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ROSSIA
SEPIOLID
CEPHALOPOD
BURYING

ABSTRACT. – Although sepiolid squids commonly bury in the sand during daylight hours, little is known of their burying behavior. The burying activity of *Rossia pacifica* was examined on substrates of different grain sizes to determine burial behavior, funnel position and behavior under threat while buried. Squid settled more quickly onto sand than larger-grained gravel and did not even settle to a pre-burying posture on cryolite. They often refused to try to bury on gravel and had a much shorter latency to bury on smallest-grained subtidal sand than on larger-grained construction sand. They buried by blowing sand from underneath with jets of water through the funnel, then throwing sand over their dorsal surface with the second pair of arms. Under threat while buried, they emitted water and ink blobs, then emerged from the substrate, inked, and jetted away. A possible angling behavior was observed while the squid were partially buried. These observations emphasize the variability within the relatively fixed sequence of burying, as well as the variable sequences used across closely related species.

ROSSIA
SÉPIOLIDÉ
CÉPHALOPODE
ENFOUISSEMENT

RÉSUMÉ. – Bien que les Sépiolides s'enfouissent couramment dans le sable pendant la journée, on connaît peu de chose à propos de leur comportement fouisseur. Le fouissement a été étudié chez *Rossia pacifica*, sur substrats de granulométries différentes pour mieux cerner ce comportement. La position du siphon, et le comportement sous une menace apparente ont été observés. Les Sépioles se posent plus rapidement sur le sable que sur les graviers, et ne s'enfouissent pas dans la cryolite. Souvent, elles n'essayent même pas de s'enfouir dans les graviers et ont une latence nettement plus courte pour s'enfouir dans le sable de faible granulométrie, en comparaison avec le sable plus grossier. Elles soufflent le sable sous-jacent par des jets d'eau provenant du siphon et rejettent ainsi le sable sur leur surface dorsale avec la seconde paire de bras. Sous une menace apparente, elles émettent de l'eau et des gouttes d'encre alors qu'elles s'enfouissent, puis émergent du substrat, envoient un jet d'encre, et un comportement très curieux ("angling") a été observé chez des individus partiellement enfouis. Ces observations soulignent une variabilité au cours de la séquence d'enfouissement relativement fixe, ainsi que des séquences variables chez les espèces étroitement liées.

INTRODUCTION

The habit of burying themselves in sand or mud (Boletzky & Boletzky 1970) has made sepiid and sepiolid cephalopods interesting for comparative investigation of burying techniques (Boletzky & Boletzky 1970, Mather 1986). This is a common behavior across phyla, as fish such as flatfish, sandfish, and sand lances are well known for burying in the substrate (Eschmeyer *et al*. 1983) which allows them to hide from predators or potential prey. Crabs and shrimp also may bury themselves, especially when they molt and their soft exoskeletons make them vulnerable to predation (Jensen 1995). Among the cephalopods, octopuses also bury themselves (Norman 2000).

Sepiolids also likely bury in the substrate for concealment (Boletzky 1987), and Boletzky & Boletzky (1970) and Mather (1986) have reported the complex sequence of actions by which some sepiolids bury themselves. This process was substantially the same in the six Mediterranean species of sepiolids studied, as *Sepiola* and *Sepietta* create a depression in the sand by blowing jets of water with their funnel, first backward then forward and so on (Boletzky & Boletzky 1970). The process is finished as the second pair of arms extend forward or laterally together at the same time along the surface of the sand. With the arm tips pointed inward toward each other, they then sweep a small amount of sand over the head and body until the squid is completely covered with sand. *Sepia officinalis* Linnaeus, 1758 blows sand but does not use the arms and does not dig at all in non-preferred coarse sediments (Mather 1986). Mather (1986) called this process relatively fixed, with aspects of both stereotypy and variable aspects of a “modal action pattern” (*sensu* Barlow 1977).

Being buried in sediment obviously produces challenges to vision and respiration. Boletzky & Boletzky (1970) cite two interesting aspects of squid behavior during burial. First, the eyeballs are rotated vertically so that the pupils face upwards. Second, respiration is accomplished not by mantle expansion and contraction as is normal in cephalopods (Morton 1967), but by the use of the collar as a “skirt” attached at the base of the funnel which is pulled backward for exhalation through the funnel and pushed forward for inhalation through lateral slits when the collar gives way. They did not report the position of the funnel during this process.

