

Cuttlefish can school in the field

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Abstract Cuttlefish (Sepiidae) are usually solitary in nature, but we have found evidence that the broadclub cuttlefish (*Sepia latimanus*) forms schools. *S. latimanus* groups of various sizes were observed for 145 min in Okinawa, Japan. The groups were comprised of 2–9 members that were usually of similar body sizes. The groups continuously changed shape, forming either clusters or lines. The groups were regarded as schools and had characteristic structures such as synchronized and polarized swimming with similar distances apart from each other (~4.0 mantle length), and swam in parallel (under 20° or over 110° in angle) to their nearest neighbours, regardless of the numbers of members in the group. Small members sometimes followed larger members within the school. These characteristics were similar to those observed in schools of Teuthoidea squid. Schools comprising large numbers of members frequently exhibited hunting behaviour for small crustaceans and fish. This is the first observation of schooling behaviour in wild Sepiidae.

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Introduction

A society is generally understood to be a group of individuals belonging to the same species that have come together in a cooperative manner (Wilson 1975). Social groupings can provide benefits for individuals, such as protection from predators, cooperation in discovering and hunting food, and enhancement of offspring survival (Wilson 1975).

A wide range of societies occurs among vertebrates. For example, the chimpanzee *Pan troglodytes* lives in loosely organized social groups comprising of 20 to over 150 individuals, with groups that may be composed of various ages and genders (Goodall 1968). In these groups, male chimpanzees have a strong dominance hierarchy (Hayaki et al. 1989), and interactions between mates, such as social grooming, are usually related to the maintenance of the group (Watts 2002). Meanwhile, some fish and birds live in loose groups that remain together for social reasons, such as defence, foraging, or spawning, and these groups are called ‘shoals’ for fish (Pitcher and Parrish 1993) or ‘flocks’ for birds. In contrast, groups of fish in which every nearest neighbour keeps the same distance from each other with the same swimming velocity (synchronized behaviour) and direction (polarized behaviour) are termed ‘schools’, in which leaders readily initiate new directions to followers (Pitcher and Parrish 1993; Parrish and Edelman-Keshet 1999; Krause et al. 2000). Over 10,000 species of fishes form schools at some time in their lives (Shaw 1978). However, the characteristics of schools in fish vary according to species. For example, the herring *Clupea harengus* spends all of its life schooling, and becomes agitated if separated from the group (Blaxter 1965; Breder 1967). In contrast, the cod *Gadus morhua* forms schools specifically at feeding grounds (Partridge et al. 1980; Deblois and Rose 1996).

The shapes of schools in fish are oblong rather than spherical (Partridge et al. 1980; Hemelrijk et al. 2010), and the main function of schooling is considered to be a reduction in the risk of predation (Krause and Ruxton 2002).

In Cephalopoda, it has been reported that Octopodidae octopuses are generally solitary, but Teuthoidea squids form schools (Mather 1995; Hanlon and Messenger 1996; Boal 2006). For example, the California market squid *Doryteuthis opalescens*, the Caribbean reef squid *Sepioteuthis sepioidea*, and the oval squid *Sepioteuthis lessoniana* form schools consisting of 10–100 individuals (Moynihan and Rodaniche 1982; Adamo and Weichelt 1999; Hunt et al. 2000; Sugimoto et al. 2013). Schools of *D. opalescens* are composed of individuals of the same approximate body size (Hurley 1978), while schools of *S. sepioidea* and *S. lessoniana* usually contain large and small individuals of both sexes and maturation stages (Moynihan and Rodaniche 1982; Hanlon and Messenger 1996; Sugimoto et al. 2013). It is believed from the composition of the schools that young *S. sepioidea* may acquire many different kinds of information by watching and following individuals, especially larger squid (Moynihan and Rodaniche 1982). Additionally, schools of *S. sepioidea* and *S. lessoniana* form shapes of ragged-lines, spheres or sheets (Moynihan and Rodaniche 1982; Boal and Gonzalez 1998; Adamo and Weichelt 1999; Sugimoto et al. 2013). In schools of *S. sepioidea*, almost all individuals arrange themselves by facing in the same direction; however, some individuals face in the opposite direction, acting as sentinels (Moynihan and Rodaniche 1982; Hanlon and Messenger 1996). Furthermore, during the reproductive season, *S. sepioidea* and *S. lessoniana* migrate to spawning grounds in larger schools, where they then mate and spawn eggs as a single pair or in smaller schools (Moynihan and Rodaniche 1982; Segawa 1987; Segawa et al. 1993). Thus, it is assumed that the forming of schools in cephalopods confers some of the same advantages on individuals as seen in fishes, such as a reduction in the risk of predation, social learning, as well as increasing the opportunity of finding and selecting mates (Hanlon and Messenger 1996).

