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Ontogenetic changes in behaviour transmission among individuals in the schooling of Pacific bluefin tuna *Thunnus orientalis*

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Abstract – To reveal the kinematical aspects of schooling development in the Pacific bluefin tuna *Thunnus orientalis*, changes in its schooling behaviour traits, local behaviour transmission among school members and morphological traits were investigated as fish developed from the larval to the juvenile stage. Schooling was first observed at around 24 days post-hatching (27 mm body length) in *T. orientalis*. Behaviour transmission among individuals took much longer among 24 d post-hatching individuals than among older fish. The compactness and polarity of the school progressively improved as the time required for behaviour transmission decreased. One cause of the reduction in the time required for behaviour transmission was the development of manoeuvrability, which resulted from further morphological development of the caudal fin and other organs related to swimming.

Key words: Early life stage / Development of behaviour / Schooling behaviour / Morphological trait / Pacific bluefin tuna

1 Introduction

The Pacific bluefin tuna *Thunnus orientalis* is one of the most commercially valuable fish species. Demand for bluefin tuna is increasing and there is a need for the development of a sustainable means of utilizing this species. To manage fish stocks, accurate assessment of recruitment is essential. Although such information can be obtained from detailed biological studies of early life stages, stocks suffer their highest mortalities during this period (Tanaka et al. 2006), and such information is scarce for *T. orientalis*. One reason for the lack of information on the early life stages of *T. orientalis* is that it is difficult to obtain swimming juveniles for experimental purposes. This issue has been addressed recently as the Fisheries Laboratory at Kinki University (FLKU) has developed full-cycle culture of *T. orientalis*, where the fish complete their entire life cycle under aquaculture conditions (Sawada et al. 2005).

Using *T. orientalis*, we previously examined how schooling behaviour develops in this species (Fukuda et al. 2010). Schooling is a common anti-predatory behaviour in teleost fishes (Pitcher and Parrish 1993), and we first observed short-term coordinated behaviour between two *T. orientalis* individuals (26.2 mm total length) 25 days after they hatched. Our data also indicated that swimming ability is important for the onset of schooling. As the tuna grew, the number of individuals who joined in the schooling behaviour increased and the fish began to form constantly coordinated schools. Swimming in a coordinated manner requires recognition of the swimming direction of neighbours and a decision on whether to follow these neighbours or to be followed by them. This leading/following behaviour occurs instantaneously and suggests that the behaviour of each fish is transmitted to its neighbours.

Many studies have suggested that behaviour transmission within schools of fish is a key element in the anti-predatory function of schooling behaviour. Gerlotto et al. (2006) noted the speed of information transfer within an anchovy (*Engraulis ringens*) school. Nakayama et al. (2007) reported developmental changes in information transmission among chub mackerel (*Scomber japonicus*) that related to changes in the number of individuals involved in information transfer. However, these studies focused on behaviour transmission among multiple school members and did not provide information about local behaviour transmission between a fish and its neighbour. In birds, Nagy et al. (2010) found a hierarchy among flock members by estimating local interactions within a flock. This approach required high-resolution spatio-temporal data on a free ranging flying flock and enabled local interactions within

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the flock to be shown. Although this approach can be applied to elucidate the mechanism of behaviour transmission, few studies have attempted to use it for the observation of local interactions within a fish school.

The aim of this study was to reveal the role of swimming ability in the development of schooling behaviour in *T. orientalis*. Changes in schooling behaviour traits, local behaviour transmission among school members and morphological traits of *T. orientalis* were investigated as the fish developed from the larval to the juvenile stage. It was hoped that these ontogenetic results would throw some light on the kinematical aspects of schooling development in this species.

2 Materials and methods

The *T. orientalis* individuals used in this study were hatched at the Oshima station of the FLKU. Fertilized eggs were collected from a sea net pen and transferred into a fine mesh net placed in a land-based tank. Hatched larvae were observed in the morning 2 days after spawning, which we specified as the hatching date. The hatched larvae were transferred to a concrete tank (5.5 m × 5.5 m × 1.2 m deep) where they were fed rotifers (*Brachionus rotundiformis)* from 2 days posthatching (dph).