Although it is a common bottom dweller in the northeastern Pacific, little has been studied about the biology, ecology, or natural history of *Rossia pacifica* Berry, 1911 (Hochberg 1998). Brocco (1971) gave general descriptions of its feeding behavior, reproductive behavior and predators. Anderson (1991) described the behavior of this species in a public aquarium setting and Post (1994) listed the color patterns and behavior of *R. pacifica* in the face of potential predators.

This investigation and a companion study on the burying behavior of *Euprymna scolopes* Berry, 1913 (Anderson *et al*. 2002) were inspired by a need for cross-group comparisons to build on the initial work of Boletzky & Boletzky (1970) and Mather (1986). Does *R. pacifica* discriminate between different substrate types? What sequence of behaviors does *R. pacifica* use when it digs and how does the substrate grain size affect this? Does it have a substrate grain size preference like *Sepia* (Mather 1986) and how does it react to predation threats while buried? These questions are partially answered by the present study.

METHODS

Rossia pacifica (mean mantle length ML 28 mm) were collected while scuba diving at night, by placing a Ziploc^R bag over them while they were resting on the substrate (per Anderson 1987). They were then transferred to the holding facilities of the Seattle Aquarium. Substrate of origin (subtidal sand, mean grain size 0.468 mm, N = 25, S.D. = 0.41) was collected and served as one type of substrate tested. Other substrates provided a variety of other grain sizes and were construction sand of mean grain size 0.56 mm (N = 25, S.D. = 0.26), cryolite sand (mean grain size 2.2 mm, N = 25, S.D. = 0.59), and quartz aquarium gravel of mean grain size of 5.2 mm (N = 25. S.D. = 1.50). Cryolite is nearly transparent in water (Hurlbut 1959) and should have aided attempts to observe respiration while the squid were buried. Squid were also released individually into a tank with no substrate.

Each substrate was spread in a 40 l aquarium to a depth of 2.5 cm and rinsed with running sea water until the water became clear. During testing of the squid, sea water was constantly supplied at approximately 1 l per minute. Inking, time to settle, refusal to bury, latency to bury, and duration of burying of 10 *R. pacifica* were recorded for each substrate. Refusal to bury (*sensu* Mather 1986) was arbitrarily set at 10 minutes, based on preliminary studies, although squid were observed longer. Responses to a “threat”, a quick hand movement toward a buried squid not contacting the tank, were noted. Persistent threats were repeated hand movements after each squid response was noted.

To view details of burying behavior of *R. pacifica* more clearly, the test tank was placed on an elevated platform that allowed viewing from underneath. Subtidal sand was added to the tank to a depth of 10-15 mm depth, and 10 *R. pacifica* were separately allowed to partially bury.

RESULTS

Settling behavior

Upon being placed in the experimental aquarium, squid either settled onto the glass sides and later moved down to the substrate (24%) or settled directly onto the bottom (76%). Their times to settle differed significantly among the five substrate conditions, $F_{(4,45)}=5.67$; $p<0.01$. The significant differences were isolated by a Tukey t-test and were between gravel and subtidal sand and gravel and construction sand ($p<0.025$). The values for bare substrate and cryolite were between those (Table I). When squid settled onto a substrate, they assumed an Alert Posture, raised off the sand anteriorly on the 1st, 2nd and 4th arms with the longer 3rd arms held laterally along the side of the body (Fig. 1a). Their heads and bodies were dark and the funnels pale and directed downward. Squid settling on cryolite substrate did not change from this posture or body pattern in 30 min. and did not bury. Squid settling on the other three substrates changed to a Horizontal Posture (Fig. 1b) in approximately one min. (Table I) and did not differ in their time to assume this position, $F_{(2,27)}=0.834$, n.s.

Burying (Stage 1)

Although squid settled to the horizontal posture on subtidal sand, construction sand and gravel, this was not always followed by burying activity. Seven of the ten squid refused to bury into gravel, three into construction sand, and none into subtidal sand (Table I). These differences were significant, $X^2(2)=7.38$, $p<0.05$. Latency to bury differed sig-

Table I. – Mean times in seconds for the sepiolid *Rossia pacifica* (N=10) to settle to the bottom, change from an Alert to a Horizontal posture, begin to bury and complete the burying process on different substrates.