In contrast, Sepiidae cuttlefish are thought to be semi-solitary as they are benthic like Octopodidae (Mather 1995; Boal et al. 1999). Two possible exceptions are the species *Sepiella inermis* and *Sepiella maindroni*, which have been observed to form groups when they are young in laboratory settings (Choe 1966; Nabhitabhata 1997). Field research on the reproductive behaviour of Sepiidae (e.g. *Sepia latimanus* and *Sepia apama*), investigating agonistic disputes and mating, also suggests that these species may be solitary most of the year and aggregate solely during the reproductive season (Corner and Moore 1980; Hall and Hanlon 2002; Hanlon et al. 2005). However, to date, there has been no clear evidence of schooling behaviour in wild Sepiidae.

Here, we report the first documented instance of schooling in the family Sepiidae observed in the broadclub cuttlefish *S. latimanus* off the western coast of Okinawa Island, Japan.

Materials and methods

Observations were conducted by SCUBA diving on a reef slope off the coast of Cape Zanpa, Okinawa Island, Ryukyu Archipelago, Japan (26°25'N, 127°42'E), on 1, 4, 6, 9, 11, and 26 August 2013. The total duration of SCUBA diving was 340.6 min across six diving days. Three or four observers usually dived together each day. The reef slope descends gradually to a depth of 8 m, and then drops rapidly to 20 m, which has a sandy bottom with rocks and coral rubble. The area in which we surveyed was from 5 to 8 m in depth and from 20 to 25 m in width. The bottom of the survey area consisted of rubble, with agglomerated coral and small-sized colonies of *Acropora*. The seawater temperature in this area was recorded with a dive computer (Edy II, Cressi-Sub) during each diving session and ranged between 28 and 30 °C. On encountering *Sepia latimanus*, we immediately recorded their behaviour using digital video cameras (Cyber-shot DSC-RX100, SONY and LUMIX DMC-TZ20, Panasonic) at a horizontal and/or vertical angle at a distance of 1–2 m. The recording continued until *S. latimanus* disappeared or divers had reached the safe limit of oxygen volume in their tanks.

The recorded videos were analysed with imaging software (ImageJ v1.47). Based on the videos, we estimated the dorsal mantle length (ML), sex, and maturity (Boletzky and Villanueva 2014). Sex and maturity were determined by body colouration [males with closely set irregular transverse lines exhibited on mantle and fin; females with no transverse lines exhibited on body but elongated iridescent spots exhibited on the fin, female body appears to be more translucent than males (Corner and Moore 1980)], and mating behaviours. If we could not observe these characteristics, we determined the *S. latimanus* to be a juvenile. In the videos, we defined *S. latimanus* as being 'grouped' if an individual spent time with conspecifics within a distance of ca. 3 m over 10 s. The individuals that constituted the groups were defined as members of the group. From the recorded videos, we determined the numbers of members within a group in the area for each observed occasion (>10 s), and then also calculated the number of occasions each size of group was encountered, and the duration of these encounters. The shapes of the groups in *S. latimanus* were described in a geometric configuration, following the methods used in fish (Partridge et al. 1980; Hemelrijk et al. 2010) and *Sepioteuthis* (Moynihan and Rodaniche 1982; Boal and Gonzalez 1998; Adamo and Weichelt 1999;

Sugimoto et al. 2013). Outlines and dimensional measures, such as areas or lengths, of each shape of the groups were estimated by connecting members with lines. In cases when a member began to separate from the group and subsequently the remaining members in the group followed it, we judged this as ‘following behaviour’ and counted the number of occurrences. Following behaviour is one of the characteristics of schools of fish (Krause et al. 2000) and *Sepioteuthis* (Moynihan and Rodaniche 1982; Sugimoto et al. 2013). Furthermore, we recorded body patterns, such as texture, posture, and colouration of the body, in accordance with Hanlon and Messenger (1988). Additionally, hunting behaviours were described based on models of hunting in *Sepia* (Messenger 1968; Hanlon and Messenger 1996), and we recorded the positioning, as well as numbers of seizures and capture of prey for each hunting behaviour.

