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PATTERNS OF SCHOOLING BEHAVIOUR IN *ALLOTEUTHIS SUBULATA* (CEPHALOPODA : LOLIGINIDEA)

by

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ABSTRACT

This paper describes and quantifies some observations on the patterns of schooling behaviour in captivity of the small squid *Alloteuthis subulata*.

The effect of predator, food and light on schooling is described. It is shown that squid are quite capable of grouping together in complete darkness, indicating that information from the mechanoreceptors of the head could also contribute to determine individual position in the school. In fact, two clusters of what is believed to be sensory hair cells were found in the central post-anterior axis of the head.

These behaviour and physiology patterns related to schooling in squid and fish may be considered to be convergent adaptations.

Introduction

A school, defined as "synchronised and polarised swimming groups" (Pitcher & Parrish, 1993), offers substantial benefits to its participants (Shaw, 1978). The advantages of schooling seem to be related to several functions, such as predator avoidance (Pitcher & Parrish, 1993), increasing the chances of finding food (Pitcher *et al.*, 1982), orientation of migrating animals (Larkin & Walton, 1969) and reproductive behaviour (Reisman, 1968).

It has been suggested that schooling is a common feature in some pelagic squids (Packard, 1972; Cousteau & Diolé, 1973) and laboratory studies have shown that squid form school-like structures in captivity (Hurley, 1978; Mather & O'Dor, 1984). Nevertheless, major questions remain unanswered, namely, a) can the structure of squid 'groups' be truly considered to be schools, b) do squid use similar schooling mechanisms to fish, profiting from identical benefits, and c) which sensory mechanisms participate in schooling?

This paper provides some information on the schooling behaviour of the squid, *Alloteuthis subulata*. The compactness and the degree of parallel orientation have been studied and the role of the sensory cells of the head is discussed.

Methods

Video recordings with groups of 3, 5, 7, 9 and 11 individuals were made in a isolated 2 m diameter tank in the MBA Laboratory (Plymouth, UK). The small tank depth (50 cm) made possible the use of two dimensional image analysis system.

The mean distance to the nearest neighbour (MNN) and the mean separation distance (MSD) were used to estimate the group compactness, and mean angular deviation (MAD) was used to estimate the degree of parallel orientation. These parameters were estimated with the same measures (MAD was adapted for squid behaviour) that have been used in fish schooling (Hunter, 1966).

The following experiments were implemented to study the effect of predation and food availability on squid schooling: 1) a natural predator of *A. subulata*, a semi-anesthetised cuttlefish, was placed inside a Plexiglass cage, and submerged in the centre of the tank, and 2) squids were fed with 0.5 cm live mysids (4/5 per squid) after a 24 hour starvation period.

The MNN, the MSD and the MAD were calculated at 30 second intervals before, during and after the two stimuli referred to above.

The effect of darkness on squid schooling was assessed by exposing the animals to a light flash after 5, 15 and 30 minutes of complete darkness. Having into account that a light flash induces an escape response, the first frame during a flash was used to measure the schooling indices. These experiments were repeated three times under the same conditions of light, salinity and temperature, with different sets of animals, each set with the same number individuals and sex ratios.

Scanning electron microscopy (SEM) was used to identify the cellular structures of the head and the upper tentacle area. An area (1 cm) covering all the indified cellular structures on the head of the squid was covered with a layer of superglue and all the experiments referred to above repeated in complete darkness.

The Mann-Whitney U test (Siegel, 1975) was used to compare the values of the MNN, MSD and MAN calculated before, during and after the stimulus (predator, food and light).

Results

The average values obtained for MNN, MSD and MAD are shown in table 1.

The variation of these indices before and during the introduction of the predator is shown in figure 1. There is a significant difference ($p<0.001$) of the values calculated for the three parameters before and during the introduction of the predator.

Similar results were obtained after squids captured the mysids (figure 2) but no differences were found ($p>0.1$) when comparing the behaviour before and during feeding.

SEM observation reveals the presence of two areas containing what appear to be clusters of sensory hair cells found in the central post-anterior axis of the head.

Figure 3 shows that, after a period of 30 minutes in darkness, the values of both the MNN and the MSD decrease significantly ($p<0.001$), whereas the values of the MAD increase significantly ($p<0.001$). When the sensory area of the head is covered with superglue, the squids schooled under light, but were unable to do so after 30 minutes in the dark.

