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Best among unequals? Effect of size grading and different social environments on the growth performance of juvenile Atlantic halibut

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Abstract In order to study the effect of rearing juvenile halibut in different social environments, individually tagged juvenile halibut were size-graded into two size classes (Large, L, and Small, S) with ungraded fish as control. After ca 6 weeks, the two size-graded groups were again graded into two size classes creating four experimental groups: Large of the Large (LL), Small of the Large (SL), Large of the Small (LS), and Small of the Small (SS). Grading (overall mean of the four grading groups) improved growth rate by 10% compared with ungraded controls, but the effect was also significantly affected by social environments, because in the latter half of the experiment overall growth was improved by 11 and 12% in the two groups with larger size variation (i.e. SL and LS, respectively) compared with the two other groups (i.e. LL and SS). Significant size rank correlations were maintained during the experiment, these were higher in the ungraded (Control) group and the SS and LL groups than in the SL and LS groups. Further, the degree of mean rank position changes varied between the experimental groups and was higher in the SL (20.7) and LS (25.6) groups than in the Control (10.5), LL (15.1), and SS (15.4) groups. This could possibly indicate a stronger social hierarchy in the last three groups. Growth rate differences may be the product of different degrees of interactions among individuals, and based on the higher overall growth rates in the groups with larger size variation (i.e. SL, LS) it is concluded that juvenile halibut should not be too intensively size graded.

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Introduction

Social interactions between fish of the same size has been proposed as an explanation of reduced growth observed in some size-grading experiments (Doyle and Talbot 1986; Baardvik and Jobling 1990) and in the culture of salmonids (Jobling et al. 1993; Jobling 1995; Jobling and Koskela 1996). Imsland et al. (1998) showed that social hierarchies form in groups of cultured turbot *Scophthalmus maximus* Rafinesque, and that they lead to an increase in size variation and to lower overall growth of the group. However, there were also indications that when stable hierarchies have been formed they tend to prevail over time and that in such groups fish grow faster compared with groups where stable hierarchies have not been formed (Imsland et al. 1998). In fact, some authors have shown that intraspecific competition and agonistic interaction is greater when fish of similar size are reared together (Doyle and Talbot 1986; Baardvik and Jobling 1990). In line with this, Sunde et al. (1998) indicated that social interactions (measured as repartitioning of size rank order) were greater in juvenile turbot of similar size compared with the largest and smallest individuals. Large differences in individual growth have been observed in juvenile halibut *Hippoglossus hippoglossus* L. (Jonassen et al. 1999), as have stable size hierarchies (Aune et al. 1997) and aggressive behaviour (Hallaråker et al. 1995). It is therefore hypothesized that grading may improve the growth rate of Atlantic halibut, but that such growth gain may be modulated by the social environment the fish are reared under. Thus, the following experiment was designed to investigate the effects of size grading, creating different social environments, on growth performance of juvenile halibut.

Materials and methods

Fish stock and rearing conditions

Juvenile halibut of mixed parental background were used in this experiment. The eggs were spawned and hatched at Stolt Sea Farm Aga, Western Norway. Prior to first feeding the larvae were transferred to Stolt Sea Farm Øye (Kvinesdal, Southern Norway), and reared under intensive conditions. From 20 May 1996 the larvae were fed *Artemia* nauplii and metanauplii in a green-water system indoors at 12°C and continuous light. After weaning to commercial formulated feed (Nutra Marin; T. Skretting, Stavanger, Norway), the juveniles were transferred to rearing tanks (1.3 × 1.3 m) with a temperature of 12°C and continuous light. On 15 October 1996 the juveniles were brought to the Industrial and Aquatic Laboratory at the Bergen High Technology Centre and reared at 11°C with a fixed photoperiod regime of 20 h light:4 h dark (LD 20:4) until the end of the experiment. On 14 November 1996 all the fish were anaesthetised (metacain, 0.05 g l^{-1}) and individually tagged under anaesthesia with Fisheagle PIT tags. No fish died during tagging and no tags were lost during the experiment. A 36-W fluorescent daylight tube integrated in the tank-cover provided light. Photoirradiance measured at the bottom of the tanks was ca. 5 μE m^{-2} s^{-1}. More details concerning fish and larval rearing are given elsewhere (Jonassen et al. 1999).

