

Stocking density, growth and growth variation in juvenile turbot, *Scophthalmus maximus* (Rafinesque)

S. Irwin^{a,b}, J. O'Halloran^{b,*}, R.D. FitzGerald^{a,b}

^a Aquaculture Development Centre, University College, Cork, Ireland

^b Department of Zoology and Animal Ecology, University College, Cork, Ireland

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Abstract

Although high stocking densities of turbot have been achieved in culture using supplementary oxygenation, this rearing strategy ignores the possibility that high densities may interfere with behavioural interactions between individuals and thereby affect biomass gain. This study describes the effect of stocking density on the growth of juvenile turbot populations. Groups of juvenile turbot were reared at four different densities (initial densities: 0.7, 1.1, 1.5 and 1.8 kg/m²) for 45 days. Treatment density had a significant effect on turbot growth rates over the experimental period. Fish held at the highest density showed lower growth rates and mean weights at the conclusion of the study than fish held at lower densities. The dispersion in fish weights was also affected by stocking density. The variation in fish weights was greatest in the highest density group and as stocking densities increased the growth of some individuals was suppressed. It is concluded that growth of juvenile turbot can be significantly increased and more homogeneous weights achieved by stocking the fish at lower densities than previously reported. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Turbot; *Scophthalmus maximus*; Growth rate; Variation; Hierarchies; Stocking density

1. Introduction

In recent years the commercial culture of turbot, *Scophthalmus maximus* (Rafinesque), has benefited from improvements in larval rearing methods, and nutrition and husbandry practices in the ongrowing phase (Cowey et al., 1976; Paulsen and Andersen, 1989;

* Corresponding author. Department of Zoology and Animal Ecology, University College, Cork, Ireland. Tel.: +353-21-904-193; Fax: +353-21-270-562; E-mail: johalloran@ucc.ie

Devesa, 1994; Minkoff and Broadhurst, 1994). Limited attention has been directed towards the manipulation of environmental factors, particularly biotic factors (e.g., feeding frequency, ration size and behavioural interactions), to improve our understanding of turbot culture. Such manipulations could enhance fish growth rates whilst decreasing size variation. This would serve to improve uniformity in growth rates and shorten the time required by groups of farmed turbot to reach market size.

One important biotic factor that influences the growth of fish is the development of hierarchies, mediated by intraspecific competition for food, and this is greatly affected by stocking density (Brett, 1979). Jobling and Baardvik (1994) showed that the manipulation of stocking densities may inhibit the formation or reduce the effects of such hierarchies in Arctic charr, *Salvelinus alpinus*.

Stocking density has been shown to affect behavioural interactions in several fish species (Brown et al., 1992; Christianssen et al., 1992) and may ultimately affect growth rates. The effect of stocking density on growth has been reported for a range of cultured fish species, such as halibut *Hippoglossus hippoglossus* (Bjørnsson, 1994), Arctic charr (Jørgensen et al., 1993), rainbow trout *Oncorhynchus mykiss* (Zoccarato et al., 1992) and Atlantic salmon *Salmo salar* (Refstie and Kittelsen, 1976). Both positive and negative relationships between stocking density and growth have been reported, and the pattern of this interaction appears to be species specific. Brett (1979) suggested that, in addition to affecting overall growth rates, intraspecific competition may influence the variation in growth of fish reared in groups. This has been supported by observations on a number of aquatic species, including chum salmon *O. keta* (Davis and Olla, 1987) and freshwater prawns *Macrobrachium rosenbergii* (Ra'anan and Cohen, 1984). However, such an effect has not been reported previously for turbot, a species in which there is marked variation in growth rates (FitzGerald et al., 1996).

Wohlfarth (1977) found that weight differences arising in very young carp, *Cyprinus carpio*, from competition for an inadequate food supply could persist in older fish even where food supply was adequate. Bagley et al. (1994) suggested that stress responses of young rainbow trout to stocking density may be quite different to the responses shown by older fish. Therefore, it is important to study the effects of density on the growth of young fish, as behavioural interactions leading to the formation of hierarchies are likely to commence at this stage. Differences in growth in very young fish may be magnified with age, consequently, control of differential growth within populations of juvenile fish may improve control over the change in size variation with time.

