Development of schooling behavior in Spanish mackerel *Scomberomorus niphonius* during early ontogeny

Reiji MASUDA,[1]* Jun SHOJI,[2] Shinnosuke NAKAYAMA[2] AND Masaru TANAKA[2]

[1]*Fisheries Research Station, Kyoto University, Maizuru, Kyoto 625-0086, and [2]Division of Applied Biosciences, Graduate School of Agriculture, Kyoto University, Sakyo, Kyoto 606-8502, Japan*

ABSTRACT: Development of schooling behavior was studied in hatchery-reared Spanish mackerel *Scomberomorus niphonius*. Behavior of larvae and juveniles was video recorded from above in a 500-L rearing tank from day 7 up to day 23 at 1–2-day intervals. For the video image analysis, separation angle (SA), nearest neighbor distance (NND), separation swimming angle (SSA) and separation swimming index (SSI) were defined and measured. Schooling behavior developed from day 17 (15.9mm in standard length (SL)) to day 19 (19.6mm in SL). During this period, SA and NND decreased significantly, suggesting that they started aggregation forming parallel orientation. Separation swimming angle and SSI also decreased dramatically in this period. After day 17 and up to day 23 (26.6mm in SL), these parameters of schooling behavior did not show much change, suggesting that schooling behavior of Spanish mackerel juveniles was completed by day 19. Relatively high values of NND (1.2–1.5-fold SL compared to <1.0 in most other species) and SSI (0.6–0.8 compared to 0.15–0.29 in chub mackerel *Scomber japonicus*) reflected a loose school as pelagic fish juveniles, and in this way they might have been minimizing the risk of cannibalism in this piscivorous species.

KEY WORDS: nearest neighbor distance, ontogeny, piscivory, schooling behavior, *Scomberomorus niphonius*, Spanish mackerel.

INTRODUCTION

Schooling is one of the most typical behaviors in pelagic fishes. The major function of schooling is supposed to be predator avoidance, such as early detection of, and confusion of the attacks from, predators.[1] Pioneer works on schooling have been conducted mostly on herviborous or planktivorous fish species such as mullet *Mugil cephalus*,[2] sliversides *Menidia menidia*,[3] northern anchovy *Engraulis mordax*,[4] guppy *Poecilia reticulata*[5] and minnow *Phoxinus phoxinus*,[6] probably due to their consistent schooling with less aggressive behavior. However, piscivorous species such as bluefin tuna *Thunnus thynnus*[7] and giant trevally *Caranx ignobilis*[8] also form schools and sometimes hunt prey fish in a cooperative manner.

Spanish mackerel is an exclusively piscivorous species from the very first feeding.[9] Their morphological characteristics, such as a large mouth with teeth[10] and digestive physiology,[11] are adapted to early piscivory, but yet they form schools from juvenile to adult stage both in the wild and in captivity. The purpose of the present study was to scrutinize the ontogenetic changes of schooling behavior in Spanish mackerel to elucidate the significance of schooling in this highly piscivorous species in the juvenile stage.

MATERIALS AND METHODS

Spanish mackerel eggs were provided from the Yashima Station of the Japan Sea-Farming Association. Broodstock were collected on 15 May 2001, then spawned on the same day. The eggs were fertilized the next morning and approximately 20 000 of them were transferred on 17 May to the Fisheries Research Station of Kyoto University. Most of the eggs hatched in the afternoon of 18 May with a hatching rate of approximately 50%. About 10 000 of the larvae were then stocked in three 500 L tanks and one of these was used for our experiment. Red sea bream *Pagrus major* larvae (0–7 days after hatching) were fed from day 3 at a frequency of two to three times a day. Fish were kept at ambient temperature $(20.0 \pm 0.8°C)$ and light intensity $(\approx 500 \text{ lx in the daytime})$.