The studies were carried out between 7 April 1997 and 1 July 1997. The 1 m^2 square, grey, covered fiberglass experimental tanks had a rearing volume of 400 l. Seawater (34.2 ± 0.2‰) was pumped from a depth of 90 m. Water flow was set to 8 l min^{-1} in all tanks. Oxygen saturation measured with a hand held Oxygard Handy Alpha meter (Oxyguard International, Birkenrød, Denmark) in the effluent water of all tanks was over 80% at all times. Prior to the start of the experiment the fish were gradually introduced to a new feed (Marin Kveite; T. Skretting; 48% protein, 25% fat, and 11% carbohydrate). Pellet size was adjusted depending on fish size according to the feed producer's recommendations, with gradual introduction of bigger pellets. The feed was distributed from automatic feeders every 10 min from 0800 to 1600 h every day.

Experimental design

On 7 April 1997 all fish ($N = 370$) were anaesthetised (metacain, 0.05 g l^{-1}) weighed and graded into two size groups (mean (SE) weights): Small (S) 38.9 (1.3) g and Large (L) 84.2 (1.8) g and one group kept ungraded as Control: 57.5 (2.0) (Table 1). These groups were distributed into ten tanks i.e. two control tanks, and four tanks for each of the other two groups. On 22 May the two graded groups were size-graded again and redistributed into two size groups within each original group, to create four new experimental groups (Table 1). From the original Small group two groups were made i.e. one group consisted of Large fish from the initial Small group (Large of the Small, LS) and one consisted of Small fish from the initial Small group (Small of the Small, SS) and. Similarly, from the original Large group two groups were made i.e. one consisted of Large fish from the initial Large group (Large of the Large, LL) and one group consisted of Small from the initial Large group (Small of the Large, SL). Ungraded fish were kept as Control (Table 1). As all fish in this experiment were individually tagged it was possible to compare individual growth rates before and after size grading in order to investigate possible social effects.

Data analysis and statistical methods

All fish were weighed individually to the nearest 0.1 g at 21–25 days intervals during the experimental period. Specific growth rate (SGR) was calculated according to the formula:

$$\mathrm{SGR} = (\mathrm{e}^{g} - 1) \times 100$$

where $g = (\ln W_2 - \ln W_1)(t_2 - t_1)^{-1}$ and W_2 and W_1 are wet weights (g) at days t_2 and t_1, respectively.

Individual growth trajectories were analysed using a growth-curve analysis (GCM) multivariate longitudinal analysis of variance (MANOVA) model (Timm 1980; Chambers and Miller 1995). The model equation of the GCM had the form:

$$\mathbf{Y}(n \times p) = \mathbf{X}(n \times q)\mathbf{B}(q \times p) + \mathbf{E}(n \times p)$$

where $\mathbf{Y}(n \times p)$ are the growth at age vectors

$$\mathbf{y} = (y_1, y_2, \ldots, y_p)$$

for each p (age) measurement on n individual fish; $\mathbf{X}(n \times q)$ is the design matrix or the set of extraneous variables measured for each individual, i.e., $q = \mathrm{age}_p + \mathrm{grading\ group}_i + \mathrm{replicate}_j$; ($i$ = Control, LS, SS, LL and SL), (k = replicate a, replicate b); $\mathbf{B}(q \times p)$ is the matrix of parameters estimated by the model; and $\mathbf{E}(n \times p)$ is the matrix of deviations for each individual from the expected value of $\mathbf{Y} = \mathbf{XB}$.

Table 1 Mean weights (g) of Atlantic halibut, size graded into three, and later five experimental groups, throughout the study

