Field Observations on the Reproductive Behavior of *Sepia latimanus*

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Abstract—*Sepia latimanus* displays a variety of colorings and behavior when interacting with another individual. The male expresses the greater variety of patterns including: the Upward V-curl, the Yellow Light, the Zebra, and the courting posture and coloring. The less elaborate postures, movements, and colorings of the female nevertheless appear to convey information to males (and possibly to predators). Paling of the arms, a leathery texture of the mantle, and greying of the body occur when she is ready to mate. A nonreceptive female displays a predominately white body with Center Bar.

Sepia latimanus gathered for reproduction each year in shallow (30 m) water during January through May. Males positioned themselves along the margin of the reef slope, each at his own limestone mound or pinnacle, locations where they intercepted females as they came from deeper water toward the site to deposit eggs. Larger males normally gained possession of the females as they arrived, sometimes after challenging the male already escorting the female. When the female was receptive, she mated with the male nearest to her. Females were seen to mate with several different males throughout the mating period.

Repeated copulation is characteristic of *Sepia latimanus*. After a female has deposited fertile eggs, copulation with a waiting male follows. After 15 to 20 minutes she deposits fertile eggs again. Identifiable females released fertile eggs during each of the 30 days that they were present in the observation area.

The critical factor determining the location of the gathering seemed to be crevices deep and narrow enough for egg deposition. Dead colonies of *Lobophyllia* usually provided the crevices, but such alternatives as sunken root systems of palm trees occasionally sufficed.

Crevices where eggs were placed in dead colonies of *Lobophyllia* were about 1 cm in diameter and 15 to 20 cm deep. The eggs averaged 1.8 cm to 2 cm in diameter, so they were retained inside the coral when they became detached. The developing *Sepia* spent about 38 to 40 days in the egg cases.

Unhatched as well as newly hatched *Sepia* employed a variety of color patterns and postures. The activities of *Sepia* inside the transparent egg included expression of a semi-Upward V-curl, a lifting of all arms in an exaggerated cone shape, propulsion by means of their funnel, and a releasing of ink.

Introduction

Little is known of the social behavior of pelagic cephalopods. Most surveys of the social reactions of cephalopods in nearshore or benthic species are fragmentary or anecdotal, some exceptions being *Sepioteuthis sepioidea, Octopus vulgaris,* and *Sepia*

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officinalis (Tinbergen 1939; Holmes 1940; Wells 1962a; Boycott 1965; Packard and Sanders 1969, 1971; Wells and Wells 1972; Moynihan 1975). The studies of the behavior of cuttlefish have been mainly aquarium studies of *Sepia officinalis* in temperate waters (Holmes 1940; Hardy 1956). We record field observations of the social behavior of *Sepia latimanus* Quoy and Gaimard 1832 which were conducted on the western coast of Guam.

Study Site

Observations were limited to a small area of the reef slope on the west coast of Guam. All sightings were made between depths of 15 and 36 m with the majority of activity occurring between 17 and 30 m. The reef slope begins at 12 m, descends gradually to 22 m, then drops rapidly to a sand bottom at 34 m. The area is a combination of a man-made cut in the reef and a natural depression; the cut is 9 to 15 m wide. The area is covered with rubble, coral mounds, and various sized colonies of dead *Lobophyllia*. The separation of the corallites of *Lobophyllia* from each other and the tendency of this type of coral to grow into tall stalks apparently made the corals an appropriate place for egg deposition by *Sepia*.

Water temperature at 20 m depth was measured nearly every day during the observations and it was consistently 27°C.

Morphological Characteristics of the Sexes

The males and females of *S. latimanus* were easily distinguished. The male has closely set, irregular, transverse lines across the mantle extending onto the upper one-third of the fin and forming a fairly even band on the fin. However, the lines are interrupted on the dorsal middle portion of the mantle. These transverse lines are normally reddish to yellowish white on the mantle and are iridescent bluish green to white on the fin. These lines are apparent throughout all the color changes that will be described. The outer edge of the fin has a distinctive dark narrow line and a broader band of pinkish white to white; the intensity apparently varies with the type of display or coloration manifest at the time.

The arms of *S. latimanus* are short and stout at their bases but they taper rapidly. The dorsal, dorsolateral, and ventrolateral arms (arms I, II, and III) are equal in length, but the ventral arm (arm IV) is approximately one-fifth longer. The arms are compressed on the distal half, forming a keel on the lower portion of the arms. Arm IV is keeled for its entire length. There is a well developed web between the arms.

On Arm IV of the male, beginning at its base and running to a sharp point, are distinctive irregular transverse lines similar to those found on the mantle and upper edge of the fin (Fig. 1). These lines are confined to the conspicuous broad flattened surface of the arm. The lines normally are the same reddish color as found on the mantle, although the color changes according to the type of behavior. Similar lines are found on the broad surface of Arm III but are fewer in number, more widely

spaced, and not as distinctive. The lateral surface of Arms I and II bear widely spaced, broad, bar-like transverse lines which are normally reddish. These can appear bold because of the dark reddish brown usually found on the arm surfaces. These transverse lines are absent along the outer keeled edge of each arm with the fourth arm having only a narrow band free of them.

The female has no transverse lines on the mantle or fin (Fig. 2). Along the extreme edge of the mantle and upper one-third to one-half of the fin are iridescent turquoise green elongated ocelli. There is no band or border on the fin and overall it appears to be more translucent than the brownish fin of the male. Arms of the females have no distinctive markings, transverse lines, or bars.

A difference detectable only when both sexes are present for direct comparison is that the male's overall coloration is darker than that of the female. The male's basic coloring in the natural light environment is reddish brown.

General Observations

We encountered *Sepia latimanus* on 75 out of 124 dives in the study area from 11 February 1976 to 18 May 1976. Two dives were usually made each day. Observations were discontinued for six days (10 April through 15 April) because of Tropical Storm Marie and ended 18 May 1976 with the arrival of Typhoon Pamela. *Sepia* eggs were first found inside *Lobophyllia* coral on 17 February and eggs in various stages of development were subsequently noted on 120 of the 124 dives. On 24 subsequent dives following Typhoon Pamela, 31 May 1976 to 12 October 1976, we sighted no more *Sepia* and all eggs were gone. All observations were made between 0900 and 1500 hr. We could not find them at the site at night.

In 75 encounters, a total of about 120 to 130 observations of males and about 55 to 65 observations of females were made. Initially, the differences between males and females were not noted, therefore the number of males and females observed was an approximation. Thereafter, we could easily distinguish males and females at distances up to nine meters. The number of *S. latimanus* encountered on a single dive varied between one and five. There were never more than five *Sepia* seen together or in the vicinity of each other except for one case involving four males and two females. Individual recognition of the subject was restricted to certain animals with scratch marks, so there was no way to determine the exact number of individual *Sepia* we saw throughout the observation period. However, based on distinguishing marks, we estimated that no more than nine to eleven males and five to seven females were involved. During the observation period there were basically three, perhaps four, groupings of *Sepia*, with the possibility of some overlapping of groups. Each group apparently persisted 27 to 30 days.

Even at the onset of observations, the cuttlefish readily accepted our presence especially when we were prone. When we first arrived, the cuttlefish circled at a distance of one to two meters until we assumed the same position as the cuttlefish (i.e., prone body 0.5 meters off the bottom with hand and fingers hanging in a downward

position), and moved slowly and deliberately. The cuttlefish then came closer. When one of us slowly extended a hand the cuttlefish approached and rubbed the tips of its cone-shaped or cupped arms across the fingers. After four to six encounters with one individual male, it accepted being rubbed across the dorsal and ventral surfaces and along the edge of the fourth arm.

With the initial group of *Sepia*, we initiated no challenges or disturbances toward them. *Sepia* approached from distances of 20 meters or more even though we had already arrived at the egg-laying site. The group appeared to be undisturbed by us even to the point of mating beneath one of us leaning on a coral mound.

With later groups of *S. latimanus*, we sometimes charged and chased the animals, attempting to separate the male from the female. These cuttlefish did not allow themselves to be handled afterwards, but their social interactions seemed otherwise undisturbed by our presence.

