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## FOOD COMPETITION IN SMALL GROUPS OF JUVENILE GILTHEAD SEA BREAM (*SPARUS AURATA*)

Oded Goldan, Dan Popper\*\*

National Center for Mariculture, P.O. Box 1212, Eilat 88112, Israel

Ilan Karplus\*

Agricultural Research Organization, Department of Aquaculture,  
P.O. Box 6, Beit Dagan 50250, Israel

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### Abstract

Four groups of single-size and four groups of mixed-size gilthead sea bream (*Sparus aurata*) were raised in small observation cells for 16 days. Each group consisted of four individually marked juveniles. Agonistic behavior, motor activity and feeding behavior were monitored on days 1, 4, 10 and 16. At the end of the study, the weight gain was measured. Aggressive interactions occurred almost exclusively during feeding. A linear dominance hierarchy stabilized sooner in the mixed groups than in the single-size groups. Rank in the hierarchy had a profound effect on the behavior and growth of all group members. The dominant fish in each group carried out more aggressive acts and bit at food particles more often than the other group members. The dominant fish also had the highest relative specific growth rate. Direct competition for food is probably the major social mechanism regulating growth in small groups of juveniles of this species when food is limited and defendable. The relevance of these findings for the commercial culture of this species is discussed.

### Introduction

The gilthead sea bream *Sparus aurata* is one of the most important species of marine fishes raised in intensive culture systems in the Mediterranean. Millions of juveniles are routinely raised in commercial nurseries until they reach the size at which they can be stocked in

floating cages. Size grading (with mechanical graders) of juveniles, which is both labor intensive and stressful to fish, is carried out periodically to reduce size variation and subsequent losses through cannibalism, and to obtain better growth by enabling optimum size-related

\* Corresponding author. Tel.: + 972-3-9683388; fax: + 972-3-9605667; E-mail: karplus@agri.gov.il

\*\* Dan Popper died on March 1, 1995, after courageously fighting a terminal disease

management procedures (regarding, e.g., pellet size, water flow velocity) to be applied. In a controlled laboratory study, growth distribution in *S. aurata* and the effects of size grading and raising fish in isolated cells were described in detail (Szifi, 1990). Growth distribution may be extremely high in *S. aurata*. At the age of 26 days, the size difference between the largest and the smallest individuals may reach 600% and cannibalism starts, resulting in the disappearance of the smaller individuals. Culturing juveniles individually in separate containers resulted in a more uniform size, indicating that social interactions play an important role in the development of size variation.

In a pioneering study on growth in brown trout (*Salmo trutta*), Brown (1946) was the first to emphasize the importance for growth of social interactions among fish and the rank of a fish in the size hierarchy. Most studies on social control of growth in fishes were carried out on salmonids. To date, four major non-exclusive mechanisms related to social rank have been hypothesized as affecting growth variation in communally reared fish (Ruzzante, 1994). (1) *Direct competition for food*. Large fish deprive smaller fish of access to food and thereby consume more; this increases the growth of the larger fish and reduces that of the smaller. This mechanism is particularly effective when food is defendable and limited in time and space (Magnuson, 1962; Symons, 1971; Kristiansen, 1999; Webster and Hixon, 2000; Maclean and Metcalfe, 2001; Irwin et al., 2002). (2) *Social stress*. Large dominant fish induce social stress in smaller subordinate ones, resulting in reduced food intake by the latter (Koebele, 1985; Knights, 1987), and/or a reduced food conversion efficiency due to reduced digestibility and/or a metabolic shift related to their lower social status (Peters, 1982; Abbott and Dill, 1989; Volpato and Fernandes, 1994; Olsen and Ringo, 1999). (3) *Motor activity*. Small subordinate fish may be continuously engaged in maneuvering to evade large dominant fish, which increases their energy expenditure and reduces their growth (Knights, 1987). (4) *Dominance cost*. Large fish, that are continuously engaged in territorial or rank-related disputes, have a larg-

er energy expenditure and may grow less than lower ranked individuals that engage in fewer aggressive interactions (Yamagishi et al., 1974; Rubenstein, 1981; Sakakura and Tsukamoto, 1998).