First grading	N		Date			Second grading	N		Date		
			7 April	28 April	22 May				22 May	11 June	1 July
Control	116	Mean (SE)	57.5 (2.0)^{b}	71.4 (2.9)^{b}	89.7 (3.2)^{b}	Control	115	Mean (SE)	89.7 (3.2)^{c}	109.2 (3.9)^{c}	131.8 (4.5)^{d}
		Max − min, CV	17.0–107.3, 38	22.8–132.6, 36	26.4–167.0, 37			Max − min, CV	26.4–167.0, 37	30.4–200.0, 36	32.4–244.5, 36
Small (S)	127	Mean (SE)	38.9 (1.3)^{c}	50.7 (1.7)^{c}	66.6 (2.1)^{c}	Large of the Small (LS)	62	Mean (SE)	84.1 (3.7)^{d}	115.6 (5.1)^{c}	154.4 (6.4)^{c}
		Max − min, CV	10.4–59.6, 35	14.7–79.4, 35	17.0–109.8, 35			Max − min, CV	41.4–109.8, 35	49.0–142.2, 33	67.8–184.3, 34
						Small of the Small (SS)	61	Mean (SE)	49.3 (1.3)^{e}	63.9 (2.0)^{d}	75.3 (2.5)^{e}
								Max − min, CV	17.0–100.2, 21	21.3–114.0, 25	24.1–132.1, 26
Large (L)	127	Mean (SE)	84.2 (1.8)^{a}	105.0 (2.3)^{a}	133.4 (3.0)^{a}	Large of the Large (LL)	61	Mean (SE)	161.8 (3.4)^{a}	190.7 (4.2)^{a}	229.8 (5.2)^{a}
		Max − min, CV	59.5–137.5, 23	68.3–172.9, 23	85.0–221.7, 24			Max − min, CV	105.2–221.7, 18	128.2–269.1, 17	164.1–325.6, 18
						Small of the Large (SL)	60	Mean (SE)	108.7 (4.1)^{b}	145.3 (5.6)^{b}	188.6 (7.4)^{b}
								Max − min, CV	85.0–135.0, 30	98.1–178.6, 31	121.9–225.6, 31

Results are given as mean (standard error), max − min sizes, and coefficient of variation (CV) for weight; N = number of fish in each experimental group. Superscript letters indicate statistical differences (Student–Newman–Keuls test, $P < 0.05$). The two size-sorted groups (Small and Large) were split into two groups on 22 May (giving a total of four grading groups from 22 May). Control group is composed of ungraded fish

Two-way nested ANOVA (Searle et al. 1992), where the two replicates were nested within experimental groups, was used to calculate the effect of different social environments on mean weights and specific growth rates. The model equation of the nested ANOVA had the form:

$$X_{ijk} = \mu + \alpha_i + B_{ij} + \varepsilon_{ijk}$$

where μ is the general level; α_i is the treatment effect (i.e. Control, LS, SS, LL and SL); B_{ij} is the contribution caused by replicate (here: tanks a and b) j in group i, and ε_{ijk} is the error term. In cases of significant ANOVA, a Student–Newman–Keuls multiple comparison test was used to locate differences among treatments (Zar 1984). Size ranking (initial size rank vs. final size rank) and growth rate ranking (initial growth rate vs. final growth rate and growth in adjacent periods) were tested using Spearman's rank correlation (r_{Sp}) (Zar 1984). Change (%) in individual rank position during the trial was calculated by use of the formula:

$$|\text{Initial rank} - \text{Final rank}|/N \times 100$$

where N is the number of fish in the respective experimental group.

Coefficient of variation of weight (CV_W) within each group was calculated as:

$$CV_W = \text{Standard deviation/mean weight}$$

One way ANOVA was used to test for possible differences in CV_W among the experimental groups. CV_W was regressed against weight and analysed by linear regression (Zar 1984).

Results

Mortality

A total of 11 fish (3.0%) died during the experiment (Table 1). No differences in mortality were found between the experimental groups ($\chi^2 = 0.9$, $P > 0.35$). Mortality occurred in all experimental groups with no systematic trend.

Mean weight and coefficient of variation

There were significant differences in initial mean weights among the three grading groups (two-way nested ANOVA, $P < 0.05$, Table 1) and these weight increases increased up to 22 May. After the second grading, mean weight was different in all five groups (Student–Newman–Keuls test, $P < 0.05$), and apart from the change in mean weight ranking between the Control and LS groups, these differences were sustained throughout the study. During the first part of the experiment coefficient of variation of weight (CV_W) was similar the Control (37) and the Small (34) group, but lower in the Large (24) group (one way ANOVA, $P < 0.05$, Table 1). During the second part of the experiment CV_W differed (one way ANOVA, $P < 0.05$) among the groups following the second grading (22 May, Table 1) and was: 37, 34, 24, 18 and 31 for the Control, LS, SS, LL, and SL groups, respectively. CV_W did not change in any group during the first or second half of the experiment (linear regression, $P > 0.5$, Table 1).

