = low density, density B = high density).

augmenting the effect of time on CV$_w$. The relationship between these two variables was described by the equation:

$$CV_{sm} = 4.06CV_w - 9.22$$

$$(R^2 = 0.36, df = 14, P < 0.05).$$

When the mean share of the group meal (MSM) was used to assign feeding rank to individual fish, there was a linear correlation between growth (SGR) and rank in both density groups (density A: Rs = 0.66, $n = 30$, $P < 0.01$; density B: Rs = 0.64, $n = 54$, $P < 0.01$) (Fig. 3). There was, however, a significant difference between these two regression lines ($F_{1,80} = 19.37$, $P < 0.001$), demonstrating that growth increased more rapidly with tank in density A).

Inter-individual differences in food consumption were assessed using the mean share of the group meal (MSM) consumed by individual fish, and intra-individual variation in food consumption was assessed using the coefficient of variation for food intake (CV$_{sm}$). Highly significant negative correlations between MSM and CV$_{sm}$ were seen in both density groups (density A Rs = −0.68, $P < 0.01$; density B Rs = −0.39, $P < 0.01$) (Fig. 4).

4. Discussion

The radiographic method of measuring consumption employed in this study was found to be very reliable in measuring gut content of turbot. There was no loss of tag

marks during the course of the study and all X-radiographs taken were suitable for use in analysis. The recovery of food delivered to each tank was very high (almost 90%) and inclusion of the radio-opaque marker did not reduce consumption. These are important considerations in the use of this technique to investigate individual consumption rates and meal distribution.

Growth performance was similar in both density groups and intraspecific variation in growth (CV_w) increased through the 82 days of this study (Fig. 1). This pattern is widely reported for cultured fish populations (Purdom, 1974; Jobling and Reinsnes, 1986) where, as average weight increases, the relative difference between the largest and the smallest members also increases. The increase in CV_w was not linear, but increased rapidly at first and then began to level off over time. The initial rapid increase suggests that there may have been high levels of competition during a period of hierarchy formation, which then decreased as the group became more stable, similar to the situation reported for wild caught turbot held in the laboratory (Purdom et al., 1972). Although such an increase in weight frequency distributions over time within groups of fish has been well documented, the exact mechanisms involved are not well understood, but differential consumption is believed to be a major contributing factor (Carter et al., 1996).

A consumption–growth relationship for juvenile turbot using data from individual fish has not been previously described, and in this study a strong positive correlation was seen between the two, as is often reported for fish (Brett, 1979). As food consumption increases so does growth, a situation similar to that reported for many fish species including rainbow trout, *Oncorhynchus mykiss*, (McCarthy et al., 1991) and flounder *Rhombosolea taparina*, (Carter et al., 1996) and Atlantic halibut, *Hippoglossus hippoglossus*, (Tuene and Nortvedt, 1995).

Given the positive correlation between individual consumption and growth rates, the range of meal sizes consumed by a group of fish is an important factor governing the degree of size variation within a group. Fig. 2 demonstrates the large spread of meal sizes consumed by individual turbot and shows that certain individuals, particularly in the tanks stocked with 30 fish, were seen not to consume any food. This effect of fish density was also seen to affect growth variation in turbot held at four different densities, where those held at the highest density showed the highest inter-individual growth variation (Irwin et al., 1999). The range of meal sizes can be affected not only by the number of fish competing for a resource, but equally by an increase in the availability of food (McCarthy et al., 1992; Jobling et al., 1995a). The spread of meal sizes within a group, as described by the coefficient of variation for the share of meal (CV_{sm}), was also seen to increase over time as the fish grew, and was positively correlated with the coefficient of variation for weight (CV_w). These results demonstrate the mechanism for increased growth variation over time; as growth variation increases, so too does meal apportionment, thus magnifying the size hierarchy effect. The relationship between the weight of individual fish on each radiographic occasion and the mean share of the meal consumed (Table 1) indicates that in the majority of cases, the larger fish consumed a greater share of the group meal and consequently grew more than the smaller fish, thus augmenting any existing size variation over time. This is further exemplified by the observed relationship between feeding rank (assigned using MSM (%)) and SGR (%)

(Fig. 3), where it appears that available food resources are monopolised by a number of individuals with a high weight relative to the group mean weight. Higher-ranking individuals in this respect showed higher specific growth rates than their lower-ranking counterparts. Together, these results suggest that differences in consumption between large and small turbot within groups explain, at least in part, the increase in CV_w over time as previously described (Howell, 1998; Sunde et al., 1998; Irwin et al., 1999).

There was a highly significant negative correlation between inter-individual and intra-individual variations in food consumption. This suggests that those individuals obtaining a larger share of the group meal show less day-to-day variation in consumption, than their counterparts that obtain a smaller share of the meal. This is considered indicative of the formation of feeding hierarchies within groups (Carter et al., 1992; Jobling and Baardvik, 1994; Houlihan et al., 1995), and a phenomenon not observed in groups of halibut within a higher weight range (90–662 g) (Tuene and Nortvedt, 1995). This observation suggests that 'dominant' turbot within these feeding hierarchies are consistently able to feed to satiation, while 'subordinate' individuals appear to feed opportunistically on the remaining share of the meal, thus exhibiting higher day-to-day variation in consumption. This variability in consumption is subsequently translated into growth variability resulting in increased size variation within groups over time.

Acknowledgements

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