Postures, Movements, and Colorings of Males

Normal Postures and Colorings

The most frequent posture of the male was considered the normal one. In this, the male is usually Dark (dark reddish brown with a scattering of white and black spots on the smooth mantle and arms, normal transverse lines, with a greying of the fin's white band). The arms are held in a drooping, downward position (Table 1), hovering 0.5 to 1 meter off the bottom. From a short distance to one side or from above, the male appeared as a hole or shadow among the coral rubble, thereby making it inconspicuous. Only after becoming familiar with the area were we able to locate a cuttlefish expressing this posture and color.

Individual males normally hovered by the coral mounds along the margin of the reef slope overlooking the deeper waters, which allowed an unobscured view of a large area of the reef slope and sand bottom. From this position, rival males, individual females, and predators could be sighted by the male facing the deeper waters.

Usually, no more than three males were present in the area at any one time. There appeared to be two mature adults (sizes nearly equal) and one young (smaller) adult in the first group. An additional young adult male appeared near the end of the first group's residence; this individual rarely penetrated the observation area; it stayed in a Dark normal posture at a depth of 30 to 34 m.

Males frequently displayed the Dark normal posture when in the company of a female who was in the early stage of egg laying and therefore not stimulated toward mating, and when no other males were present. A male also assumed this posture when stationary near us. We conclude that the Dark normal posture indicated that external stimuli were minimal.

Another color pattern of the male that appeared to promote crypsis was a Blotched or mottled coloration. The Blotched normal posture was produced when yellowish white chromatophores expanded into large blotches and the reddish brown

Table 1. Body postures and chromatic patterns of male *Sepia latimanus* in relation to behavior.

	MALE		
BEHAVIOR	COLOR PATTERNS	SKIN TEXTURE	ARM POSTURE
Normal	Dark or Blotched	Smooth	Downward hanging, relaxed
Low Level Alarm	Dark or Blotched	Smooth or hint of papillae	Downward hanging w/Upward V-curl Downward pointing w/Upward V-curl Lifting pointing w/Upward V-curl
Moderate Alarm	Dark, Dark w/hint of Zebra, Dark w/Center Light, Dark w/Transverse Bar, or Blotched	Smooth or papillae lifted in varying degrees	Lifting, forward pointing w/any degree of Upward V-curl slight proximal puffiness
High Level Alarm	Moderate Zebra, Yellow Light	Smooth or papillae lifted in varying degrees	Horizontal arms, pointing, hooked Upward V-curl; Puffiness of arms or Downward pointing w/hooked Upward V-curl
Aggression	Zebra, Zebra w/Black Spot	Smooth or papillae lifted	Any degree of lifting and pointing of arms; Arms stretched forward; Arms flairing and enlarging; Body enlarging, webbing stretched; or Umbrellaing of arms
Courting	Light grey w/complete retraction of spots and transverse lines	Smooth	Semi-cone shape, confluent, tips of arms curled
Mating	Blotched, Predominately white Blotched, Center Light Dark, or semi-Zebra	Smooth or hint of papillae	Center arms on females forehead, modified arm inserted in female, other arms surrounding female
Traveling	Paled brownish grey Greyish brown	Smooth	Arms forward (somewhat retracted), curled, and confluent
Flight	Olive grey brown or Oliver grey brown w/Black Spot	Smooth	Arms forward, confluent, puffy (somewhat retracted), hint of Upward V-curl

chromatophores contracted into small blotches with some dark spots slightly expanded in the center of each of the reddish brown blotches. Some of the dark spots were also expanded into blotches; these vaguely outlined a Chevron Bar across the middle of the dorsal surface. The arms and head had a mottling of all the above colors (Table 1). Raised papillae on the dorsal surface also occurred during this color pattern, with the ventral surface being lightly mottled. The raising of white spots into

papillae usually happened when there was a conspicuous external stimulus; it therefore seemed to indicate alarm (Table 1).

The normal posture with a Blotched pattern was assumed when the *Sepia* settled down only 5 to 15 cm off a bottom on which dark and light coral rubble formed a strongly contrasting background. When viewed from the side, the *Sepia* was usually obscured by the rubble around him. When viewed from above, his mottled back made him almost invisible. We noted that a diver could descend within 1 to 2 meters of a cuttlefish in this coloration and, as with the Dark coloration, not see it.

Alarm Postures and Colorings

A posture described by Packard and Sanders (1969, 1971) as the "flamboyant" in *Octopus vulgaris*, and by Moynihan (1975) as the "Upward V-curl" in *Sepioteuthis sepioidea*, was also observed in *S. latimanus*. This Upward V-curl (Fig. 3) was assumed frequently by adults and was also seen in unhatched and newly hatched individuals.

As with *Octopus vulgaris* and *S. sepioidea*, the Upward V-curl seemed to indicate alarm. This posture also appeared to be a warning to conspecifics as well as to predators (and to us). If a male *Sepia* or the observers moved toward a male too quickly or approached too close, the center arms were lifted from the rest of the arms in a slight bend or V-pattern. The position of these arms seemed to vary with the intensity of the threat. A low intensity posture consisted of slight lifting of the center arms with the other arms hanging in a downward, relaxed position. As the threat intensified, the arms were lifted higher and higher until the outer arms were nearly horizontal to the body and the center arms were raised to an angle (to the horizontal arms), of 75° to 85° with the ends hooked and the beak area somewhat exposed (Fig. 3). Sometimes a puffiness at the base of the arms, caused by the partial closing of the funnel beneath the arms, was also shown (Table 1). The *Sepia* appeared larger to the observer when the arms were extended and/or enlarged. This posture was sometimes accompanied by aggressive behavior.

The variety of arm movements was combined with several color arrangements which apparently also reflected the intensity of the stimulus. In most cases, the Upward V-curl posture was combined with the Dark coloration which indicated stimulation of low intensity. This was most often the posture initiated toward observers. In most instances, when predators or competing males were seen, the Dark pattern with the Upward V-curl was the first posture expressed, followed by a more complicated combination. On only three occasions was it the only posture shown when competing males or predators appeared.

The more complicated combination consisted of the Dark remaining basically the same as in the normal posture but with a Center Light or a Transverse Bar coloration. The Center Light pattern was characterized by the Dark having an expanded blotch or patch of yellow ochre to each side of the middle portion of the dorsal mantle. This patch was iridescent at times. The white spots on the mantle and arms were also intensified and slightly expanded. The dorsal surface appeared

Fig. 1. Arm posture of a young adult male, *Sepia latimanus*, in a normal Dark color.

Fig. 2. A female *Sepia latimanus* in normal coloration over most of the body, but with a trace of Center Bar to each side of the middle portion of the body. This female was cleaning her arm and tentacle pads upon completion of laying eggs as she blew from beneath the relaxed arms and rubbed the tentacle pads across the inner surface of the arms in a final cleaning ritual.

Fig. 3. A male *Sepia latimanus* in semi-Zebra with forward pointing and Upward V-curl of arms III and IV.