Discussion

The effect of group size (larger groups schools more tightly) has been described both in squids *Loligo pealei* (Hurley, 1978) and *Illex ilecebrosus* (Matter & O'Dor, 1984), and in fish *Trachurus symetricus* (Hunter, 1966). It is important to consider the possibility than this effect could be due to limited space, since all these studies were made in captivity. The values obtained in this study were larger but of a similar order to those found in the two referred works on squid and in fish (Hunter, 1966), particularly the values for *mean separation distance* MSD. Nevertheless, the formation of two different groups in the schools of *A. subulata* which may be associated with the mating behaviour observed in this species (unpublished data), influenced MSD and no MNN.

The compactation and polarisation of *A. subulata* in response to the predator is similar to the behaviour of some fish schools, referred by Keenleyside (1979), Partridge (1982) and Gerking (1994). This behaviour might be related with the mechanism of predator avoidance described as "dilution of attack" and "the abatement effect" (Pitcher & Parrish, 1993). These theories state that an individual group member gains advantages simply trough a reduced probability of being the one attacked in an encounter with a predator. This probability reduces as the reciprocal of group size.

The decrease of MNN, MSD and MAD during and after feeding was found in fish after a similar starvation period (Hunter, 1966). This tendency was also observed in squid (figure 2), but only after the feeding phase, which may reflect different foraging strategies. There is field evidence suggesting that squid schools frequently scatter to hunt (Moyniham & Rodaniche, 1982; Sauer & Smale, 1993) whereas fish can act in a joint action to catch prey (Keenleyside, 1979).

Previous studies (Hurley, 1978; Mather & O'Dor, 1984) referred to vision as the only sense employed in squid schooling. Hurley (1978) showed that *L. pealei* were attracted to one to another using visual reference, since two squid placed in opposite sides of Plexiglas barrier swam in parallel though further away than without the barrier.

The sensory area of the head may play an important role in detecting the presence of other squids. These hair like structures might be related to the epidermal head lines described in *Sepia* hatchlings and adults of *Lollinguncula sp.* (Budelmann & Bleckmann, 1988). According to these authors, these structures are analogous to the lateral line system of fish. Furthermore, Budelman *et al.* (1989) concluded that these structures enable cuttlefish to catch small shrimps in the absence of light.

This study suggests that squid show a schooling pattern similar to that described in fish. However, more information is needed about the physiological basis of this behaviour, particularly under conditions of restricted vision. It would be interesting to investigate the presence of the external hair receptors in the cephalopods living in deeper waters.

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	MNN	MSD	MAD
3 animals	2.5	4.9	28.5
5 animals	2.0	4.8	43.3
7 animals	1.8	4.5	35.8
9 animals	1.7	4.4	40.4
11 animals	1.6	4.1	36.6

Table 1. Average values of *mean nearst neighbour* MNN, *mean squid distance* MSD and *mean angular deviation* MAD per group size. MNN and MSD are given in body length and MAD in radian degrees (SI).