In a review of the effects of domestication on aggressive and schooling behavior in fish, Ruzzante (1994) suggested that the relative importance of the mechanisms that influence the relationship between social hierarchy and growth is both species and environment specific; generalizations from one species to another and from one competitive environment to another should be avoided. Social mechanisms affecting the growth of fish in groups also depend on group structure and size, and on the type and amount of feed and its mode of presentation (i.e., continuously or at intervals, predictably or unpredictably in space and time, and whether it is defendable or not; Grant and Kramer, 1992; Grant and Guha, 1993; McCarthy et al., 1999; Linner and Brannas, 2001).

Present knowledge of the social behavior of *S. aurata* is limited and mainly concerned with feeding behavior, food preferences, group operation of demand feeders and self-feeding activity patterns (Kentouri et al., 1981, 1994; Anthouard et al., 1986; Fernandez-Diaz et al., 1994; Parra and Yufera, 2000; Paspatis et al., 2000; Andrew et al., 2002). To the best of our knowledge, there are no published studies on this species that address competitive social interactions during feeding, the agonistic ethogram, dominance hierarchies, or the impacts of these factors on food acquisition and growth.

The aim of the present study was to describe the agonistic ethogram of juvenile *S. aurata* and the competitive aggression in the presence and absence of defendable food. This study also aimed to determine the effect of group structure (single or mixed-size fish) on hierarchy formation and the effect of social rank on feeding and growth.

#### Materials and Methods

*S. aurata* were hatched and reared in the laboratory of the National Center for Mariculture, Eilat. At the age of  $82 \pm 2$  days they were size

graded and randomly assigned to eight groups, four comprising fish of a single size and four containing fish of mixed sizes. Single-size groups consisted of four fish weighing  $780 \pm 160$  mg, with the weight differences within any group not exceeding 50 mg. The mixed-size groups contained one fish belonging to each of four size categories:  $250 \pm 60$  mg,  $470 \pm 90$  mg,  $780 \pm 160$  mg and  $1100 \pm 220$  mg, with approximately 250 mg difference between adjacent weight classes. All fish were marked with a subcutaneous injection of Alcian blue to facilitate recognition of individuals. The color was applied after 5 sec of sedation with  $0.75 \mu\text{g/l}$  benzocain. The fish were marked on both sides with a single dot applied to various parts of the body. Fish were marked 24 h prior to their transfer to the observation cells. Only healthy fish with clear markings were used. The stocking density in the observation cells (1.6 fish per liter) was about half that used for similar size *S. aurata* in commercial nursery units.

Eight small (2.5 l) observation cells, each stocked with four fish, were installed in a 25-l aquarium. The cells were white and box-shaped with an area of  $250 \text{ cm}^2$ , each, and a depth of 10 cm. One of the opaque  $250 \text{ cm}^2$  side panels of each observation cell was removed and this side of the cell was pressed against the front panel of the aquarium, providing a transparent surface for viewing and filming. Fresh sea water (40 ppt salinity), at a temperature of  $25 \pm 1^\circ\text{C}$ , was continuously supplied at a rate of  $1 \pm 0.2 \text{ l/min}$  to each cell. Oxygen levels were close to saturation and ammonia levels did not exceed  $0.015 \text{ mg/l}$ . Light was provided 13 h per day (07:00-20:00) at an average intensity of 1600 lux, measured at the front panel of the observation cell.

On day 1, the fish were fed dry pellets of a uniform small size (which could easily be ingested by all fish) at a rate of 12% of the stocking biomass of each observation cell. Subsequently, the ration was increased daily by 4%. During days of no filming, one third of the food was manually administered at 08:00, one third at 14:00 and the rest at 17:00. During filming sessions, the morning feeding extended over several hours. The pellets

(6.3% moisture) were manufactured at the National Center for Mariculture in Eilat and consisted of 53.9% protein, 13.2% ash, 13.2% lipids and 19.7% carbohydrates. Food was provided to the fish in one corner of the observation cells and, apparently, was insufficient since it was usually eaten within 15 min of administration. All cells were without food in the morning.

