Marine Biodiversity Records, page 1 of 11. © Marine Biological Association of the United Kingdom, 2013
doi:10.1017/S1755267213000067; Vol. 6; e34; 2013 Published online

Observations of schooling behaviour in the oval squid *Sepioteuthis lessoniana* in coastal waters of Okinawa Island

CHIKATOSHI SUGIMOTO[1], RYOKO YANAGISAWA[1,3], RYUTA NAKAJIMA[2] AND YUZURU IKEDA[1]

[1]Department of Chemistry, Biology and Marine Sciences, University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan, [2]Department of Art and Design, University of Minnesota, Duluth, Minnesota 55812-3041, USA, [3]Present address: Ocean Planning Corporation, Urasoe, Okinawa 901-2102, Japan

The schooling behaviour of the oval squid Sepioteuthis lessoniana *was observed over 4 summers at 3 observation sites in the coastal waters of Okinawa Island, Ryukyu Archipelago, Japan. During this field study, 3 static appearances (belt, ball and sheet shape) and 2 transitional appearances (high and low density) were noted, recorded and described. In addition to formations, a member of* S. lessoniana *schools also displayed particular and repeated behavioural patterns such as vanguard and intimidating display. The 3 observation sites were tropical coral reefs near the coastline at a depth of 1 to 15 m on an average. All participating observers snorkelled and were equipped with various underwater digital video and photographic cameras. The schools observed consisted of 8 to over 100 members with a wide range of body sizes. Despite these biological and locational differences, both static and transitional appearances were consistently observed with equally consistent individual behavioural patterns. There have been studies on related species,* Sepioteuthis sepioidea, *at the San Blas Islands along the Caribbean coast of eastern Panama, and the same species,* S. lessoniana, *at a different geographical location, Casuarina Beach on Lizard Island, Australia. The findings of this study are consistent with those reported previously, with some notable differences.*

Keywords: Cephalopoda, oval squid, follower, leader, school, vanguard

Submitted 3 August 2012; accepted 14 January 2013

INTRODUCTION

Unlike many vertebrate species, very few invertebrates are known for their group behaviour, excluding social insects. Among these invertebrates, the squids are known to form large aggregations. However, in contrast to the number of studies conducted for analysing fish schooling behaviour (Pitcher & Parrish, 1993), squid school studies are scarce considering their equal importance to the world fisheries and their ecological niche in marine environments.

Cephalopods possess a well-developed nervous system. Their brain weight relative to body weight is intermediate between that of the fish–reptile group and the bird–mammal group (Packard, 1972). This advanced neural feature is reflected in their cognitive abilities such as short- and long-term memories (Messenger, 1973) and visual imprinting (Darmaillacq *et al.*, 2006). These abilities might also be the contributing factors to their social features such as schooling behaviour.

Moynihan & Rodaniche (1982) in natural environment observed schools (from 2 to more than 150 squid) of the Caribbean reef squid *Sepioteuthis sepioidea* (Blainville, 1823) at the San Blas Islands along the Caribbean coast of eastern Panama (Table 1). They observed *S. sepioidea* forming schools with semi-diagonal (successive order of body size from large to small) and crescent (large individuals at both ends and small individuals at the center) appearances upon encountering potential predators (Moynihan & Rodaniche, 1982). In these schools, squid arranged themselves laterally by facing in the same direction and sometimes contained individuals continuously watching for predators as scouts or sentinels (Moynihan & Rodaniche, 1982).

Other studies also showed similar *Sepioteuthis* schooling behaviours (Table 1). Boal & Gonzalez (1998) observed a size-based arrangement of captive oval squid *S. lessoniana* (Férussac, 1831 in Lesson 1830–1831) without complex social behaviour. Adamo & Weichelt (1999) observed a natural population of *S. lessoniana* (10 to 186 squid) at Casuarina Beach on Lizard Island, Australia, and reported a ragged-line and size-based arrangement for *S. lessoniana*, visually similar to that reported for *S. sepioidea* schools. Schools of the California market squid, *Doryteuthis opalescens* (Berry, 1911), which numbers were similar to those of *Sepioteuthis* spp. (tens or hundreds: Hunt *et al.*, 2000) consisted only of similar-sized schoolmates (Hurley, 1978). These past reports function as foundations; however, they are not enough to clarify the complex dynamics of squid schools and their appearances. Our knowledge about squid schooling behaviour in nature is still very limited.

We feel that in order to elucidate the social aspects of squid school in nature, more extensive observation of school

Corresponding author:
Y. Ikeda
Email: ikeda@sci.u-ryukyu.ac.jp

Table 1. Difference of characteristics for schooling behaviour among some squid species. n/a, not applicable; ML, dorsal mantle length.

Measurements	Squid species			
	Sepioteuthis lessoniana		*Sepioteuthis sepioidea*	*Doryteuthis opalescens*
Observation sites	Field[1]	Laboratory[2]	Field[3]	Field[4] and laboratory[5]
School shape	Ragged-line	Roughly spherical	Jumbled, semi-diagonal, crescent	Not recorded
Number of schoolmates	10–186	4–18	2–150 <	10–100 <
Water depth from the surface	7.2 m	n/a	0.2–20.0 m	<400 m
Interindividual distance (median nearest neighbour distance)	1.8 ML	2.7 ML	Varies	1.4–7.0 ML
Interindividual angle (median angular deviation)	15°	Not recorded (50% squid oriented in the same direction)	Varies	18°
Size-based arrangement	Obvious	Obvious	Obvious	Not obvious
Group fidelity	Low	Low	Low	Not recorded
Cannibalism	None	Not recorded	None	Not recorded
Less synchronized movement by squid at periphery	None	Obvious	Not recorded	Not recorded
Some social roles of a particular individual	None	None	Obvious	None

[1]Adamo & Weichelt (1999), [2]Boal & Gonzalez (1998), [3]Moynihan & Rodaniche (1982), [4]Hunt *et al.* (2000), [5]Hurley (1978).

appearance and schoolmate dynamics is necessary. In this study, we traced patterns of school dynamics for *S. lessoniana* in its natural environment. In addition, we defined several types of squid school appearance and discussed their morphological traits and possible social functions.