For morphological measurements, 14 different ages were used, namely 5, 7, 9, 12, 15, 18, 21, 24, 27, 31, 35, 40, 45 and 50 dph. Ten fish were randomly selected from the group and their body lengths measured. After measurement, each fish was fixed in Bouin's solution for 24 h. After fixation, the fish were photographed under a light microscope and the body length (L_B), body height (H_B), upper jaw length (L_J), eye diameter (D_E), caudal peduncle height (H_P), caudal fin height (H_F), caudal fin length (L_F) and area of the caudal fin (A_F) were measured using Adobe Photoshop CS4 (Adobe). To take into account any contraction induced by the fixation process, the measured lengths and area were converted into a proportion relative to body length (for length) or to the second power of body length (for area). We also estimated the aspect ratio (AR) of the caudal fin as an index of hydrodynamic characteristics due to caudal fin shape (Magnuson 1978). AR can be expressed by the following equation:

$$AR = \frac{(H_F)^2}{A_F}.$$

We studied the behaviour of *T. orientalis* at 6 different ages, namely at 15, 21, 24, 27, 31 and 45 dph. To regulate the conditions in the behaviour experiment, such as lighting and water temperature, the experiments were conducted in circular tanks placed in a room partitioned with black curtains. The size of the tanks ranged from 0.22 m to 1.86 m in diameter depending on fish size. Shallow water at a depth of 50–150 mm was maintained during the experiment to ensure that the fish swam in two-dimensional space. We observed the behaviour of 4 individuals for 20 min using a digital video camera (DCR TRV-50; Sony, Tokyo, Japan). We also used a high-speed digital video camera (EX-F1; CASIO, Tokyo, Japan) to record 300 digital images per second, which facilitated observation of behaviour transmission.

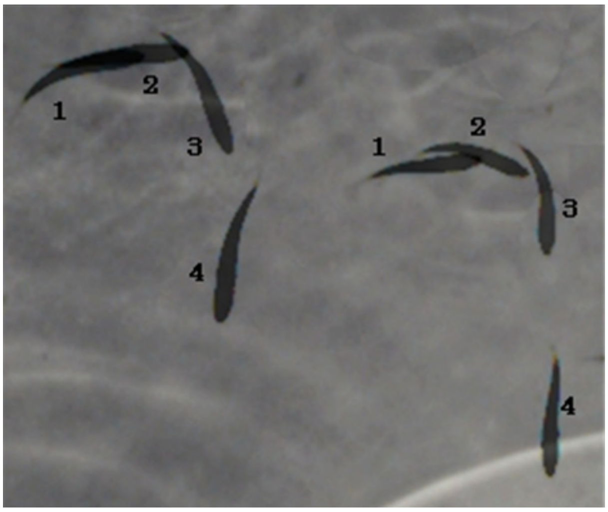

Fig. 1. Superimposed pictures showing a behaviour transmission between two *Thunnus orientalis* individuals.

To evaluate schooling behaviour traits, two schooling indices, namely the nearest neighbour index (I_{NN}, Fukuda et al. 2010) and the separation swimming index (I_{SS}, Nakayama et al. 2003), as well as swimming speed were calculated from the video images recorded with the digital video camera. The positions of the snouts of each fish were obtained as two-dimensional coordinate data at 0.1-s intervals over 2 min. I_{NN} was defined as the proportion of the distance between a fish and its nearest neighbour relative to the expected distance between a fish and its nearest neighbour when the fish were randomly distributed in the tanks (Clark and Evans 1954). I_{NN} is less than one when each individual is positioned closer to its neighbour. I_{SS} was defined using an index of parallel swimming for schooling fish and was estimated in accordance with Nakayama et al. (2003). These indices were estimated every 10 s. The swimming speed of each individual was also calculated from the distance travelled in 0.4 s every 2 s.