The fish were filmed with a JVC video camera positioned behind a black screen (with small holes for the camera lens) so as not to disturb the fish. All four fish in each group were always in focus because of the small size of the observation cells. Filming was carried out on days 1, 4, 10 and 16, and the order in which the groups were filmed was determined with random number tables. Each group was filmed for eight minutes prior to feeding and an additional eight minutes after the feed was introduced. To analyze the fish behavior, the 8-min films were subdivided into four 2-min segments. In each segment all the social interactions and maintenance activities of one fish - a different one in each segment - were carefully analyzed by the focal animal sampling method (Altman, 1974). The order of analyzing the behavior of the four fish in each group was randomly determined by throwing a die. Because of the very rapid movements of the fish, transcription of the behavior was based on very slow playbacks, often with single-frame analyses. Analyses addressed agonistic behavior, position, time spent swimming vertically, mobility and frequency of biting at food.

The agonistic ethogram of juvenile *S. aurata* (80-100 days old) was based on over 1600 videotaped interactions of similarly and differently sized individuals maintained in groups of four. Agonistic behavior was analyzed by recording the frequency of performance of nine agonistic acts: (1) *frontal approach* ("front") - one fish approaches within one body length of the head of another fish. The approaching fish must cover a distance of at least two body lengths in its approach; (2) *rear approach* ("rear") - one fish approaches within one body length to the rear end of another fish. The approaching fish must cover a distance of

at least two body lengths in its approach; (3) *turn to front* ("turn") - one fish rotates up to 180° towards the head of another fish, while covering a distance not exceeding one body length; (4) *head-to-head* - two fish, both with expanded fins, are positioned very close head-to-head for at least 1 sec; (5) *circling* - two fish chase one another head to tail in a circular motion, completing at least one circle; (6) *chase* - one fish rapidly follows another fish over a distance of at least three body lengths; (7) *nip* - one fish rapidly closes its mouth on or in the immediate vicinity of another fish; (8) *retreat* - one fish moves away from within one body length of another fish, covering a distance of at least two body lengths; (9) *flee* - one fish moves rapidly away from within one body length of another fish, through a distance of at least two body lengths.

Fish body length always refers to the larger of the two interacting fish. The three acts in which the distance between fish decreased (i.e., front, rear and turn) were combined ("approach"). Similarly, the acts in which the distance between the fish increased (i.e., retreat and flee) were combined. Since the defensive acts, retreat and flee, were used to determine social rank, they were not used to analyze the effect of social rank on behavior. Therefore, for the analyses, the nine behaviors were reduced to five.

An exchange of agonistic acts between two fish was considered an agonistic interaction. An interaction usually starts with the approach of one individual but may also start by a mutual approach. Similarly, an interaction usually terminates with the retreat of one fish, but it may also end in a mutual retreat. Genuine agonistic interactions had to be distinguished from neutral approaches, which were merely the result of the small size of the observation cells.

Fish position was computed by subdividing the monitor screen into three similarly sized horizontal zones (upper, intermediate, lower) and recording the fish's position every ten seconds. The amount of time the fish spent swimming vertically with its head pointed upward in the upper layers of the water was recorded. Fish mobility was analyzed by

subdividing the monitor screen into four similar-size quadrates and counting the number of times the fish moved from one quadrate to another. The number of times each fish bit at food particles was counted, to provide a rough estimate of food intake. The dominance rank was determined, based on retreating and fleeing acts, by constructing and rearranging dominance matrixes, as recommended by Brown (1975).

Every fish was carefully placed on a blotting pad, blotted and individually weighed at stocking and at the end of the experiment. The specific growth rate was calculated as:  $SGR = 100(\ln w_t - \ln w_0)/t$ , where  $w_0$  and  $w_t$ , respectively, are the weights recorded initially and after  $t$  days (Ricker, 1975). The relative SGR of each fish was its own SGR divided by the sum of the SGRs of all the fish in his group.

Statistical analyses were carried out with the SAS (1987) computer software package. Descriptive statistics were computed from the raw data, which were subjected to repeated-measures three-way ANOVA tests following log transformation of the data. Relative SGRs were subjected to one-way ANOVA following arcsin transformation.

## Results

The majority of agonistic interactions (close to 80%) were of short duration and consisted only of approach and retreat; the rest were longer and included additional acts. The longest such interactions were of high intensity and involved similarly ranked fish; they included, as well as approach and retreat, a mutual frontal threat display (head-to-head), circling, chasing and nipping. Some of these elements were repeated more than once in a single interaction.

