

Onsets of schooling behavior and social transmission in chub mackerel *Scomber japonicus*

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Received: 1 September 2006 / Revised: 28 January 2007 / Accepted: 31 January 2007 / Published online: 24 February 2007
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Abstract Grouping behavior has various types of anti-predator functions. Some of these functions require social transmission of information, such as the many-eyes effect, whereas others do not, such as the dilution and confusion effects. Functions of grouping behavior would enhance with social transmission among group members. We investigated and compared the onsets of schooling behavior and social transmission of information in chub mackerel *Scomber japonicus*. Onset of schooling behavior was observed in rearing tanks by calculating the degree of parallel swimming. Onset of social transmission was examined by using visual cues from conspecifics. A group of five individuals was put in each of three experimental chambers from which they could see a group of conspecifics in the neighboring chamber. A weak electric stimulus was given to one of these chambers, and information transfer among individuals was observed. We found that

social transmission by visual cues started on 30 days posthatching (25.1 mm in standard length), which was 2 weeks after the onset of schooling behavior. The late onset of social transmission relative to schooling behavior might be attributed to different predation pressure with development, or by underdevelopment of optic tectum, as the volume of the optic tectum did not increase just after the onset of schooling behavior.

Keywords Grouping behavior · Information transfer · Optic tecta · Visual cue

Introduction

Behavioral development is considered to be an ontogenetic adaptation to the environment (Gould 1977). Organisms alter their behavior with development or environmental change so that they can enhance their fitness. For example, tadpoles of *Xenopus laevis* end their aggregative lifestyle and become solitary after metamorphosis (Wassersug 1973), and American lobsters *Homarus americanus* change their antipredator behavior from escape to aggression with the growth of claws (Lang et al. 1977). Knowing the ontogeny of behaviors can reveal critical aspects of fitness associated with different developmental stages and environments.

Grouping behavior is an advantageous strategy in many environments (reviewed by Krause and Ruxton 2002). Each group member receives benefits, such as a decrease in predation pressure or an increase in food searching or mating efficiencies. However, grouping also increases conspicuousness to predators (Krause and Godin 1995), food competition within groups (Krause 1994), and risk of infection by parasites (Brown and Brown 1986; Côté and

Communicated by Jens Krause

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Poulin 1995). The decision to join or leave a group therefore involves a trade-off between these advantages and the co-occurring disadvantages assessed against the need of different developmental stages and environments.

Some antipredator functions of grouping behavior operate simply because the members are in a group, whereas other functions require information transfer among group members. For example, large group size itself creates the dilution (Calvert et al. 1979; Foster and Treherne 1981) and confusion effect (Milinski 1984; Jeschke and Tollrian 2005), whereas information transfer among group members increases vigilance against predators (many-eyes effect; Bertram 1980). Information transfer within groups is an important component of the antipredator functions, in addition to dilution and confusion effects, as it allows individuals in groups to receive vital information that are difficult or risky to obtain as solitary individuals. Information about a predator was visually transmitted to conspecifics in minnows *Phoxinus phoxinus* (Magurran and Higham 1988). A group of five individuals displayed more effective escape responses than a pair of rainbowfish *Melanotaenia duboulayi* (Brown and Warburton 1999). These results suggest that being in groups is beneficial for escaping from predators because individuals are warned earlier, giving them more time to perform antipredator maneuvers.

Ontogenetic timing of both grouping behavior and social transmission are important factors for survival. In addition to dilution and confusion effects of schooling behavior, social transmission ability is required for group members to benefit from many-eyes effect. Visual recognition of and response to the fright behavior of conspecifics is one of the important components of social transmission in decreasing predation risk (Magurran and Higham 1988; Brown and Warburton 1999). Although there is substantial literature on grouping behavior and the social transmission of the visual fright response, no reports have linked the ontogenetic timing between them.

In this study, chub mackerel *Scomber japonicus* was used as a model organism to investigate the ontogenetic timing of grouping behavior and social transmission of information. Shoaling is an important antipredator behavior for chub mackerel because they occupy the open ocean, which provides no physical refuge from predators. We examined whether the ontogenetic onsets of schooling and social transmission of information coincide. Onset of social transmission was examined by using visual stimuli, which would be particularly important for schooling fishes living in a clear open ocean. We also observed the development of the optic tectum, the hub of visual information (Vanegas and Ito 1983), as one of the possible factors to explain the onset of social transmission. These results are discussed in ecological, evolutionary, and physiological contexts.