*Corresponding author: Tel: 81-773-62-9063.
Fax: 81-773-62-5513. Email: reiji@kais.kyoto-u.ac.jp

Video recording of behavior started from day 7 up to day 23 at 1–2-day intervals using a digital video recorder (DCR-PC100; Sony Corp., Tokyo, Japan). Two reflective panels, each semicircular, were put on the tank bottom approximately 5 min before the recording to give a good image contrast. Recording was started at 15.00 h and lasted 15 min each day. Water and aeration was stopped while video recording in order to minimize the effect of current on behavior. Last feeding was approximately 3 h ahead of video recording to reduce the effect of prey animals, although there remained some prey fish larvae during the recording. Fish standard lengths were measured on 10 individuals randomly sampled on each video recording day.

Four parameters of schooling were defined for video analysis as separation angle (SA), nearest neighbor distance (NND), separation swimming angle (SSA) and separation swimming index (SSI). Separation angle and NND, after Masuda and Tsukamoto,[12] were criteria of parallel orientation and aggregation, respectively, calculated on a still frame. A fish closest to the center of the video frame was focused (focal fish), then the fish closest to the focal fish was defined as the neighboring fish (Fig. 1). The angle between the body axes of the focal fish and the neighboring fish was measured on the TV monitor and was defined as the SA. As Spanish mackerel larvae and juveniles tend to use only the caudal part for propulsion, body axes was defined as the line connecting the snout and the fulcrum of the tail beat. On the same frame, three other individuals close to the focal fish were selected, then the distance between each fish to the closest individual from each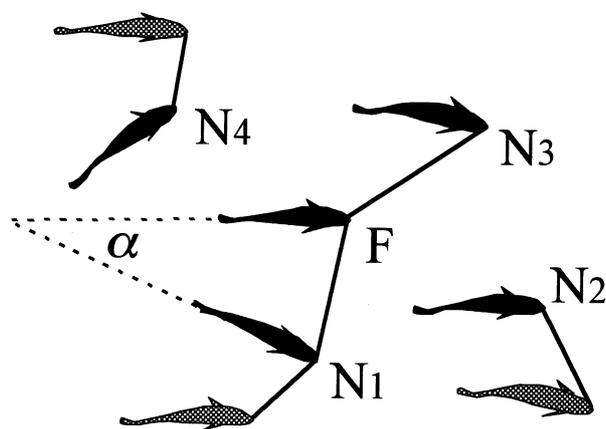 was measured. The average of these five measurements was defined as the NND of this frame. Separation angle and NND were sampled from 30 frames with a 20-s interval. Separation angle, ranging from 0° to 180°, was expected to be 90° when fish were located in a random direction and was expected to decrease as they developed a parallel orientation. NND was also expected to decrease as they started to show an aggregated location. NND was divided by average SL to facilitate the comparison among different age groups.

Separation swimming angle and SSI, after Nakayama *et al.*,[13] were analyzed from the same video frames as SA and NND measurements with the addition of frames 1 s after these. We developed these parameters in order to describe the tendency of parallel swimming be-havior that is typical in the early stage of schooling. For the measurement, vectors of the focal fish and the neighboring fish were defined as the movement in 1 s (Fig. 2). Separation swimming angle was then defined as the angle made by these two vectors (Fig. 2a). To measure SSI, the starting points of the neighboring fish vector was parallel-translated to that of the focal fish, then the distance of the endings of two vectors was divided by the average length of two vectors (Fig. 2b). SSA ranges from 0° to 180° and is expected to be 90° when fish swim in a random direction, and to be close to 0° when they swim in a parallel direction. SSI ranges from 0 when two fish swim together keeping the same distance, to 2 when they swim in the opposite direction, and is
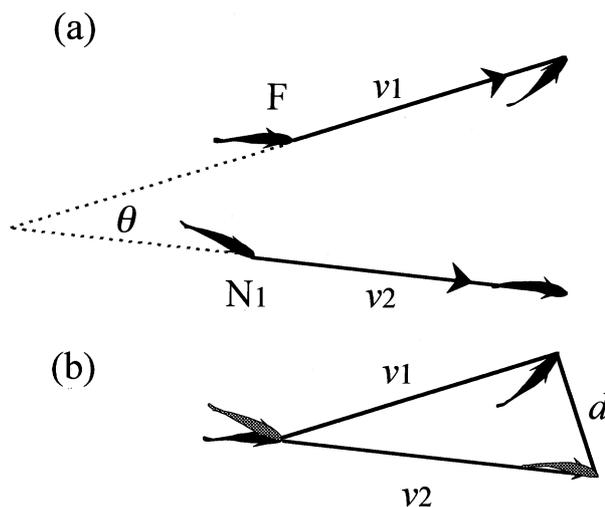

