

Social rank in schools of juvenile yellowtail, *Seriola quinqueradiata*

Yoshitaka Sakakura* and Katsumi Tsukamoto

Division of Fisheries Ecology, Ocean Research Institute, The University of Tokyo,
Minamidai 1-15-1, Nakano, Tokyo 164, Japan

(* Present address: Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada)

Summary

The composition, stability and biotic factors of social rank in the schools of juvenile marine fish are demonstrated, using juvenile yellowtails *Seriola quinqueradiata* (Temminck et Schlegel: Carangidae). According to the frequency of aggressive behaviour, members within a school were divided into three categories; dominants (10-20 %), intermediates (10-20 %) and subordinates (60-80 %). Social rank was reset with the same composition of hierarchy when dominants and intermediates were gathered. Observation of individual aggressive behaviours using video image analysis system revealed that starvation and an increase in fish densities accelerated only aggression of dominants. In order to determine the durability of social rank, otoliths of dominant fish in 8 experimental groups were labeled and the fish were returned to their groups. Six labeled dominants appeared after one day and three after one week rearing, respectively, indicating that social rank was maintained for at least one week (binomial distribution; $p < 0.05$). Total lengths of dominants were larger than those of subordinates in one day rearing, whereas dominants were smaller in one week rearing. Social rank of this species is decided upon by individual aggressive tendency, but is not beneficial for feeding or growth.

Introduction

Many fish species develop social responses to conspecifics as schooling behaviour in their early life stages (Noakes and Godin 1988). Schooling behaviour is closely associated with survival in the wild through its functions in foraging enhancement and predator avoidance (Hamilton 1971; Noakes 1978; Magurran 1990; Pitcher and Parrish 1993). Recently, the presence of individual differences in the behaviour of members of fish schools, such as positioning among individuals, are reported (Magurran 1993; Pitcher et al. 1982), although long considered to be egalitarian and leaderless societies (Breder 1954; Shaw 1962; Shaw 1978).

The inconsistent behaviours, schooling behaviour and aggressive behaviour, appear simultaneously in the juvenile stage of the yellowtail *Seriola quinqueradiata*, which is a highly migratory marine species and one of the most important commercial species around Japan (Sakakura and Tsukamoto 1996). Previous studies claimed that there is individual difference in aggressive behaviour among the school members (Sakakura and Tsukamoto 1996), and that a social rank is present in the juvenile schools of this species (Sakakura and Tsukamoto 1997a; Sakakura et al. 1997). Since aggressive behaviour and social rank can cause a high mortality in fish culture including yellowtail (Hecht and Pienaar 1993; Imaizumi 1993), there is a need to understand the mechanism of the social rank in the early life stages of this species. However, little is known of the detail of the social rank in the juvenile yellowtail schools, such as composition, stability and environmental factors.

In this study, we examined the composition, stability and environmental factors on social rank in a school of the juvenile yellowtails, by observing school members individually. We use the term 'schooling' in the sense of a polarized synchronized swimming group (Pitcher 1983).

Materials and Methods

Experimental Fish

Three batches of juvenile yellowtails were used in this study in year 1992, 1993, and 1995. Yellowtail were matured artificially by human chorionic gonadotropin injection and were allowed to spawn naturally in a 90-m³ indoor tank at the Goto station of the Japan Sea Farming Association (JASFA) in Nagasaki Prefecture. Fertilized eggs were maintained in a 0.5-m³ tank, and after 2 days, approximately 1,000,000 larvae were obtained (April 30, 1992; April 24, 1993; May 10, 1995). Two days after hatching (day 2), larvae were transferred to a concrete rearing pond (90 m³). Larvae were fed with the rotifer *Brachionus plicatilis* cultivated with *Nannochloropsis* sp. between days 3 and 20, with newly hatched *Artemia salina nauplii* enriched with feed oil (Riken feed oil, Riken Co.) between days 7 and 24, and with dry pellets (for fish 1992, Larval fish feed, Nissui Co.; for fish 1993 and 1995, C-400 and C-1000, Kyowa Co.) from day 22 until the end of the experiment. Water temperature ranged from 22 to 24°C under natural light conditions.

Experiment 1: Social rank

One-hundred fish of comparable size (total length, TL \pm SD, 23.7 \pm 2.5 mm) were selected from the rearing pond (day 39, 1993). Ten fish were transferred to each of ten white round experimental tanks, each containing 10-L seawater (30 cm in diameter, 12 cm in depth). The tanks were kept in a water bath at 22°C under natural light conditions.