Thus, differences in growth rates of juvenile turbot held at four different stocking densities were examined with the aims of studying the effect of stocking density on growth rate and variation within groups over time.

2. Materials and methods

2.1. Source of fish

The turbot were obtained as 133 day old juveniles from a commercial hatchery on the Isle of Man and transported to Cork, Ireland, by air. Fish were acclimatised in a

recirculation system for 14 days prior to the start of the experiment. At the beginning of the experiment, all fish were weighed individually and, from a total of 714 fish, 280 individuals were selected for the experiment. Selection was made such that the weights of the experimental fish lay within one standard deviation of the mean weight of the source population.

2.2. *Experimental design*

The experimental design was based on the growth of turbot at four different stocking densities. Juvenile turbot ($n = 280$, mean live weight \pm standard error (S.E.): 8.62 ± 0.06 g) were divided into 16 groups (four replicates each of four stocking densities) of similar mean weight, ranging from 8.46 ± 0.26 to 8.74 ± 0.23 g. Experimental stocking densities (groups I, II, III and IV) comprised 10, 15, 20 and 25 fish per tank, respectively, corresponding to biomass stocking densities (\pm S.E.) of $0.71 (\pm 0.01)$, $1.45 (\pm 0.01)$ and $1.79 (\pm 0.01)$ kg/m² tank bottom, respectively. The numbers of fish in each tank were held constant for 45 days, during which time biomass increased as the fish grew. This resulted in final stocking densities of $3.39 (\pm 0.08)$, $4.76 (\pm 0.04)$, $5.87 (\pm 0.20)$ and $7.07 (\pm 0.21)$ kg/m² tank bottom, respectively.

Fish were held in circular white PVC tanks of 50-l capacity, with a central drain, an operating depth of 30 cm and a bottom area of 0.12 m². Groups were assigned to tanks at random. All tanks were connected to a single settlement tank and biological filter through which water was continuously recirculated. Environmental parameters (pH, oxygen saturation (%) and salinity (‰)) were measured once per week. Oxygen saturation was maintained at approximately 90%, salinity varied between 33.6 and 35.8‰, and pH between 6.90 and 7.85. The water flow rate was manually controlled and adjusted as fish density increased to levels not exceeding 2.5 l/min. Light was provided by overhead fluorescent tubes on a 12-h light:12-h dark cycle. Water temperature was not controlled, and ranged between 20.0 and 23.0°C.

2.3. *Food and feeding regime*

The fish were hand fed three times daily, at four hourly intervals during the light period. Fish were not fed on census days to minimise handling stress. Dry pellets (0.35 mm diameter, 58.1% protein, 13.8% fat, 9.3% water and 16.3% ash) were provided at 3% of the tank biomass per day, spread evenly over the three feeding occasions. Daily food consumption was recorded for each tank and actual quantities of food offered were increased daily to allow for projected growth, taking cognisance of food conversion ratio and the amount consumed daily. On days 15, 30 and 45, individual live fish were weighed (following removal of excess water) to the nearest 0.01 g on an electronic balance.

2.4. *Data analysis*

Growth, expressed as specific growth rate (SGR, %/day), over the intervals between each weighing and for the entire experiment were calculated using the formula

$100 \times [(\ln(w_t) - \ln(w_i))/t]$, where $\ln(w_t)$ and $\ln(w_i)$ are the natural logarithms of the weight at time t and of the initial weight, respectively, and t is the time interval in days. The coefficient of variation for weight (CV, %) within tanks was calculated for each census day using the formula, tank standard deviation/tank mean weight, and was used to assess size variation. The percent coverage of the tank bottom at the conclusion of the experiment was estimated for all treatment groups. Area was derived from individual fish weights using the formula:

$$A = 102.5W + 3595.0 \quad (r = 0.98, P < 0.01)$$

where A = area (mm^2) and W = weight (g). This formula is applicable to turbot only within a very limited size range less than 100 g (Irwin, unpublished data).