	Bare tank	Subtidal sand	Construction sand	Gravel	Cryolite
Time to settle	25	17	22	33	31
Alert to Horizontal posture	---	67	70	78	---
Horizontal posture to bury	---	155	505	---	---
Complete burying	---	213	423	---	---

A dash indicates the squid did not perform the given activity on that substrate within 10 min.

nificantly between subtidal sand (156 sec.), and construction sand (476 sec.), $t_{(9)}=3.57$, $p<0.01$. On the other hand, time to bury was 215 sec. and 430 sec., respectively, but did not differ significantly, $t_{(9)}=2.02$, n.s., because of the large variance.

The squid began Stage 1 of the burial process (per Boletzky & Boletzky 1970) by directing a single jet of water forward, followed by a short pause. In the finer-grained substrates the squid blew the substrate out from under its body with its water jet directed alternately forward and backward until a depression was created in the bottom under the squid.

Covering (Stage 2)

After a pause (mean 83 sec.), the squid began Stage 2 of burial by extending its 2nd pair of arms forward synchronously at a 45° angle lateral to the longitudinal axis of its body, curled the distal end of the armtips downward and forward, thus "cupping" a bit of sand in each armtip and then threw the sand straight back onto its head and body by curling the arm upward while retracting it. It repeated this action until covering was achieved (Fig. 1c). The sand-throwing movements were smooth and continuous and the arms always moved synchronously.

Burying in gravel presented some difficulties for *R. pacifica*. They started the burial process by settling onto the gravel, maintaining a dark red/brown color, and assuming an Alert posture, as on other substrates. They then blew 1-3 water jets, first forward, then backward, as on other substrates. After several minutes the squid removed gravel grains from under their bodies by curling the distal tips of its 2nd arms around 1-3 gravel grains, curling the middle portions of the arms upward, and throwing them forward in a sweeping motion, arms extended, to a 45° angle forward of the body. Squid repeated this process up to six times, forming a depression under the body, with gravel piles left at a 45° angle forward of the body on each side. Afterward, they attempted to place gravel grains on top of their bodies. The second pair of arms went forward at a 45° angle and curled as it attempted to pick up and throw substrate on top of themselves, using the same method as with sand, but no gravel grains were actually picked up by the squid in this effort.

Respiration

Rossia pacifica used several methods of breathing during different burying stages. In the Alert Posture, the funnel was directed ventrally below the head. While squid were partially buried and/or sitting in the resting posture, the funnel was pointed laterally. The squid was seen to be performing rhythmic contractions of the mantle during these stages of burial (normal respiration movements).

When squid were mostly buried, particularly in fine sediments, the squid would eject several strong water jets through the funnel accompanied by fine sand grains. This was called Sand Geyser by Anderson (2000) (Fig. 1d). At this point the funnel was extended and aimed dorsally, with its opening flush with the surface of the substrate. There were three variations of this latter funnel position. First, the funnel protruded through a thin slit at the back of the head formed by the division between the mantle and the head. Secondly, it protruded upward from a slit made between a third arm and one side of the mantle, as the long arm was held close alongside the body. Thirdly, it protruded through a single small opening in the sand, directly posterior to one of the eyes. During these stages of burial, respiration was accomplished as described by Boletzky & Boletzky (1970), where the funnel