Overall growth

The fish reared in the different grading groups differed in their growth patterns (Figs. 1 and 2) and the GCM analyses revealed differences between the individual growth trajectories (IGT) of the grading groups ($\text{MANOVA}_{(\text{grading group})}$, Wilk's $\Lambda_{16, 941} = 0.69$, $P < 0.001$). Mean overall growth rates were 0.96, 1.06, 1.12, 0.92, and 1.18% day^{-1} for the Control, LS, SS, LL and SL groups, respectively, and overall the growth rate was 10% higher in the grading groups (mean of LL, SL, LS, and SS individual growth-at-age trajectories) compared with the ungraded fish (Control group).

Growth: prior to and after second grading

During the first part of the trial the fish in the Small group had higher growth rate compared with fish in the Large and the Control groups (two way nested ANOVA, $P < 0.05$, Fig. 1), whereas the second grading changed this growth pattern. Mean growth rates in the Large group did not differ from the Control group after the second grading, and no differences in growth between the three groups were seen in the final period (Fig. 1).

New grading groups were established on 22 May. Comparison of growth in these groups prior to and after the second grading (individual growth-at-age trajectories) revealed that after the second grading growth rate in groups with lower size variation (i.e. SS and LL) declined (Student–Newman–Keuls test, $P < 0.05$, Fig. 2) compared with the other two grading groups (i.e. LS and SL). After being redistributed in May the Large of the Small (LS) and Small of the Large (SL) grading groups performed 11 and 17% better compared with being reared together with either smaller conspecifics, i.e. LS reared with SS prior to 22 May, or larger conspecifics, i.e. SL reared with LL prior to 22 May. Accordingly the difference in growth rate between SS and LS evaporated, but growth rate was 10% higher in the SS group prior to second grading. Further, growth difference between LL and SL

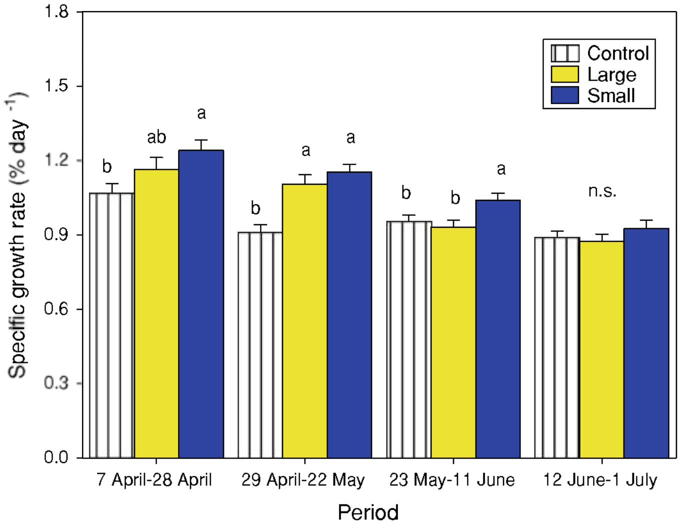

Fig. 1 Mean (+SE) specific growth rates (SGR) of juvenile Atlantic halibut size-graded into two grading groups (*Large* and *Small*) and with ungraded fish as *Control* group. *Different letters* indicate statistical differences (Student–Newman–Keuls test) within each time interval

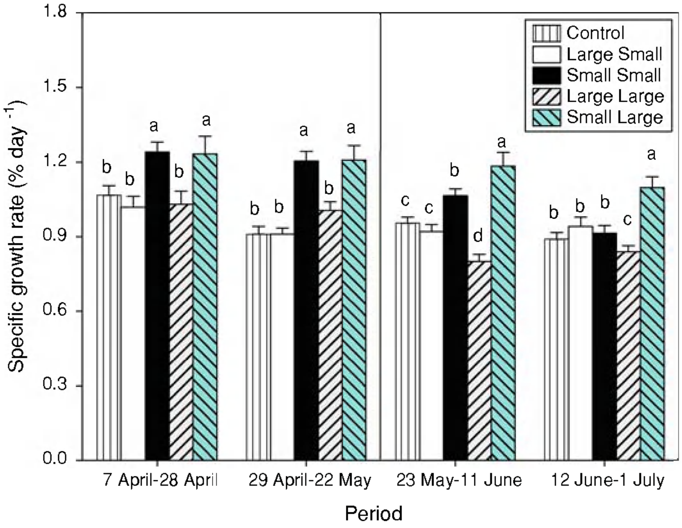

Fig. 2 Mean (+SE) specific growth rates (SGR) of juvenile Atlantic halibut size graded into five experimental groups. In order to visualize possible effect of different social environment, SGR is shown for each experimental group prior to, and after, the second grading (22 May, indicated by *vertical line*). *Different letters* indicate statistical differences (Student–Newman–Keuls test) within each time interval

increased in the latter half of the experiment as these were 20% prior to second grading but 39% after second grading.