MATERIALS AND METHODS

Schooling behaviours of *Sepioteuthis lessoniana* were observed in the field between July and August of 2005–2011. Observations were conducted in the coastal waters of Okinawa Island, located in the Ryukyu Archipelago, Japan. The specific locations are as follows: Cape Maeda, 26°26′N 127°46′E, 1- to 30-m depth (Figure 1A); Cape Zanpa, 26°25′N 127°42′E, 1- to 3-m depth (Figure 1B); and Sunabe beach, 26°19′N 127°44′E, 1- to 5-m depth (Figure 1C). At Cape Maeda, the edge of the coral reef is close to the shoreline (less than 50 m), and observations were conducted mainly at the edge of the reef. At Cape Zanpa and Sunabe beach, the reef edge is far from the shore (100 m and 1000 m, respectively), and observations were conducted near the shore within the coral reef. At all locations, 2 to 5 observers separately snorkelled and searched for a school of *S. lessoniana*. Once a *S. lessoniana* school was found, all observers joined to watch an identical school, then, it was followed and video recorded using one or more of the following equipment: Canon IXY Digital 610, SONY DCR-TRV900, Canon PowerShot A650 IS and Canon EOS Kiss X3 cameras. The recording was usually started immediately after a school was found; however, at some occasions, recording was started several minutes after spotting a school to allow the squid to acclimate. Recordings were made from some distance (~5 to 10 m). At all occasions, *S. lessoniana* did not swim away and would often move closely under and between the observers. This indicated that they had been acclimated to our presence. The recording was continued until the squid voluntarily moved out of the field of vision. Each observation lasted for 1 to 2 hours between 0800 and 1700. In this study, 16 recordings were analysed (1 to 7 recordings per day; recording duration, 10 to 903 seconds), which were recorded on: 2 July 2005; 20 July 2008; 25, 27 and 28 August 2010; and 18 August 2011 (SCHOOL 1 through to 16).

For each recording, the numbers of schoolmates were counted and the changing process of school appearance with time was traced. The school appearance was categorized on the basis of geometrical traits. The trait of the school appearance was evaluated by calculating the nearest neighbour distance (NND), angular deviation (AD) and shape deviation (SD) from the video still frames by using a video imaging software (ImageJ 1.45, Figure 2). NND was the distance of 2 points between the eyes of the 2 closest squid (Sugimoto & Ikeda, 2012). AD was calculated by setting a base line. This line was the horizontal line connecting 2 points between the eyes of 2 squid that were situated at the most peripheral position of both the sides when schoolmates oriented toward the longitudinal direction. AD was the angle between the base line and a schoolmate. Since squid could move backward and forward, AD was less than 90°. NND and AD were measured for 10 squid that were evenly distributed in whole school per video frame. Each value was averaged across 10 schoolmates; next, the median and quartile for these distances and angles were calculated from 5 video frames for each school appearance in 1 recording. The video frame that contained more than 10 clearly visible schoolmates was selected as the analysis frame.

For SD, a polygon was drawn to connect the tip of the arm and the mantle (opposite side of the head) of peripheral schoolmates, and a perpendicular line was drawn to the base line between 2 farthest cross-points of the polygon and the perpendicular line. SD was the difference between the length of a base line and the perpendicular line. The median and quartile for this length were calculated from 5 video frames in the same way as NND and AD. Dorsal mantle length (ML) for *S. lessoniana* in a school and the water depth from the surface at which they formed the school were visually estimated. Since the accurate length of the field could not be estimated easily, NND and SD were normalized to ML.

For statistical analysis, NND, AD and SD were compared among different schools and school appearances by using the Kruskal–Wallis test, followed by the Scheffé test and

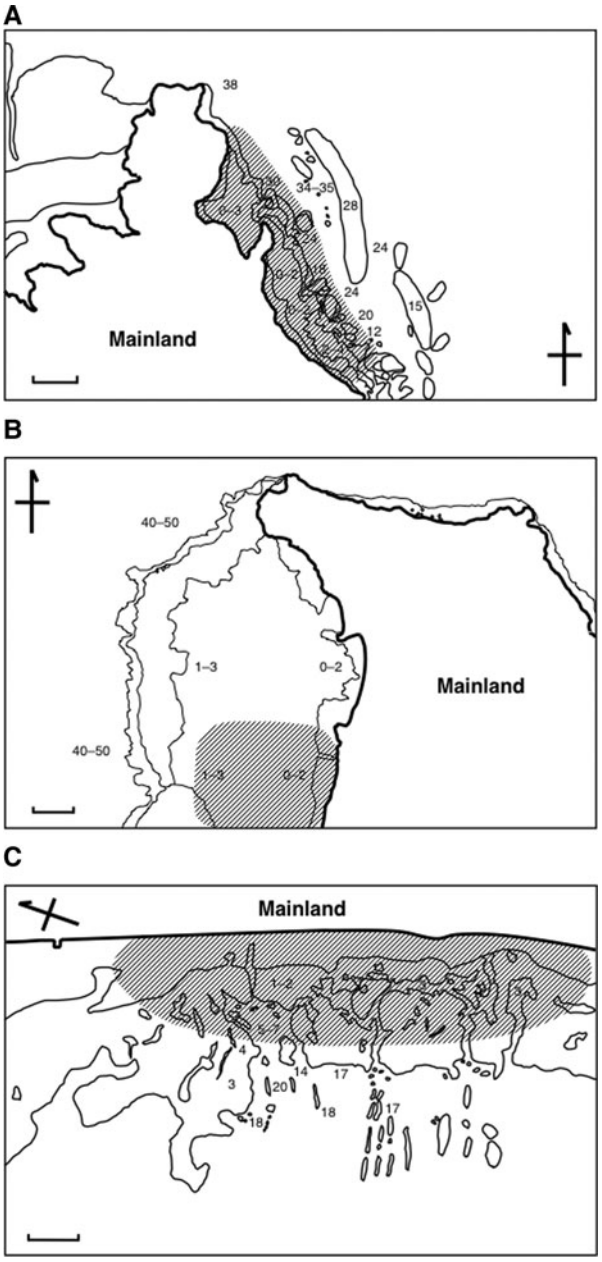

Fig. 1. A simplified map of the observation sites for the schools of the oval squid *Sepioteuthis lessoniana*: (A) Cape Maeda; (B) Cape Zanpa; (C) Sunabe beach. The numbers show the depth (m) from the water surface. The cross indicates bearing. The bold line indicates the boundary of the mainland. Other lines show the landscape of the sea bottom. The slashed area indicates the observational area. Scale bars: (A & C) 50 m; (B) 200 m.