To evaluate behaviour transmission, we focused on the time lag between the motion of one fish and that of its neighbour. High-speed camera images were examined (Fig. 1) and sequences of fish turning were captured on a computer. Fish turning was defined as changes in swimming direction greater than 30°. To avoid tankwall obstruction effects on the turning behaviour, we chose the turning fish positioned more than 1 body length away from the tank walls (Eaton and Emberley 1991). The positions of the snout and midpoint between the right and left pectoral fins of each individual were digitized as two-dimensional coordinate data in a time series at about 3-ms intervals. The segment from the midpoint between the pectoral fins and the snout was defined as the body axis of the fish and the bearing angle of the fish (B) was calculated on the basis of this axis (Fig. 2a). The time lag of behaviour transmission between two fish, a "leader" and a "follower" could be isolated during 2 periods based on the behaviour of the follower fish. One such period was the latency period, which occurred between the turning of a leader fish and the turning of a follower (Fig. 1; 1–2). The other was the period in motion, which was the time period between the point where the follower started to turn and that when it adjusted its direction to match that

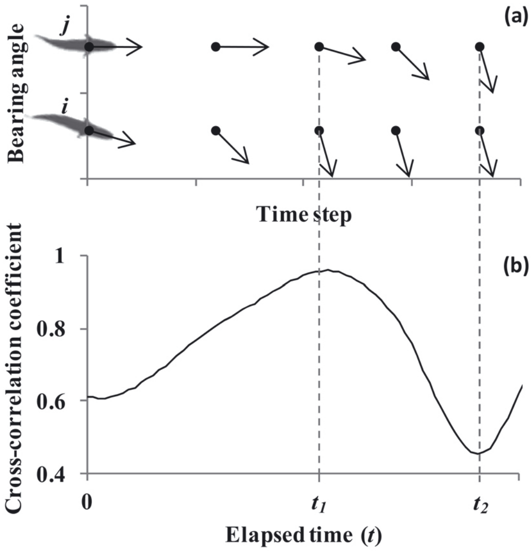

Fig. 2. Quantification of the latency period and period in motion. The bearing angles of fish *i* and *j* in each time step are shown in (a). In (b), the directional cross-correlation between *i* and *j* were determined as a function of elapsed time (*t*).

of its neighbour (Fig. 1; 2–4). To quantify these periods, we determined the directional cross-correlation between each individual (*i*) and its neighbour (*j*) (Fig. 2b). The latency period then corresponded to the elapsed time between $t = 0$ and t_1 and the period in motion corresponded to the period between t_1 and t_2. The latency period and the period in motion were calculated for more than 10 individuals of each fish age class.

3 Results

T. orientalis specimens used in this study ranged from 3.7 mm to 121 mm in average body length (Fig. 3; each data point: $N = 10$). Growth was particularly good from 15 dph (9.6 mm L_B). Morphological analysis indicated 1–2 allometrical turning points during the 5 to 50 dph period (Fig. 4; $N = 140$). At around 10 mm body length, H_B, L_J, D_E, H_P and H_F reached peak ratios in relation to L_B (Figs. 4a–4e). Thereafter, all these indices all began to decrease except for H_F. H_B and H_P approached constant values around 30 mm L_B and were independent of further growth. L_J began to decline from 10 mm L_B, and gradually approached a constant value at 60 mm L_B. D_E continued to decrease over the time span of the experiment in the present study. The ratio of the caudal fin area (A_F) and L_F showed similar trends: peak values were reached at 15–20 mm L_B and decreased until around 100 mm L_B (Fig. 4g). In contrast, the aspect ratio of the caudal fin (AR) tended to increase over the growth period, rapidly increasing in the period fish measured 4 to 20 mm L_B and then only gradually increasing in the period they grew between 20 to 80 mm L_B; no growth trend was detected in the stage after L_B reached 80 mm (Fig. 4h).

The swimming speed of *T. orientalis* showed slight increases between 15 and 24 dph (9.6–27 mm L_B) and rapid increases from 24 dph onwards (Fig. 5a). The fish began to swim in parallel at 24 dph (27 mm L_B). Before this age, I_{SS} was constant with growth and was not significantly different from 1.27, which is the expected value when fish swim in a random direction in a tank (Steel multiple comparisons, each data point: $N = 60$, $p > 0.05$) (Fig. 5b). I_{SS} began to decrease at 21 dph (19 mm L_B) and reached a value significantly different from 1.27 at 27 dph (Steel multiple comparisons, each data point: $N = 60$, $p < 0.01$). I_{NN} maintained a high value from 15 to 24 dph, but decreased from 27 dph onwards (Steel-Dwass multiple comparisons, each data point: $N = 60$, $p < 0.05$) (Fig. 5c).