Materials and methods

Fish husbandry

Hormone-induced fertilized eggs of chub mackerel *S. japonicus* were purchased from a private hatchery company (Nichimo Marifarm, Kumamoto, Japan) and transferred to the Fisheries Research Station of Kyoto University (Kyoto, Japan) on 18th June, 2003. Eggs were immediately stocked in two 500-l black polycarbonate tanks, 2,000 eggs in each. Water temperature and light were kept at ambient conditions (21–23°C, 14L:10D) during a 33-day rearing period. Water was supplied at 1 l min⁻¹ (approximately three exchanges day⁻¹), and light intensity on the water surface was about 400–500 lx during daytime.

Food was provided ad libitum in each rearing tank. From 2 to 7 days posthatching (dph), fish were fed L-type rotifers *Branchionus plicatilis* at 3–5 rotifers ml⁻¹ enriched with two different types of nutritional supplements (Marine Gross, Nisshin Marineteck, Japan; Plus Aquaran, BASF Japan, Japan). From 8 dph onward, fish were fed with *Artemia* sp. nauplii at 0.1–0.3 individuals ml⁻¹ enriched with a supplement containing highly unsaturated fatty acids (HUFA; Biochromis, Chlorella Kogyo, Japan). To shift their diet smoothly, rotifers were also provided to each tank at three rotifers ml⁻¹ for the first 3 days after changing food items (8–10 dph).

Schooling behavior

The development of schooling behavior was observed by recording the behavior of the fish in the rearing tanks every 2 days from 8 to 18 dph using a digital video camera (Sony Handycam, Sony, Japan). Video recording was conducted for 15 min for each tank at 1400 hours, about 7 h after feeding to prevent the influence of foraging behavior. Two semicircular white reflecting boards (Reflective Panel NT-A041S, Nihon Tentosha, Japan) were put on the tank bottom 15 min before recording to cover the bottom and enhance the contrast of the recorded images. Fish resumed normal behavior within 5 min after placing the white boards. The video camera was set above the tank so as to record approximately one-quarter of the tank.

To measure the degree of schooling behavior quantitatively, the separation swimming index (SSI) was calculated following Nakayama et al. (2003). On a still frame of the video image, the fish that was nearest to the center of the video image was defined as the focal fish, and the one that was nearest to the focal fish was defined as the neighboring fish. The position of the snout was marked for each fish and marked again after the videotape was forwarded 0.5 s. Movement of the snout in 0.5 s was expressed as a speed vector for each fish. After a starting point of one vector is

parallel-translated to that of the other, the SSI was calculated as:

$$SSI = 2d(v_f + v_n)^{-1}$$

where d is a distance between two vector endpoints, and v_f and v_n are the magnitudes of the vector for the focal fish and neighboring fish, respectively.

The SSI represents how far the two neighboring individuals are separated from each other in a given time, which is adjusted by an average speed of two individuals. The value of SSI ranges between 0 and 2; 0 when two individuals show perfect parallel swimming with the same speed and direction, about 1.5 when swimming speeds and directions of two individuals are at random, and 2 when two individuals swim in opposite directions. The SSI can be calculated without parallel transformation of the vectors by measuring an angle between two vectors (θ) and transforming d in the function below:

$$SSI = 2\sqrt{v_f^2 + v_n^2 - 2v_f v_n \cos \theta} \times (v_f + v_n)^{-1}$$

$(0^\circ \leq \theta \leq 180^\circ)$

There are two merits for adopting the SSI as an indicator of schooling behavior. First, it reflects typical movement of schooling individuals more precisely by its definition than the conventional methods based on still images, such as a nearest neighbor distance and a separation angle. Secondly, it reduces the artifact caused by the difference in density of fish between tanks because it is calculated only using the speeds and angles of a randomly selected individual and its nearest neighbor.