*Effects of food availability, size differential and time on number of agonistic interactions.* There was a highly significant ( $p < 0.001$ ) effect of food on the number of interactions. The vast majority of interactions occurred during feeding (89.6% in mixed and 87.6% in single-size groups). Since interactions in the absence of food were rare, further behavioral analyses were carried out during feeding ses-

sions. There were no significant differences ( $p > 0.05$ ) in number of agonistic interactions between the single and mixed-size groups. However, there was a significant effect of time on the number of interactions. The number of agonistic interactions was lower on day 1 than on days 4, 10 and 16 ( $p < 0.05$ ). There was no significant interaction between or among tested variables.

*Effect of size differential and time on rank in dominance hierarchies.* Thanks to the high rate of agonistic interactions, sufficient data were available to rank the dominance of each fish during every observation. Dominance hierarchies were clearly linear; fish were dominant over all those ranked below them and submissive to all those ranked above. Despite the linear structure of the dominance hierarchies, changes in rank did occur in the course of time (Fig. 1). In groups of mixed-size fish, rank usually matched size. Only on day 1, in half the groups, the second and fourth biggest fish occupied the first and third rank, respectively. The dominance hierarchies seemed to have stabilized on day 4. In contrast, in groups of single-size fish, the dominance hierarchy stabilized only by day 10. The rank attained by each fish on day 10 was the same on day 16 in all groups. Since rank was monitored only on specific days, the changes in rank could have happened on that day or sometime between that day and the previous monitoring session.

*Effect of rank, size and time on frequency of aggressive acts - approaches.* Rank had a highly significant ( $p < 0.001$ ) effect on the frequency of approaches (Table 1). In both single and mixed-size groups, the dominant fish carried out the largest number of approaches per 2-min time segment (Table 2). Size differential and time had no effect on the frequency of approaches. However, significant interactions were found between rank and time (Table 1), and among rank, size differential and time. In groups of single-size fish, the number of approaches carried out by the dominant fish was significantly ( $p < 0.05$ ) lower on day 1 than on days 4, 10 and 16. In groups of mixed-size fish there were no significant day-to-day differences.

*Head-to-head.* The frequency of the head-to-head threat display was affected by both rank and time (Table 1). This act is, by definition, displayed simultaneously by two interacting fish that are usually closely matched. The frequencies of performing this act, therefore, were quite similar between the first and second ranked fish, and between the third and fourth-ranked fish, but the fish of the two higher ranks performed it more often (Table 2). The frequency of performance on day 1 was significantly ( $p < 0.05$ ) lower than on days 4, 10 and 16. Neither effects of size differential nor any interactions were found in the frequency of performing the head-to-head display.

*Circling.* Circling was affected only by the rank of the fish (Table 1). It, by definition, is carried out by two fish that are usually closely matched. This act is performed most often by the first and second-ranked fish, occasionally by the third ranked and much less by the lowest ranked (Table 2).

*Chase.* Chase was affected only by social rank, and not at all by size differential or time (Table 1). Clearly the most dominant fish performed the majority of chases, with the second-ranked next, the third-ranked still fewer and the lowest ranked hardly any (Table 2).

*Nipping.* Nipping was affected by the social rank but not by size differential or time. However, there were two significant interactions: between social rank and size differential, and between social rank and time (Table 1). In groups of single-size fish, the most dominant fish carried out the majority of nipping, about three times as many as the rest of the fish combined (Table 2). There was no difference in rate of nipping among the second, third and fourth-ranked fish. In contrast, in groups of mixed-size fish, nipping was also carried out relatively frequently by the second-ranked, which did not differ significantly from the most dominant. However, the third and fourth-ranked fish nipped very rarely. In groups of single-size fish, the most dominant performed fewer nipping acts on day 1 than on days 4, 10 and 16, whereas in groups of mixed-size fish the rate of nipping was similar throughout the study.