Data are presented as arithmetic mean \pm S.E. One-way ANOVA (following Levene's F -test for homogeneity of variance) was used to test for differences between treatments. Where differences were found ($P < 0.05$) in multiple comparisons, Tukey's honestly significant difference (HSD) test was used to determine which specific pairs differed. The relationships between initial biomass stocking density and both SGR and CV were analysed using linear regression analysis. Differences in the slopes of the regression lines between treatments were analysed using a t -test. Where multiple comparisons were made the observed significance level was adjusted according to the Bonferroni correction. Differences in the weight frequency distribution were analysed using the Kolmogorov–Smirnov two-sample test. All statistical analysis were carried out using the MINTAB package for the Macintosh.

3. Results

3.1. Effects of stocking density on growth

The mean fish weight (\pm S.E.) at the start of the experiment was 8.62 ± 0.06 g. There were no significant differences ($F_{264,15} = 0.15$, $P > 0.05$) between fish weights in any experimental tanks at the beginning of the experiment. No significant differences were found between replicate groups ($n = 4$, $P > 0.05$) over the course of the experiment and so data from replicate groups were pooled for each treatment prior to analysis. Significant differences between treatments were seen on day 45 ($F_{12,3} = 5.38$, $P < 0.05$), when the weights of fish held at the highest stocking density (IV) were significantly lower than those held at the lowest density (I) (Fig. 1, Tukey's HSD $P < 0.05$). The mean weight of all experimental fish at the conclusion of the experiment was 37.70 ± 0.42 g. A single fish from the highest stocking density group died on day 41, and was not replaced to avoid disruption of social interactions within that tank. On day 45 the percent cover of the tank bottom by turbot in the lowest density group (I) was 67.41 (0.78)%, in density group II it was 93.69 (0.43)%, in density group III it was 125.80 (2.00)% and in the highest density group (IV) it was 149.31 (3.00)%.

The highest SGR (4.38%/day) recorded during the course of this experiment was for a replicate tank in group I stocked with 10 fish, over the first time interval of the experiment. SGR decreased over time as mean fish weight increased; however, the SGR of the lowest stocking density group (I) decreased at a slower rate than all others

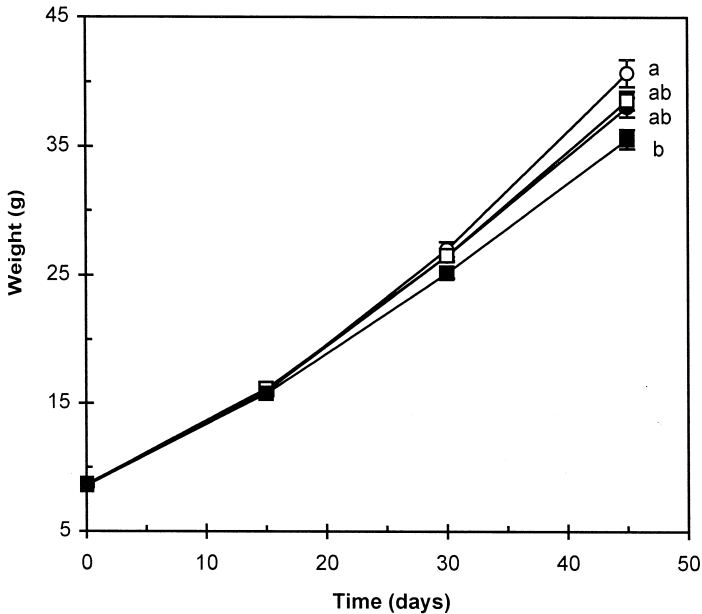


Fig. 1. Mean weight (\pm S.E.) (g) over the experimental period of juvenile turbot held at four different densities. ● Density I, 0.71 (0.01) kg/m²; ○ density II, 1.07 (0.01) kg/m²; ■ density III, 1.45 (0.01) kg/m²; □ density IV, 1.79 (0.01) kg/m². Treatments with a common letter are not significantly different ($P > 0.05$).