Mann–Whitney *U*-test with Ekuseru–Toukei 2006 (Social Survey Research Information Co., Ltd.).

RESULTS

In all, 16 schools of *S. lessoniana* were observed, containing 8 to more than 100 squid of sizes ranging from 50 to 200 mm ML (Table 2). Squid schools were divided into 4 categories as containing ~100 squid, ~40 squid, ~20 squid and ~10 squid. SCHOOLS 1 through to 4 contained different sizes of squid (100 to 200 mm ML for SCHOOL 1; 150 to 200 mm ML for SCHOOLS 2, 3 and 4). SCHOOLS 5 through to 16

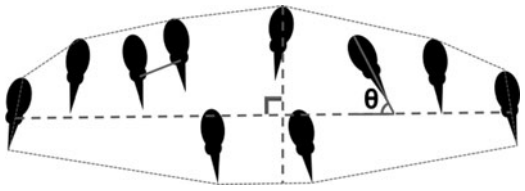

Fig. 2. Definition of the nearest neighbour distance (NND), angular deviation (AD) and shape deviation (SD) for the schools of the oval squid *Sepioteuthis lessoniana*: NND (solid line) was measured as the distance between the midpoint of the eyes of randomly selected squid and their own closest neighbour; AD (θ) was defined as the angle between the base line (dashed horizontal line) and squid; SD was defined as the difference between the length of the base line and the perpendicular line (dashed vertical line) that was drawn between 2 farthest cross-points of the polygon (dotted line). For the details of each measurement, please refer to the text.

mainly contained squid of the same size (50, 100, or 150 mm ML). All these schools were found at a depth of 1.0 to 3.0 m on an average in clear water.

Further, the schools were divided into 5 school appearance types: static appearances (belt, ball and sheet shape) and transitional appearances (high and low density). If a school retained a specific appearance for more than 5 seconds with hovering of schoolmates, it was judged as static and the others as transitional appearance. Many observed schools often changed their appearances within the time of recording. The frequency of these appearances was as follows: belt-shaped appearance by 9 schools; ball-shaped appearance by 3 schools; sheet-shaped appearance by 1 school; high-density transition by 12 schools; and low-density transition by 13 schools (Table 2). These appearances were quantitatively defined by calculating NND, AD and SD, and selecting SCHOOL 1 as schools containing ~100 squid, SCHOOL 3 as schools containing ~40 squid, SCHOOL 6 as schools containing ~20 squid and SCHOOL 13 as schools containing ~10 squid. During this study, no cannibalism and gender or group fidelity were observed or recorded among schoolmates because of the difficulty of accurately identifying individual schoolmates within a school.

The belt-shaped appearance of *S. lessoniana* was used by schools of all sizes (Figures 3A & 4A; Table 3). This appearance was formed at the depth of 0.5 to 4.0 m. The schools continuously maintained this appearance for 5.0 to 139.6 seconds (first quartile, 14.8 seconds; second quartile, 23.5 seconds; and third quartile, 50.1 seconds). In this appearance, schoolmates hovered and aligned themselves laterally and horizontally into a rectangular arrangement while maintaining a parallel orientation with neighbouring individuals. Interindividual distances between schoolmates were highly varied (see NND below). In the schools with ~100 squid, schoolmates arranged themselves according to their body sizes: larger squid were positioned at the front end of the school (i.e. closer to human observers), while smaller squid were scattered across the entire school (Figure 3A). The NND ranged between 1.3 and 11.1 ML (Table 4). AD ranged between 30.9 and 78.4°. The SD ranged between 0.9 and 129.9 ML. In the schools with ~20 squid, NND and SD were significantly larger than those of the schools with ~10 squid (both $P < 0.05$, Scheffé test). The AD did not show a significant relationship with school size. School size and NND were inversely proportional to each other. However, the relationship seemed insignificant.

The ball-shaped appearance of *S. lessoniana* was used by the schools with ~40 and ~10 squid (Figures 3B & 4B; Table 3).

Table 2. Details of oval squid *Sepioteuthis lessoniana* schools observed in coastal water of Okinawa Island, Ryukyu Archipelago, Japan.

School number	Recording date	School size	Mantle length (mm)	Recording depth (m)	Recording duration (s)	Appearance duration (s)	Static appearance	Transition appearance	Individual behaviour
1	2/7/2005	100 <	100–200	2.0–3.0	48	48	Belt		
2	25/8/2010	43	150–200	1.0–3.0	644	25.67	Belt		
						15.00		Low	
						19.00	Belt		
						8.33		High	
						102.00	Ball		In-and-out
						39.00		Low	
						17.67		High	
						20.00	Belt		
						76.33		High	
						50.83	Belt		
						27.83		High	
						66.67	Ball		In-and-out
						17.33		High	
						7.67		Low	
						9.33		High	
						6.67	Belt		
						27.33		Low	
						11.67	Ball		
						26.67		High	
						19.33		Low	
						12.33	Belt		
						37.23		High	
3	25/8/2010	40	150–200	1.0–4.0	272	49.67		High	
						14.67	Belt		
						14.67		Low	
						17.00		High	
						8.00	Sheet		
						10.00		High	
						39.33	Sheet		
						24.67		High	
						12.67	Ball		
						28.00		High	
						40.67	Belt		
						8.67		Low	
4	25/8/2010	39	150–200	1.0–2.0	28	27		Low	
5	27/8/2010	20	50	2.0–3.0	97	96	Belt		
6	28/8/2010	20	100	0.5–3.0	585	119.33		High	
						23.00		Low	
						8.67		High	In-and-out
						18.00		Low	In-and-out
						15.00	Belt		
						20.67		Low	
						32.00		High	