After one hour of acclimation, the behaviour of fish in each experimental tank was observed from above for a duration of ten minutes, and the first series of aggressive fish (1 to 3 fish per tank), which showed an incidence of chase behaviour toward another fish more than 5 times \cdot min⁻¹ as an index of aggressive behaviour (Sakakura and Tsukamoto 1996), were quickly scooped out by a hand net. These fish were held thereafter in a 2-L white plastic beaker with aeration. Four hours after removal of the first group of aggressive fish, a second series of aggressive fish (1 to 3 fish per tank), which appeared after the removal, were also taken out of the tank in the same manner as described

above and pooled with the first group of aggressive fish. The behaviour of fish in each experimental tank was observed for an additional hour after which the remaining fish were anesthetized in MS222 and preserved in buffered solution of 10% formalin in seawater.

A total of thirty aggressive fish pooled in the white beaker during first and second series of treatments, were transferred to a white round tank (35 cm in diameter) containing 30-L seawater. After one hour of acclimation the first group of aggressive individuals, termed 'dominants' were removed immediately by a hand net. Four hours after this treatment, the second group of aggressive fish, termed 'intermediates', were scooped out in the same way. The fish remaining in the tank were termed as 'subordinates'. The fish of all categories were anesthetized with MS222 and preserved in a buffered solution of 10% formalin in seawater, followed by TL measurement using a caliper.

Experiment 2: Effects of starvation and density

Fish used for this experiment were randomly sampled from the rearing pond with a 13-L bucket, and 20 fish were selected to minimize size variation (20.3 ± 2.7 mm, day 39, 1992). Fish were introduced into three experimental tanks using a white 1-L plastic beaker at 7:00am as follows: the first tank contained five fish (1 fish L^{-1}) which were fed with sufficient artificial diet (Larval feed, Nissui Co.) with 4 hours intervals (control); the second tank containing five fish (1 fish L^{-1}) were kept starved for 12 hours (starved); the third tank consisted of ten fish (2 fish L^{-1}) fed sufficiently for 4 hour intervals (high density). Sufficient feeding was estimated from a typical expansion of belly size. A density of 1 fish L^{-1} corresponded roughly to the mean density of juveniles in the rearing pond. After acclimation for 12 hours, the behaviour of fish in each tank was recorded from above by an 8 mm video camera (Handycam CCD, Sony Co.) for 60 minutes simultaneously. After observation, all fish were anesthetized with MS222 and TLs were measured.

The experimental tanks used were white round tanks containing 5-L of seawater (30 cm in diameter, 7 cm water depth) immersed in a water bath at 22°C. Lighting was provided by a video lamp (Brom Cine Light, LPL Co.) at 2000 lux throughout the experiment. Both water temperature and light intensity were adjusted to match those of the indoor rearing pond at noon in good weather.

The individual fish on the video recording of each tank were discriminated by a video image analysis system (LA525, PIAS Co.), which recognizes fish from their background by thresholding of brightness. The behaviour of each individual fish was traced throughout the all video recordings (60 min). "Chase" behaviour as an index of aggressive behaviour (Sakakura and Tsukamoto 1996) was counted individually, and the mean frequency of aggressive behaviour (count min^{-1}) of each fish was obtained.

Experiment 3; Stability of social rank

One thousand juveniles (TL ca. 50 mm) were transferred from the rearing pond to a round black poly-carbonate tank containing 500-L seawater on July 10, 1995 (day 66). Fish were kept as a stock in running seawater (25°C, flow rate $8 \text{ L} \cdot \text{hour}^{-1}$) and were fed a commercial diet (C-1000, Kyowa Co.) at a rate of 3% of the body weight, three times per day.

Eight white round tanks (35 cm in diameter) containing 20-L seawater were set up in a water bath at 25 °C and aerated. At 5:00pm on July 19 (one-day experiment) or July 11 (one-week experiment), a total of 80 fish from the stock tank were introduced into the experimental tanks ($10 \text{ fish tank}^{-1}$) and were acclimated for one hour. Based on a 10-minute observation of each tank, the most aggressive fish (dominant), with the highest frequency of chase behaviour, was identified and removed by a hand net (first treatment). According to Tsukamoto (1988), the dominants were labeled individually in 400 ppm of ALC (Alizarin complexone; Wako Co.) in another group of 8 separate tanks (30 cm in diameter, 20-L) for 15 hours. The following morning at 9:00am, the dominants were again returned to the previous tanks from which they originated. Otolith marking can be almost only one

method applicable for marking of larval and juvenile fishes in behavioural experiments, because this treatment is known to not affect on fish behaviour, growth and survival (Tsukamoto 1985,1988).