Fig. 1 Measurements of separation angle (SA) and nearest neighbor distance (NND). SA (α in this figure) was defined as the angle made by body axes of the focal fish (F) and the neighboring fish (N1). NND, represented by solid lines, were measured from the focal fish and four other adjacent individuals (N1–N4).

Fig. 2 Measurements of separation swimming angle (SSA) and separation swimming index (SSI). Movements of the focal fish and the neighboring fish in 1 s were expressed as vectors (v1 and v2). SSA (θ) was defined as the angle made by v1 and v2 (a). The latter vector was then parallel-translated to give the separation distance (d) of two vectors (b). SSI was defined as $2d/(v1 + v2)$.
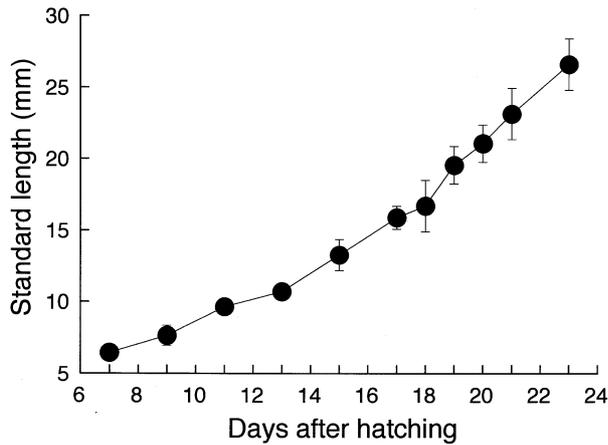
Fig. 3 Growth curve of Spanish mackerel (average standard length ± SD in 10 specimens) during the period of experiment.

expected to be close to 1.41 when they swim in a random direction.

All four parameters were compared among different age groups using ANOVA followed by the Tukey test for multiple comparisons. Separation angle, SSA and SSI in each age group were also compared to 90°, 90° and 1.41, respectively, the values expected in random location or movement, using Student's *t*-test.

RESULTS

Average SL ± SD on day 7 was 6.5 ± 0.31 mm and fish grew to 26.6 ± 1.76 mm on day 23 (Fig. 3). According to the direct observations on the rearing tank, the first sign of schooling-like behavior as the parallel swimming of two individuals for a short period was observed on day 17 (15.9 ± 0.84 mm), although this was limited in relatively large individuals in the tank. Schooling was obvious on day 19 (19.6 ± 1.33 mm) or later.

Separation angle decreased as fish grew (Fig. 4a). Significant difference among groups was observed between day 9 and day 19, or between day 18 and day 20. SA ranged from 80° to 101° from day 7 to day 15, but ranged from 33° to 44° from day 19 to day 23. SA on day 17 or older was significantly lower than 90° ($P < 0.05$, *t*-test), suggesting the sign of parallel orientation. NND ranged from 2.6 to 4.4 SL during the period from day 7 to day 17, but decreased to 2.1 SL on day 18, and showed 1.5 SL or lower on day 19 or older (Fig. 4b). NND was significantly lower on day 18 compared to the younger stage ($P < 0.05$, Tukey test).