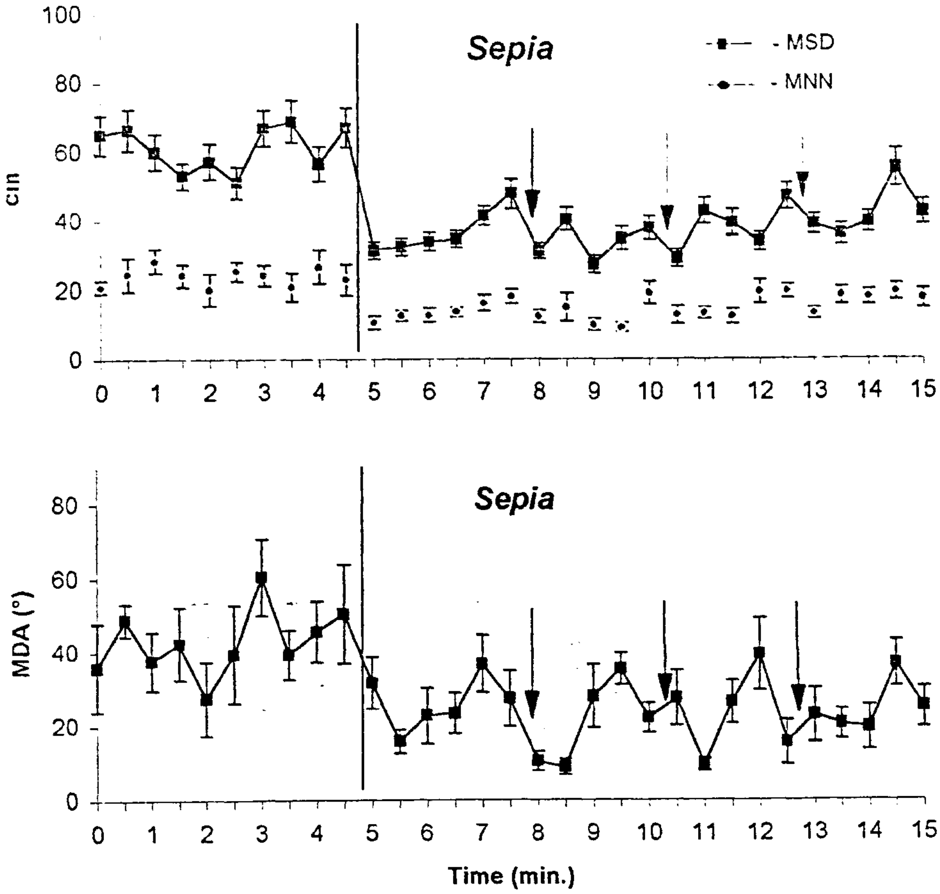

Figure 1.. MNN, mean distance to nearest neighbour, MSD, mean separation distance and MAD, mean angular deviation (+/- SEM) of a 9 animals school. *Alloteuthis* schooling before, during and after the presentation of a semi- anaesthetised cuttlefish in a Plexiglass box located in the centre of the tank.

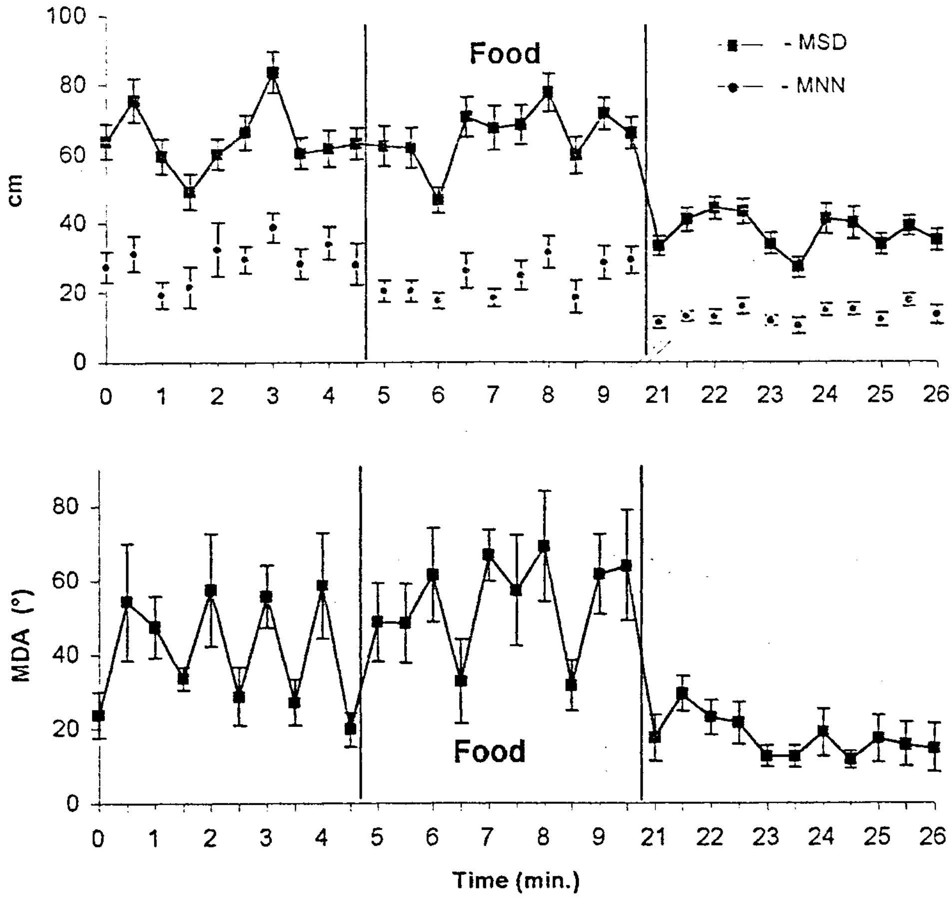

Figure 2.. MNN, mean distance to nearest neighbour, MSD, mean separation distance and MAD, mean angular deviation (+/- SEM) of a 9 animals school. *Alloteuthis* schooling before, during and after feeding.