The SSI of 20 pairs of fish was calculated in each tank for each observing day, and the data from two rearing tanks were pooled because there was no effect of tanks (analysis of variance [ANOVA], $F_{1, 318}=0.059$, $p=0.81$). The SSI was compared among age using Kruskal–Wallis test followed by Dunn's test. The SSI was also compared with 1.49, the expected average value when two individuals swim randomly, using one-sample t test with the Bonferroni correction (adjusted $\alpha=0.0063$). The expected average value 1.49 was obtained from 10,000 simulations of the SSI with random speeds of two individuals and random angle between them.

Social transmission

To investigate social transmission among individuals in shoals, three transparent experimental Plexiglas chambers (30 by 40 cm, 10 cm depth) were arranged side by side so that the fish in each tank could see each other from inside, except that fish in chamber 1 and chamber 3 were not able to see each other because of an opaque plastic board

between them (Fig. 1). Two electrode plates were set on the side walls of chamber 1 so that an electric stimulus was given uniformly throughout the water in chamber 1. The electrical stimulus was 20 V, the lowest voltage at which fish showed startle responses (S. Nakayama, unpublished data). Timing of the electric stimulus was indicated by a light bulb connected to the electrode plates with a parallel circuit.

Fifteen fish were selected randomly from each rearing tank, and five individuals were put into each experimental chamber. After a 30-min acclimatization, fish in all chambers were recorded simultaneously from above by using three video cameras (Sony Handycam, Sony) for 3 min. Then, five electric pulses (each 0.5 s at 30-s intervals) were applied to chamber 1. As a control, the same observation was conducted without giving stimuli to the fish just before each experiment. If social transmission occurred, it was expected that behavioral changes displayed by individuals in chamber 1 would be transmitted first to those in chamber 2, and then to those in the chamber 3.

All experiments were conducted between 900 and 1200 hours on 16, 20, 24, 30, and 33 dph, with five trials from each of the two rearing tanks each day. Water temperature was 21–23°C, and light intensity was about 200 lx on the water surface of experimental chambers. After each trial, fish were anesthetized immediately with MS222, and their standard length was measured. Five individuals were randomly chosen on each experimental day and fixed for histological analysis.

From the video images, the number of individuals out of five that responded to the stimulus (responsiveness) was counted in each chamber. Fish were regarded to have responded to the stimulus when they showed C-start (Eaton et al. 1977) followed by an abrupt increase in swimming

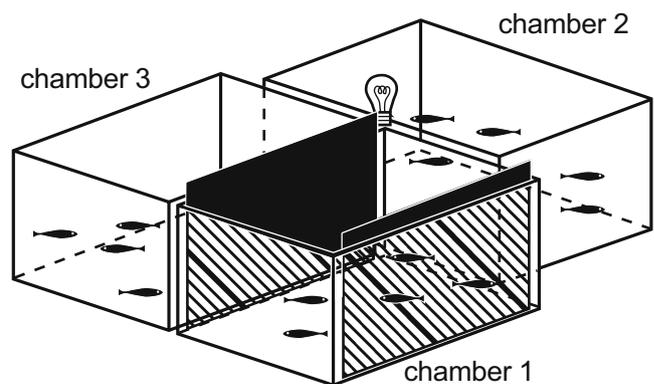


Fig. 1 Schematic illustration of experimental tanks for social transmission experiment. Two electrode plates were set on the two facing sides of chamber 1 with a light bulb. Electricity was provided from a transformer. The experimental chambers were set so that individuals in chamber 2 were able to see those in chamber 1, and individuals in chamber 3 were able to see those in chamber 2, but individuals in chamber 3 were not able to see those in chamber 1

speed or rapid change of direction. Swimming speeds of individuals 0.2 s before and after each stimulus were measured for 0.2 s, respectively, in each chamber.

Responsiveness of tested fish from two rearing tanks were pooled because there was no difference between the rearing tanks (analysis of covariance [ANCOVA], $F_{1, 143}=0.61$, $p=0.44$). The pooled data were compared with age and chamber number as main effects in a 2-way ANOVA ($\alpha=0.05$). In cases where information was transferred between chambers, the difference of the responsiveness between chamber 2 and chamber 3 was tested by ANCOVA with responsiveness in the informer's chamber (chamber 2 with 1, chamber 3 with 2) as a covariate, and chamber (chamber 2, 3) as a factor ($\alpha=0.05$). For swimming speed of the individuals after stimulus presentation, data from the two rearing tanks were also pooled because there was no difference between the rearing tanks (ANOVA, chamber 1; $F_{1, 498}=0.97$, $p=0.33$, chamber 2; $F_{1,498}=1.40$, $p=0.24$, chamber 3; $F_{1, 498}=1.68$, $p=0.20$). The swimming speed after stimulus presentation was compared with that of control using ANCOVA with the swimming speed before stimulus presentation as a covariate and treatment (experiment/control) as a factor. Significant α level was adjusted with the Bonferroni correction (adjusted $\alpha=0.01$).