In the one-day experiment, fish in all the experimental tanks were fed with the commercial diet (C-1000, Kyowa Co.) at a rate of 3% of the b.w. at 10:00am one hour after reintroduction of an ALC-labeled individual, and acclimated for 6 hours thereafter. We observed fish in each tank for 10 min, and scooped the dominant fish from each tank with a hand net (second treatment) and anesthetized them with MS222. The dominant fish and the fish remaining in the experimental tanks were anesthetized in MS222 and preserved in 90% ethanol in order to prevent degradation of otoliths (Brothers 1984).

In the one-week experiment, all experimental fish were fed the commercial diet (C-1000, Kyowa Co.) twice a day (10:00am, 4:00pm) at a rate of 3% of the body weight. Half volume of the seawater was exchanged with fresh seawater after every feeding time. Fish were reared for one week; then the dominant fish of each tank were identified and scooped by a hand net, and all fish preserved as in the one-day experiment.

The TLs of the fish of both experiments were measured using a caliper and sagittal otoliths were also extracted. ALC label in the otolith was examined under a UV-light microscope (Tsukamoto et al. 1989). Binomial distribution was carried out to determine the theoretical possibility that the dominant fish at the second treatment coincided with the dominant fish with the ALC marking in the first treatment for both the one-day and the one-week experiments.

Results

Experiment 1

Fish showed typical schooling behaviour as well as chase behaviour in all tanks. Numbers of the first series of aggressive fish were one to three fish (10 to 30 %) from each tank, and the mean number \pm SD was 1.4 ± 0.7 fish (14.0 ± 6.6 %, $n=10$). Second series of aggressive fish appeared 10 to 60 minutes after removing the first series of aggressive fish. Second series of aggressive fish were found at same numbers (1 to 3 fish, 11.1 to 42.9 %), and mean aggressive fish number \pm SD was 1.6 ± 0.8 (9.1 ± 10.8 %, $n=10$). There was no significant difference between aggressive fish occurrence at the first and second observation (T-test, $t = -1.22$, $p=0.24$). After the second observation, no further aggressive fish were noted. No significant difference was found between TLs of aggressive fish (23.5 ± 2.1 mm, $n=30$) and non-aggressive fish which remained in the experimental tanks (23.8 ± 2.7 mm, $n=70$; T-test, $t = -0.58$, $p = 0.57$).

In the experimental tank where 30 aggressive fish were introduced, we found three categories: dominants (the most aggressive fish which showed chase behaviour over 5 times min^{-1}), intermediates (the secondary aggressive fish which appeared after the removal of dominants), and subordinates (non-aggressive fish). The occurrence ratio of dominant was 13.3 %, that was around the same value of the previous treatment (14.0 ± 6.6 %). The occurrence of intermediate was 23.3% and subordinate was 63.4 %, respectively. There was no significant difference of TLs among dominant, intermediate, and subordinate fish (ANOVA, $df= 2$, $F = 0.88$, $p = 0.43$).

Experiment 2

Fish showed typical schooling behaviour in all tanks and sometimes aggressive behaviours were observed among individuals in the schools. From the frequencies of individual aggressive behaviours (Fig.1), all individual fish were separable into three categories: highly aggressive fish (0.5 to $1.2 \text{ times min}^{-1}$: dominant), low aggressive fish ($>0.5 \text{ times min}^{-1}$: intermediate), and non-aggressive fish (subordinate). Dominant was Fish A ($0.67 \text{ times min}^{-1}$) in the control and Fish J ($1.44 \text{ times min}^{-1}$) in the starved. Intermediates were Fish B ($0.11 \text{ times min}^{-1}$) and Fish C ($0.17 \text{ times min}^{-1}$) in the control, whereas Fish G ($0.11 \text{ times min}^{-1}$) and Fish H ($0.05 \text{ times min}^{-1}$) in the starved. Between control and

starved group, frequency of aggressive behaviour was at the same level as intermediate fish, while aggression of dominant of starved group was twice than that of control. In the high density group, dominants were Fish L (0.94 times min^{-1}) and Fish O (1.22 times min^{-1}), and intermediates were Fish M (0.22 times min^{-1}) and Fish Q (0.11 times min^{-1}). Comparing aggressive behaviours between control and high density group, intermediates showed approximately same levels, whereas dominants of high density showed 1.4 to 1.8 times as high as that of control. Each dominant showed aggressive behaviour mainly toward subordinates, and each intermediate chased subordinates or other intermediates but not dominant.