*Effects of rank, size differential and time, on location, vertical swimming, mobility and*

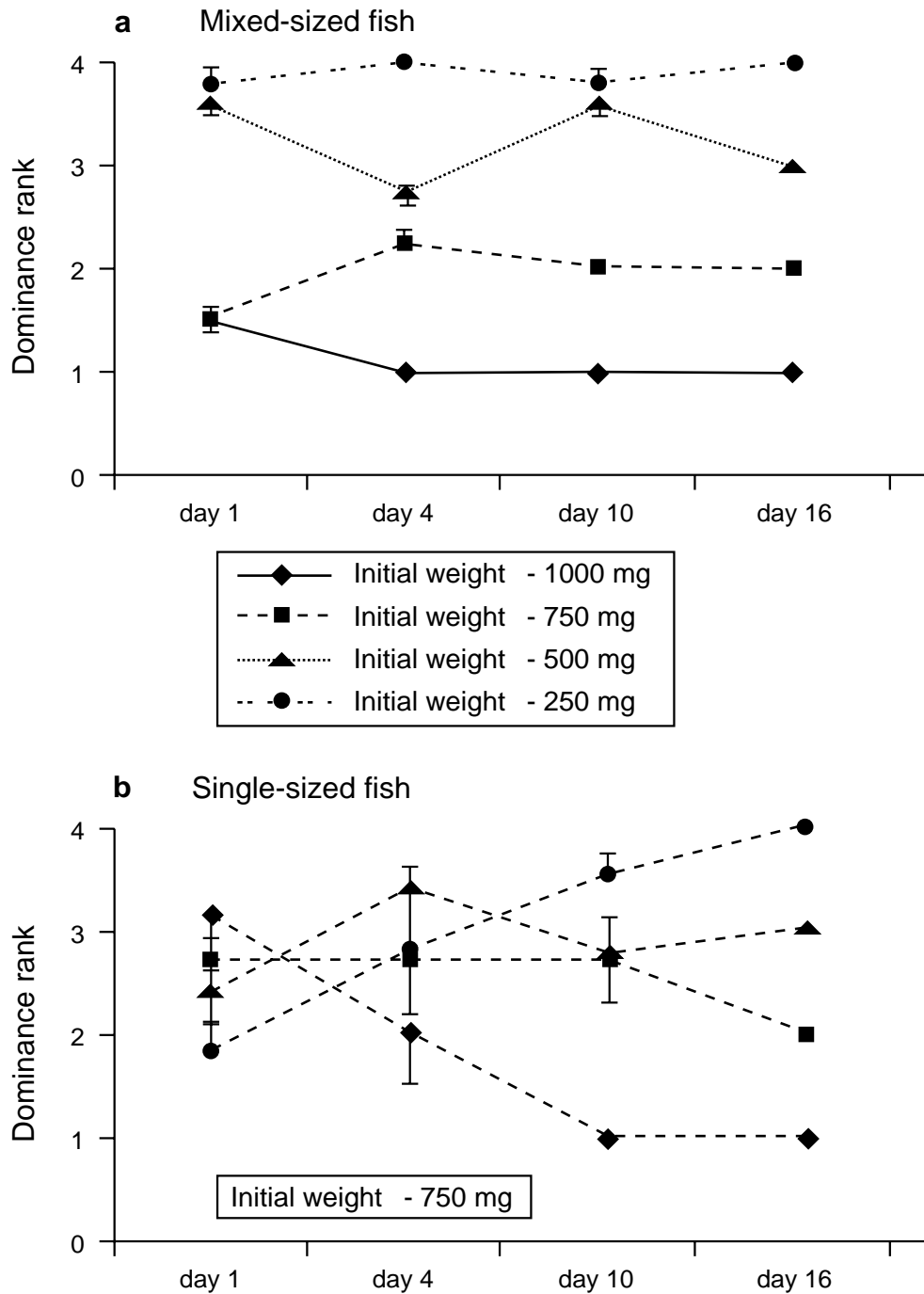


Fig. 1. Rank of juvenile *Sparus aurata* in dominance hierarchies in groups of (a) mixed-size and (b) single-size individuals during a period of 16 days. Bars designate standard error of the mean.

Table 1. Effects of rank, size and time on the frequency of performing five aggressive acts by juvenile gilthead sea bream *Sparus aurata*, results of three-way repeated measures ANOVA (F values).