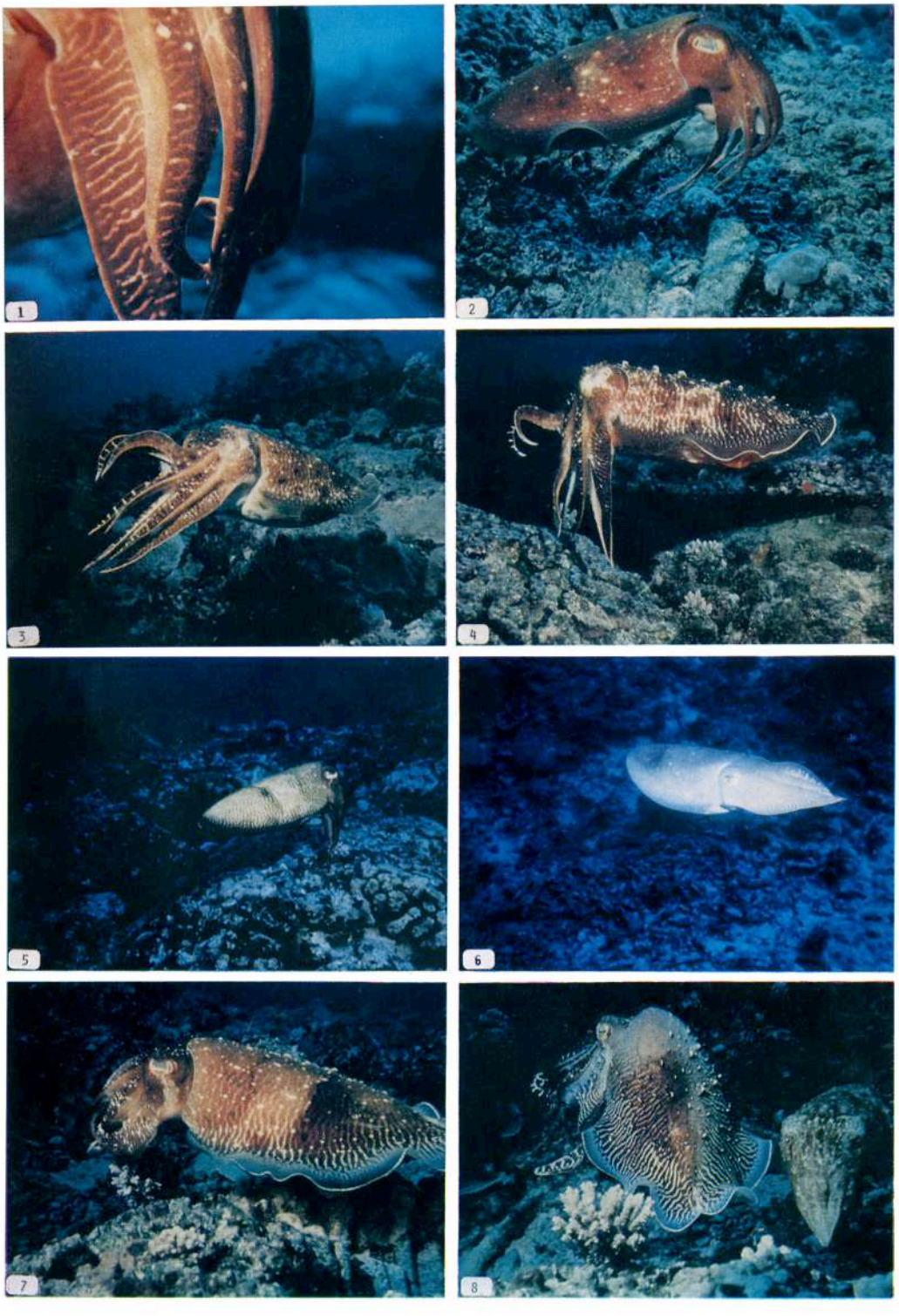
Fig. 4. An adult male *Sepia latimanus* with transverse lines, a trace of Blotching, and Center Light on the back. It was assuming a low intensity downward pointing arm posture. With the addition of the Upward V-curl and raised papillae on the dorsum, a higher level of stimulation was indicated.

Fig. 5. Male *Sepia latimanus* in a Yellow Light pattern displayed toward an approaching barracuda. The iridescent Yellow Light posture with the Upward V-curl (which is not shown) appeared to be stimulated by the approach of a potential predator.

Fig. 6. A male *Sepia latimanus* in retreat following encounter with the observers.

Fig. 7. An adult male *Sepia latimanus* in a Zebra pattern with additional false eye spots on either side toward the rear of the body and around the eyes and a lifting of papillae over the dorsum.

Fig. 8. The Zebra pattern of a male *Sepia latimanus*. This male to the left, was being challenged by another male for possession of the female by his side. Arms and webbing were stretched forward, the body was swollen, papillae were raised on the dorsum, and there was a hint of a black spot around the eyes. These patterns indicated hostility toward the challenger. The female was in a Blotched coloration with a hint of the papillae being raised on the white spots. These patterns usually indicated alarm.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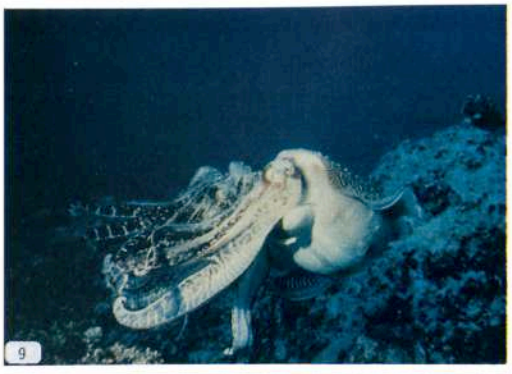
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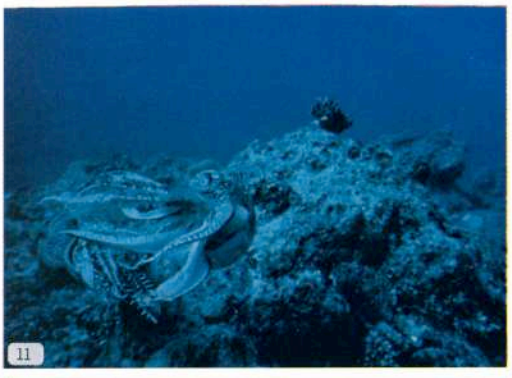
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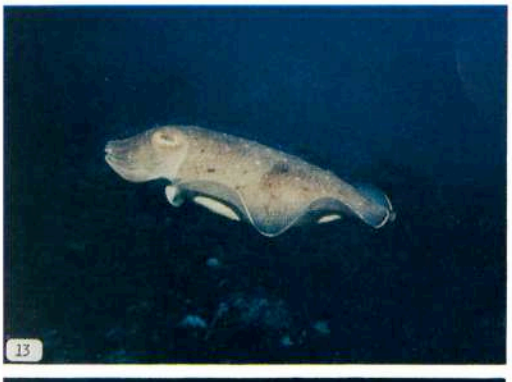
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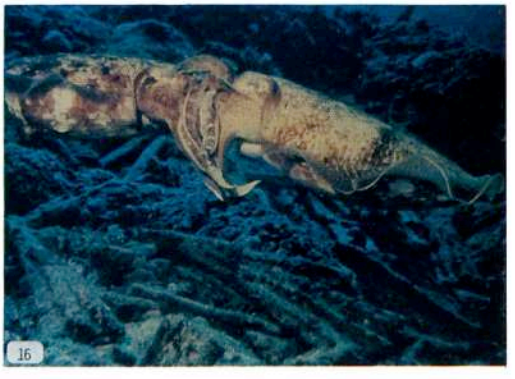
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Fig. 9. Two male *Sepia latimanus* in an aggressive Zebra pattern. As the female's display indicated that she was ready to mate, the males' interactions became more frequent. All transverse lines intensified, papillae were raised on the dorsum, arms and webbing were stretched, and the funnel was closed. This pattern was displayed by both males as the challenging male tried to pass the possessing male to gain possession of the female who was still placing eggs in the coral.

Fig. 10. A male *Sepia latimanus* in the Umbrella posture which was assumed as the challenging male became more persistent. As the funnel was closed, the body enlarged, became nearly circular; arms flaired upward and outward in a circle; the mouth, beak, and tentacle pads were exposed; all transverse lines were intensified. The female, to the right, was in a discouraging color pattern as she carried her egg to the coral.

Fig. 11. Two males in an extreme aggressive posture. When all else failed to stop the challenging male, the possessing male, from a side position, assumed the aggressive posture and colorings as he twisted his head and arms over the challenging male in an apparent attempt to bite the challenging male.

Fig. 12. The male in his courting posture and coloration. As the male approached the female, he twirled the tips of his arms in an attempt to rub her forehead. When rejected by the female, he blew at the coral where the female was placing her eggs. The female (lower) was in the process of changing from her Leathery texture, which was displayed when she was ready to mate, to her discouraging color pattern where the body was chalky white with a transverse line to the rear, with a false eye spot over each eye, and a row of confluent dots down the keeled edge of arm III. She was still carrying an egg in her arms.

Fig. 13. A male *Sepia latimanus* in an undisturbed forward swimming posture and coloration.

Fig. 14. A female *Sepia latimanus* in the Shriveled Trunk posture. This posture was assumed when passing an egg down to her arms. The male in the background was changing from an aggressive Zebra pattern used against an intruding male to a paled courting pattern.