(Table 1). There was a significant difference ($t = 2.03$, $d.f. = 20$, $P < 0.05$) in the slopes of the regression lines between time and SGR for the groups stocked at the lowest (I) ($SGR = -0.05t + 4.86$, $r > 0.99$, $P < 0.01$) and highest (IV) ($SGR = -0.06t + 5.09$, $r = 0.99$, $P < 0.01$) densities. During the final 15 day interval of the experiment, there was a significant difference between the growth rates of groups I and IV ($t = 3.33$, $d.f. = 7$, $P < 0.05$). SGRs of fish held at different densities were determined over the 45-day period, and are shown in Table 1. There was a significant negative correlation ($r = -0.95$, $d.f. = 12$, $P < 0.05$) between initial stocking density and overall SGR (Table 1).

Table 1
SGR (S.E. in parenthesis) of juvenile turbot, *S. maximus*, held at four stocking densities

| Stocking density | Interval 1 (day 0–15) | Interval 2 (day 16–30) | Interval 3 (day 31–45) | Overall (day 0–45) |
|-----------------------|--------------------------|---------------------------|---------------------------|---------------------------|
| Group I ($n = 4$) | 4.13 (0.11) | 3.53 (0.22) | 2.73 (0.08) | 3.46 (0.05) ^a |
| Group II ($n = 4$) | 4.15 (0.06) | 3.38 (0.18) | 2.41 (0.16) | 3.31 (0.02) ^{ab} |
| Group III ($n = 4$) | 4.12 (0.02) | 3.32 (0.14) | 2.50 (0.15) | 3.31 (0.07) ^{ab} |
| Group IV ($n = 4$) | 4.04 (0.04) | 3.13 (0.04) | 2.23 (0.15) | 3.13 (0.06) ^b |

Initial biomass stocking densities: group I: 0.71 (0.01), group II: 1.07 (0.01), group III: 1.45 (0.01) and group IV: 1.79 (0.01) kg/m². Values in columns with a common superscript are not significantly different ($P > 0.05$).

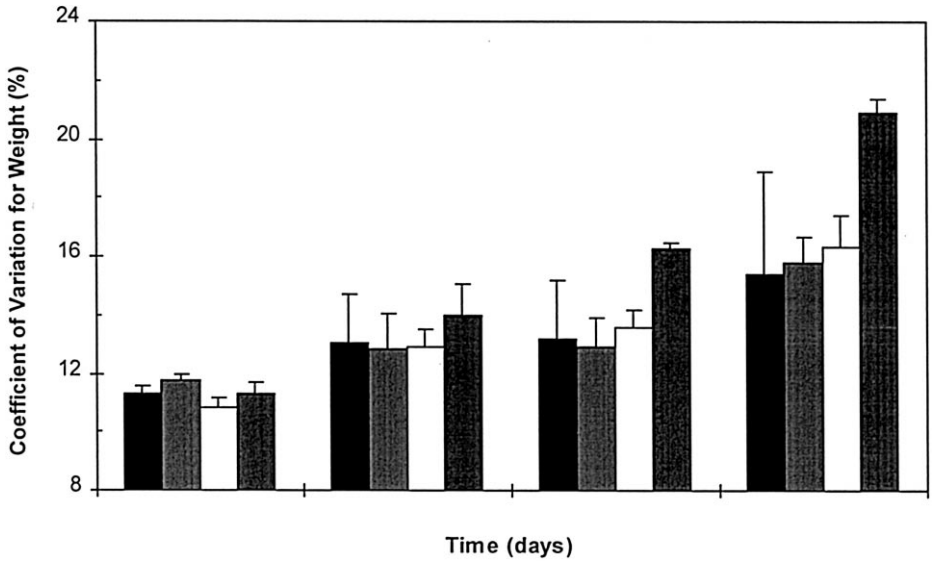


Fig. 2. The CV for weight (%) on days 0, 15, 30 and 45 for each stocking density (I, II, III and IV, see text) of juvenile turbot. Vertical bars represent one S.E.