The number of individuals used and the intensity of the electrical stimulus were minimized as recommended by the ethical guidelines of Association for the Study of Animal Behaviour (1997). Throughout the experiments, fish resumed normal routine swimming behavior right after a brief startle response, and we did not observe any cases where fish behaved abnormally after the stimulus. Although electricity is not a natural indicator of predatory threat for this species, it reliably elicits startle responses with C-start. C-start is the typical escape behavior seen in fish, as reported in yellow perch *Perca flavescens* and bluegill *Lepomis macrochirus* (Webb 1980). Therefore, the information on predatory threat is expected to be transmitted in a shoal in the same manner as in our experiments. Furthermore, this experiment is not designed to test the response to the electric stimuli, but to investigate social transmission by visual cues from conspecifics. Our method gives a stimulus to focal individuals without disturbing other individuals in the neighboring chambers.

Histological observation

Of the 30 individuals used in the social transmission experiment in each day, five fish were fixed in 15% formalin. They were then transferred to Bouin's solution for 24 h and preserved in 70% ethanol. The heads were sectioned transversely at 8- μ m intervals with a microtome. The sections were stained with hematoxylin-eosin, and the area of optic tectum was measured

every 24 μ m with NIH image (National Institutes of Health, <http://rsb.info.nih.gov>). The total volume of the optic tectum was calculated for each individual by integrating the measured areas and compared with standard length.

Results

Schooling behavior

From 8 and 12 dph, the SSI maintained a value of about 1.5, a value that reflects pairs of fish swimming at random direction and speed (one-sample t test with the Bonferroni correction, adjusted $\alpha=0.0063$, 8 dph: $t_{39}=0.627$, $p=0.535$; 10 dph: $t_{39}=0.012$, $p=0.990$; 12 dph: $t_{39}=2.099$, $p=0.042$, Fig. 2). At 14 dph and thereafter, the SSI was significantly different from an expected random value and gradually decreased with age (14 dph: $t_{39}=2.925$, $p=0.006$; 16 dph: $t_{39}=3.709$, $p=0.001$; 18 dph: $t_{39}=6.973$, $p<0.001$; 20 dph: $t_{39}=20.309$, $p<0.001$; 22 dph: $t_{39}=43.994$, $p<0.001$, Fig. 2). Morphological observations showed that all the fish completed metamorphosis on 16 dph (7.9 mm in standard length [SL]) by attaining the adult number of fin rays. The SSI began to decrease sharply on 18 dph (9.6 mm SL), just after the metamorphosis, indicating a strong schooling behavior (Kruskal–Wallis, $H=140.5$, $df=7$, $p<0.001$; Fig. 2). The continuing decline in the SSI meant that the degree of parallel swimming between neighboring individuals became greater. Onset of schooling behavior was also observed directly in the rearing tanks. At 18 dph and thereafter, almost