Both SSA and SSI decreased significantly from day 17 to day 19 (Fig. 5a,b). SSA were slightly but
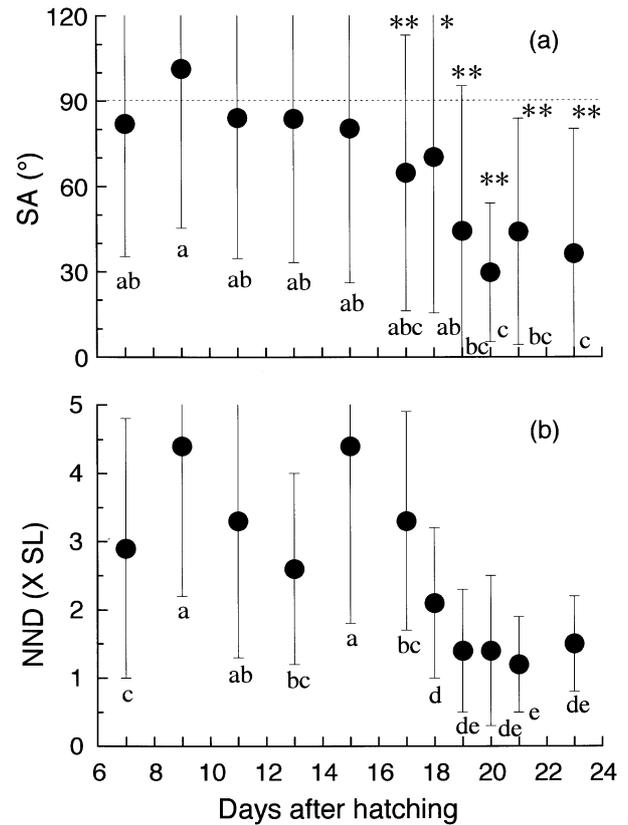

Fig. 4 (a) Ontogenetic changes of separation angle (SA) and (b) nearest neighbor distance (NND) in Spanish mackerel. Plots sharing a letter are not significantly different ($P < 0.05$, ANOVA followed by Tukey test, $n = 30$). Asterisks above bars show that the value is significantly smaller than the value expected when fish were located randomly (*$P < 0.05$, **$P < 0.01$; *t*-test, $n = 30$).

significantly lower than 90° on days 11 and 15 ($P = 0.048$ and 0.013, respectively, *t*-test). SSA was lower on day 19 or older fish and more significantly departed from 90° ($P < 0.001$, *t*-test). SSI also ranged around the value expected for random movement (1.41) from day 7 to day 17. SSI started to decrease on day 18 up to day 19, then the value stabilized at 0.6–0.8.

DISCUSSION

Among the four parameters of schooling behavior we analyzed, NND is the most commonly used. To understand the ontogenetic changes of schooling, however, the measurement of NND only could be misleading, as early fish larvae that cannot form a school may show a patchy distribution[14] and result in a relatively low value of NND. The density in a tank may also bias the NND and mislead results.
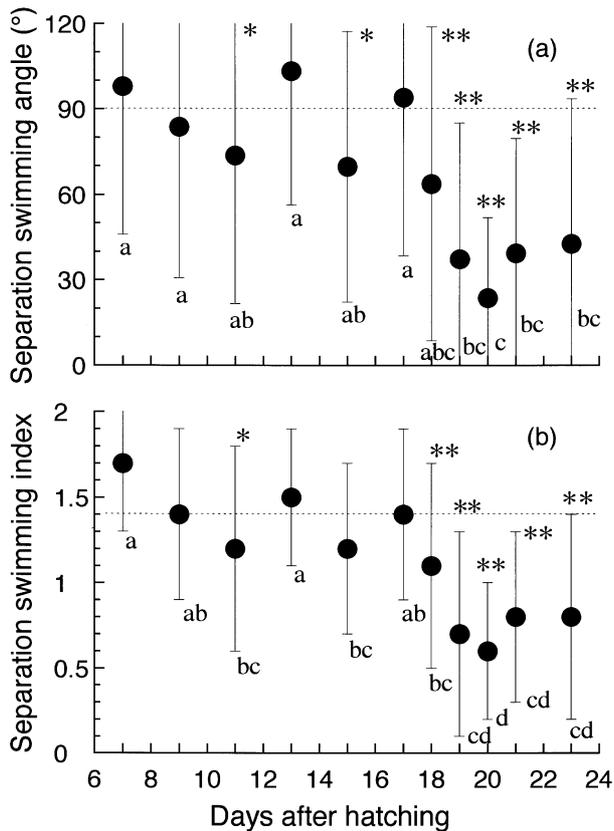
Fig. 5 Ontogenetic changes of separation swimming angle (a) and separation swimming index (b) in Spanish mackerel. Plots sharing a letter are not significantly different ($P < 0.05$, ANOVA followed by Tukey test, $n = 30$). Asterisks above bars show that the value is significantly smaller than the value expected when fish moved randomly (*$P < 0.05$, **$P < 0.01$; *t*-test, $n = 30$).