3.2. Effects of stocking density on growth variation

The CV for weight for all groups of turbot increased over the course of the experiment (Fig. 2), but there were significant differences among groups over time ($F_{60,3} = 13.42, P < 0.01$). The relationships between time and the CV for weight for each of the density treatment groups are shown in Table 2. The fish stocked at the highest density showed a more rapid increase in CV over time than all others, with the slope of the regression of CV against time being steeper than those of groups I and II (Fig. 3) (group IV vs. group II: $t = 2.30, d.f. = 28, P < 0.05$; group IV vs. group I: $t = 3.22, d.f. = 28, P < 0.01$).

There was a pronounced increase in the distribution of fish weights within experimental groups over the 45 days of the experiment (Fig. 3). Fish weights in lower stocking density groups were, however, more uniform at the conclusion of the experiment. The

Table 2

Equations describing the relationship between time (t) and the CV for weight (%) for groups of juvenile turbot held at the four initial treatment densities, 0.71 (0.01), 1.07 (0.01), 1.45 (0.01) and 1.79 (0.01) kg/m², for 45 days

| Stocking density | Relationship between time (t) and CV (%) |
|------------------|--|
| I | $CV = 1.24 + 10.13t, r = 0.96, P < 0.01$ |
| II | $CV = 1.22 + 10.29t, r = 0.91, P < 0.01$ |
| III | $CV = 1.73 + 9.09t, r = 0.98, P < 0.01$ |
| IV | $CV = 3.10 + 7.86t, r = 0.99, P < 0.01$ |

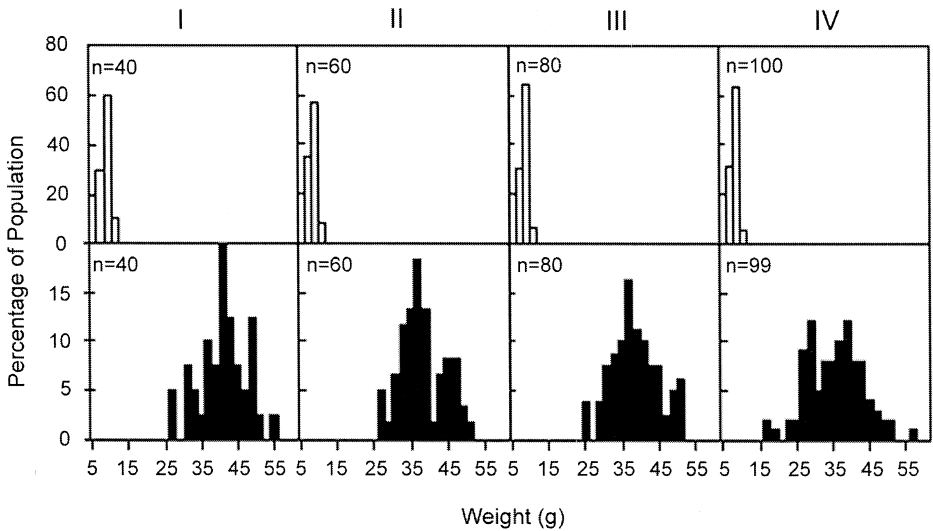


Fig. 3. Size frequency histograms of juvenile turbot held at four different stocking densities at day 0 (□) and day 45 (■), n = number of fish weighed.

initial size range of fish in all groups was between 7.0 and 11.0 g. The final size ranges of fish in groups I, II, III and IV were 27.1–54.6, 26.8–51.1, 24.6–51.3 and 16.5–56.8 g, respectively. By the end of the experimental period significant differences in weight distributions had developed between groups stocked at the lowest and highest densities ($d_{\max} = 0.30$, $d.f. = 0.19$, $P < 0.05$). These differences were primarily due to the depressed growth of a number of individuals in the high stocking density group (Fig. 3). The smallest fish at the lowest stocking density achieved higher weights than the smallest fish at the highest density by the end of the experiment. The mean weight of all experimental fish on day 45 was 37.70 ± 0.42 g. In tanks stocked at the lowest density (I) 67.5% of individuals were greater than this weight, compared to only 43.0% of individuals in the tanks stocked at the highest density (IV).