Dominant occurred at 20% and intermediate appeared 20 to 40 % from total fish among each experimental tank. TL of dominant was the second largest fish in control and starved, and was the second and fifth largest in high density (Fig.1).

Experiment 3

In the one-day experiment, six labeled fish were found from the 8 dominant fish of second treatment (75%; Table 1). The theoretical possibility was $p=0.000023$, indicating that dominant fish at first treatment coincided with the dominant fish at second treatment significantly ($p<0.01$; Table 1). Mean TL of dominants (63.1 ± 6.8 mm, $n=8$) was significantly larger than that of subordinates (58.4 ± 5.9 mm, $n=72$; T-test, $t = -2.13$, $p<0.05$; Table 1).

In the one-week experiment, three of 8 dominant fish (37%) had ALC label (Table 1). The theoretical possibility was $p=0.038$, indicating that dominant fish at first treatment corresponded with the dominant fish at second treatment significantly ($p<0.05$; Table 1). TLs of dominants (54.4 ± 7.1 mm, $n=8$) was significantly smaller than those of subordinate (59.4 ± 5.9 mm, $n=72$; T-test, $t = -2.22$, $p<0.05$; Table 1).

Discussion

The most significant findings in our study are that: (1) the presence of a social rank in the schools of juvenile yellowtails with dominance hierarchy, (2) occurrence of each component of dominance hierarchy at a constant ratio based on a relative strength of individual aggressive tendency, (3) biased effect of environmental factors only on aggressive tendency of dominant fish, and (4) comparatively long duration of social rank for more than one week, are firstly demonstrated among the school of highly migratory marine fish juveniles.

Composition of social rank

Our results reflect not only the presence of social rank in a school of juvenile yellowtails, but also the presence of individual difference in aggressive tendency, as reported in schools of Midas cichlid *Cichlasoma citrinellum* (Francis 1990). In all experiments, aggression was observed toward fish belonging to lower rank one-sidedly. Therefore, the social rank of this species resembles the 'peck order' of chickens (Schjelderup-Ebbe 1935), and is coincided with a social rank of rainbow trout *Oncorhynchus mykiss* (Abbot et al. 1985; Yamagishi 1962) in which territoriality and competition for limited space and food resources are concerned.

The social rank of juvenile yellowtails were divided into three grades: dominant (10~20 % of a fish group), intermediate (10~20 %) and subordinate (60~80 %) with constant ratio, respectively (Experiment 1 ~ 3). It is noteworthy that even when aggressive fish (dominant plus intermediate) gathered in one tank social rank appeared with same ratio components in one hour (Experiment 1), suggesting that the social rank of juvenile yellowtail is decided upon the relative dominance hierarchy between the members in a school.

In the experiment 3, the dominant fish were re-introduced into the previous tanks after 15 hours isolation for marking, although this isolation period included about 11 hours nighttime when juvenile

yellowtails stop swimming and agonistic interactions (Sakakura and Tsukamoto 1997b). During this period, a new hierarchy seems to be established in a short time less than one hour after removal of a dominant fish, since aggressive behaviour and social rank occurred in 15 min when fish exposed to a new environment in *Betta splendens* (Bronstein 1988). However, most of ALC-labeled dominants at least in one-day experiment (Table 1), destroyed a possible new hierarchy and reestablished the former social rank again, when returned to the previous tank after 15 hours isolation. This also supports the presence of individually different aggressive tendency which decides the social rank in a school.

No agonistic interactions were observed among the subordinates after the removal of dominants and intermediates (Experiment 1). It is reported that subordinates hardly become dominants despite the removal of dominant fish because of learning the position in social rank, as e.g. in European eel *Anguilla anguilla* (Knights 1987), paradise fish *Macropodus opercularis* (Francis 1983) and rainbow trout (Abbot et al. 1985). The social rank of yellowtail may be decided upon not only individual aggressive tendency and relative aggression strength between school members, but also learning position in a school.