						17.67		Low	
						108.33		High	
						18.67		Low	In-and-out
						28.67		High	In-and-out
						24.67		Low	In-and-out
						14.67		High	In-and-out
						11.00		Low	In-and-out
						14.00		High	In-and-out
						111.00		Low	
7	18/8/2011	20	50	0.5–3.0	795	40.75		High	
						135.25		Low	
						17.50		High	
						7.50		Low	
						244.00		High	
						25.50		Low	
						21.50		High	In-and-out
						81.00		Low	
						48.00		High	
						10.00		Low	
						163.85		High	
8	18/8/2011	20	50	0.5–3.0	671	5.50		High	
						51.00		Low	
						350.50		High	In-and-out
						36.00		Low	
						67.00		High	
						52.00		Low	
						29.50		High	
						79.55		Low	
9	25/8/2010	18	150–200	1.0–2.0	155	15.67		High	
						23.33	Belt		
						27.67		High	
						63.67	Belt		
						24.67		Low	
10	28/8/2010	13	100	1.0–3.0	137	23.67	Belt		
						48.33		High	
						28.33		Low	
						36.27		High	
11	28/8/2010	13	100	1.0–2.0	56	15.33		Low	
						40.17		High	
12	28/8/2010	13	100	1.0–2.0	10	10.00		Low	
13	20/7/2008	10	100	1.0–2.0	903	56.50	Ball		
						47.33		High	
						6.67	Belt		
						19.00		Low	
						591.67	Ball		

Continued

Table 2. Continued

School number	Recording date	School size	Mantle length (mm)	Recording depth (m)	Recording duration (s)	Appearance duration (s)	Static appearance	Transition appearance	Individual behaviour
						42.67		High	
						139.63	Belt		Intimidating
14	28/8/2010	10	150	1.0–5.0	179	58.67		High	
						28.67		Low	
						27.67		High	
						38.00		Low	
						10.00		High	
						16.33		Low	
15	28/8/2010	10	100	0.5–2.0	176	16.33		Low	
						12.00		High	
						103.67	Belt		
						15.00		Low	
						5.00	Belt		
						24.30		High	
16	28/8/2010	8	100	2.0–3.0	45	45		High	

It was formed at the depth of 1.0 to 3.0 m. The schools continuously maintained this appearance for 11.7 to 591.7 seconds (first quartile, 23.6 seconds; second quartile, 61.6 seconds; and third quartile, 93.2 seconds). In this appearance, schoolmates hovered parallel to each other and were densely packed into a spherical arrangement. The NND ranged from 0.8 to 2.5 ML (Table 4). The AD ranged from 47.9 to 83.8°. The SD ranged 0.5 to 5.7 ML. Although these values were not significantly different between the schools with ~40 and ~10 squid, NND of the former was smaller than that of the latter.

The sheet-shaped appearance of *S. lessoniana* was used by the schools with ~40 squid (Figures 3C & 4C; Table 3). It was formed at the depth of 2.0 m. The schools continuously maintained this appearance for 8.0 to 39.3 seconds (first quartile, 15.8 seconds; second quartile, 23.7 seconds; and third quartile, 31.5 seconds). In this appearance, schoolmates hovered parallel to each other and positioned themselves in a horizontal plane with a square arrangement. The schoolmates were evenly distributed, with a similar interindividual distance. The NND ranged from 1.3 to 2.9 ML (Table 4). The AD ranged from 60.7 to 80.9°. The SD ranged from 2.7 to 13.6 ML.

SCHOOL 3 with schools of ~40 squid showed all appearance types: the belt-shaped, ball-shaped and sheet-shaped. The NND, AD and SD of this school type showed significant differences between the belt-shaped and ball-shaped appearances. The NND of the belt-shaped appearance was larger than that of the ball-shaped appearance ($P < 0.01$, Scheffé test; Table 4). The AD of the belt-shaped appearance was smaller than that of the ball-shaped appearance ($P < 0.01$, Scheffé test). The SD of the belt-shaped appearance was larger than that of the ball-shaped appearance ($P < 0.05$, Scheffé test). The NND, AD and SD of the sheet-shaped appearance were intermediate between those of the belt-shaped and ball-shaped appearances.

SCHOOL 13 with schools of ~10 squid showed both belt-shaped and ball-shaped appearances. The NND and SD of the belt-shaped appearance were larger than those of the ball-shaped appearance, although insignificant (Table 4). The AD of the belt-shaped appearance was smaller than that of the ball-shaped appearance, although insignificant.

The high- and low-density transitional appearances of *S. lessoniana* were used by the schools with ~10, ~20 and ~40 squid (Figures 3D, E & 4D, E; Table 3). These appearances were formed at a depth of 0.5 to 5.0 m. The duration of these transitional appearances ranged from 5.5 to 350.5 seconds (first quartile, 17.2 seconds; second quartile, 28.0 seconds; and third quartile, 47.7 seconds) and 7.5 to 135.3 seconds (first quartile, 15.2 seconds; second quartile, 20.7 seconds; and third quartile, 32.3 seconds). The high-density transition occurred when schoolmates moved simultaneously as a cluster. On the other hand, the low-density transition was observed in 2 cases where schoolmates began to move away from individuals located at the school's periphery or simultaneously moved into a belt-shaped arrangement. Since schoolmates aligned themselves laterally and longitudinally, the school's appearance became elongated. In both the high- and low-density transition, interindividual distances varied over time, changing school geometry. In contrast, interindividual angle was maintained at nearly zero (i.e. completely parallel) among schoolmates since they maintained the same directional movement.

We evaluated these 2 transitional appearances by using NND alone. When schoolmates used both high- and low-density

Table 3. Difference among the school appearances in oval squid *Sepioteuthis lessoniana* observed in coastal water of Okinawa Island, Ryukyu Archipelago, Japan. n/a, not applicable; ML, dorsal mantle length.

Measurements	School appearance				
	Belt	Ball	Sheet	High	Low
Number of schoolmates	10, 20, 40, 100	10, 40	40	10, 20, 40	10, 20, 40
Water depth from the surface	0.5–4.0 m	1.0–3.0 m	2.0 m	0.5–5.0 m	0.5–5.0 m
Interindividual distance (median nearest neighbour distance)	2.6 ML	1.1 ML	2.1 ML	2.1 ML	3.0 ML
Interindividual angle (median angular deviation)	42.0°	64.1°	70.2°	Nealy 90°	Nealy 90°
Size-based arrangement	Obvious	Not obvious	Not obvious	Not obvious	Not obvious
Less synchronized movement by squid at periphery	Not obvious	Not obvious	Not obvious	Not obvious	Not obvious
Individual behaviour	Intimidating	In-and-out	n/a	In-and-out	In-and-out

transitions, schools with ~40 and ~20 squid were often separated into two groups, which smoothly merged together within a few seconds to several minutes. The NND of the high-density transition ranged from 1.0 to 2.8 ML (Table 4). The NND of the low-density transition ranged from 1.5 to 9.1 ML. In the low-density transition, the NND of the schools with ~40 squid was significantly smaller than that of the schools with ~20 squid ($P < 0.05$, Scheffé test). In the schools with ~20 squid, the NND of high-density transition was significantly smaller than that of low-density transition ($P < 0.01$, the Mann–Whitney *U*-test).