To reveal the structures of *S. latimanus* groups, within groups we calculated neighbour distance (ND), the nearest neighbour distance (NND), nearest neighbour angle (NNA), and the percentage of the nearest neighbour looking in the same direction, as these criteria are used during evaluation of group structures in fish (Pitcher and Wyche 1983) and Teuthoidea schools (Hurley 1978; Boal and Gonzalez 1998; Adamo and Weichelt 1999; Sugimoto and Ikeda 2012; Sugimoto et al. 2013). As was done in these past studies (Pitcher and Wyche 1983; Boal and Gonzalez 1998; Adamo and Weichelt 1999; Sugimoto and Ikeda 2012; Sugimoto et al. 2013), we defined ‘neighbours’ as members positioned alongside each other inside of a group. All measurements were from a set base point between the eyes of *S. latimanus*. ND was defined as the distance between the base points of all neighbouring pairs of squids. NND and NNA were the distance and angle between the base points of nearest neighbours, respectively. ND and NND were normalized to ML. Since most *S. latimanus* looked in either the same or opposite direction, we divided NNA into 0°–90° and 91°–180°, respectively, for analysis. For the percentage of the nearest neighbour looking in the same direction, we calculated the number of nearest neighbours which exhibited NNA between 0° and 90° within the groups. From recorded footage, we took the image that was deemed the clearest from each 60 s stretch of footage for each group. Based on these images, we calculated the median and quartile range for ML, ND, NND and NNA. Due to criteria for schooling in fish (Pitcher and Parrish 1993; Parrish and Edelstein-Keshet 1999) and in the squid *Doryteuthis opalescens* (Hurley 1978), we determined the group to be a school if every member of *S. latimanus* displayed synchronised and polarized swimming at an approximately equal distance (i.e. no large variation in NND) and in a way parallel (i.e. <69° or >111° in NNA) to the nearest neighbours.

To compare ND, NND, NNA, and the percentage of the nearest neighbour looking in the same direction between the different group sizes, a Kruskal–Wallis one-way ANOVA was used to determine statistical differences. When significant differences were observed between the different group sizes, Scheffé’s method was performed for multiple comparisons. For all statistical tests, the significance level was set at $p < 0.01$. Statistical analyses were performed using Ekuseru-Toukei 2006 (Social Survey Research Information Co. Ltd.).

Results

We encountered a total of 28 *Sepia latimanus* across six dives (Table 1). ML for all *S. latimanus* was ~80–150 mm, except for *S. latimanus* observed on 26 August 2013, in which ML was ~150–250 mm. The cuttlefish we observed did not exhibit the irregular transverse lines pattern on the body or fins that are characteristic of subadults and adults, nor did they show any reproductive behaviour. Hence, all *S. latimanus* we encountered were classified as juveniles. It was difficult to distinguish the sex of juvenile *S. latimanus* based on their external morphometry, such as ML and body patterns, contrary to with the subadult and adult phases.

When groups of *S. latimanus* hovered in the water column or above low-contrast backgrounds such as a horizontally extended pale rock surfaces, they usually exhibited a weakly disruptive colour pattern (overall body colouration was light or had scattered small spots, but clearly exhibited two dark transverse lines on the dorsal mantle) (Fig. 1a–c). On the other hand, *S. latimanus* exhibited a dark mottled colour pattern (overall body colouration was darkened and scattered with white and black patches), or a disruptive colour pattern (a white bar between two dark transverse lines on the dorsal mantle were clearly exhibited on a darkened body colouration scattered with white and black patches) just above the bottom of high-contrast or dark backgrounds, such as coral reefs, dark macroalgae, and rocks (Fig. 1d). Most members in groups held their arms against their smooth or coarse skin texture. Within groups, all members usually displayed similar postural and textural body patterns, although selected colour patterns differed based on the locations the groups were at.

When a fish (e.g. *Prionurus*) of similar body size to *S. latimanus* approached, group members sometimes extended their fourth arm pair and exhibited dark rings around their eyes. When groups moved away from observers, they usually exhibited a uniformly light colour pattern (overall body colouration was light and sometimes exhibited numerous small white and black spots). However, *S. latimanus* did not change their body patterns before and after joining and

Table 1 Summary of the field observations for *Septia latimanus* during schooling in the coastal waters of Okinawa Island, Ryukyu Archipelago, Japan