Fig. 15. A female *Sepia latimanus* placing eggs in the coral. The Blotched color pattern with the white spots raised into lappets and with the horn-like protrusion above each eye, indicated a high intensity level of disturbance as the males' challenges intensify nearby.

Fig. 16. The mating of *Sepia latimanus*. The male (on the right) and female (on the left) assumed a variety of color patterns during the mating.

"bumpy" from a lifting of the white spots into papillae (Fig. 4). Whenever the papillae on the dorsal surface were raised, regardless of the color pattern being used, it accompanied an intensified threat. The fin band or stripe was usually greyed. The arms could assume any degree of the Upward V-curl depending upon the strength of the alarm (Table 1).

This combination was employed when a male was accompanying a female laying eggs with the observers in close proximity. When we tried to place ourselves between the male and female, the male changed to this Center Light pattern with Upward V-curl, circled around us, and got near the female. This pattern was observed during our first encounters with any particular male. As that individual became habituated to our presence, he would display the normal posture and allow us to move freely between the female and himself.

This habituation toward us was consistent among individuals that were identified by distinctive scars, injuries, or scratch marks. It was only after five to eight days of encounters that the individual male did not move in order to place himself next to the female when we intervened between the pair. When an unrecognized individual or group of *Sepia* occasionally reacted to us with the Center Light pattern, the reluctance to allow us to separate the pair was evident once again, disappearing after a few days. We interpreted this to mean that the individual or group was new to the area since we began observations. From periodic encounters with unhabituated groups, we concluded that more than one group of *Sepia* was involved in our observations.

The Blotched pattern with Upward V-curl was a variation of the Center Light pattern with Upward V-curl (Table 1). Unlike the normal posture, the Blotched pattern with Upward V-curl was performed higher in the water column, usually 0.6 to 2 meters off the bottom and in the open. This posture was elicited by the sudden appearance of a potential predator or observer. Although the Blotched pattern with the normal posture appeared cryptic, its association with the Upward V-curl posture suggested that it might indicate alarm. It was rarely used and then for only a few seconds.

The Transverse Bar and the Yellow Light patterns (described below) combined with the Upward V-curl were a transition from the Center Light and were the most extreme expression of the Upward V-curl. This transition was associated almost exclusively with the approach of a potential predator such as a large fish. When a potential predator first appeared, a male displayed an exaggerated Upward V-curl and a Center Light. After the *Sepia* held this posture and coloring for a few seconds, a broad Transverse Bar appeared in the middle dorsal area, often intensifying to an iridescent yellow (Fig. 5). This Yellow Light pattern over the entire dorsal surface was different from the Center Light pattern. The Transverse Bar was held for an instant, followed by a complete yellowing of the entire dorsal surface. The dorsal yellowing was initially of low intensity but rapidly changed to a complete iridescence that was reminiscent of a light organ display of deep water species (Table 1). On seven occasions, we saw either a large (1–1.5 m) unidentified fish or a large barracuda

swiming along the margin of the reef slope over deep water. At other times we could see nothing, but the *Sepia* appeared to be tracking something because it gradually turned from one direction to the other. After a few seconds it would return either to a Center Light with Upward V-curl, a Dark with Upward V-curl, or a Dark normal posture. Of the six times a diver approached from directly above or from deeper water to shallower water, the *Sepia* displayed these same color patterns in quick succession, holding each for only a few seconds. This transition from Transverse Bar to Yellow Light could also be reached from a Blotched coloration, normal posture (Table 1). As with the Dark, the Upward V-curl was the first indication of alarm. The white, ochre, and brown blotching with the exaggeration of papillae over the entire animal, followed by the intensifying of the blotches on each side of midmantle (Center Light) with the progression to the yellow Transverse Bar, and finally the Yellow Light, appeared to be a deterrent. Indeed, on one occasion, a barracuda was swimming rapidly toward a *Sepia* when the *Sepia* followed this sequence. The barracuda abruptly changed direction and left the area.

Another reaction to alarming stimuli was the production of two black spots toward the rear and sides of the mantle (Fig. 6) and occasionally the formation of black rings around the eyes. Young (1962) named this the "Dymantic display" in *Sepia*. This display of *Sepia latimanus* is probably homologous with the Dymantic display of *Octopus* (Wells 1962; Packard and Sanders 1969, 1971; Packard and Hochberg 1977), *Sepioteuthis* (Boycott 1965), and *Sepia officinalis* (Holmes 1940). In *Sepia latimanus* this display is additionally characterized by the body being a pale olive grey accompanied by pinpoint dark, or sometimes white, spots. The fin is also pale with the fin stripe grey and somewhat retracted. There is a puffiness or thickening of the arms at their bases as they are pointed forward with the dorsal arms lifted slightly and held together in horizontal "V." The transverse lines and bars are somewhat pale on all arms. However, because of a pale longitudinal streak on the inner surface of Arm IV and along the keeled edge of the other arms, the transverse lines and bars are still distinct (Table 1).

The Black Spot pattern was used by male or female *Sepia* whenever one of us approached a cuttlefish quickly from directly above. This pattern was followed by a paling of the entire body. As with the squid, *Sepioteuthis* sp., cuttlefish do not move to escape when approached in this manner. However, if approached from the same level and repeatedly charged, the cuttlefish used the Black Spot pattern as he quickly darted backward out of reach of the pursuer (Fig. 6). As the pursuit subsided, the attempt to escape subsided. This coloration was retained only as long as challenges were being initiated.

Aggression in Competition for Females

A Zebra pattern was assumed by two or more males during encounters in competition for a female. When a female approached the area, the male turned brownish grey, streamlined his body with the arms forward, confluent and curled to one side, and quickly converged on the female while traveling 1.5 to 2 m off the

bottom. He usually moved within 0.3 to 0.6 m of the female, swimming alongside her. The larger male was normally the first to reach the female, possibly because of his having the position along the reef-slope margin closest to the *Lobophyllia* colony to which she was heading. As the other males approached the pair, all males began an exaggerated Zebra pattern (Fig. 7). Arms were either lifted forward or spread simultaneously. The body coloring was bold black and white transverse lines across the body. The arms with the black and white transverse lines appeared bold as the arms were spread or stretched forward (Fig. 8). The keeled edges of the arms were white or red. These longitudinal lines made the arms appear longer than they were; the entire posture conveyed increased size. Around each eye was a false black eye spot. A black blotch was also noted occasionally along each side of the middle mantle and slightly to the rear (Fig. 7 and Table 1).

In the male interactions, the participants dashed toward each other a short distance, exhibiting this exaggerated Zebra pattern. The smaller male was typically the one to halt, reduce the transverse lines and back away; he sometimes paled his entire body, withdrew several feet, and returned to the Dark normal or Dark with Upward V-curl. This was a typical reaction of the smaller male, especially when additional males participated in the contests. Each male could be accompanied by a female and still participate in interactions (Fig. 8). In some instances, a male and female were together at the egg-laying site when another male, or male and female, approached the area. The males confronted each other whenever close. Once, when two males with females and a small male without a female were facing off, the pursuit took them several meters away from the females. After several encounters, the males with females returned to them but in the process they switched mates.

As the female began to exhibit the precopulatory patterns, interactions between males became more frequent and intense (Fig. 9). The males repeatedly dashed toward each other. If neither retreated, the males then simultaneously flaired their arms upward and outward with all webbing stretched between the arms (Fig. 10 and Table 1). If this failed to result in the submission of one combatant, the arms were extended to an Umbrella pattern and the mouth was exposed for a few seconds. In six out of nine encounters, this display finally ended the contest. If unable to keep an opponent at bay, the larger male resorted to an exaggerated Umbrella as he dashed toward the intruder and, from a side position, twisted his arms over the head of the intruder as if to bite him (Fig. 11 and Table 1). This invariably resulted in the intruding male paling his body and retreating several meters, presenting the rear portion of his body to the attacker, and switching to the Dark or Blotched pattern in either a normal or Upward V-curl posture.