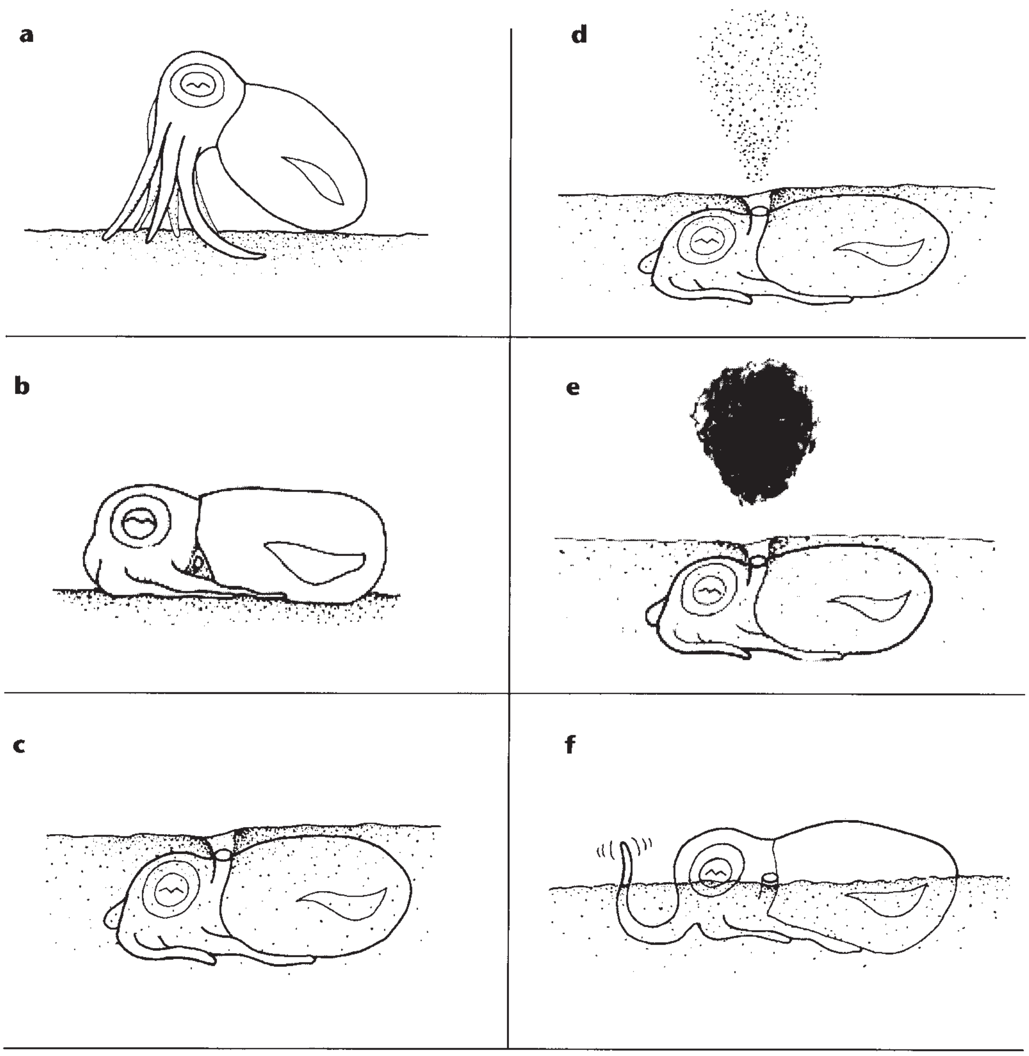

Fig. 1. – a, After settling to the substrate, the squid maintained an Alert Posture with eyes maximally extended upward. b, After approximately one min., the squid settled down into a Horizontal Posture on the substrate before beginning to bury. c, After burying themselves, the squid respired with water movements around and through the funnel. d, After burying themselves, the squid cleared a breathing hole above the funnel with forceful ejections of water upward through the funnel. This was called a Sand Geyser by Anderson (2000). e, Under threat, the squid would either eject a diffuse Ink Plume or a thick Ink Blob upward into the water. f, While partially buried and with eyes above the substrate, a possible angling behavior was observed, where a pale arm tip (arm L1) wiggled in front of the squid.

collar acted as a diaphragm that pushed water back and forth, out through the funnel and in through mantle slits.

Response to Threats

Squid occasionally blew a Sand Geyser, a diffuse ink plume or a thick ink blob up from the sand while buried (Fig. 1e), but their main response to a threat was to first partially emerge from the substrate while still pale, leaving the eyes and the mantle openings fully exposed. In the face of a persistent, repeated threat, squid emerged fully from the substrate, rested on the sand, assumed an Alert Posture and turned dark brown. If a threat was then repeated, they jetted up into the water column, released an ink blob, turned pale and jetted away.