Date	Duration of dive (min)	Number of <i>S. latimanus</i>	Mantle length, ML (mm)	Number of occasions for encountering the different-sized groups						Duration for maintaining the different-sized groups (min)						Number of occasions for observing the following behaviour						
				2 Members		3 Members		4 Members		5 Members		2 Members		3 Members			4 Members		5 Members		Over 6 members	
				Members	Over 6 members	Members	Over 6 members	Members	Over 6 members	Members	Over 6 members	Members	Over 6 members	Members	Over 6 members		Members	Over 6 members	Members	Over 6 members	Members	Over 6 members
1 Aug 2013	34.6	6	80–120	17	3	7	5	8	3	9.2	3	8	6.95	3.9	0							
4 Aug 2013	84.1	9	80–120	11	17	6	8	6	13.7	7.4	6.2	7.9	42.9	0								
6 Aug 2013	51.9	5	120–150	3	–	1	0	0	2.2	0	0	0.75	–	0								
9 Aug 2013	60	3	120–150	4	–	1	–	–	7.5	4.9	–	–	–	1								
11 Aug 2013	60	3	80–150	6	–	3	–	–	4.6	14.7	–	–	–	3								
26 Aug 2013	50	2	150–250	1	–	–	–	–	0.8	–	–	–	–	0								
Total	340.6	28	–	42	20	18	14	13	38	30	14.2	15.6	46.8	4								

leaving the group, and new members often synchronized their body patterns with those of group members.

We were able to observe *S. latimanus* groups of various sizes for a total of 145 min. They formed groups containing 2–9 members that were usually of similar body sizes (Fig. 1; Online Resource 1: Video S1). We frequently encountered groups of two members during the period of observation (42 times; Table 1), and they maintained these groups for long periods of time (a total of 38.0 min; Table 1). Smaller groups were encountered more often than larger groups. However, in groups containing greater than six members, maintained group time was the same as that of the pairs (a total of 46.8 min; Table 1). *S. latimanus* in groups usually hovered and swam slowly in the water column 0.5–1 m above the bottom. While they moved as a group, members often joined and left the group, which caused the observed duration of each group to vary accordingly (Table 1). We observed following behaviour four times in groups consisting of three *S. latimanus* (Table 1). In three cases, when a larger member began to leave the group, the remaining two smaller members immediately followed the larger member. In the remaining case, in which the sizes of the three *S. latimanus* were similar, two members immediately followed the other member that began to leave the group.

Groups gently and continuously changed in their shapes between clusters and lines. In the cluster shape, *S. latimanus* were grouped together by hovering or swimming slowly at approximately equal distances and in the same direction. The outline of the shape seemed to form a triangle, square, or trapezium (Figs. 1a, b, d and 2a, b, d). The area of cluster shapes was in the range of ~0.2 m² (3 members) to 4.5 m² (9 members). Groups maintained this shape continuously for 0.2–9.9 min. In the line shape, *S. latimanus* were aligned horizontally or laterally by hovering at approximately equal distances and in the same direction (Figs. 1c and 2c). The length of lines was in the range of approximately 1.0 m (3 members) to 2.5 m (6 members). Groups continuously maintained this shape for 0.2–6.0 min.

As the number of members in groups increased, neighbours moved significantly away from one another (median of absolute distance to neighbour: 2 members, 376 mm; 3 members, 410 mm; 9 members, 544 mm; median of ND: 2 members, 3.3 ML; 3 members, 4.1 ML; 9 members, 5.4 ML) (Scheffé's method, $df = 7$, $p < 0.01$, Fig. 3A). However, regardless of group size, distance to the nearest neighbour within groups was located within 4.0 ML (median of absolute distance to the nearest neighbour: 3 members, 382 mm; 9 members, 286 mm; median of ND: 3 members, 3.8 ML; 9 members, 2.9 ML) (Fig. 3B). Meanwhile, the nearest neighbours within groups mostly looked in either the same ($NNA < 20^\circ$; median of NNA , 0° – 90° ;