Biotic factors such as starvation and high-density only accelerate the aggression of dominant fish, but do not affect on those of intermediate and subordinate fish (Fig.1). No size advantages were observed between dominants and subordinates (Table 1). These results indicate the presence of individual difference in aggressive tendency in juvenile yellowtails, which is not strongly affected by body size in the same body size group.

Stability of social rank

There are few studies on the stability and durability of social rank in fishes (Elwood and Rainey 1983; Oliveira and Almada 1996). The instability of social rank for long period (1 to 4 weeks) is reported in cichlid fish *Oreochromis mossambicus* (Oliveira and Almada 1996), whereas stability in 5 days is reported in green sunfish *Lepomis cyanellus* (McDonald et al. 1968). Stability of dominant yellowtail was statistically one week (Table 1), which is firstly revealed in a school of juvenile marine species.

In one-day experiment, almost all the dominants were also previously dominant fish and were larger in size, whereas hierarchy relatively changed after one week and TLs of both previous and new dominants became smaller (Table 1). This result indicates that social rank of this species is not stabilized strictly and has some flexibility to experience a rank reversal within dominant and intermediate fish in long-term period. The reversal of social rank will be caused by relationships in relative physical strength of fish, in which dominant tend to loss much energy in long-term by chasing other fish resulting in depression of growth rate, and intermediates have a chance to come over the previous dominant.

Social rank in wild and rearing conditions

In wild condition, juvenile yellowtails aggregate to drifting seaweeds in current rips with uniformed body size (Uchida et al. 1958; Sakakura and Tsukamoto 1996) and age (Safran 1990; Sakakura & Tsukamoto 1997b). These juvenile yellowtails forage pelagic copepods and fish larvae which do not associated with drifting seaweed (Anraku and Azeta 1965; Sakakura and Tsukamoto 1996).

Therefore, juvenile yellowtails of one school under a drifting seaweed mass are in scramble-competition over the food (Wootton 1990), in which the drifting seaweed is not functional for the food resources and the base for territory. Moreover, there were the reversal of social rank (Experiment 3) and weakness in size advantages in this species (Experiment 1 and 2). Thus, social rank in the schools of this species may not bring the benefit on growth to the dominant fish as reported in many salmonid species (e.g. Abbot and Dill 1989; Ruzzante 1994).

In the rearing ponds, cannibalism among juvenile yellowtails of one batch causes high mortality (Imaizumi 1993). Chase behaviour is observed not only in every sequence of aggressive behaviour but also in cannibalism, and cannibalism is interpreted as an final phase of aggressive behaviour

(Sakakura and Tsukamoto 1996). Size variations of body size (coefficient of variation; CV) in a rearing pond, is depressed from the onset of aggressive behaviour and cannibalism (CV < 0.2; Sakakura and Tsukamoto 1996). Larger fish (dominants), which can cannibalize smaller fish in a school with less than 50 % of body size (Sakakura and Tsukamoto 1996), are supposed to lose their energy in chasing other subordinates or preys, and to lose benefit for growth (Table 1). Then, the reversal of social rank and body size of dominants shown in this study (Table 1), may act to minimize the size variation leading to the uniformity in body size of school members. Field observation also shows that size variations in body sizes of school members are uniformed (CV = ca.0.15), and cannibalism is found among school members (Sakakura and Tsukamoto 1996), and each school was formed by almost the same batch estimated from age composition (Sakakura and Tsukamoto 1997b). Therefore, aggressive behaviour and social rank in the schools of yellowtail are supposed to have a function for making the body size of school members as uniformed both in wild as well as rearing conditions. The uniformity in body size among fish school is considered that it may minimize the predation risk individually by the predator's confusion (Pitcher and Parrish 1993). Social rank of the yellowtail seems to be inconsistent with schooling behaviour at a glance, but the balance between schooling and social rank derived from aggression regulate the size of school members as uniformed and it is interpreted as a strategy to raise the benefit of predator avoidance in early life stages.