Size ranking and size ranking changes

A significant size rank correlation (initial weight vs. final weight) was maintained in all groups ($r_{sp} > 0.38$, $P < 0.05$, Table 2), but was higher in the Control ($r_{sp} = 0.89$), LL ($r_{sp} = 0.78$), and SS ($r_{sp} = 0.78$) groups than in the SL ($r_{sp} = 0.38$) and LS ($r_{sp} = 0.34$) groups. Further, an overall positive correlation between adjacent periods (i.e. period$_n$ and period$_{n+i}$) growth rates was only found in the Control, LL, and SS groups ($r_{sp} > 0.42$, $P < 0.05$, Table 2). When comparing initial versus final growth rates a positive correlation was found in the Control ($r_{sp} = 0.25$, $P < 0.05$, Table 2) and SS groups only ($r_{sp} = 0.47$, $P < 0.05$, Table 2). The degree of mean rank position changes varied between the experimental groups and was higher in the SL (20.7) and LS (25.6) groups than in the Control (10.5), LL (15.1), and SS (15.4) groups.

Discussion

Growth rates were significantly affected by grading and social environments (Fig. 1; Tables 1, 2) as overall growth was 10% higher in the graded groups compared with control. Growth rate was improved by 15 and 12% in the two groups with a higher level of size variation (i.e. SL and LS, respectively) compared with the two other grading groups (i.e. SS and LL) in the latter half of the experiment. Accordingly, these findings suggest that an optimum size variation exists for growth in groups of juvenile halibut, above and below which growth is reduced. Accordingly, juvenile halibut should be graded, but not into

Table 2 Results from Spearman rank analysis of correlation for weight and size ranking of Atlantic halibut in the experimental groups

Experimental group	Rank comparison	Spearman rank (r_{Sp})
Control	W_1 vs. W_5	0.89*
	G_1 vs. G_2	0.58*
	G_2 vs. G_3	0.51*
	G_3 vs. G_4	0.46*
	G_1 vs. G_4	0.25*
Large of the Small (LS)	W_1 vs. W_5	0.34*
	G_1 vs. G_2	0.26
	G_2 vs. G_3	0.12
	G_3 vs. G_4	0.16
	G_1 vs. G_4	−0.03
Small of the Small (SS)	W_1 vs. W_5	0.78*
	G_1 vs. G_2	0.49*
	G_2 vs. G_3	0.42*
	G_3 vs. G_4	0.55*
	G_1 vs. G_4	0.37*
Large of the Large (LL)	W_1 vs. W_5	0.78*
	G_1 vs. G_2	0.19
	G_2 vs. G_3	0.38*
	G_3 vs. G_4	0.43*
	G_1 vs. G_4	0.11
Small of the Large (SL)	W_1 vs. W_5	0.38*
	G_1 vs. G_2	0.17
	G_2 vs. G_3	0.24
	G_3 vs. G_4	0.16
	G_1 vs. G_4	0.04

Results are given for size ranking (initial, W_1 vs. final weight, W_5), growth rank in adjacent periods (i.e. $G-\text{period}_n$ and $G-\text{period}_{n+i}$) and initial and final growth rank (G_1 vs. G_4). Significant correlations are indicated by *. The Control group is composed of ungraded fish