Commonly reported values of NND in fishes are just below 1.0 times fish body length (BL). Pitcher studied the 3-D structure of a school of minnow and reported their NND as 0.9 BL.[6] Striped jack *Pseudocaranx dentex* at 30 mm in total length (TL) had 0.79 ± 0.15 TL of NND.[12] The NND of coho salmon *Oncorhynchus kisutch* (130 mm in fork length (FL)) was reported to be 0.60–0.66 FL when they were provided with enough (4–4000 lux) light intensity.[15] A school of Atlantic herring *Clupea harengus* (350 mm in BL) had an average NND of 0.77 BL.[16] Compared to these values, the NND of Spanish mackerel (1.2 SL on day 21 and 1.5 SL on day 23) in the present study seems to be large. That was also the case with SSI in which Nakayama *et al.*[13] reported an SSI of 0.15–0.29 in 18–21-day-old chub mackerel *Scomber japonicus*, whereas the SSI in Spanish mackerel in our experiment stabilized at a much higher value (0.6–0.8 in 19–23-day-old juveniles; Fig. 5b). Those findings were coinci-

dent with our visual observation that Spanish mackerel juveniles in both rearing tanks and in the wild form relatively loose schools (J Shoji, unpubl. obs., 2000). Threatened schools tend to have a high degree of compaction with low value of NND.[16] As Spanish mackerel juveniles are voracious piscine predators, they may tend to have dispersed schools and thus reduce a risk of sibling cannibalism in an individual level. Because of their extreme piscivory, Spanish mackerel larvae and juveniles may require such a strategy to avoid cannibalism. Indeed, even at the larval stage, where the abundance is much higher than in the juvenile stage, cannibalistic incidence in the sea is as low as 1% of fish examined.[10] Alternatively, they develop highly efficient feeding capability in the early juvenile stages but not as much maneuverability of schooling and thus fail to maintain a tight and well-organized school.

Onset of schooling is observed to be coincident or right after the metamorphosis in many fish species, such as silversides,[3] northern anchovy,[4] Atlantic herring,[17] striped jack,[12] yellowtail *Seriola quinqueradiata*[18] and Pacific threadfin *Polydactylus sexfilis*.[14] The major change of relative growth in Spanish mackerel was observed at 12 mm SL and the completion of fin rays was at 19 mm SL.[10] In the present experiment, schooling was observed to start from day 17 to day 19 (15.9–19.6 mm in average SL), which was markedly delayed after the major change of relative growth but coincident with the completion of metamorphosis. Shoji *et al.*,[10] based on the prey size in the stomach contents of wild Spanish mackerel larvae and juveniles, reported that their prey-capture capability improves drastically after 12 mm SL. These authors suggested the importance of morphological development to support the capability of piscivory, although Spanish mackerel feed exclusively on fish larvae from right after the first feeding.[9] In general, morphological development precedes to the relevant ecological and/or behavioral changes in the early ontogeny of fishes, as is demonstrated for the digestive system development and feeding habits shift in flatfishes.[19] The developmental timing of morphology and behavior may not be as straightforward in the case of Spanish mackerel because of its extreme piscivory.

We found that Spanish mackerel formed a school from day 17 to day 19 (15.9–19.6 mm SL). Their school in the juvenile stage was markedly loose compared to other pelagic fishes, reflecting their highly piscivorous feeding strategy and thus sacrificing antipredator performance in schooling. Further research related to this subject will be quantitative measurement of antipredator performance in this species as well as other pelagic fish larvae and juveniles, particularly in fishes with a

flexible feeding strategy of piscivory and zooplanktivory like chub mackerel.

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