Courtship and Mating

The male precopulatory pattern consisted of a complete retraction of the white and black spots, lines, and blotches until the body and arms were overall light grey. The arms had only a hint of the white transverse lines. The body was streamlined, the arms were held together in a semicone shape, slightly lifted, with the tips of the arms

curled (Fig. 12 and Table 1). As a male approached the female, he attempted to rub these curled arm tips across the female's forehead or cheek. (This arm position was also used by a young male that consistently came to us, apparently to be petted; this could possibly be a form of "Greeting"). If she did not respond to him, he then moved between the female and the coral head where she was placing the eggs, which must have been fertilized during a previous mating. As he neared the coral, the male puffed or blew at the coral and then shot backward a meter or so. This pattern continued until the female responded.

This grey precopulatory pattern was never assumed by the male unless the female also exhibited precopulatory behavior. When other males tried to intervene, the male displayed the precopulatory pattern and arm position toward the female with one half of his body while the other half of his body displayed an aggressive Zebra pattern toward the intruder. This ability to display patterns simultaneously to more than one receiver is characteristic of several species of cephalopods (Young 1962a; Moynihan 1975).

As the female backed away from the coral after placing an egg, the male approached and rubbed her head with the tips of his arms. If she accepted him, the female then opened her arms, forming a bowl with both the male and female placing their center arms on the others' head. The male then inserted his modified copulatory arm into her mantle cavity while she wrapped her arms around those of the male. As soon as mating began, both sexes again changed color. The male displayed either a Blotched, a Blotched that was predominately white, a combination of Center Light and Dark, or a semi-Zebra pattern (Table 1), the last of which indicated that another male was in close proximity. During mating, which lasted 0.5–1.5 min., the pair either remained stationary a few centimeters off the bottom or moved slowly about one meter off the bottom.

Generally, as the pair separated, the male let his arms hang in a downward stretched position and blew through them several times as if to clean them. The female also went through a "cleaning ritual," but her arms were lifted forward and held open or apart while blowing. At times, the upper arms folded upward over her head, exposing the ventral surfaces of all arms. The dilated mouth appeared to contract as the female blew across the exposed area. After mating, both sexes typically assumed a swimming pattern, i.e., greyish brown with most of the spots obscured and with the arms forward and slightly cupped to one side. They usually left the area swimming toward deeper water side by side about two meters off the bottom.

In two encounters, mating took place just as the females arrived in the observation area. In those instances the females deposited their eggs after copulation. On another occasion the pair stayed in the vicinity after copulation and the female had not begun to oviposit after eleven minutes, after which we had to surface. In eight of the thirteen observations of mating, the mated pair left the area. On two of these eight occasions, the mated pair returned after 15–20 minutes. The females went directly to a coral head and began placing eggs. In instances when mating took place on our first dive, females were found to be depositing eggs 2–2.5 hrs later. When we

returned on our second dive the male in a Dark normal posture was near the female. The other two matings took place just as we had to ascend. Consequently we could not determine the actions following mating.

Interpreting Colors

Males seen while traveling from one point to another exhibited pale greyish brown (Fig. 13). When pursued or retreating from a threat, they assumed another pale coloring—olive grey brown with or without black spots (Fig. 6). When approached by a female, males became pale brownish grey. The colors might seem the same to the casual observer, but with experience we were able to predict the next event by the male's coloring and posture. This ability to interpret the colors of the males enabled us to locate other males, approaching females, and predators.

Postures, Movements, and Colorings of Females

Female *Sepia latimanus* always approached the site from beyond the reef-slope area, traveling alone or in the company of a male, but never accompanied by another female. Their color and posture were the same as the males when traveling from one point to another. Unaccompanied females were always quickly intercepted by waiting males, but they never altered their forward movement as the male approached and joined them. Like the males, when traveling 1.5 to 2 meters off the bottom, the body was streamlined, colors subdued, arms confluent and forward with the ends folded to one side (Table 2). With only a few exceptions, females entering the area moved directly to a coral mound, hovered 0.3 to 0.7 meters off the bottom about a meter away from it, and then began laying eggs.

Transfer of Eggs from Mantle to Arms

When passing an egg down to her arms, the female *Sepia latimanus* exhibits the Shriveled Trunk posture (Fig. 14). This was characterized by Arms I, II, and III being tucked or drawn down tightly about the head, with a few centimeters of the distal portion of the arms confluent and pallid. The broad surfaces of the fourth arms were held horizontally with the lower portion curled upward and the funnel tucked between these arms. The mantle coloring was normally the same as the Dark coloring of the male, but deeper red in tone (Table 2). The area across the forehead was darker and at times appeared to flash an even darker brown, contrasted with a paling of the middle portion of the arms, when the rate of egg transfer decreased. Transfer of an egg while in Shriveled Trunk took an average of 32–35 seconds, but at the end of the sequence it took as long as 2.5 minutes to produce an egg.

When an egg appeared in the upper portion of the arms, the female moved toward the coral colony where the eggs were being placed. Moving 0.3 meters off the bottom, Arms I, II, and III were brought forward in a cone shape, with the fourth arm held horizontally and the funnel now free to be used for forward movement. The arms moved up and down against each other as the egg was pushed down until it was

Table 2. Body postures and chromatic patterns of female *Sepia latimanus* in relation to behavior.

FEMALE			
BEHAVIOR	COLOR PATTERN	SKIN TEXTURE	ARM POSTURE
Normal (not laying eggs)	Dark or Blotched	Smooth	Downward hanging, relaxed
Normal (acquiring eggs)	Dark	Smooth	Shriveled Trunk
Alarm (acquiring eggs)	Blotched w/Center Bar w/or w/out Dark posterior	Smooth	Shriveled Trunk
	Center Light, Yellow Light	Smooth	Shriveled Trunk or carrying egg posture
Nearing Mating	Dark w/paling of mid-arms. Leathery, pinkish paled brown	Smooth Leathery	Shriveled Trunk
Traveling to Coral	Dark, Leathery pinkish paled brown	Smooth	Cone shape
Near Coral (placing eggs)			
Normal	Blotched	Smooth	Cone shape
Low Level Alarm	Blotched	Papillae lifted	Cone shape
High Level Alarm (Discouraging)	Center Bar White w/or w/out posterior blotch and arm spots or stripe	Smooth	Cone shape
Courting	All over light grey	Smooth	Arms forward, confluent, semicone shape, tips curled
Mating	Blotched, Paled Blotched, Center Light Dark or Normal Dark	Smooth or hint of papillae	Center arms on males forehead other arms surrounding male's head

held near the end of arms I and II, with arms III and IV holding it from beneath.

Color patterns varied during movements toward the coral to deposit eggs. In the early stages of egg laying, when transfer of eggs was frequent, the female retained the normal Dark coloration as she moved forward and until she approached the coral mound. As she neared the coral, a few centimeters off the bottom, she changed to a Blotched pattern, with or without papillae over the mantle and head. The white spots were elevated various degrees into papillae whenever the female appeared to be disturbed by either males or the observers (Fig. 15). As the female displayed the paling of the arms more frequently, while transferring the egg in the Shriveled Trunk

posture, the mantle changed to a Leathery texture with most of the spots retracted and with the predominant color being pinkish pale brown (Table 2). The males now became more active and challenged each other more frequently or approached the female in a courting posture and pattern.

At various times, a female exhibited an additional combination of color patterns while passing the egg down to her arms. This was either a Blotched, barred pattern (Fig. 14), or the front portion of the mantle was Blotched, the rear portion Dark, with a center band of pale brown or light ochre. These color combinations were displayed at the beginning of our observation of an individual female. When one particular female (recognizable because the last few centimeters of arm IV were missing) first appeared in the observation area, she exhibited a Blotched, barred pattern while in Shriveled Trunk. After a few encounters with the observers, she discontinued this color combination and exhibited only the Dark pattern with Shriveled Trunk while acquiring eggs from the mantle cavity. This behavior also allowed us to identify individual females from separate groups.

As the female continued to deposit eggs, she moved back from the coral after each egg placement and settled into Shriveled Trunk (Fig. 14). After each deposition, the pallid area of the arms seemed to broaden progressively across the arms until the dorsal surface was almost totally pale at the end of the egg laying sequence. After this paling appeared on the female, the male usually moved to within 0.3 or 0.6 meters of the female.