4. Discussion

4.1. Effect of stocking density on growth

When the effects of stocking density on the growth of fish have been examined, different terms of expression have been used and density has been expressed in terms of either biomass or numbers of fish per unit area or volume. Sometimes, numbers of fish are reduced as the fish grow so as to maintain constant biomass stocking densities (Refstie, 1977; Papst et al., 1992). In this study, numbers of turbot were held constant for the duration of the experiment, and so biomass density was allowed to increase with time due to the growth of the fish. There is evidence that removing fish may disrupt

hierarchies, and the resulting high levels of interactions between individuals following changes in group structure may affect growth rates (Baardvik and Jobling, 1990). Purdom (1974) showed that social interactions between marine flatfish led to high levels of variance prior to the establishment of a stable hierarchy.

Initial biomass stocking densities used in this experiment ranged between 0.71 and 1.79 kg/m² tank bottom (1.71 and 4.30 kg/m³ water), similar to stocking densities used in several previous turbot growth trials (Iglesias et al., 1978; Fernández-Pato et al., 1990). In these previous trials initial biomass stocking densities varied between 1.0 and 5.0 kg/m³ water. Turbot can be reared at very high stocking densities, and in commercial operations stocking densities generally range from 25 to 30 kg/m³ (Iglesias et al., 1978) with a maximum reported sustainable density of 75 kg/m³ for large fish (Jones et al., 1981). The ability of turbot to withstand conditions of very high stocking density may be related to their benthic habit, low levels of spontaneous activity and low oxygen requirements (Jones et al., 1981). Such rearing conditions, do not, however take into account behavioural interactions between individuals which may unfavourably affect biomass gain.

In this study the turbot reared at the higher stocking densities showed significantly slower growth rates than those held at lower stocking densities (Table 1), and significant differences in weight were evident after 45 days (Fig. 1). This supports the view that increasing stocking densities have a negative impact on growth rates of turbot populations, as observed by Danielssen and Hjertnes (1991) particularly among fish of smaller sizes. At the conclusion of this study the percent cover of the tank bottom by fish in the highest density treatment group (149.3%) was more than twice that of the lowest density group (67.4%) where growth rates were significantly higher. Björnsson (1994) estimates the optimal density of halibut in circular tanks to be between 100% and 200% coverage of the tank bottom. The results of this study suggest that this value is lower for turbot where significantly improved growth rates were seen at densities well below 100% coverage of the tank bottom. Although high densities are a favourable consideration in determining production costs in aquaculture, in juvenile turbot populations elevated stocking densities result in an increase in the length of the ongrowing phase through decreased SGR.

Martínez-Tapia and Fernández-Pato (1991) examined the effect of two stocking densities (0.25 and 0.5 kg/m²) on the growth of turbot and found no significant differences in weight between groups. Experimental fish weights were, however, much higher than those under investigation in this study. On the other hand, Danielssen and Hjertnes (1991) reported reduced growth when turbot were held at much higher stocking densities (150 kg/m³). Growth improved when the density was reduced, indicating that density has a certain influence on growth. Danielssen and Gulbrandsen (1989) attributed the reduced growth observed as the fish grew to the increase in stocking density that occurred during the experiment with noticeable differences at densities above 23.3 kg/m³. Improvements in SGR were observed when density was reduced.

Studies on the effects of stocking density on the growth of fish show inverse relations for a range of species (Rubenstein, 1981; Zoccarato et al., 1992; Björnsson, 1994). In some species, however, a positive effect of density on growth is reported (Papst et al., 1992). The negative impact of stocking density on growth may be due to increased

social interactions between individuals. These interactions lead to intraspecific size variation in groups resulting from the suppression of growth of subordinate individuals by larger conspecifics (Yamagishi et al., 1974; Jobling, 1985; Koebele, 1985). For example, Wickins (1985) reported that when stunted European eels, *Anguilla anguilla*, were taken from large populations and held in isolation they showed a marked growth recovery.