Effect	d.f.	Behavioral pattern				
		Approach	Head-to-head	Circling	Chasing	Nipping
Rank in hierarchy (1, 2, 3, or 4)	3, 96	73.61**	4.12*	4.13*	6.06**	7.6**
Size differential (single or mixed)	1, 96	0.65	0.38	2.68	0.23	1.46
Time (day 1, 4, 10, or 16)	3, 96	0.94	4.25*	2.04	2.28	2.02
Rank x size differential	3, 96	1.31	0.62	0.63	0.76	3.1*
Rank x time	9, 96	1.99*	0.87	0.74	0.84	2.2*
Size differential x time	3, 96	1.41	0.71	0.14	0.09	0.62

Significance of effects: \*  $p < 0.05$ , \*\*  $p < 0.01$ .

Table 2. Number of agonistic interactions carried out by juvenile *Sparus aurata* according to rank in dominance hierarchy in groups of single and of mixed-size individuals. Size differential refers only to approaches and nipping because there was a significant interaction effect between the factor and rank only in these behaviors. Numbers represent means over a period of 2 min.

Rank	Behavioral patterns						
	Approach		Nipping		Head-to-head	Circling	Chasing
	Single size	Mixed size	Single size	Mixed size			
First	32.8a	26.6a	2.9a	1.31a	1.0a	1.4a	1.0a
Second	7.7b	9.9b	0.63b	1.27a	0.9a	1.2a	0.4b
Third	2.5b	1.3c	0.47b	0.12b	0.4ab	0.63ab	0.1b
Fourth	1.0b	0.0c	0.0b	0.0b	0.2b	0.25b	0.04b

Values in the same column marked with the same letter are not significantly different ( $p < 0.05$ ).



Table 3. Effects of rank, size and time on the location, vertical swimming, mobility and biting-at-food behavior of juvenile gilthead sea bream *Sparus aurata*, results of three-way repeated measures ANOVA (F values).

	<i>d.f.</i>	<i>Behavioral patterns</i>			
		<i>Location</i>	<i>Vertical swimming</i>	<i>Mobility</i>	<i>Biting at food</i>
Rank in hierarchy (1, 2, 3, or 4)	3, 96	9.1**	3.81*	6.58**	20.0**
Size differential (single or mixed)	1, 96	0.77	0.44	11.1**	0.18
Time (day 1, 4, 10, or 16)	3, 96	3.12*	1.08	1.59	4.48**
Rank x size differential	3, 96	0.74	0.25	0.68	0.8
Rank x time	9, 96	0.7	0.73	1.29	0.66
Size differential x time	3, 96	1.51	1.54	2.19	0.94

Significance of effects \* $p < 0.05$ , \*\* $p < 0.01$ .

Table 4. Location, vertical swimming, mobility and biting-at-food behavior by juvenile *Sparus aurata*, according to rank in dominance hierarchy. Numbers represent means over a period of 2 min.

<i>Rank</i>	<i>Behavioral pattern</i>			
	<i>Location</i>	<i>Vertical swimming</i>	<i>Mobility</i>	<i>Biting at food</i>
First	2.52 <sup>a</sup>	0.0 <sup>b</sup>	67.0 <sup>a</sup>	37.0 <sup>a</sup>
Second	1.89 <sup>b</sup>	0.0 <sup>b</sup>	65.6 <sup>a</sup>	22.5 <sup>b</sup>
Third	1.86 <sup>b</sup>	9.4 <sup>a</sup>	48.1 <sup>b</sup>	15.8 <sup>b</sup>
Fourth	1.84 <sup>b</sup>	9.6 <sup>a</sup>	47.0 <sup>b</sup>	14.8 <sup>b</sup>

Values in a column with the same superscript are not significantly different ( $p > 0.05$ ).

*biting at food*. Both social rank and time (Table 3) affected fish location. The most dominant fish spent much more time in the lower third of the observation cells, where food accumulated, than the rest of the fish (Table 4). Fish spent more time in the lower

third of the cell on day 1 than on day 4. Their positions on days 10 and 16 did not significantly differ from those on days 1 and 4.

Vertical swimming in the upper level of the water was affected only by the social rank (Table 3) and was seen only in third and

fourth-ranked fish (Table 4), probably to avoid social interactions.

Rank and size differential had highly significant effects on mobility (Table 3). The mobility of the first and second-ranked fish was similar; they were much more active than the third and fourth-ranked (Table 4). Similar-size groups were significantly more active than the mixed-size groups (mean numbers of quadrates crossed within 2 min were 65.2 and 50.7, respectively).