Discouraging the Male

When a male approached a female with a courting display (Fig. 12), while she was transferring or depositing eggs, the female appeared to discourage his advances by employing a near-white Center Bar. Females displaying Center Bar never responded favorably to males. If a male became more persistent, the female exaggerated papillae over the entire mantle and forehead and extended horn-like papillae over each eye (Fig. 15). As responses to the male intensified, the chromatophores retracted further until the body became chalky white. Normally, a dark bar or line traversed the mantle to each side of the middle portion, outlining a Center Bar (Table 2). Above each eye, and on the pointed posterior, a dark red brown blotch appeared. If the male continued to display his courting actions and interfered with the female's placing of the egg, she flashed a row of dark red dots along the keeled edge of arm II. These dots became confluent, forming a dark longitudinal stripe. When this occurred, the male quickly darted back away from the coral and from the female, while still exhibiting his precopulatory coloring.

Egg Deposition

To deposit an egg, a female approached the coral, hovered a few centimeters off it, and then inserted her arms a few centimeters into the head (Fig. 17a). At times, she turned sideways to the coral and cocked her head as if to see into the coral. This was the only time any portion of the iris was visible. Using her suckers, she alternately

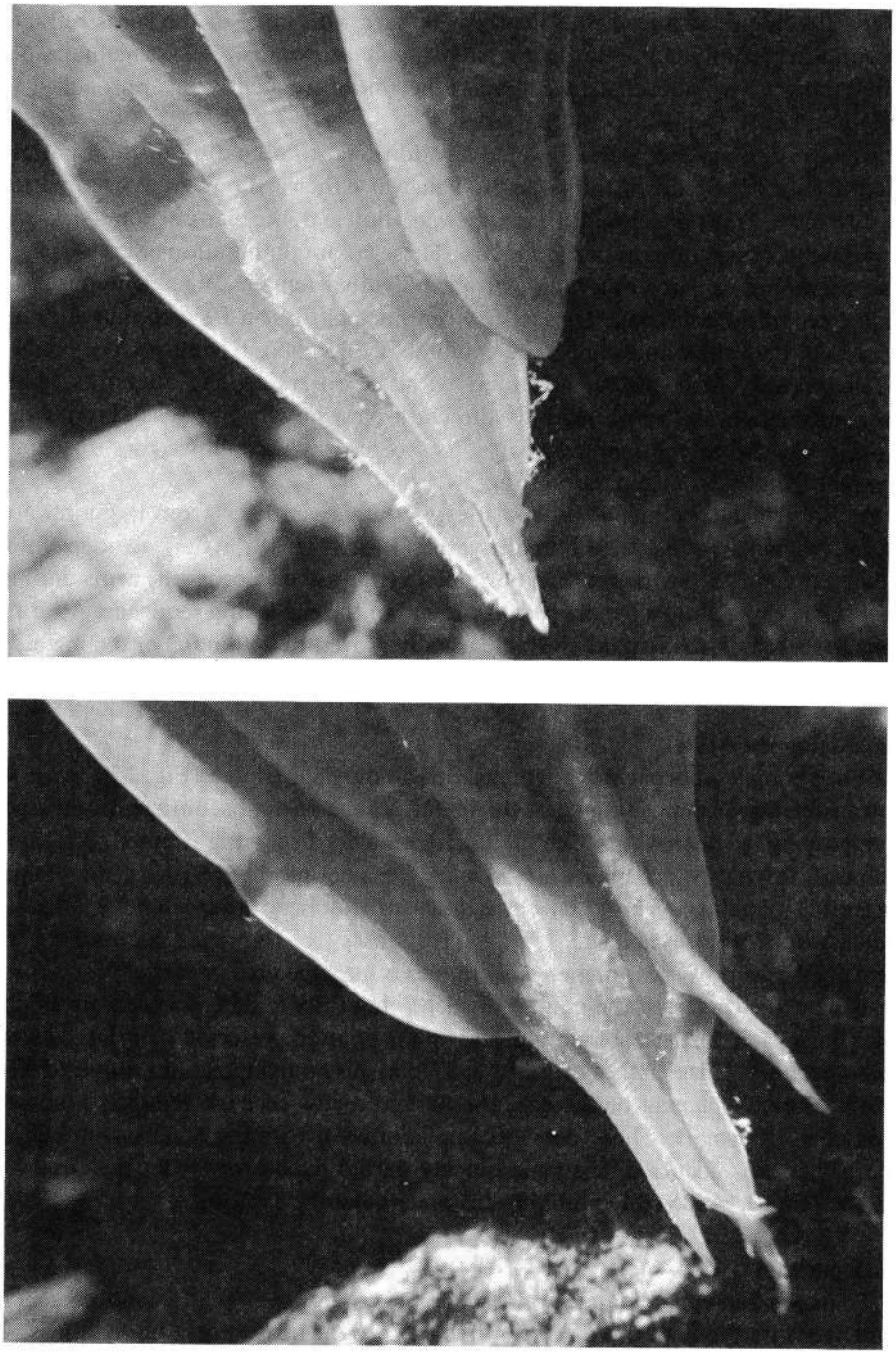

Fig. 17. (a) Arm posture of a female *Sepia latimanus* while holding the egg in her arms just prior to placing the egg into the *Lobophyllia* colony. (b) The female tested the hole size between the corallites; she puffed as latex-like substance flowed between her arms and as the egg was placed deep inside the coral head.

moved the egg down her arms and tested the size of the hole between the dead corallites. After two to four tests, she puffed under her arms, inserted her arms deeply inside the coral head, puffed again, and withdrew her arms with the egg which was still about 5 centimeters from the ends of the arms. After withdrawing, a creamy latex-like substance was seen along the tips and edges of the arms (Fig. 17a). She then brought all arms together into an exaggerated cone shape and placed all arms and the egg into the coral until her head was nearly touching the coral. While making one or two additional puffs, the arms were moved up and down as she pushed the egg down and left it (Fig. 17b). Unlike *S. officinalis*, the eggs were not individually colored with a squirt of ink (Burton and Burton 1969).

On all other occasions, upon removing her arms from the coral the female *S. latimanus* relaxed her arms, puffed three or four times while stationary and then backed off to begin the sequence again. Puffing apparently rid the arms of the excess latex-like substance. On one occasion the female blew six or seven times and finally dislodged a large wad of the latex-like substance. After that, she backed off and went into Shriveled Trunk.

The length of the egg-laying bouts varied considerably. The time for laying a single egg ranged from 3′4″ to 9′55″. In one thirty-five minute observation period, five eggs were deposited into the coral with a sixth egg in place in her arms when we were forced to leave.

Mating

When the female began another sequence of events in the early stages of egg laying, she exhibited the normal Dark coloration. When near mating, she displayed Leathery texture, then changed to Shriveled Trunk while maintaining Leathery texture on the mantle and additionally paling the center of the arms. When she was ready to mate, she removed her arms from the coral, paled her entire body to pinkish grey, cupped her arms forward, and twirled the tips of her arms as the male (Table 2). The male responded immediately by rubbing her head with his arm tips. She then spread all arms in a bowl shape with mouth open and swam toward the approaching male.

Upon mating (Fig. 16) the female either changed to greyed Dark with white spots raised, ventral surface mottled, and lappets on the ventral surface extended, or to Blotched with center bar paled yellow, or to Blotched that was predominately white (Table 2). The duration of each copulation (in the thirteen matings observed) was between thirty and seventy-five seconds. Most of the matings occurred in the area adjacent to the egg-laying site. On two occasions, however, they took place just as the female approached the area.

Additional Postures

On only three occasions was the female seen in a yellow light pattern, i.e., alert pattern. Once turned on, it remained on only while the threat was present. However, only after all her eggs had been laid did the female exhibit normal Dark posture or the

Upward V-curl near the coral mounds.

Sites for Egg Deposition

The eggs of *Sepia latimanus* were found in our study area only between the corallites of dead *Lobophyllia* colonies. The widths of the spaces between the corallites were about 1 cm in diameter at the coral-head surface with the usual depths of the spaces between the corallites being 15 to 20 cm. The eggs were 2 cm in diameter. In order to place her eggs in the coral interstices, the female must have temporarily compressed and elongated each egg between her arms as she placed it through the opening. The spacing at the surface appeared to be the most important criterion for selecting of sites for depositing. No eggs were found in coral heads in which the corallites were closely knit, or covered with various marine organisms.