too-similar-sized groups as this will lead to lower growth in such groups compared with rearing the fish in groups with larger initial variation in weight (e.g. SL and LS in this study). Stefánsson et al. (2000) reported 18% lower growth in juvenile halibut reared with similar sized fish compared with groups where medium sized fish were reared with either larger conspecifics (defined as dominates) or smaller conspecifics (defined as subordinates). This is line with current findings that individual halibut grow better when they are reared in mixed-sized grading groups. Further, Sunde et al. (1998) graded juvenile turbot into three size groups (small, medium, large) in addition to ungraded controls and investigated the effect of size-grading on growth and survival. No differences in growth rate between the medium sized and ungraded groups were found in that study, indicating that grading does not improve growth of juvenile turbot (Sunde et al. 1998). Similar results have been found for Arctic charr *Salvelinus alpinus* L. (Wallace and Kolbeinshavn 1988; Baardvik and Jobling 1990), Atlantic cod *Gadus morhua* L. (Jobling et al. 1991), and eel, *Anguilla anguilla* L. (Kamstra 1993). These findings suggest that for some fish species separating small and large individuals from each other will not necessarily lead to better growth in these groups compared with groups with larger variation in size. Although our data show better growth of graded fish compared with ungraded, the degree of growth enhancement is linked to the social environment of the fish. One possible explanation might be a higher level of intraspecific competition and agonistic interaction in similar-sized groups (Doyle and Talbot 1986; Baardvik and Jobling 1990).

Another possible explanation of the positive growth effects seen in SL and LS could be linked to the removal of possible dominates (as in the case of the SL group) and subordinates (as in the case of the LS group). Doyle and Talbot (1986) introduced the term "resource-dependent competition" to describe the process where resource competition, e.g. for food, controls the relative growth rates and there are cases in which size hierarchies develop in the presence of excess food (Jobling 1982; McCarthy et al. 1992). It was suggested that size hierarchy (with larger fish dominating smaller ones) forms where the dominant fish consumes a greater proportion of the group meal (Huntingford et al. 1990; McCarthy et al. 1992; Jobling 1995). Less resource-dependent competition after grading would explain the positive effect seen in the SL group in this study. In the case of the LS group, removal of subordinates could change the social structure within the group and lead to less intraspecific competition, thus allowing the larger fish to fulfil their growth potential. The findings of Imsland et al. (1998) support this explanation as indications of size-dependency in formations of size hierarchies, because different forms of size hierarchy were seen within three grading groups (large, medium, small). For the smallest group there were more intraspecific interactions than among medium and large fish. Comparing this with the data in this study, the split into LS and SS may have reduced intraspecific interactions in the LS group with possible positive effects on growth rate, which is in line with our findings. Hence, both scenarios (dominate suppression and subordinate competition) are supported by our findings.

The formation of size hierarchies in fish is generally found to have negative effects on overall biomass gain, leading to inconsistency of growth among groups and heterogeneity in growth among individuals within a group (Jobling 1995; Jobling and Koskela 1996; Stefánsson et al. 2000). Imsland et al. (1998) used individual-based models to investigate the causes of size variation in a culture population of juvenile turbot. Two variants of size hierarchies were included in their models. One variant (A) was a dominance hierarchy in which every fish is subordinate to a larger individual; the other (B) was size-related dominance into dominant (the largest fish) and subordinates (the smallest fish). The study of Imsland et al. (op cit.) showed a difference in the sensitivity of the two types of size hierarchy tested in different grading groups at different times, indicating formation of different types of size hierarchy in different size groups in juvenile turbot. They concluded that social interactions related to size-dependent hierarchies contribute to size variation in juvenile turbot. In the current study the groups displaying the lowest size ranking correlation and the highest rate of rank position changes i.e. SL and LS had the largest size variation. This indicates the size hierarchies form in juvenile halibut in accordance with earlier findings on halibut (Aune et al. 1997; Stefánsson et al. 2000) and turbot (Imsland et al. 1998). It is, also, notable that the correlation between adjacent growth rates is more profound in the similar sized groups (LL and SS) compared with the more dissimilar sized grading groups (SL and LS). This could indicate a stronger social hierarchy and a higher level of intraspecific competition in the former groups, with a possible negative effect on growth.

Conclusions

Grading and social environment affects growth in juvenile Atlantic halibut. Overall growth is improved by 10% in the grading groups compared with control, but the growth enhancement is larger in grading groups with larger initial coefficients of variation i.e. amongst unequals. Concurrent with higher growth, a lower level of intraspecific competition was anticipated in the groups with a higher level of size variation (i.e. SL and LS) fish compared with more tightly graded groups (i.e. SS and LL). It is concluded that observed growth suppression seen in tightly graded groups may be the product of intraspecific interactions between similar sized individuals, and that juvenile halibut should not be too intensively size graded.

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