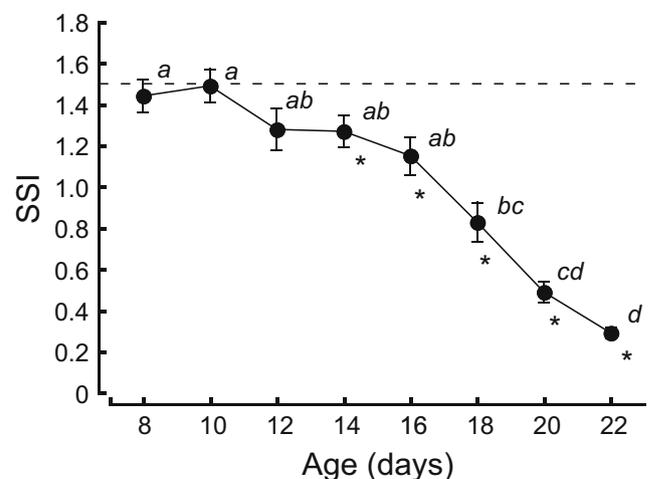


Fig. 2 Relationship between age and separation swimming index (SSI). Data are mean \pm 1SE. Dashed line indicates the average value of SSI when each individual swims randomly (1.49). Different letters indicate the significant difference among ages (Kruskal–Wallis followed by Dunn, $\alpha=0.05$). Asterisks indicate significant differences from the expected mean value of random swimming (one-sample t test with the Bonferroni correction, $\alpha=0.0063$). $n=40$

2.942, $p=0.090$), and 30 dph ($F_{1,97}=5.354$, $p=0.023$). Swimming speed significantly increased at 33 dph ($F_{1,97}=37.296$, $p<0.001$).

Histological observation

The volume of optic tectum showed little increase from 16 to 20 dph, when all individuals completed metamorphosis, whereas it increased dramatically after 20 dph (Fig. 5). The volume of optic tectum was proportionally increased with the standard length of fish (Fig. 6, $R^2=0.95$). Because of the curvilinear regression line, the increment of the volume of optic tectum was small when the standard length was small, whereas it became steeper when fish became larger.

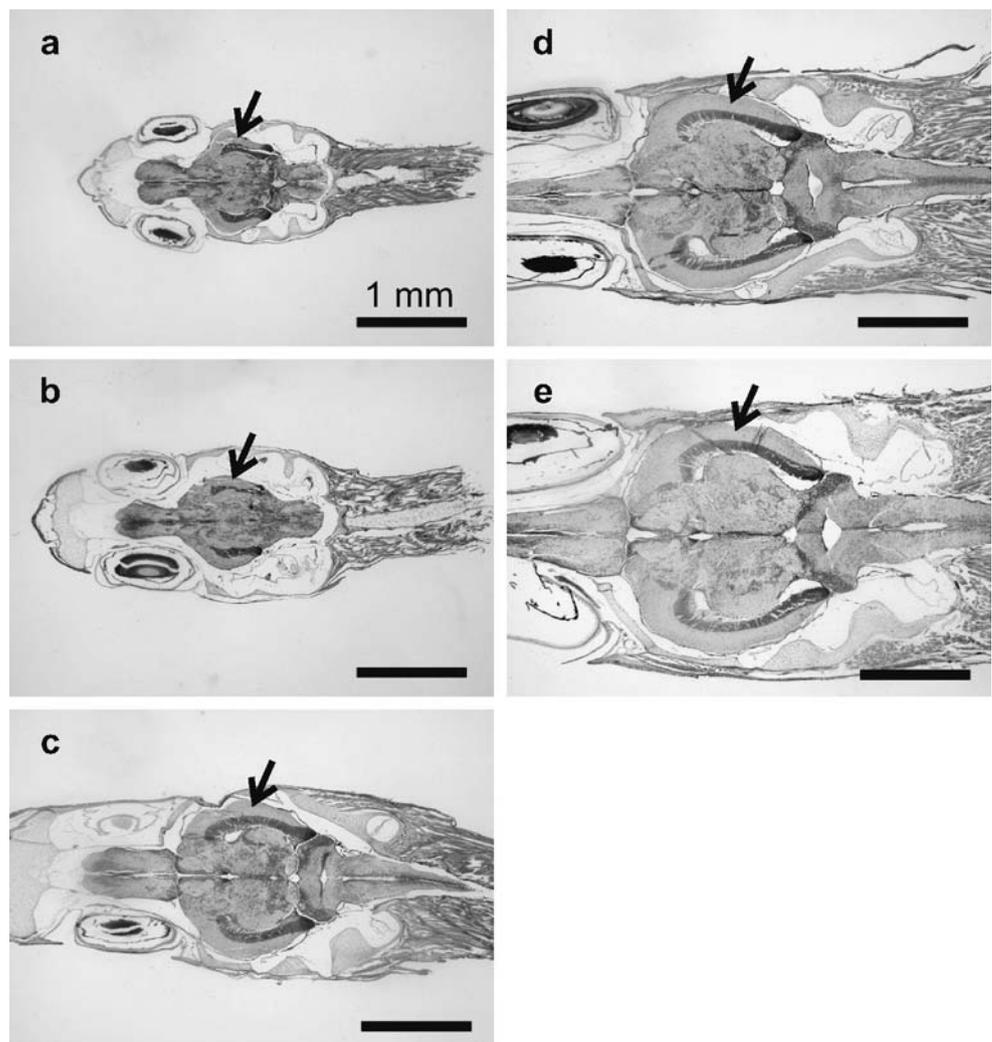
Discussion

In this study, we found that fish started coordinated swimming at 14 dph, and schooling behavior became