Both rank and time affected the number of bites directed at food pellets (Table 3). The first-ranked fish directed significantly more bites at pellets than the others (Table 4). The mean numbers of bites directed at food were significantly higher on day 4 than on the rest

of the days (mean frequencies of 29.6 and 20 bites per 2 min, respectively).

*Effects of rank and size differential on growth.* All fish gained weight during the study, but the variations among replicates of each treatment were large. Rank had a significant effect on relative SGR (Fig. 2). In both single and mixed-size groups, the most dominant fish had the highest relative SGR. In groups of single-size fish, the relative SGR of the most dominant fish more than doubled that of the rest of the fish, which were similar to each other. In contrast, in mixed-size groups, the most dominant fish had only a slightly higher relative SGR than the second and third-ranked fish and was significantly different only from the fourth.

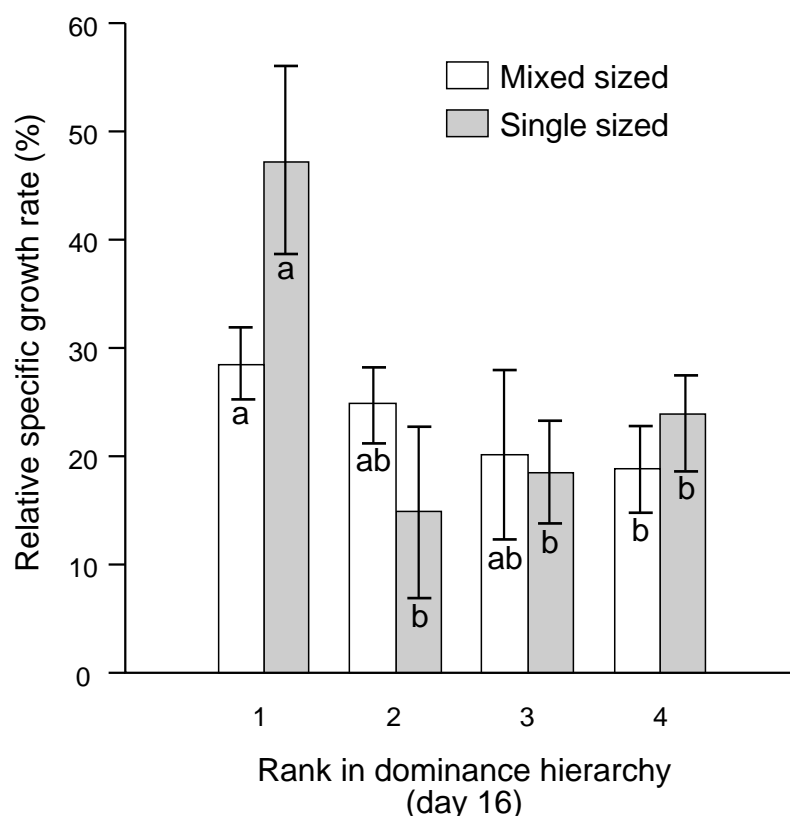


Fig. 2. Relative specific growth rate and rank of juvenile *Sparus aurata* in dominance hierarchies in groups of single and mixed size fish.

### Discussion

We found that a major social mechanism controlling growth in small groups of *S. aurata* was competition for food when this resource was both limited and defensible. The most dominant fish, irrespective of group structure, prevented food from reaching lower ranked fish by continuously attacking and chasing them away, as long as food was present. The dominant fish, which occupied the lower sections of the observation cells where food accumulated, bit at food twice as often as lower-ranked fish, which mostly occupied the upper layers of the cell.

Frequency of biting does not necessarily reflect the amount of food ingested (Carrieri and Volpato, 1991) and an objective measure of food consumption, e.g., radiography (Talbot and Higgins, 1983; Jobling et al., 1995; Kristiansen, 1999; McCarthy et al., 1999), provides a better means of determining food ingestion. Nevertheless, we believe that the much higher biting rate of the dominant fish genuinely reflected a higher rate of food ingestion; and this was manifested in a clear growth advantage. These results are in accord with a study of *S. aurata* under conditions of limited and defensible food (Karplus et al., 2000) in which the SGR of medium-sized juveniles was three times as high when they were surrounded by small rather than large fish. Karplus et al. (2000) attributed this to monopolization of food by the larger fish. A similar phenomenon of subordinate fish being denied access to food by aggression from dominant fish, with subsequent disproportionate food acquisition and growth in the dominant fish, has been described in other fish species (Magnuson, 1962; Symons, 1971; Kristiansen, 1999; Webster and Hixon, 2000; Maclean and Metcalfe, 2001; Irwin et al., 2002).