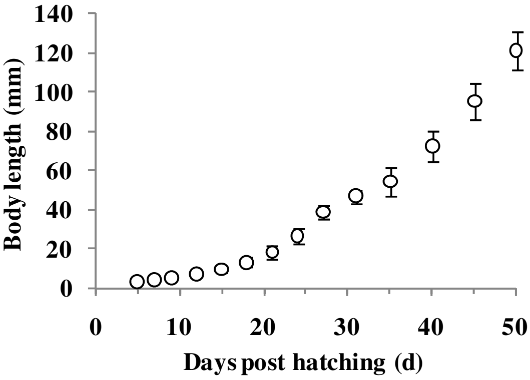

Fig. 3. Changes in mean body length of Pacific bluefin tuna during the experimental period. The vertical bars indicate the standard deviation.

No behavioural transmission was observed in fish younger than 24 dph. The mean latency period was more than 1 s and the mean period in motion was 0.55 s at 24 dph (Fig. 6). Both these indices decreased rapidly to 0.29 and 0.27 s, respectively, at 27 dph (39 mm L_B) (Kruskal-Wallis test: each data point: $N > 10$, $p < 0.05$). The indices remained constant from 27 dph onwards.

4 Discussion

In the present study, momentary parallel swimming behaviour was observed in *T. orientalis* at 24 dph (27 mm L_B) and a more coordinated school was formed at 27 dph (39 mm L_B) (Fig. 5b). We therefore suggest that in the course of the ontogeny of *T. orientalis*, schooling behaviour occurs at around 24 dph. This result is consistent with previous studies on the ontogeny of schooling behaviour in terms of fish size and developmental stage, i.e., immediately after the metamorphosis from larva to juvenile (Fukuda et al. 2010; Sabate et al. 2010). In a similar way to *T. orientalis*, the cub mackerel *Scomber japonicus* showed coordinated swimming at 14 dph and schooling was then stronger at 18 dph immediately after metamorphosis (Nakayama et al. 2007). The striped jack *Pseudocaranx dentex* and the Japanese Spanish mackerel *Scomberomorus niphonius* have also been reported to begin to form schools immediately after the completion of metamorphosis (Masuda and Tsukamoto 1998; Masuda et al. 2003). Metamorphosis would be expected to be involved in developmental changes in fish behaviour, but the exact trigger that induces fish to begin to form schools remains unknown. Ishizaki et al. (2001) suggested that the development of the