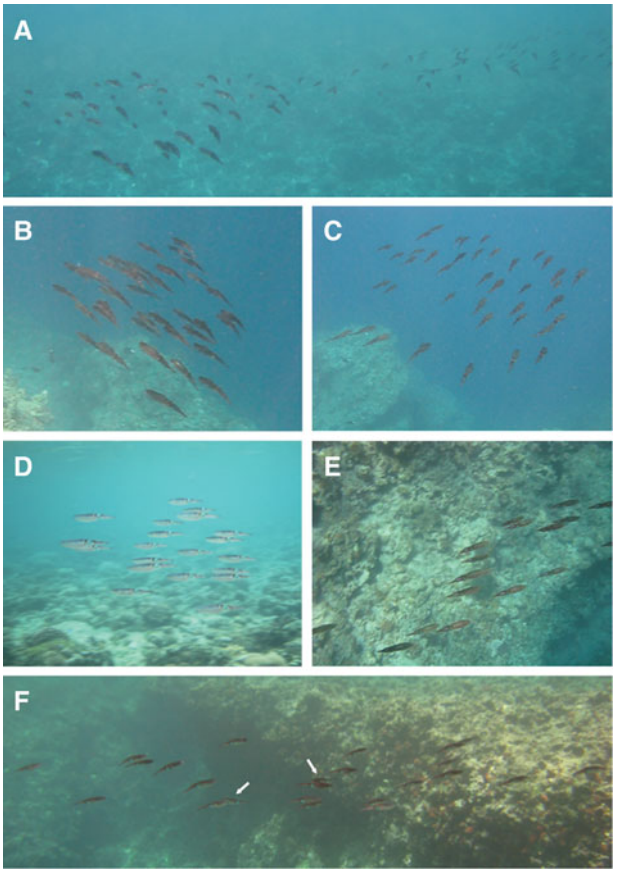

Fig. 3. Photographs of the schools of the oval squid *Sepioteuthis lessoniana*: (A) belt-shaped appearance (SCHOOL 1); (B) ball-shaped appearance (SCHOOL 3); (C) sheet-shaped appearance (SCHOOL 3); (D) high-density transition (SCHOOL 8); (E) low-density transition (SCHOOL 3); (F) two individuals (arrow) facing in opposite directions (SCHOOL 1). Note that some larger schoolmates are positioned at the front end of the school in the belt-shaped appearance (see the lower left of (A)). All photographs were taken at Cape Maeda.

The NND of the belt-shaped appearance for the schools with ~10, ~20 and ~40 squid was larger than that of the high- and low-density transitions, and that of high-density transition was smaller than that of low-density transition, although insignificant (Table 4). The NND of the ball-shaped appearance of the schools with ~40 and ~10 squid was smaller than that of the high- and low-density transitions, particularly showing a significant difference between the ball-shaped appearance and low-density transition ($P < 0.05$, Scheffé test). Furthermore, the NND of the sheet-shaped appearance of the schools with ~40 squid was larger than that of the high- and low-density transitions, and that of the high-density transition was smaller than that of the low-density transition, although insignificant.

Several interactions were observed among the schoolmates of *S. lessoniana*. In SCHOOL 7, a larger individual suddenly moved out of the school and moved in the opposite direction from the school. Immediately, the schoolmates turned around and followed this larger squid (Figure 5A–C). On the same day, in SCHOOL 8, a larger squid dashed out of a school, but the schoolmates did not follow this individual. Instead, 43 seconds later, the larger squid rejoined the school. In another instance, a large squid (ML ~200 mm) moved near the school but did not join this school, and none of the schoolmates responded to the movement of this squid. This type of in-and-out behaviour was observed during the high-density transition in both SCHOOLS 7 and 8.

In-and-out behaviour by a larger squid was also noted in SCHOOL 2. The larger individual left the school and then returned to it after 21 to 72 seconds. This particular squid repeated this process 4 times over a period of 10 minutes. In SCHOOL 6, a larger squid left the school and rejoined it after 14 to 35 seconds (Figure 5D–F). This squid repeatedly joined and left the school 3 times over a period of 10 minutes. The in-and-out behaviour in SCHOOLS 2 and 6 was observed during the ball-shaped and transitional appearances, respectively. These in-and-out behaviours in SCHOOLS 2 and 6 differed from those in SCHOOLS 7 and 8 in terms of relative location of the larger squid to the other schoolmates. The larger squid in SCHOOLS 2 and 6 always maintained the same distance from the other schoolmates and never moved away from the school. In the case of SCHOOLS 7 and 8, however, the larger squid moved away from the school.

In SCHOOL 13, a larger squid was located at one end of the belt-shaped school closest to the human observer. This squid

Table 4. Details of measurements for the school appearances in oval squid *Sepioteuthis lessoniana* observed in coastal water of Okinawa Island, Ryukyu Archipelago, Japan. Nearest neighbour distance (NND), angular deviation (AD) and shape deviation (SD).