In the present study, increased motor activity and energy expenditure of subordinate fish can be ruled out as a growth-regulating mechanism because of the reduced motor activity in the subordinate *S. aurata*. Contradictory findings on motor activity of subordinates are probably related to the territoriality of the dominant fish (Ruzzante, 1994). In cases of strictly solitary territorial fish, subordinates are continu-

ously evicted and forced into sustained pelagic swimming, as in the case of the European eel (Knights, 1987), or maintaining positions in areas of high stream velocity as in the case of rainbow trout (Li and Brocksen, 1977) with consequently increased levels of energy expenditure. The motor activity of subordinates whose presence in the vicinity is tolerated by dominants is usually reduced (Abbot and Dill, 1989; Ruzzante, 1994), a situation also observed in the present study of *S. aurata*.

In this study, the cost of dominance in *S. aurata* was relatively low since, in all the groups, the dominant fish had the highest relative growth rate and their aggressive acts were mostly restricted to defending the food from subordinates. In the absence of food, there were few aggressive interactions. In other species that often engage in territorial or rank-related dominance conflicts, the highest-ranking individuals often bear the cost of extra conflicts by growing more slowly than some of the subordinates (Yamagishi et al., 1974; Rubenstein, 1981; Sakakura and Tsukamoto, 1998).

The size differential among group members had a profound effect on the behavior of the individuals in each group. Dominance hierarchies were already stabilized after four days in groups of mixed-size fish, whereas in groups of single-size fish the dominance hierarchy stabilized some time between days 1 and 10. The overriding importance of size in determining social rank has been established in a variety of teleostean species (Frey and Miller, 1972; Barlow and Balin, 1976; Gorlik, 1976). In some species, a size difference of only 5% was sufficient to ensure dominance of the larger individuals (Abbot et al., 1985). In the absence of a clear size cue, dominance hierarchies may take more time to stabilize, as was found in the present study and also suggested by Jobling and Reinsnes (1986) for stunted Arctic charr, *Salvelinus alpinus*.

Nipping, the most offensive aggressive act, was carried out at different rates by similarly ranked members of the single and mixed-size groups. Except for the dominant fish, which behaved in a despotic manner, the

rates of nipping in single-size groups were relatively low and similar among group members. In mixed-size groups, the nipping rates of the various group members were relatively high and followed the size hierarchy. These results can be understood as subordinates refraining from attacking fish of a similar size, since the costs involved in attacking such individuals may be too high (Maynard-Smith and Parker, 1976).

Extrapolation of insights gained from studying the relationship of behavior and growth in small groups raised in a restricted space to schools composed of thousands of individuals in large culture units should be done cautiously. It was believed that one of the fundamental behavioral differences between the two was that fish in small groups gradually establish hierarchies based on recognition of individuals or individuals displaying certain behaviors, whereas fish in large groups are egalitarian anonymous social units. However, recent studies revealed that, also in fish schools, there are individual differences in the behavior of members, e.g., in positioning (Pitcher et al., 1982; Krause et al., 1992; Krause, 1993). Individual differences in aggressive tendency were reported in schools of the Midas cichlid *Cichlasoma citrinellum* (Francis, 1990) and the presence of social rank was reported in schools of juvenile yellowtail, *Seriola quinqueradiata* (Sakakura and Tsukamoto, 1998). Thus, some of the findings of the present study could be considered with regard to their relevance to commercial fish culture. In particular, attention should be paid to the finding that direct competition for food is a major social mechanism controlling growth in juveniles of this species. Earlier studies (Goldan et al., 1997, 1998) of how changes in food particle size, feeding frequency and the live/dry food ratio could reduce food competition indeed show that these measures result in a change in growth, reducing the need for labor-intensive fish-stressing grading operations in this species.

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