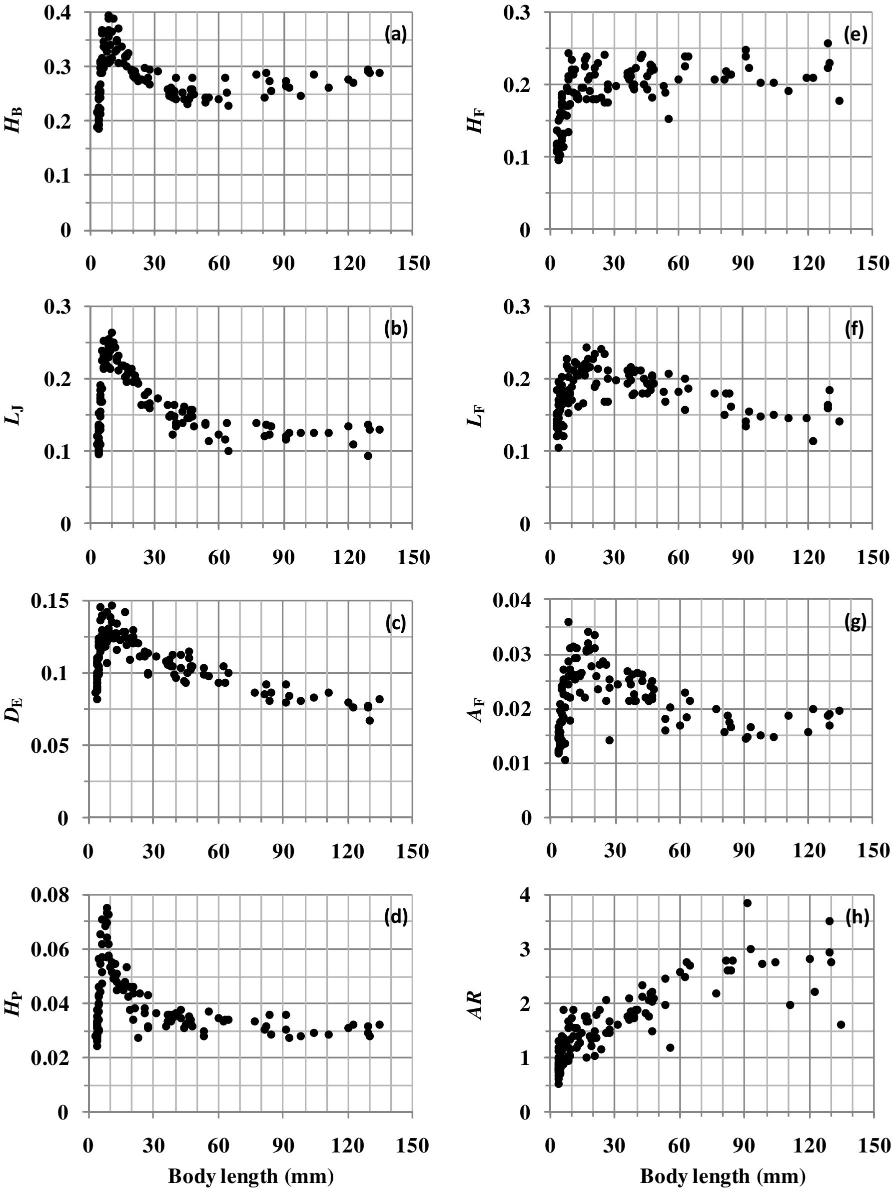

Fig. 4. Changes in proportion of (a) body height, (b) upper jaw length, (c) eye diameter, (d) caudal peduncle height, (e) caudal fin height, (f) caudal fin length, and (g) area of caudal fin relative to body length (for length) or to the second power of body length (for area) and change in (h) aspect ratio during the experimental period.

central nervous system (CNS) was important for the onset of schooling. Nakayama et al. (2007) suggested that environmental cues, such as conspicuousness to predators, as well as the development of the CNS, are important in initiating schooling behaviour. Another possible environmental cue could be the hydrodynamic environment (Fukuda et al. 2010), which also changes dramatically during the early life history of fishes and would affect their mode of swimming (Weihs 1980; Webb and Weihs 1986). Our present results do not conflict with the above mentioned studies. Instead, they highlight the important role of kinematics in school formation.

At 24 dph (27 mm L_B), when *T. orientalis* formed a slightly parallel school, behaviour transmission took approximately 1.3 s longer than at the later stages at which stably coordinated schools were formed (Fig. 6). After the latency period and the period in motion decreased at 27 dph, I_{SS} reached a value that was stable and lower than 1.27 (the expected random value) (Fig. 5b). Thus, behaviour transmission over a shorter period of time appears to make it possible for *T. orientalis* to swim stably in parallel with neighbouring fish. It remains unclear what the factors contribute to the reduction of the latency period, but the period in motion would be brought about by the development of the manoeuvrability of *T. orientalis*. Gibb et al. (2005) showed an improvement in the escape manoeuvrability of rainbow trout *Oncorhynchus mykiss* and suggested that the improvement in escape manoeuvrability was due to the developmental morphology of the caudal fin and stiffness in the axial skeleton. The morphology of *T. orientalis* also changed significantly over the time span of the present study (Fig. 4).