School number	Measured values	School appearance and measurements										
		Belt			Ball			Sheet			High	Low
		NND (ML)	AD (°)	SD (ML)	NND (ML)	AD (°)	SD (ML)	NND (ML)	AD (°)	SD (ML)	NND (ML)	NND (ML)
SCHOOL 1 (~100 squid)	First quartile (25%)	2.3	45.6	46.0	–	–	–	–	–	–	–	–
	Second quartile (50%)	2.5	45.6	57.8	–	–	–	–	–	–	–	–
	Third quartile (75%)	2.5	48.8	77.5	–	–	–	–	–	–	–	–
SCHOOL 3 (~40 squid)	First quartile (25%)	2.2	34.1	27.1	0.8	78.7	3.8	2.0	70.1	2.7	1.0	1.6
	Second quartile (50%)	3.5	34.9	42.8	0.9	78.7	4.2	2.1	70.2	5.4	1.6	1.9
	Third quartile (75%)	3.7	37.0	46.5	1.1	81.2	4.3	2.4	71.5	7.2	2.0	1.9
SCHOOL 6 (~20 squid)	First quartile (25%)	7.3	36.9	47.2	–	–	–	–	–	–	2.1	4.3
	Second quartile (50%)	9.9	37.4	64.9	–	–	–	–	–	–	2.3	6.9
	Third quartile (75%)	10.5	49.6	88.7	–	–	–	–	–	–	2.7	8.5
SCHOOL 13 (~10 squid)	First quartile (25%)	1.4	38.4	3.8	1.4	58.0	1.3	–	–	–	1.9	2.0
	Second quartile (50%)	2.2	56.2	7.4	1.5	61.1	2.3	–	–	–	2.5	3.2
	Third quartile (75%)	2.5	70.7	18.6	2.0	62.0	2.8	–	–	–	2.7	3.6

exhibited distinct body pattern with conspicuous striped coloration, with its arms held upward or downward (Figure 6A–C). The remaining schoolmates did not show such a distinct body pattern and oriented themselves parallel to each other. During all the other school appearances observed, *S. lessoniana* consistently exhibited a clear counter-shading pattern with darker dorsal side and lighter ventral side. No other body patterns or body postures were observed during both static and transitional appearances. In addition, 1 or 2 schoolmates sometimes moved facing in opposite directions from all the other schoolmates, while maintaining the same moving direction and speed.

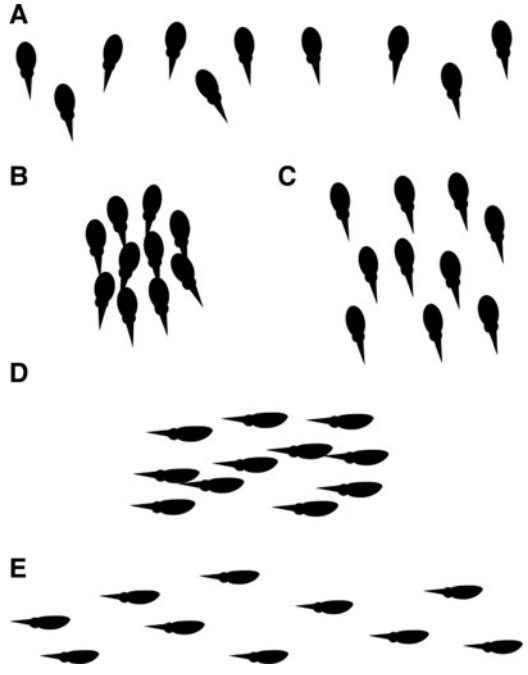

Fig. 4. Schematic drawings of the school appearance in the oval squid *Sepioteuthis lessoniana*: (A) belt-shaped appearance; (B) ball-shaped appearance; (C) sheet-shaped appearance; (D) high-density transition; (E) low-density transition.

DISCUSSION

In this study, we described and defined 5 types of school appearances (3 static appearances: belt shape, ball shape and sheet shape; and 2 transitional appearances: high and low density) of *Sepioteuthis lessoniana* in the field. Of these

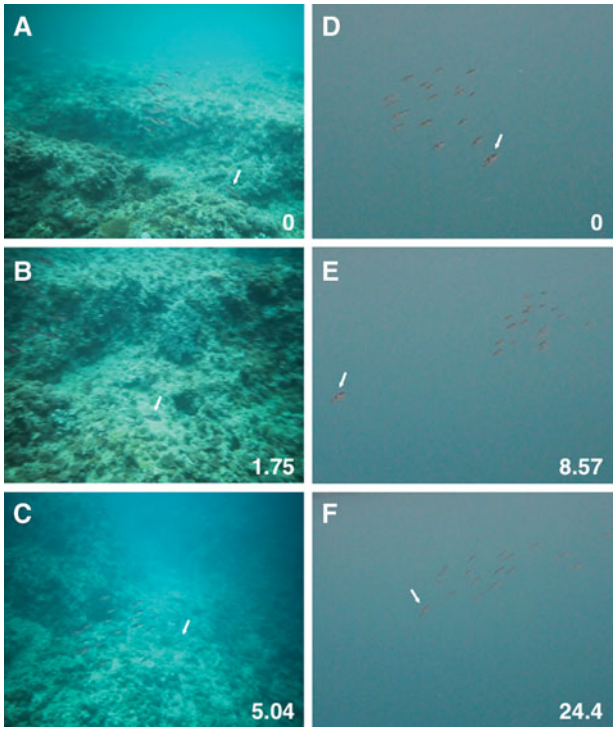

Fig. 5. Photographs of in-and-out behaviour and following behaviour in a school of the oval squid *Sepioteuthis lessoniana*: (A) a larger squid dashes out of the school; (B) the schoolmates follow the larger squid; (C) the larger squid rejoins the school; (D) a larger squid moves to the periphery of the school; (E) the larger squid moves out of the school; (F) the larger squid rejoins the school. Arrows indicate the larger squid. Numbers show time-lapse in seconds. A–C, SCHOOL 8; D–F, SCHOOL 6. All photographs were taken at Cape Maeda.

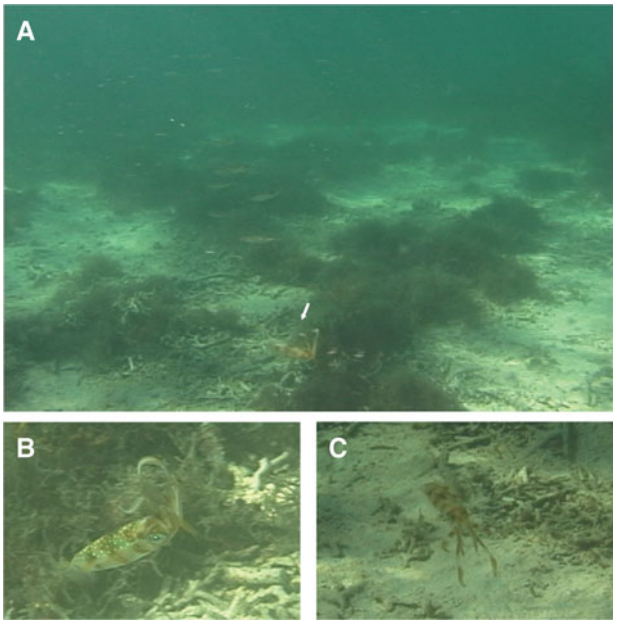

Fig. 6. Photographs of intimidating behaviour by a large oval squid *Sepioteuthis lessoniana* individual in a school: (A) a larger squid moves to the periphery of a school with a belt-shaped appearance and lifts its arms; (B) enlargement of the squid in (A); (C) same squid in (A), with its arms down. All photographs were of SCHOOL 13 at Cape Zanpa.