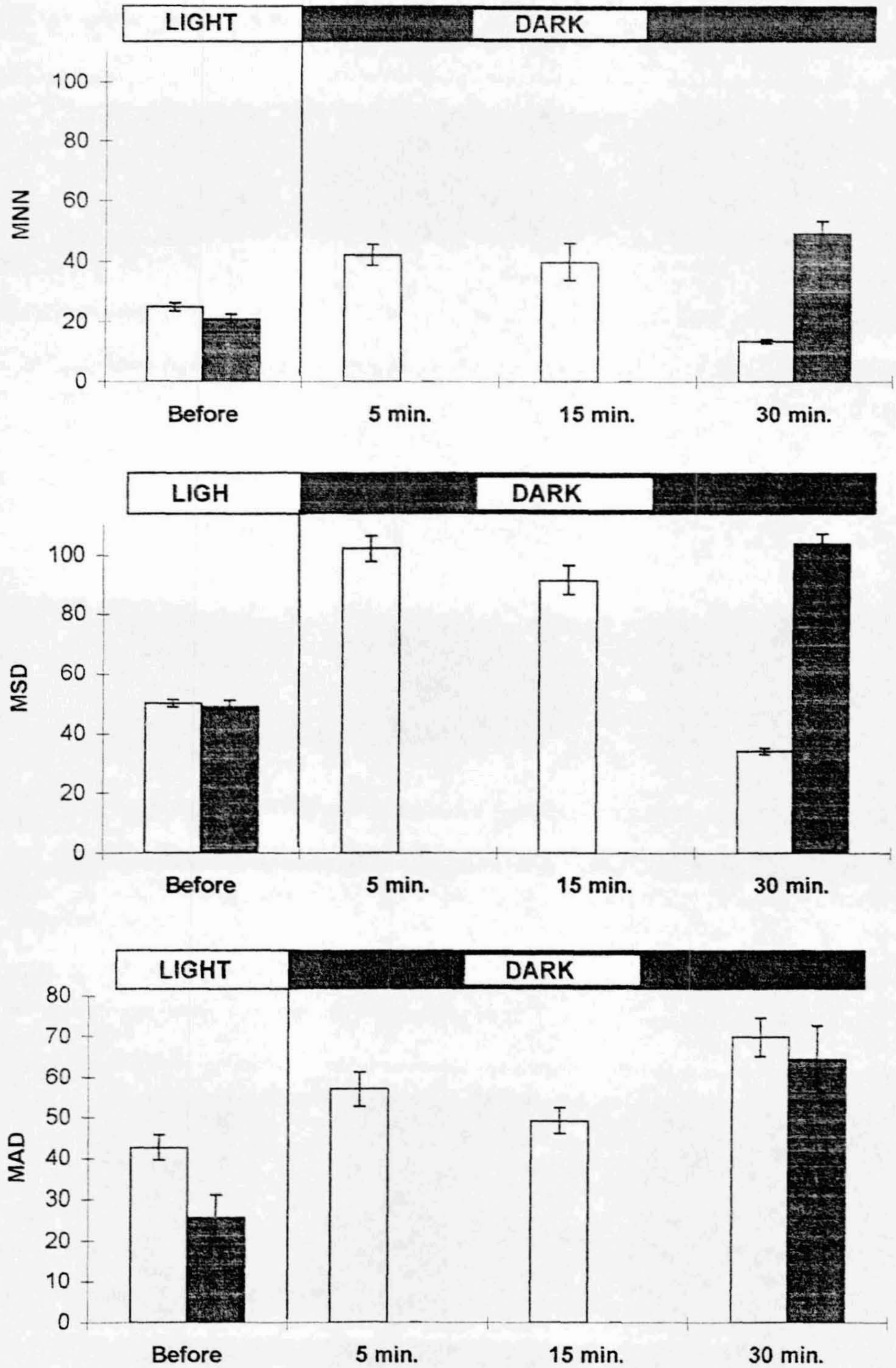

Figure 3.. MNN, mean distance to nearest neighbour, MSD, mean separation distance and MAD, mean angular deviation (+/- SEM) of a 9 animals school. *Alloteuthis* schooling before and after 5, 15 and 30 minutes in complete darkness under 'normal' conditions ('empty' bars) and after superglue had been applied to the head region.