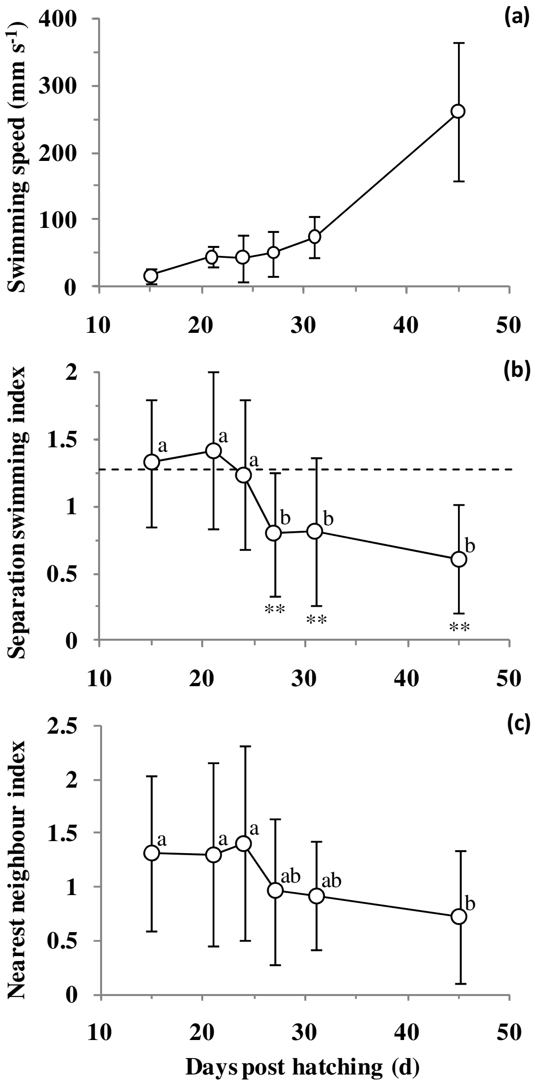

Fig. 5. Changes in (a) swimming speed, (b) separation swimming index and (c) Nearest Neighbour Index during the experimental period. The vertical bars indicate the standard deviation. In (b) and (c), significantly different groups are indicated by lower-case letters (Steel-Dwass multiple comparisons, each data point: $N = 60$, $p < 0.05$). In (b), the dotted line indicates the expected value (1.27) for randomly swimming fish and asterisks above the bars indicate that the recorded value is significantly smaller than this expected value (Steel multiple comparisons, each data point: $N = 60$, $*p < 0.05$, $**p < 0.01$).

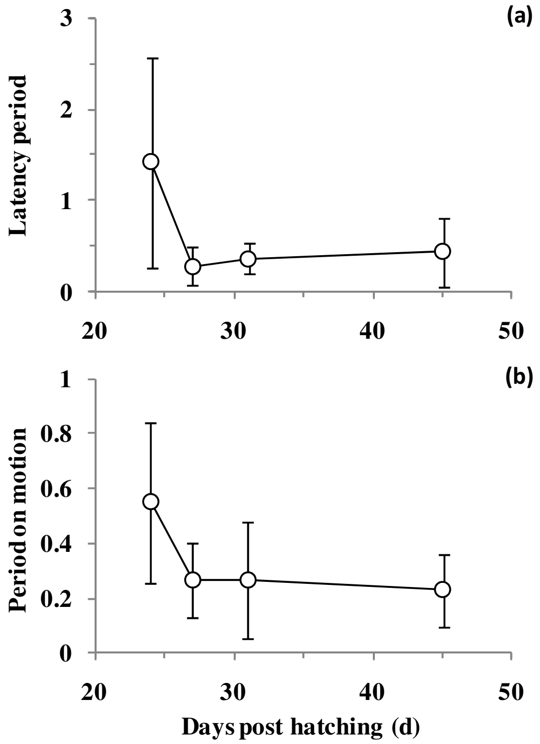

Fig. 6. Changes in (a) latency period and (b) period in motion during the experimental period. The vertical bars indicate the standard deviation.