appearances, the belt-shaped appearance has been reported by following researchers during their field study of *Sepioteuthis* (see Table 1). The semi-diagonal and crescent appearance (Moynihan & Rodaniche, 1982), the picket line appearance (Hanlon & Messenger, 1996) for *S. sepioidea*, and the ragged-line appearance (Adamo & Weichelt, 1999) for *S. lessoniana* can be categorized together with the belt-shaped appearance described. Adamo & Weichelt (1999) quantitatively defined belt-shaped appearance among *S. lessoniana* schoolmates by using the interindividual distance (1.8 ML) and deviation of angle (15°) method, and these values are also similar to our result (2.6 ML and 12.5°, respectively; see Table 3). Besides geometric similarity, in a belt-shaped appearance, school size (~10 to ~100 squid) and body-size based arrangement are concomitant with those reported by the pioneer studies. The *Sepioteuthis sepioidea* school usually includes 20 to 40 squid (Hanlon & Messenger, 1996) and shows marked size-based arrangement in the belt-shaped appearance (Moynihan & Rodaniche, 1982; Hanlon & Messenger, 1996). In this study, however, the size-based arrangement was not obvious in the belt-shaped appearance of the schools with ~20 and ~40 squid (half of all records) and was observed only in the schools with ~100 squid. This difference may be caused by the difference in the amplitude of schoolmate body-size variation. The body size variation of *S. lessoniana* schoolmates in the schools with ~10 to ~40 squid was smaller than that of the schools with ~100 squid. A wide size-range of schoolmates in *S. sepioidea* has been reported previously (Moynihan & Rodaniche, 1982; Hanlon & Messenger, 1996). That is, in a belt-shaped appearance of *Sepioteuthis* school, the larger the size variation of schoolmates, more is the size-based arrangement.

Unlike belt-shaped appearance, which has been reported in the past studies, the ball shape and sheet shape as static appearances have not yet been reported (see Tables 1 & 3). Ball-shaped and sheet-shaped appearances are similar to those of a rough assemblage of relaxed *S. sepioidea* in the field (Moynihan & Rodaniche, 1982) and/or of *S. lessoniana* in a laboratory tank (Boal & Gonzalez, 1998). However, the deviation angle between schoolmates differs. Almost all schoolmates in this study faced the same direction unlike the previous studies (just half of the schoolmates faced the same direction; Boal & Gonzalez, 1998).

To our knowledge, we are the first to define transitional appearances in terms of schoolmate density (high and low). The school appearance while moving was described as the tight appearance against approaching predators in *S. sepioidea* (Hanlon & Messenger, 1996). Moreover, Adamo & Weichelt (1999) reported that the interindividual distance in a *S. lessoniana* school decreased while jetting away. These descriptions are similar to the high-density transition of *S. lessoniana* since the schoolmates are densely packed and facing the same direction. A school of *S. lessoniana* might be constantly expanding (fission) and contracting (fusion) according to various environmental necessities. This trait of static and transitional appearances of *S. lessoniana* is also similar to the schooling behaviour of *S. sepioidea* (Moynihan & Rodaniche, 1982).

School appearances described in this study can also be found in other animals. Fish, birds and dolphins show similar group appearances in their three-dimensionally manoeuvrable living environments (Table 5). The belt-shaped appearance is reported in birds and dolphins. Birds use a line flight formation (e.g. front or V formation), which they use during their long migration (Heppner, 1974; Hainsworth, 1987). This appearance in bird flocks possesses two major functions: reducing energetic costs of flight through aerodynamic advantages and facilitating visual contact with neighbouring birds for communication (Heppner, 1974; Cutts & Speakman, 1994). Dolphins also use a line formation (e.g. a front formation; Pryor & Norris, 1991) by 20–30 individuals maintaining an equal

Table 5. Difference of characteristics related to grouping behaviour among animals. n/a, not applicable.

Characters	Animals				
	Fish[1]	Squid[2]	Bird[3]	Dolphin[4]	Elephant[5]
Brain to body-weight ratio	Low (the same as reptile)	Relatively high (close to bird and mammal)	High	High	High
Cognitive ability (e.g. learning and memory)	Relatively high	Relatively high	High	High	High
Synchronized and polarized group	Yes	Yes	Yes	Yes	Yes
Static appearance	Yes	Yes	None	None	n/a
Leader–follower relationship	None	Yes	Yes	Yes	Yes

[1]Pitcher & Parrish (1993), [2]Hanlon & Messenger (1996), [3]Nagy *et al.* (2010), [4]Pryor & Norris (1991), [5]McComb *et al.* (2001).

interindividual distance (Pryor & Norris, 1991). Dolphins' school arrangement may also be related to the above-mentioned 2 functions found in birds. Although the shape is similar, the belt-shaped appearance of *S. lessoniana* schools also has a unique characteristic. Unlike birds and dolphins, *S. lessoniana* can hover in mid-water. Hence, hydrodynamic advantages are an unlikely reason for this and other static appearances, despite the difference in the buoyancy and density effect between air and water. Instead, visual contact might be used for communication between school members, since squid possess a highly developed and laterally positioned lens and can change their body patterns. These physical attributes may suggest that squid have visual communication with members of the school.