Acknowledgements

The authors are grateful to Mr. S. Shiozawa, K. Maruyama, Y. Mizuta and T. Furusawa of JASFA for their support and kind help during the course of the experiments, without which the study could not have been made. We are also grateful to Prof. Howard A. Bern, University of California at Berkeley for critical reviewing the manuscript. Thanks are also due to Dr. J. H. Blom, Faculty of Fisheries, Kagoshima University, and Dr. Marcy N. Wilder, Japan International Research Center for Agricultural Science, Ministry of Agriculture, for their helpful comments. Y.S. was supported by the Fellowship for Japanese Junior Scientists and the Postdoctoral Fellowships for Research Abroad of the Japan Society for the Promotion of Science.

References

- Abbott, J. C.; Dunbrack, R. L.; Orr, C. D., 1985: The interaction of size and experience in dominance relationships of juvenile steelhead trout (*Salmo gairdneri*). Behaviour, **92**, 241-253.
- Abbot, J. C.; Dill, L. M., 1989: The relative growth of dominant and subordinate juvenile steelhead trout (*Salmo gairdneri*) fed equal rations. Behaviour, **108**, 104-113.
- Anraku, M.; Azeta, M., 1965: The feeding habits of larval and juveniles of yellowtail, *Seriola quinqueradiata* Temminck et Schlegel, associated with floating seaweeds. Bull. Seikai Reg. Fish. Res. Lab. **33**, 14-15.
- Breder, C. M., 1954: Equations descriptive of fish schools and other animal aggregations. Ecology **35**, 361-370.
- Bronstein, P. M., 1988: Socially mediated learning in male *Betta splendens*. III: Rapid acquisitions. Aggressive Behav. **14**, 415-424.
- Brothers, E. B., 1984: Otolith studies. In: Ontogeny and systematics of fishes. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. J. Kendall and S. L. Richardson (Eds). The American Society of Ichthyologists and Herpetologists, Lawrence, pp. 50-57.
- Elwood, R. W.; Rainey, C. J., 1983: Social organization and aggression within small groups of female Siamese fighting fish, *Betta splendens*. Aggressive Behav. **9**, 303-308.
- Francis, R. C., 1983: Experimental effects on agonistic behaviour in the paradise fish, *Macropodus opercularis*. Behaviour **85**, 292-313.
- Francis, R. C., 1990: Temperament in a fish: A longitudinal study of the development of individual differences in aggression and social rank in the Midas cichlid. Ethology **86**, 311-325.