Stocking density and growth rates are often reported to be related, however, the relationships between the two may not be uniformly positively or negatively linear for a given species. For example, Baker and Ayles (1990) suggested that growth of Arctic charr increased with stocking density up to a threshold of 40–50 kg/m³ and then declined at higher densities. Björnsson (1994) reported that stocking density affects the growth of halibut only above a certain threshold level corresponding to approximately 100% coverage of the tank bottom. In the present study, there was a significant decrease in SGR of the turbot within the range of densities examined (Table 1), but at initial densities lower than 0.5 kg/m² (final density: 68 kg/m²) the growth of turbot has been reported to be independent of stocking density (Martínes-Tapia and Fernández-Pato, 1991).

4.2. The effect of stocking density on growth variation

In this study stocking turbot at higher densities resulted in decreased mean growth, and a more pronounced increase in the variation in body weight over time (Fig. 2). Examination of the frequency distributions of weights for fish held at different densities (Fig. 3) revealed that the growth of a number of fish in the highest density group was depressed. Thus, it seems that it was this decrease in growth which resulted in an increase in variation in these groups, and which ultimately gave rise to the reduced rate of overall biomass gain. A direct effect of stocking density on growth variability has been reported by a number of authors (Rubenstein, 1981; Papst et al., 1992; Jobling and Baardvik, 1994) with great inter-specific variation in results. When growth of subordinates is affected by dominants due to numbers, space or size of individuals, the relative size difference between members of the population usually increases. This is thought to be an adaptive strategy to optimise survival in a restricted space (Volpato and Fernandes, 1994).

Furthermore, an increase in the CV for weight within a population is considered to be indicative of the establishment of hierarchies and the suppression of growth of certain individuals (Purdom, 1974; Brett, 1979; Zoccarato et al., 1992). In this study, the CV increased more rapidly in groups of turbot held at the highest stocking density than in all others (Fig. 2), indicating that behavioural interactions had a more significant effect on growth rates in these groups than in groups stocked at lower densities. Several hypotheses have been proposed to explain the social dependence of differential growth within populations. The most widely stated is that competition between individuals for a limited food supply results in disproportional food acquisition and this ultimately gives rise to differential growth (Brett, 1979; Davis and Olla, 1987). Carter et al. (1996) demonstrated a positive relationship between food consumption and growth in flounder, *Rhombosolea tapirina*, and suggested that growth depensation in flatfish is a result of

differential rates of food consumption. Martínez-Tapia and Fernández-Pato (1991) reported increased aggressiveness and competition in turbot under conditions of food scarcity, but no overt acts of aggression were discernible in the current study in which food was provided in excess. Although direct competition for food may result in disproportional food acquisition, considerable variation in food consumption and growth has been reported under conditions where rations are not limiting, e.g., plaice, *Pleuronectes platessa* (Purdom, 1974). In marine flatfish, variation in individual growth rates are reported to be related more to social interactions than to food availability (Purdom, 1974) and, in juvenile cichlids, Koebele (1985) demonstrated that dominant fish ingested more food by either acquiring a limiting ration first, preventing subordinates from acquiring food or behaviourally inhibiting the subordinate's feeding behaviour. Abbott et al. (1985) suggested that subordinate steelhead trout (*S. gairdneri*) individuals may reduce food intake voluntarily. Abbott and Dill (1989) suggested several alternative causes of variation in growth between dominant and subordinate individuals: differences in feed conversion efficiency, differences in activity levels and differences in metabolic rates due to complex physiological conditions occurring in subordinate individuals. Although differential growth rates were observed in this study and have previously been reported for turbot (FitzGerald et al., 1996), the precise mechanisms involved have not yet been elucidated.

In conclusion, the results of the present study demonstrate that there is a significant negative effect of increasing rearing density in juvenile turbot populations. Increasing densities result in heterogeneous growth rates and the depression of growth of some individuals.

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