The ball-shaped appearance and the high- and low-density transitions are similar to the group appearance of fish, birds and dolphins. The school appearances of squid are similar to ball, cruise and hourglass manoeuvres in fish (Pitcher & Wyche, 1983); globular, extended and column formations in birds (Heppner, 1974); and tight group, team and line formations in dolphins (Pryor & Norris, 1991). In fish, the ball manoeuvre is employed when stationary and at the highest density when fish are introduced in a new environment (Pitcher & Wyche, 1983). In the ball-shaped appearance observed, *S. lessoniana* also aggregate with the highest density compared to other appearances. The dense pack of schoolmates may have some anti-predator functions in terms of the morphological feature (Pitcher & Parrish, 1993). In fish, birds and dolphins, several group appearances during movement might have appropriate functions for defence or migration. The same might be true for squid. The switch between the high- and low-density transition and in-and-out behaviour in these appearances might enhance some functions related to defence and/or navigation.

In addition to its appearance, for a squid, the size variation among schoolmates and the number of schoolmates relates directly to the functions of a school. In SCHOOL 8, when a school of ~20 small squid (ML ~50 mm) encountered a large squid (ML ~200 mm), they did not form a single school. Forming a school with similar-sized schoolmates has been reported in natural populations of *Doryteuthis opalescens* (Hurley, 1978). This is also common in fish schools (Pitcher & Parrish, 1993). From the principle of the oddity effect of groups (i.e. predators may preferentially target the least common phenotype in a group), evolutionary pressure for grouping with similar individuals is produced (Krause & Ruxton, 2002). The feature of forming a school with similar-sized schoolmates was particularly common in the smaller *S. lessoniana* observed in this study. Smaller *S. lessoniana* (ML less than ~100 mm) form a small school (schools of ~10 and ~20 squid) and exhibit narrow size-variation among schoolmates. In contrast, larger *S. lessoniana* (ML more than ~100 mm) tend to form a large school (schools of ~40 and ~100 squid) with various-sized schoolmates. In a school with ~100 squid, the size-range of the schoolmates is wider than that in a school with ~40 squid. Adamo & Weichelt (1999) reported that *S. lessoniana* of 25 to 160 mm ML formed a school of less than 186 squid that showed a size-based arrangement. In this study, 75% of the observed schools had ~10 or ~20 schoolmates (12 schools out of all schools observed). This suggests that a school with ~10 or ~20 squid is the smallest natural unit of a *S. lessoniana* school. These units are then integrated to create a larger squid school. Hence, schools with ~40 and ~100 squid contain squid of different body sizes. In fact, schoolmates in schools with ~100 squid had the widest body-size variations (ML ~100 to 200 mm) and thus showed the size-based arrangement. During this study, we observed and analysed very interesting facts regarding the schooling behaviour of *S. lessoniana*. However, there are many more questions that need to be answered in our future investigation.

ACKNOWLEDGEMENTS

We thank members of the Ikeda laboratory for their assistance with field observations. We also acknowledge H. Shirakawa and H. Aniya for assistance in drawing the map of the observation sites. This study was partially supported by a Grant-in-Aid for Scientific Research (C), Project No. 18580188, MEXT; a Research Fellowship for Young Scientists, Project No. 23·4156, JSPS; and University of Minnesota Grant-in-Aid and Imagine Grant for which we are very grateful.

REFERENCES

Adamo S.A. and Weichelt K.J. (1999) Field observations of schooling in the oval squid, *Sepioteuthis lessoniana* (Lesson, 1830). *Journal of Molluscan Studies* 65, 377–380.

Boal J.G. and Gonzalez S.A. (1998) Social behaviour of individual oval squids (Cephalopoda, Teuthoidea, Loliginidae, *Sepioteuthis lessoniana*) within a captive school. *Ethology* 104, 161–178.

Cutts C.J. and Speakman J.R. (1994) Energy savings in formation flight of pink-footed geese. *Journal of Experimental Biology* 189, 251–261.

Darmaillacq A.-S., Chichery R. and Dickel L. (2006) Food imprinting, new evidence from the cuttlefish *Sepia officinalis*. *Biology Letters* 2, 345–347.

Hainsworth F.R. (1987) Precision and dynamics of positioning by Canada geese flying in formation. *Journal of Experimental Biology* 128, 445–462.

Hanlon R.T. and Messenger J.B. (1996) *Cephalopod behaviour*. Cambridge: Cambridge University Press.

Heppner F.H. (1974) Avian flight formations. *Bird Banding* 45, 160–169.

Hunt J.C., Zeidberg L.D., Hamner W.M. and Robison B.H. (2000) The behaviour of *Loligo opalescens* (Mollusca: Cephalopoda) as observed by a remotely operated vehicle (ROV). *Journal of the Marine Biological Association of the United Kingdom* 80, 873–883.

Hurley A.C. (1978) School structure of the squid *Loligo opalescens*. *Fishery Bulletin* 76, 433–442.

Krause J. and Ruxton G.D. (2002) *Living in groups*. New York: Oxford University Press.

McComb K., Moss C., Durant S.M., Baker L. and Sayialel S. (2001) Matriarchs as repositories of social knowledge in African elephants. *Science* 292, 491–494.

Messenger J.B. (1973) Learning in the cuttlefish, *Sepia*. *Animal Behaviour* 21, 801–826.

Moynihan M. and Rodaniche A.F. (1982) *The behavior and natural history of the Caribbean reef squid* Sepioteuthis sepioidea. *Advances in Ethology*. Berlin and Hamburg: Verlag Paul Parey.

Nagy M., Ákos Z., Biro D. and Vicsek T. (2010) Hierarchical group dynamics in pigeon flocks. *Nature* 464, 890–893.

Packard A. (1972) Cephalopods and fish: the limits of convergence. *Biological Reviews* 47, 241–307.

Pitcher T.J. and Parrish J.K. (1993) *Behaviour of teleost fishes*. 2nd edition. London: Chapman & Hall.

Pitcher T.J. and Wyche C.J. (1983) Predator avoidance behaviour of sand-eel schools: why schools seldom split? In Noakes D.L.G., Linquist D.G., Helfman G.S. and Ward J.A. (eds) *Predators and prey in fishes*. The Hague, The Netherlands: Junk, pp. 193–204.

Pryor K. and Norris K.S. (1991) *Dolphin societies*. Los Angeles, CA: University of California Press.

and

Sugimoto C. and Ikeda Y. (2012) Ontogeny of schooling behavior in the oval squid *Sepioteuthis lessoniana*. *Fisheries Science* 78, 287–294.

Correspondence should be addressed to:
Y. Ikeda
Department of Chemistry, Biology and Marine Sciences
University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan
email: ikeda@sci.u-ryukyu.ac.jp