Possible Angling Behavior

A possible "angling" behavior by several *R. pacifica* was noted on several occasions during burial in subtidal substrate and was videotaped for further analysis. The squid partially buried themselves using standard methods, leaving the top half of the mantle and the eyes above the substrate surface. They then protruded one arm vertically out of the sand directly in front of the left eye of the squid, extending about 8 mm (Fig. 1f). The skin, head, and mantle were dark red/brown but the arm tip was pale. The arm tip wiggled irregularly, sometimes back and forth laterally and sometimes curling on the substrate. Close examination of a video recording of the behavior revealed that the squid were always using a dorsal arm (L1) for this behavior.

DISCUSSION

The burying sequence of *Rossia pacifica* appeared relatively fixed in its normal substrate, probably a modal action pattern *sensu* Barlow (1977); cuttlefish use a similarly fixed pattern in burying (Mather 1986). This fixity may seem unusual, since cephalopods are known for their variability of behavior within species (Hanlon & Messenger 1996) and among individuals (Mather & Anderson 1993, Sinn *et al*. 2001). Similar stereotypy of burying is reported in Mediterranean sepiolids (Boletzky & Boletzky 1970) and in *E. scolopes* (Anderson *et al*. 2002).

Why would such fixity in burying behavior be found in an animal whose hallmark is variability? If speed is important for predator evasion, it may be emphasized with a fixed action that is "hard wired". Yet these squid settled onto the substrate for minutes before burying and probably did an initial assessment of the substrate and altered their burying behavior accordingly. Mather (1986) reports a similar chemo-tactile evaluation of sand by *Sepia*. Such evaluation would allow *R. pacifica* to use a different method to dig in gravel than in sand, as did *Sepia* (Mather 1986), or not to dig in cryolite or on a bare tank bottom. But the fixity of digging behavior once begun was emphasized when one animal settled next to a tank wall; one arm collected substrate for covering and the other moved up the tank wall as if it attempted to collect substrate there. As in the grooming sequence of mice tested by Fentress (1978), the behavior appeared to follow sequence without appropriate peripheral feedback.

The modification of respiration while squid are buried suggests another aspect of cephalopod behavioral flexibility. *Sepiola*, *Sepietta* (Boletzky & Boletzky 1970), *R. pacifica* (this study) and *E. scolopes* (Anderson *et al*. 2002) all change their method of respiration while buried, from mantle expansion and contraction, the respiratory action for most cephalopods (Morton 1967), to flexing of the skirt at the base of the funnel collar to cause inhalation and exhalation. Thus they adapt the method of breathing to the physical constraints of the situation.

While we think of being buried as rendering an animal insensitive to the environment, this was not the case with the *R. pacifica*, which was responsive to visual threats. There may just be a thin layer of substrate over the eyes, allowing the squid to see between the sand grains. Whatever method it uses to see while buried is effective, as it used water jets and inking to perceived threats. These responses belie its reputation for behavioral flexibility as they are an example of a normal reaction in a wrong place, calling attention to a hidden animal.

Rossia pacifica showed the normal cephalopod variable responses to threats. Many cephalopod species use ink ejection, either widely dispersed as "smoke screens" or mixed with mucus to form a pseudomorph "decoy", to distract predators (Hanlon & Messenger 1996). Interestingly, these two variations are seen as species-typical, but *R. pacifica* was able to vary the ink consistency sequentially to produce both ejection patterns, as also was *E. scolopes* (Anderson *et al*. 2002).

Our casual observations during this study suggest that we can add *R. pacifica* to the list of "angling" cephalopods, the first sepiolid to be so noted. Such behavior has been commonly but casually observed in cephalopods (Hanlon & Messenger 1996). Hoover (1998) mentions a possible angling behavior by the undescribed "crescent octopus", using the same dark body and pale armtip. Hanlon & Messenger (1996) describe it in the cuttlefish *Sepia officinalis*, and *S. latimanus* Quoy & Gaimard, 1832 as a "luring" behavior, and Moynihan & Rodaniche (1982) saw it in the Caribbean reef squid *Sepioteuthis sepioidea* (Blainville 1823). This behavior has now been described in four orders of cephalopods and may be a common predation technique across a wide range of species of cephalopods in many different habitats.