The *S. latimanus* at our site placed their eggs in the larger coral heads, ranging from 210 cm to 374 cm in circumference. This allowed several eggs to be placed down between the stalks. The number of eggs found between the coral stalks varied according to the depths of the space because each egg was individually attached to the sides of the coral stalks by an elongated stem until the eggs reached 3.5 cm to 9 cm from the surface (Fig. 18). In the smaller coral heads, only a limited number of eggs

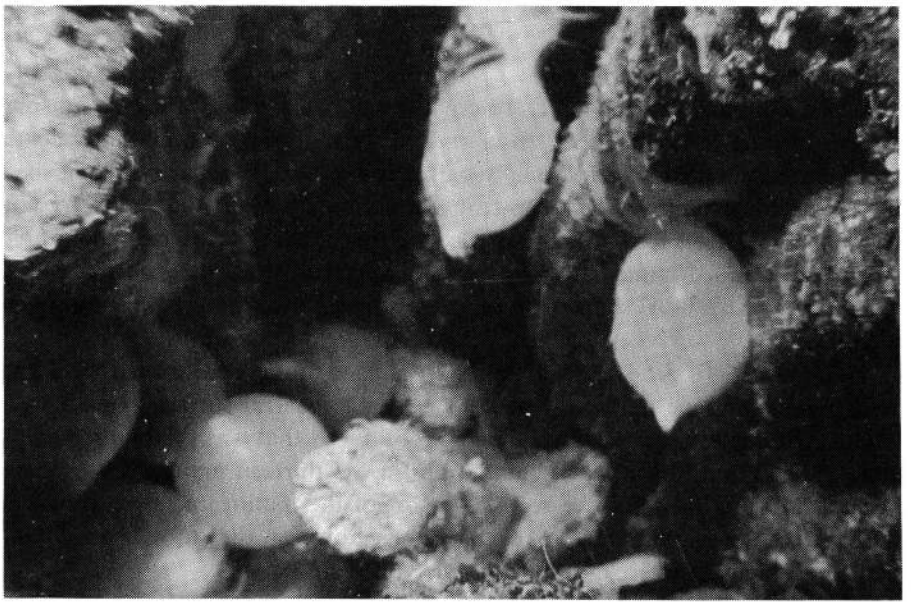

Fig. 18. Eggs of *Sepia latimanus* in a dead *Lobophyllia* colony at 20 meters depth. The eggs were placed singularly and attached to the coral. The egg in the upper portion of the picture was a newly placed egg as it was still opaque. The embryo was visible in the egg to the right. A loose portion of the coral was removed to take the picture and then replaced. Eggs averaged 2 cm in diameters.

could be deposited deep enough inside the coral to be inaccessible to predators.

Butterfly fish, *Chaetodon ulietensis*, were present throughout the observation period and readily ate any eggs accessible to them. One pair of *C. ulietensis* remained within one to two meters of a female *Sepia* as she deposited eggs for several days in early March 1976. During the first two days, the female *Sepia* tried to find a proper crevice in *Lobophyllia* mounds at a depth of 21 m, but the crevices in both large and small coral mounds were already full of *Sepia* eggs. After extensive searching during each observation period, this individual finally deposited an egg in a place where the corallites were broken away; the egg was therefore partly exposed. As soon as the female left, the two *C. ulietensis* darted to the egg and pulled it apart, eating all the pieces that came loose.

Early in our observations, the females consistently used the coral heads found between 15 and 20 meters, even when the coral heads appeared unable to contain more eggs. This use of the original corals continued even though nearby coral colonies were available and the females found it difficult to find appropriate holes to place their eggs.

The use of new coral colonies for depositing eggs coincided with the arrival of new individuals, both male and female. After an inking that took place near the 15 and 20 m coral heads, no cuttlefish were seen for four days. As far as we could tell, individuals from the first group were never observed again, with the exception of one young male. The second group of *Sepia* used the coral heads between 20 and 23 meters, beginning with the two largest mounds. After the mounds at this depth were filled with eggs, no *Sepia* were found in the area for two days until a third group was discovered; they were using the coral heads at 30 meters and possibly the one coral head at 34 meters. Later, with the hatching of the first group of eggs, which emptied the coral at the 15 to 20 meter level, females began refilling these coral heads just as we were forced to abandon observations because of hazardous seas. Consequently, we were unable to determine whether the eggs being placed at the first site we observed were from the third group of individuals or by a fourth group. Although the behavior of those laying at 30 m appeared consistent with that observed previously, the behavior of the *Sepia* at the 34 meter level was somewhat different from that noted on prior observations. This group was only observed once, from a distance, and consisted of three *Sepia*. An example of this behavior follows:

One female, in a blotched Center Bar pattern, was in the process of depositing eggs with a male beside her when this new group was first approached. A third *Sepia* was a meter or so away, confined by a cliff wall behind it. As the third *Sepia* tried to get past the pair, the male exhibited a mild Zebra pattern and darted toward the individual that was trying to pass. In past observations, a challenging male had to be moving closer to a female before the possessing male challenged. The third *Sepia* was small and exhibited flight coloring, i.e., greyish brown with subdued spots, arms together tightly and curled on the ends. It had an additional coloring not noted before. This consisted of a black spot on the I or II arm. This black spot was exhibited each time it tried to pass the male in a direction that would take the *Sepia* away from the

female. Each time the third *Sepia* tried to pass, the male displayed a semi-Zebra posture in that the arms were extended but not exaggerated or swollen. The transverse lines were bold but not predominant as in the other instances. Just as we started our ascent, the third *Sepia* got past the pair and went to another coral head in slightly shallower water. As it approached the coral head, it changed to a pale yellow and inserted its arms in the coral as if to deposit an egg. As we watched, it probed several holes in the coral; we realized its behavior was as previously observed in females. This was the only instance of (1) two females being with a single male, (2) a male exhibiting a Zebra pattern toward a female, (3) a large black spot being noted on the arm of *Sepia*, (4) a female exhibiting a center bar while depositing eggs, and (5) eggs being laid below the 30 meter level.

Behavior Patterns of Young

On February 23, an egg was collected when a male in retreat from an attacking male bumped into a female, causing her to drop the egg. The egg was kept in an aquarium with two airstones for circulation. Movement of the embryo could be observed by day 15. The mantle and head were visible on day 18. By day 20, the pinkish white cuttlebone, eyes, funnel and branchial heart were all visible. The *Sepia*

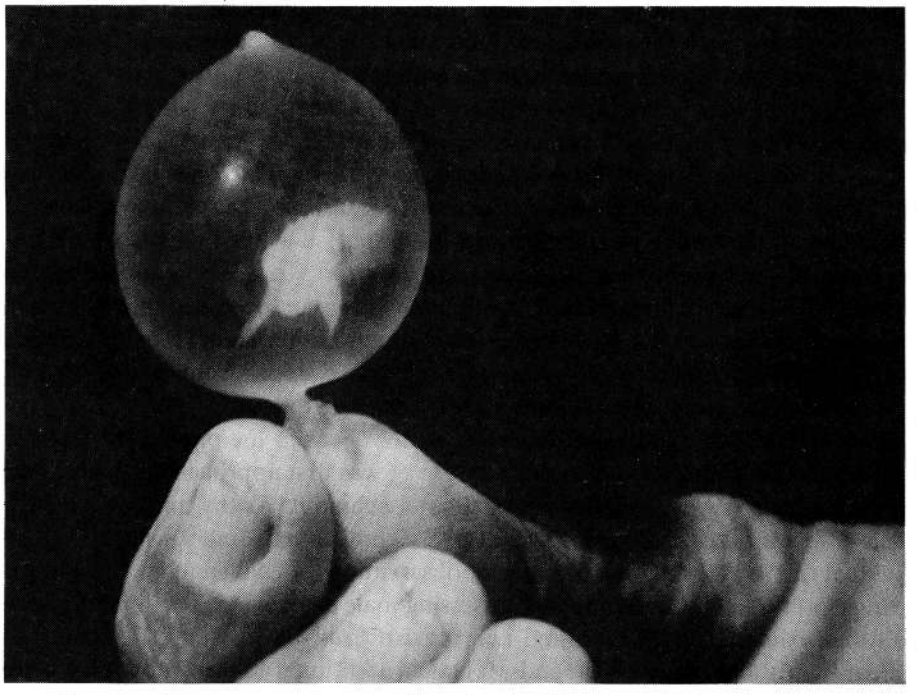

Fig. 19. Alarm pattern and posture of an unhatched *Sepia latimanus*. Egg diameter was approximately 2 cm with embryo 13–14 mm in length.