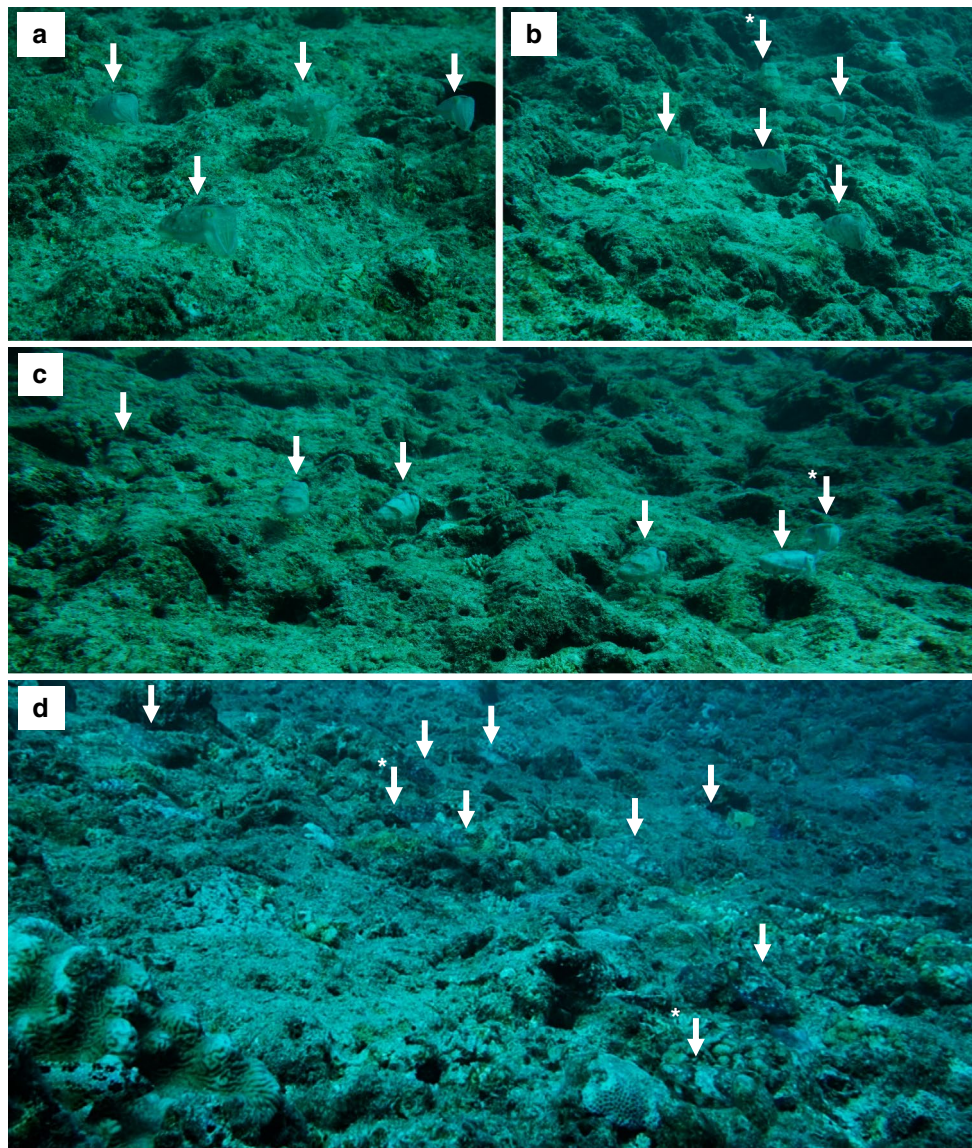


Fig. 1 School of cuttlefish *Sepia latimanus* formed particular structures in clusters or lines: **a** cluster shape in which the outline of a school of 4 has a triangular arrangement, **b** cluster shape in which the outline of a school of 5 has a square arrangement, **c** a lined shape of

2 members, 5.5° ; 3 members, 8.0° ; 9 members, 9.4°) or opposite ($NNA > 110^\circ$) direction (median of NNA , 90° – 180° : 2 members, 157.3° ; 3 members, 111.8° ; 9 members, 139.3°) (Fig. 4A). All members in small groups comprising 2–4 members looked in the same direction. Conversely, as the size of groups increased, the percentage of neighbours looking in the same direction slightly decreased (i.e. an increase in the number of neighbours looked in the opposite direction; median of the percentage of neighbours looked in the same direction; 2–4 members, 100 %; 9 members, 50 %; Fig. 4b). However, there were no statistically significant differences for these percentages between groups. Since groups of *S. latimanus* exhibited synchronising and

6, and **d** cluster shape in which the outline of a school of 9 has a trapezoidal arrangement. Arrows indicate *S. latimanus*, and those with an asterisk indicate *S. latimanus* that face in the direction opposite to their nearest neighbour

polarizing swimming at a particular distance (~ 4 MLs in NND) and in a parallel manner (under 69° or over 111° in NNA) regardless of the number of members in the group, these groups were judged to have met the criteria for forming a school.