- Hamilton, W. D., 1971: Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295-311.
- Hecht, T.; Pienaar, A. G., 1993: A review of cannibalism and its implications in fish larviculture. *J. World Aquaculture Soc.*, **24**, 246-261.
- Imaizumi, K., 1993: Recent progress of Japan Sea-Farming Association in marine finfish hatchery activities. In: *Finfish hatchery in Asia, Proceedings of finfish hatchery in Asia '91*. C. S. Lee, M. S. Su and I. C. Liao (Eds). Tungkang Marine Laboratory TFRI and The Oceanic Institute, Tungkang, pp. 173-177.
- Knights, B., 1987: Agonistic behavior and growth in the European eel, *Anguilla anguilla* L., in relation to warm-water aquaculture. *J. Fish Biol.* **31**, 265-276.
- Magurran, A. E., 1990: The adaptive significance of schooling as an anti-predator defense in fish. *Ann. Zool. Fennici* **27**, 51-66.
- Magurran, A. E., 1993: Individual differences and alternative behaviours. In: *Behaviour of teleost fishes*. T. J. Pitcher (Ed). Chapman & Hall, London, pp. 441-477.
- McDonald, A.; Heimstra, N. W.; Damkot, D. K., 1968: Social modification of agonistic behaviour in fish. *Anim. Behav.* **16**, 437-441.
- Noakes, D. L. G., 1978: Social behaviour as it influences fish production. In: *Ecology of Freshwater Fish Production*. Ed. S. D. Gerking, Blackwell, Oxford. pp. 360-382.
- Noakes, D. L. G.; Godin, J-G. J., 1988: Ontogeny of behavior and concurrent developmental changes in sensory systems in teleost fishes. In: *Fish physiology*. W. S. Hoar and D. J. Randall (Eds). Academic Press, San Diego, Vol. XI part B. pp. 345-395.
- Oliveira, R. F.; Almada, V. C., 1996: On the (in)stability of dominance hierarchies in the Cichlid fish *Oreochromis mossambicus*. *Aggressive Behav.* **22**, 37-45.
- Pitcher, T.J., 1983: Heuristic definitions of shoaling behaviour. *Anim. Behav.* **31**, 611-613.
- Pitcher, T. J.; Parrish, J. K., 1993: Functions of shoaling behaviour in teleosts. In: *Behaviour of teleost fishes*. T. J. Pitcher (Ed). Chapman & Hall, London, pp. 363-439.
- Pitcher, T. J.; Wyche, C. J.; Magurran, A. E., 1982: Evidence for position preferences in schooling mackerel. *Anim. Behav.* **30**, 932-934.
- Ruzzante, D. E., 1994: Domestication effects on aggressive and schooling behavior in fish. *Aquaculture* **120**, 1-24.
- Safran, P., 1990: Drifting seaweed and associated ichthyofauna: Floating nursery in the Tohoku waters. *La mer* **28**, 225-239.
- Sakakura, Y.; Tsukamoto, K., 1996: Onset and development of cannibalistic behaviour in early life stage of yellowtail. *J. Fish Biol.* **48**, 16-29.
- Sakakura, Y.; Tsukamoto, K., 1997a: Effects of water temperature and light intensity on the aggressive behavior in the juvenile yellowtails. *Fish. Sci. (Tokyo)* **63**, 42-45.
- Sakakura, Y.; Tsukamoto, K., 1997b: Age composition in the schools of juvenile yellowtail, *Seriola quinqueradiata*, associated with drifting seaweeds in the East China Sea. *Fish. Sci. (Tokyo)* **63**, 37-41.
- Sakakura, Y.; Tagawa, M.; Tsukamoto, K., 1997b: Whole-body cortisol concentrations and ontogeny of aggressive behavior in yellowtail (*Seriola quinqueradiata* Temminck & Schlegel; Carangidae). *Gen. Comp. Endocrinol.*, *in press*.
- Shaw, E., 1962: The schooling of fishes. *Scient. Amer.* **206**, 128-138.
- Shaw, E., 1978: Schooling fishes. *Amer. Scient.* **66**, 166-175.
- Schjelderup-Ebbe, T., 1935: Social behavior of birds. In: *Handbook of social psychology*. T. Murchison (Ed). Clark University Press, Worcester, pp. 947-972.
- Tsukamoto, K., 1985: Mass-marking of ayu eggs and larvae by tetracycline-tagging of otoliths. *Bull. Jap. Soc. Sci. Fish.* **51**, 903-911.
- Tsukamoto, K., 1988: Otolith tagging of ayu embryo with fluorescent substance. *Bull. Jap. Soc. Sci. Fish.* **54**, 1289-1295.

- Tsukamoto, K.; Seki, Y.; Oba, T.; Oya, M.; Iwahashi, M., 1989: Application of otolith to migration study of salmonids. *Physiol. Ecol. Japan* **1**, 119-140.
- Uchida, K.; Dotu, Y.; Mito, S.; Nakahara, K., 1958: The spawning and early life history of "Buri", Japanese yellow tail, *Seriola quinqueradiata* Temminck et Schlegel. *Sci. Bull. Fac. Agr. Kyushu Univ.* **16**, 329-342.
- Wootton, R. J., 1990: Biotic interactions II: Competition and mutualism. In: *Ecology of teleost fishes*. R. J. Wootton (Ed). Chapman and Hall, London, pp. 216-237.
- Yamagishi, H., 1962: Growth relation in some small experimental populations of rainbow trout with special reference to social relations among individuals. *Japan. J. Ecol.* **12**, 13-53.

Table 1. Stability of social rank in yellowtail (Experiment 3).

Rearing period		Dominant			Subordinate			
coincidence with firstly observed dominant (8 tanks)		Total length (mm) (mean±SD)		N	Total length (mm) (mean±SD)			
N	theoretical possibility							
1 day	Label	6	0.000023*	65.1±6.7	63.1±6.8	2	67.5±9.9	58.4±5.9**
Non label	2	57.2±0.6	70	58.1±5.7				
1 week	Label	3	0.038*	55.6±1.1	54.4±7.1	5	58.4±3.7	59.4±5.9**
Non label	5	53.8±6.0	67	59.4±6.3				

* significant ($p < 0.05$, binomial distribution) ** significant ($p < 0.05$, Student's t-test)

Fig. 1 Individual aggressive behaviour in different environmental conditions. Alphabet and vertical bar represents each fish and its mean frequency of aggressive behaviour in 60 minutes, respectively. Numerals on the bars indicate the total length (mm) of each fish.