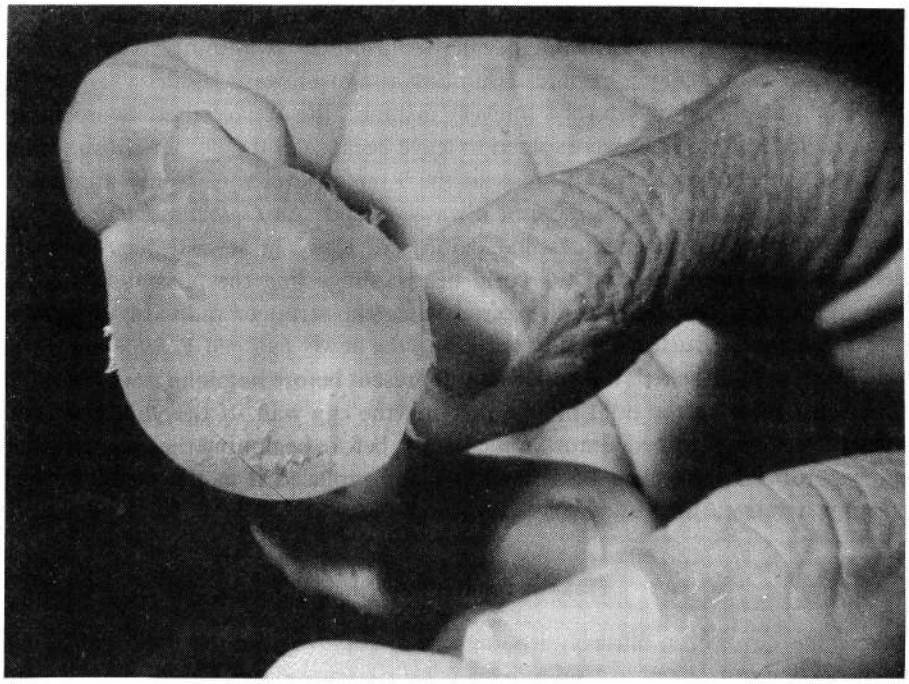

Fig. 20. *Sepia latimanus* breaking out of its egg. Egg yolk is still attached, although the yolk was usually dropped just prior to hatching. The embryo was approximately 13–14 mm and the egg was approximately 2 cm in diameter.

was propelling itself inside the egg with its funnel on day 29. By day 33, it was displaying color changes.

When the unhatched eggs were handled in the field, the unhatched *Sepia* assumed a variety of postures, including a semi-Upward V-curl and lifting all arms forward in an exaggerated cone shape. The *Sepia* in the egg employed color patterns when stimulated, but was pallid when at rest (Fig. 19).

Developing *S. latimanus* spent about 38 to 40 days in the egg case. On several occasions, we located eggs that were ready to hatch. As the egg was being held by its stem, the embryonic *Sepia* began swimming backwards with arms stretched forward, butting the inner surface of the egg until a thinning bubble formed. Then the pointed anterior end of the cuttlebone seemed to protrude outward as the *Sepia* swam backward and broke through the egg wall (Fig. 20). Upon emerging, the *Sepia* immediately took on a pinkish flesh coloring. The first specimen that was observed while hatching measured 13–14 mm with an estimated arm length of 2 mm. Respiration on the surface was 35 inhalations in 5 seconds. When an observer's finger was placed near the surface of the water in which the cuttlefish was placed, the cuttlefish turned white with dark dots on the dorsal surface. When the young *Sepia* was transferred to other container for transportation, it became bright red. One

specimen inked heavily when placed in a bag for removal from the ocean.

Upon emerging most *Sepia* began to ascend, swimming backward, at approximately 18 meters per minute, exhibiting a semi-Upward V-curl whenever our camera lens was placed too closely. In every instance, the *Sepia* halted its ascent at 9 meters and hovered until we were forced to leave because of time or air consumption. The longest we were ever able to hover at the 9 meter level was twenty minutes.

The newly hatched *Sepia* did not always ascend. As *Octopus dofleini martini* (Gabe, 1975), they sometimes descended into crevices. On several occasions, tiny cuttlebones were noted around the coral heads, suggesting the possibility that the weaker individuals descended and expired while the stronger individual ascended. Unlike *S. officinalis* (Burton and Burton, 1969), the newly hatched *S. latimanus* rarely emerged with yolk attached. If a yolk was still present before hatching it was normally detached just prior to the final plunge through the egg wall. If the yolk was intact upon exiting, it was dropped almost immediately, before beginning the ascent. Several times, we stopped the ascent of a hatchling and replaced it in the coral. In every instance, if it started the young *Sepia* reascended.

Habitat for Reproduction

Sepia has never been officially recorded from Guam before this study (Gilbert L. Voss, pers. comm.). They are seldom seen by divers around Guam and we only observed them at our study site in May 1973, February to May 1976, February to March 1977, February to March 1978, end of January to the end of June 1979, and February 1980. We only observed the reproductive behavior of *S. latimanus* i.e., courtship, mating, and egg deposition. We suspect that most of their other activity, such as foraging for food, is carried out in waters too deep for scuba.

The site of *S. latimanus* reproductive activity on Guam was characterized by the prevalence of large dead colonies of *Lobophyllia* which were apparently selected for egg deposition because of the depth and width of spaces between the corallites.

A natural experiment demonstrated the importance of crevices for suitability of habitat. One of us (HTM) dived frequently at Tarague Beach on northern Guam each year from 1970 to 1980. *Lobophyllia* was not prevalent there and *Sepia* was never seen, except from May to July 1977. At that time, a palm tree lay on the bottom at a depth of 14 m. The *Sepia* were associated with the mass of palm roots where a cluster of eggs was deposited. The spaces among the palm roots resembled the spaces between *Lobophyllia* corallites. The *Sepia* have not been seen there since the palm washed away.

While dead coral colonies of *Lobophyllia* are probably primary in selection of the place for reproduction, the various pinnacles and mounds of limestone play an important role in the location of the males. As each female approached the area from deeper waters, the male quickly left his vantage point, approached the female, and joined her as she traveled to shallower water. When more than one male was present, the larger and usually more dominant male had the best waiting spot for sighting the

female and making contact. Each additional male, in descending order of size and dominance, was progressively farther from the optimum location for making contact with the female because she consistently arrived in the same general location.

Discussion

A group of male *Sepia latimanus* returns on consecutive years to a specific area near dead *Lobophyllia* coral colonies to compete for females. Since the area is consistently used for courtship, it might be considered a lek, except that the primary reason for selection of the area by females was for egg deposition. The true lek is defined as removed from nesting areas (Wilson, 1975). The females appear to be willing to mate with whichever male is available when she is ready. Mate selection appears to be based on competition between males rather than female choice.

Octopods are generally solitary and squid are generally gregarious. *Sepia latimanus* differs from both in that males aggregate in areas only during the reproductive season to compete for females. Despite these differences in social patterns and morphology between octopods, squid, and cuttlefishes, some of the postures of *Sepia latimanus* (e.g., the Upward V-curl or "flamboyant" posture) are similar to those by the same name in *Octopus vulgaris* (Packard and Sanders 1969, 1971) and *Sepioteuthis sepioidea* (Moynihan 1975) and some of the color patterns of *Sepia latimanus* (e.g., the "Dymantic" display) are similar to those in *Octopus vulgaris* (Wells 1962; Packard and Sanders 1969, 1971; Packard and Hochberg 1977) and *Sepiotheuthis sepioidea* (Boycott 1965). Some parts of cephalopod communicative behavioral patterns may be more conservative than their patterns of social structure or morphology.

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