stronger at 18 dph just after metamorphosis (Fig. 2). The onset of social transmission by visual cue was about 2 weeks after the onset of schooling behavior (Figs. 3 and 4). Although schooling behavior itself is an antipredator strategy that promotes survival through the dilution and confusion effects, grouping behavior would become more effective when information about a predator can be transferred through the shoal members (many-eyes effect). Social transmission of information about a predator could decrease mortality by allowing school members to initiate antipredator behavior earlier than solitary individuals (Treherne and Foster 1981; Potts 1984).

The onset of coordinated swimming, indicated by the decrease in the SSI from random swimming (Fig. 2), was observed at 14 dph, and the degree of coordination became stronger after metamorphosis (18 dph). Schooling behavior is reported to start at a similar point in ontogeny in other species, such as anchovy *Engraulis mordax* (Hunter and Coyne 1982), Atlantic herring *Clupea harengus* (Gallego and Hearth 1994), yellowtail *Seriola quinqueradiata*

Fig. 5 Transverse sections of *S. japonicus* brain at **a** 16 dph (8.0 mm SL), **b** 20 dph (11.5 mm SL), **c** 24 dph (18.4 mm SL), **d** 30 dph (25.2 mm SL), and **e** 33 dph (29.1 mm SL). Each image represents the area where the optic tectum (arrow) is largest in each age. Scale is 1 mm



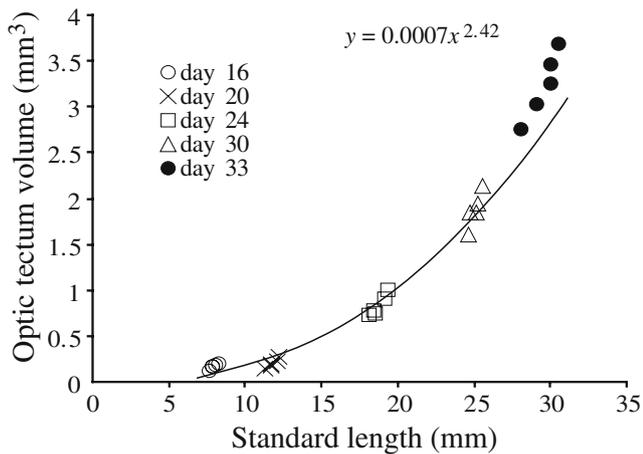


Fig. 6 Relative growth of optic tectum to the standard length in *S. japonicus*. Different symbols indicate different ages (open circle, 16 dph; cross, 20 dph; open square, 24 dph; open triangle, 30 dph; closed circle, 33 dph). Each point represents the calculated volume of the optic tectum of an individual. $R^2=0.95$, $n=25$

(Sakakura and Tsukamoto 1997), and striped jack *Pseudocaranx dentex* (Masuda and Tsukamoto 1999). Schooling behavior requires at least basic locomotor organs for sustainable swimming (Kohno et al. 1984) and sensory organs, such as eyes and lateral line systems, for adjustment of distance and swimming speed with other shoal members (Hunter and Coyne 1982). It is, however, not likely that the development of these systems causes fish to start schooling during metamorphosis, because locomotor and sensory systems necessary for coordinated swimming with conspecifics have already been acquired before metamorphosis (Masuda and Tsukamoto 1999). Schooling behavior probably begins in response to environmental changes that accompany metamorphosis. Fish change their appearance as well as their niche, such as habitat and prey preference, during metamorphosis. As a consequence, pigmentation and elevated swimming speed would lead to increased conspicuousness to predators (Fuiman and Magurran 1994), conditions under which schooling behavior becomes more effective. In addition to that, development of the central nervous system (CNS) would also be necessary for schooling behavior. It is reported that fish with underdeveloped CNS did not show schooling behavior compared to those with well-developed CNS at the same age and size (Ishizaki et al. 2001; Nakayama et al. 2003).