Interestingly, *S. latimanus* exhibited two types of hunting behaviour during schooling. One was ‘pursuit’, which is similar to that observed in *Sepia officinalis*. In pursuit, when *S. latimanus* spotted prey, they swam rapidly towards the target with the first and second arm pairs raised or extended forward and the third arm pair slightly opened. Tentacles were then ejected from the tips of arms to strike the prey at an optimal distance. The other type of hunting

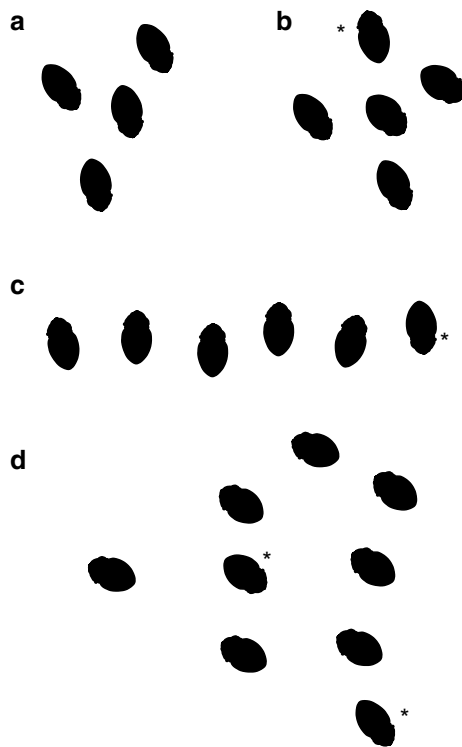


Fig. 2 Diagram of the shapes of schools of the cuttlefish *Sepia latimanus*, top view: **a** cluster shape of a school of 4 with a triangular arrangement, **b** cluster shape a school of 5 with a square arrangement, **c** lined shape of 6, and **d** cluster shape of a school of 9 with a trapezoidal arrangement. Those with an *asterisk* indicate *S. latimanus* that face in the direction opposite to their nearest neighbour

behaviour seen was ‘luring’, as previously noted for *S. latimanus*. In luring, when *S. latimanus* spotted prey, individuals swam slowly towards the target with the first arm pair raised and swaying left and right as if attracting the prey. Concurrently, the second arm pair darkened at the tips, and the second and third arm pairs wagged vertically and horizontally. Finally, tentacles were ejected at an optimal distance. *S. latimanus* hunt using these two types of behaviour for small crustaceans and fish, such as *Paguritta* or Gobiidae, which live in small holes of coral reefs. As the size of groups became larger, *S. latimanus* frequently exhibited both types of hunting behaviour for small crustaceans and fish. Although *S. latimanus* frequently exhibited such hunting behaviour, the final capture of the prey was seldom observed, which caused the success rate of hunting to be ~50 % (Table 2).

Discussion

In our observations, *Sepia latimanus* exhibited a weakly disruptive colour pattern when they were on low-contrast

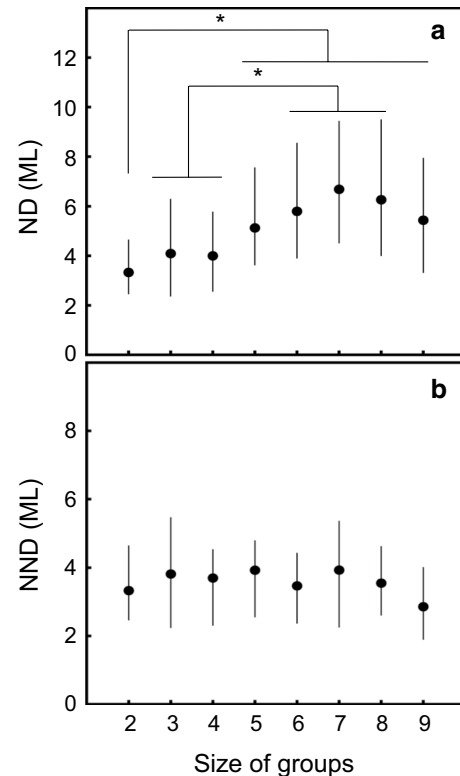


Fig. 3 Fluctuation of profiles of ND **a** and NND **b** for different-sized groups of *Sepia latimanus*. ND and NND are normalized to ML of each *S. latimanus*. Symbols and vertical bars show median and quartile range, respectively. *Statistically significant: groups contained 2 members versus 5–9 members, and 3 and/or 4 members versus 6–8 members in ND (Kruskal–Wallis and Scheffé’s method, $p < 0.01$)