As they are relatively fixed and species-typical, the burying behaviors of different cephalopods may be useful taxonomically. Many octopod, sepiid and sepiolid species bury (Boletzky 1996), and use different actions and sequences (Hanlon & Messenger 1996, Norman 2000, Norman & Reid 2000). Although no detailed analyses of movement patterns have been performed here, the relative stability of burying sequences was obvious, yet different from that of other species. *Sepia officinalis* just uses a Stage 1 form of burying (*sensu* Boletzky & Boletzky 1970), only water jetting (Mather 1986). The sepiolids *Euprymna scolopes* (Anderson *et al*. 2002) and *Sepiola* and *Sepietta* (Boletzky & Boletzky 1970) all perform stages 1 and 2. *R. pacifica* also uses Stages 1 and 2 but the sequence is performed differently than in the other sepiolids studied. Although *Sepia officinalis* is the only sepiid whose burying behavior has been studied quantitatively thus far (Mather 1986) its distinct

Table II. – Comparison of decabrachian cephalopod burial behaviors.

SPECIES	STAGE 1 (blowing)	STAGE 2 (throwing)	DIRECTION OF FIRST FUNNEL BLOW	REFERENCE
FAMILY SEPIIDAE				
Sepia officinalis	yes	no	forward	Mather, 1996
Sepia pharaonis	yes	no	backward	Nabhitabhata, pers. comm.
Sepiella inermis	yes	no	backward	Nabhitabhata, pers. comm.
FAMILY SEPIOLIDAE				
Sepietta obscura	yes	yes	forward	Boletzky & Boletzky, 1970
S. neglecta	yes	yes	forward	Boletzky & Boletzky, 1970
Sepiola affinis	yes	yes	forward	Boletzky & Boletzky, 1970
S. ligulata	yes	yes	forward	Boletzky & Boletzky, 1970
S. robusta	yes	yes	forward	Boletzky & Boletzky, 1970
S. rondeleti	yes	yes	forward	Boletzky & Boletzky, 1970
Euprymna hyllebergi	yes	yes	backward	Nabhitabhata, pers. comm.
E. scolopes	yes	yes	backward	Anderson et al., 2002
E. tasmanica	yes	yes	forward	Norman, 2000: Sinn, pers. comm.
Rossia macrosoma	yes	yes	forward	Boletzky, 1996
R. pacifica	yes	yes	forward	this study
FAMILY SEPIADARIIDAE				
Sepiadarium austrinum	yes	yes*	?	Norman, 2000; Norman and Reid, 2000
Sepioloidea lineolata	yes	yes*	?	Norman, 2000; Norman and Reid, 2000

* Squid in this family threw sand on top of themselves in Stage 2 burial actions using their 2nd and 3rd left arms, unlike the sepiolids which used their second left and right arms.

burying behavior may reflect its taxonomic distance from the sepiolids, who have recently been placed in a different order from *Sepia* (Boletzky 1999). The burying behavior of the octopuses (Norman 2000) has yet to be studied in detail.

Though easy to elicit and simple to record, burying behaviors have been studied in few cephalopods so far. The sepiolids whose behaviors have been studied have all buried themselves in the substrate (Boletzky & Boletzky 1970, Shears 1988, Anderson *et al.* 2002), but all live in relatively shallow waters. Because of difficulties in live capture and maintenance, the digging behavior of deeper water sepiolids (if present) has not been studied at all. Such deep water animals have only been caught by abrasive trawls that are deadly to such fragile, soft-bodied organisms and these deep water species are only known as battered, preserved specimens in jars of formalin on museum shelves. Knowledge of open or deep-ocean cephalopods is grudgingly and expensively coming from the recent observations from deep water submersibles and ROVs (remotely operated deep water vehicles) (Hunt & Seibel 2000, Vecchione *et al.* 2001). With these new techniques, further research on burying sepiolids is clearly possible, and will illuminate the ecological constraints and behavioral sequencing used by this fascinating group of cephalopods.

CONCLUSION

The burying behaviors of *Rossia pacifica* are relatively fixed. It uses water jets from the funnel, first directed forward, then backward, as a first stage of burying. The second stage is accomplished by "throwing" substrate on itself using the second pair of arms. The latency to bury and the time to bury vary with the consistency of the substrate. The variation in the sequence of burying behaviors across the class may give us clues to the taxonomy of the species. A possible angling behavior was seen and is added to the list of angling cephalopods. As it has now been noted in members of four orders of cephalopods, it is likely it will be found in other species when they are studied.

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