Social transmission by visual cues became obvious among individuals at 30 dph (25.1 mm SL) and thereafter, as evidenced by responsiveness (Fig. 3) and the change of the swimming speed after the stimulus (Fig. 4). It is unlikely that the responses of individuals in chambers 2 and 3 were limited by the developmental state of swimming or sensory organs, because they had already performed schooling behavior about 2 weeks earlier than the onset of social transmission. The developmental timing of visual transmis-

sion of fright response might reflect another increase in predation pressure during this time, when swimming speed exponentially increases and so does conspicuousness. Onset of social transmission of information in chub mackerel occurs in the middle of the juvenile stage, when they show a remarkable increase in swimming speed and foraging ability, which enables them to accomplish long distance migrations (Watanabe 1970). Moreover, information transfer within groups increases accuracy of decision-making in moving direction (Couzin et al. 2005). The predation pressure experienced during migration would be greatly reduced with acquisition of visual transfer of information within groups.

The delay in onset of responsiveness in chamber 3 (Fig. 3) was not caused by the reduced magnitude of response between chambers 1 and 2, but simply by a dilution effect of responsiveness because there was no significant difference in responsiveness against the number of informers in the neighboring chambers (chamber 2 against chamber 1, chamber 3 against chamber 2). That is, the effectiveness of information transfer is related to the number of individuals that responded, but not the magnitude of the response (Brown and Laland 2003). The decrease from chamber 1 to 3 in the number of individuals responding indicates that staying closer to the first responders in groups is beneficial because information is diluted through the transmission process. Individuals have a greater chance of receiving information by eavesdropping on the responders directly than indirectly, but the benefits depend on the trade-off between information and risk, because staying closer to the responders is same as staying closer to the source of risk.

Laboratory experiments have demonstrated that olfactory cues can work as an antipredator signal in freshwater fishes (Smith 1992; Chivers and Smith 1994; Kristensen and Closs 2004), but it is not likely to be plausible in the wild (Magurran et al. 1996). Pelagic fishes in the open ocean, such as our model organism, may instead depend on vision, considering the clarity of water and the presence of visual predators. We could not exclude the contribution of mechanoreception to information transfer within shoals because of our experimental design, although little is known about its importance. It is possible that the onset of social transmission would be expressed at an earlier ontogenetic stage if individuals could use mechanoreception, as it is one of the sensory organs that schooling fishes use to maintain the swimming speed and direction with the neighbors (Partridge and Pitcher 1980).

In teleost fishes, visual information received by the retina is projected to the optic tectum, which is considered to work as a hub of sensory and locomotion systems (Vanegas and Ito 1983) and to transform sensory information to motor expression (Broglio et al. 2003). Ishizaki et al. (2001) reported that yellowtail *S. quinqueradiata* did not show schooling behavior when HUFA were deficient in the diet,

and that optic tectum was smaller in HUFA-deficient fish than in the controls. The significant delay in the onset of social transmission relative to the onset of schooling behavior might be attributed to the fact that the optic tectum was not developed well enough to exercise social transmission. The optic tectum increases little with size during the early juvenile stage (Fig. 5). Although fish completed metamorphosis at 16 dph and showed strong schooling at 18 dph, it was obvious that the volume of the optic tectum was similar at 16 and 20 dph (Figs. 5 and 6). At 30 dph and thereafter, when information transfer was observed among individuals, a small increase in body length results in a huge increase in the size of the optic tectum, which might be enough to express social transmission. Although we do not know which part of the CNS governs social transmission ability, the optic tectum could play a critical role. Further histological and neurological investigations are required to confirm the role of optic tectum in social transmission.

Acknowledgements We sincerely thank Dr. M. Takahashi in National Research Institute of Fisheries Science for helping fish husbandry and A. Kobayashi in Kyoto University for teaching the microtome technique. We also thank Dr. L. A. Fuiman and Dr. A. F. Ojanguren of the University of Texas, Marine Science Institute for giving helpful comments and suggestions during the preparation of the manuscript. This experiment was conducted in compliance with current laws in Japan.

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