backgrounds, while they exhibited a dark mottled or a disruptive colour pattern against high-contrast or dark backgrounds. Many fieldwork studies and laboratory experiments on camouflage of *Sepia officinalis* have led towards an understanding of how these animals evoke their body patterns differently depending on visual stimuli, such as contrast, brightness, shape, and texture of substrates or objects (e.g. Hanlon et al. 2009). Past studies have revealed that camouflaged body patterns exhibited by *Sepia* fall into three pattern categories: (1) uniform (or uniformly stippled), (2) mottle, and (3) disruptive (Hanlon and Messenger 1988). Evoking of these three body patterns is particularly related to the characteristics of backgrounds, such as contrast or edges. The uniform pattern is evoked against pale backgrounds, the mottled pattern is evoked against backgrounds with small-scale and moderate contrast, and the disruptive pattern is evoked against backgrounds with high-contrast and defined edges (Chiao et al. 2005; Mäthger et al. 2006, 2007; Barbosa et al. 2007, 2008; Zylinski et al. 2009; Chiao et al. 2010). Therefore, it seems to be plausible that *S. latimanus* in the current study exhibited body patterns against each background type as camouflage.

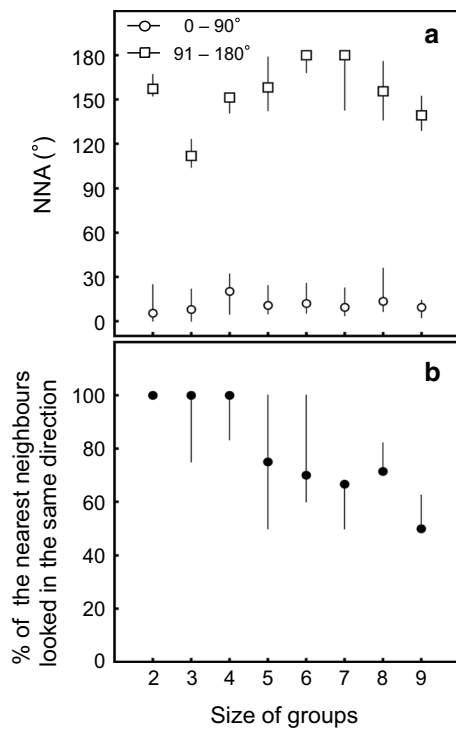


Fig. 4 Fluctuation of profiles of the NNA **a** and the percentage of the nearest neighbours that looked in the same direction **b** for different-sized groups of *Sepia latimanus*. Symbols and vertical bars indicate median and quartile ranges, respectively. There were no statistically significant differences for NNA or the percentages between the groups by Kruskal–Wallis and Scheffé’s method

From our observations, it was revealed for the first time that *S. latimanus* swam in a group with synchronization and polarization at a particular distance (~4.0 MLs in NND) and in a parallel manner (under 20° or over 110° in NNA), which leads us to conclude that this style of swimming can be categorized as a school (Pitcher and Parrish 1993; Parrish and Edelstein-Keshet 1999). Since most social animals

overlap generations, offspring receive care from their parents to enhance their survival (Wilson 1975) and hence the offspring maintain strong relationships with the parents to ensure receiving this care. Additionally, social animals obtain benefits, such as protection from predators, cooperation in discovering and hunting food, and reproductive opportunities, by forming social groups (Wilson 1975). On the other hand, with few exceptions, cephalopods die after reproduction (Rocha et al. 2001), and thereby juveniles do not receive care from their parents. However, cephalopods are capable of forming schools with members of the same generation to obtain survival advantages as they possess a well-developed nervous system and cognitive abilities (Wells 1962; Moynihan 1985; Hanlon and Messenger 1988, 1996). Schooling is a common characteristic of Teuthoidea (Hanlon and Messenger 1996). However, from our observations, it was revealed that *S. latimanus* also forms schools. It has been reported that *Sepiella inermis* and *Sepiella maindroni*, which also are members of Sepiidae, can form schools in the laboratory (Choe 1966; Nabhitabhata 1997). It is also assumed that *Sepiella japonica* migrates from deeper water to shallower water in comprehensive groups to forage and reproduce (Ueda 1985). However, there have been no descriptions in *Sepiella* that meet the criteria for a school in fish (Pitcher and Parrish 1993; Parrish and Edelstein-Keshet 1999).