All of the measured body parts had maximum ratios in relation to L_B at a size of around 10 mm or 20 mm L_B (Fig. 4). The earlier time point coincides with the change in prey, from zooplankton to fish larvae, that occurs in other tuna species in the open sea (Young and Davis 1990). Based on empirical evidence, the diet of our laboratory-reared *T. orientalis* also changed from zooplankton to fish larvae at this time point. The maximum ratios of L_J and D_E at this time point would enable them to feed on larger organisms (Figs. 4b, 4c). The latter time point (20 mm L_B) occurred as the fish were metamorphosing from the larval to the juvenile stage. Here, the ratio of L_F and A_F, namely the length and area of the caudal fin, reached a peak (Figs. 4d–4g). These changes as well as those in H_F are important features for the aspect ratio of the caudal fin *AR*. At this time point, the *AR* trend changed from rapidly to gradually increasing with growth (Fig. 4h). The rapid increment of *AR* at 4–10 mm L_B was brought about by the rapid increase in H_F. In this period, L_F also increased and eventually A_F did also. On the other hand, from size 20 mm L_B onwards, *AR* slowed as H_F remained unchanged and L_F and A_F decreased. Thus, between 4 and 10 mm L_B, the area of the caudal fin increased by the increments of H_F and L_F, but at 20 mm L_B onwards, the fin was widened due to the decrease in L_F. At the same time as the caudal fin was becoming wider, H_P approached a constant value; this indicates the disappearance of the larval fin and the independence of the caudal fin. These changes occurred at around 20–30 mm L_B and constitute the morphological development required for adaption to continuous (cruising) swimming seen in young and adult *T. orientalis*.

Fukuda et al. (2010) suggested that the onset of schooling in *T. orientalis* coincided with the transition to a continuous swimming mode and that this occured at the early juvenile stage. The present results also showed the development of schooling behaviour at the early juvenile stage. It is interesting that the morphological features of the caudal fin changed to adapt to the cruising swimming mode directly before schooling behaviour was first observed. *T. orientalis* would start to form a school with a caudal fin adapted to the cruising swimming mode. Once schooling behaviour had begun, the time required for behaviour transmission among individuals shortened and the compactness and polarity of the fish schools progressively improved. The morphological features of the caudal fin also developed during this period (27–60 mm L_B); this is evident from the change in *AR* (Fig. 4h). Thus, the development of suitable morphological features would contribute to the reduction in the period in motion and eventually to the compactness and polarity of the school.

Although the reduction in the period in motion could be explained by the development of manoeuvrability, it does not explain the reduction in the latency period. The reduction in the latency period might have a greater effect than that of the period in motion relative to the overall reduction observed in the length of time required for behaviour transmission (Fig. 6). It is unlikely that morphological features or swimming ability are involved in the reduction in the latency period. It is also unlikely that the mechano-sensory organ contributed to the observed reduction since *T. orientalis* depend strongly on their vision when forming schools (Torisawa et al. 2007), even though their lateral line canal is complete at a similar stage (Kawamura et al. 2003). Vision should become functional well before the initiation of schooling (Matsuura et al. 2010). Imada et al. (2010) showed a lack of schooling-like behaviour in *Oryzias latipes* even though they already had optomotor response ability. These findings suggest that the *T. orientalis* of 24 dph in the present study would already have enough ability for the perception of neighbouring fish, but took a longer time for the latency period.

It is possible that the development of the CNS contributed to the reduction in the latency period. Ishizaki et al. (2001) showed how the CNS was important for the onset of schooling in the yellowtail *Seriola quinqueradiata*. Nakayama et al. (2007) showed a delay in the onset of social transmission relative to the onset of schooling behaviour and suggested that the optic tectum, which is considered to act as a hub for the sensory and locomotion systems (Broglio et al. 2003), contributed to social transmission among the school members. Even though the relative volume of the optic tectum might be reduced at or after metamorphosis (Montgomery et al. 1997), the volume of the brain should increase as time passes. Further physiological studies are necessary to determine the exact role of the CNS in schooling behaviour. In addition to the CNS, the contribution of learning or training in relation to behaviour transmission is also possible. Makino et al. (2006) demonstrated that the learning capability of the striped knife jaw *Oplegnathus fasciatus* improved at the juvenile stage and peaked well after metamorphosis (7 cm standard length). *T. orientalis* might also be trained and thus learn how behaviour is transmitted. Further studies on the learning capability and comparative experiments between trained and untrained fish are needed to confirm this possibility.

5 Conclusion

In the present study, *T. orientalis* juveniles began to swim in parallel with neighbouring fish right after metamorphosis and developed a well-coordinated school within a few days. A key factor in the development of schooling behaviour was the reduction in the time required for the period in motion and latency period during behaviour transmission. The development of fin and body morphology and its contribution to the reduction of the period in motion (as defined in this study) was shown. It might be possible that the functions of sensory organs, swimming ability and development of the CNS are required for the onset of schooling and that manoeuvrability and some training are required in order to form a well-coordinated school.

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