In our observations, *S. latimanus* schools positioned and oriented themselves at an equal distance (~4.0 MLs in NND) and in parallel way (under 20° in NNA) from one another, regardless of the group size. However, as the school size increased, up to 50 % of members in the groups looked in the opposite direction (over 110°) compared to their neighbour. Additionally, schools formed particular structures in clusters or lines. These characteristics of schools in *S. latimanus* are similar to those found in Teuthoidea. The mean or median of NND and NNA in Teuthoidea, respectively, ranged from 1.0 to 5.0 ML and

Table 2 Number of steps (positioning, seizure and capture) observed in two types of hunting behaviour (pursuit and luring) by *Sepia latimanus* in the coastal waters of Okinawa Island, Ryukyu Archipelago, Japan

Date	Types of hunting behaviour					
	Pursuit			Luring		
	Positioning	Seizure	Number of capture prey	Positioning	Seizure	Number of capture prey
1 Aug 2013	36	2	2	23	4	3
4 Aug 2013	23	1	1	34	2	0
6 Aug 2013	17	4	1	0	–	–
9 Aug 2013	35	5	3	1	0	–
11 Aug 2013	0	–	–	4	0	–
26 Aug 2013	0	–	–	0	–	–
Total	111	12	7	62	6	3

9°–32° [*Sepioteuthis lessoniana*, 1.0–3.0 ML and 15°–30° (Boal and Gonzalez 1998; Adamo and Weichelt 1999; Sugimoto and Ikeda 2012; Sugimoto et al. 2013); *Doryteuthis opalescens*, 1.0–5.0 ML and 9°–32° (Hurley 1978; Hunt et al. 2000); *Illex illecebrosus*, 1.0–2.0 ML and 24°–29° (Mather and O’Dor 1984)]. These are approximately the same values to those of *S. latimanus*. Additionally, similar to schools of *S. latimanus*, ~20–50 % of members in a school of *S. lessoniana* look in the opposite direction to their neighbours (Boal and Gonzalez 1998; Adamo and Weichelt 1999), and their schools typically have a shape of spherical cluster or line (Boal and Gonzalez 1998; Adamo and Weichelt 1999; Sugimoto et al. 2013). On the other hand, the numbers of members within the schools for Sepiidae is different from those of Teuthoidea. From our observations, the schools of *S. latimanus* composed up to nine members, whereas Teuthoidea formed schools that ranged from 10 to 100 members (Moynihan and Rodaniche 1982; Adamo and Weichelt 1999; Hunt et al. 2000; Sugimoto et al. 2013). This difference might be related to reproductive strategies of these two cephalopod families. Sepiidae species lay large eggs in few numbers and are characterized by *K* selection features, and hatchlings settle immediately. However, Teuthoidea lay small eggs in large numbers, being characterized by *r* selection, and hatchlings survive as plankton or weak swimmers (Mangold 1987). These differences are reflected in the biomass of these two families [e.g. amount of catch in fisheries; ~2.5 million tonnes in Teuthoidea vs. 460 thousand tonnes for the Sepiidae (Boyle and Rodhouse 2005)].

Similar to *S. sepioidea*, some *S. latimanus* individuals in the larger schools faced in the opposite direction to their neighbours. In our observations, larger members of *S. latimanus* were clearly followed by smaller members more frequently than the reverse while schooling. It has been reported that juvenile *Sepia pharaonis* may have the potential of observational learning/conditioning within their cognitive capacity (Huang and Chiao 2013). From our observations, *S. latimanus* frequently exhibited hunting behaviours while forming schools consisting of large numbers of individuals, and under this condition individuals would have many opportunities to watch conspecifics finding or hunting prey. Therefore, it can be speculated that schools of Sepiidae may have the function of helping successful foraging by increasing opportunities for finding food. These functions in schooling would compensate for disadvantages arising from the lack of parental care in cephalopods.

We must be cautious as Sepiidae do not always form schools throughout all life phases as other examples have shown that as *Sepia* spp. grow, they stay far away from each other in captivity (*S. officinalis*, Boal et al. 1999; *S. pharaonis*, Ikeda personal observation). As well, it has been seen that *Sepia* form groups during the reproductive

season in the wild (*S. latimanus*, Corner and Moore 1980; *Sepia apama*, Hall and Hanlon 2002; Hanlon et al. 2005). We did not observe *S. latimanus* with large mantle lengths (i.e. supposed to be older member) forming large schools. Therefore, Sepiidae might have particularly strong social relationships during young and reproductive stages, although they have the tendency to spend time alone as subadults, characterized by an adult-like external morphometry even though they are not sexually mature (Boletzky and Villanueva 2014).

In conclusion, in this study, it was revealed for the first time that juvenile *S. latimanus* can form schools in which members (2–9 cuttlefish) position and orient themselves at an approximately equal distance and in parallel to their nearest neighbours. These characteristics of *S. latimanus* schools are similar to those in some squid species. The present observation on schooling behaviour in *S. latimanus* could provide a turning point in reconsidering the general belief that Sepiidae spp. are solitary (Boal 2006).

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