# The Story of Deep-Sea Squid Sputum

**Stephanie L Bush**

***Mentors: Bruce Robison, Kim Reisenbichler, Rob Sherlock, Karen Osborn***

***Summer 2003***

**Keywords: squid, deep-sea, cephalopod ink, inking, escape behavior, pseudomorph**

**ABSTRACT:** The inking behavior of deep-sea squids was studied. Dive footage from Remotely Operated Vehicles was reviewed and information on squid species, depth, ink-type, and behavior was recorded. All species continued to ink throughout their depth range. Each species had a type of ink most commonly released, however, they were not limited to it. Similarly, the type of ink released usually, but not necessarily, coincided with an individuals' behavior. Individuals of some species were also collected and videotaped in the laboratory using low-light video equipment. Attempts to provoke ink release were unsuccessful, however, probably due to animal stress. Two hypotheses are presented, the first that ink release in squids living at depths without sun-light penetration relies not on color vision, but on the use of shadows produced by bioluminescence and low-levels of down-welling light. Secondly, I suggest a chemical component to ink in order to explain its continued use at depth.

> *Cephalopods may attract predators because they are…goodies to be seized*
>
> -M Moynihan

## INTRODUCTION:

Cephalopods are a group of invertebrates that have lost an external means of physical protection (Wells 1994). They are composed solely of soft parts within a core of muscle; a chitonous beak within a powerful buccal mass remains their only hard part, excluding the gladius of squids (Norman 2000). Cephalopods also possess some of the largest brains in the invertebrate world, their complex learning and social behaviors exceeding those of their common marine counterparts, fishes (see Wells 1994).

Due to this absence of a hard outer covering and muscular build, cephalopods are ideal prey items for marine mammals, fish, and even other cephalopods (Norman 2000). Because of their complex brains, it is not surprising that cephalopods demonstrate a complex repertoire of escape behaviors. Cephalopods have highly complex eyes for invertebrates and hunt visually (Budelmann 1994). They also rely on the visual system for defense, using various strategies to deceive their predators (Hanlon & Messenger

1996). The cephalopod defense array includes the complex skin color and texture changes demonstrated by all members of the coleiod subclass, the octopus, squid, and cuttlefish (Hanlon & Messenger 1996; Norman 2000). Additionally, frequent posture change is utilized to make the animal either look large and fierce or nothing like a cephalopod at all (Hunt 1996). The release of ink may be considered a last-ditch effort to escape predation, meant to prevent an attack or cause a mistaken attack upon the ink while the cephalopod takes flight (Norman 2000).

Defense is a costly, but necessary, part of animal behavior. For cephalopods, changes in skin coloration or body shape may be relatively cheap calorically compared to the release of ink. Skin chromatophores and erector muscles are controlled by direct neural connections to the brain and posture change requires simple movement of the highly flexible appendages. Ink, however, requires the production of both melanin, mucous, and possibly other chemicals, followed by their expulsion (Norman 2000). For animals with a very high metabolism and fast growth-rates (Wells 1994), this process effectively dumps precious calories from the body. Inking is a commonly observed behavior, however, so it must be an effective, evolutionarily stable technique of predator avoidance (but see Nolen & Johnson 2001). If it were not so, this behavior would be lost over time.

Inking events are commonly grouped as one of two types: clouds/smoke screens, which are large, diffuse releases of ink, and pseudomorphs, dense blobs of ink the approximate size and shape of the animal releasing them (Lucero et. al 1994; Hanlon & Messenger 1996; Huffard & Caldwell 2002). The former presumably blocks the animal from view (Moynihan 1985), deceiving the predator as to the location of the animal. The latter is meant to resemble the animal and function as a decoy as the individual escapes the scene (Moynihan & Rodaniche 1982). Both rely on simple visual cues, or visual deception as the case may be.

The question addressed by the current research is whether squids which live in complete darkness continue to utilize ink and why, when neither the animal nor the ink can be seen. I predicted that the occurrence of inking would decrease with increases in depth, as light is attenuated by water and the environment continues to darken (Tett 1990). That is, unless ink also possesses some deterrent chemical component in addition to its visually deceptive uses (Lucero et. al 1994; Norman 2000). Testing of the chemical composition of deep-sea squid ink is beyond the scope of this study. The approach taken focuses on the determination of whether squid continue to use ink at depth and, if so, whether or not the type of inking changes with depth in order to gather an idea of how ink is employed.

Furthermore, given the light regime in the deep sea (see Robison 1995; Robison 1999), I assumed that pseudomorph release would occur more commonly at shallower depths compared to ink clouds. At deeper depths I expected to find the opposite, for two reasons. First, due to the higher ambient light at shallower depths I expected a greater reliance upon visual methods of hunting, and thus a need to make fast escapes while leaving behind a decoy to prevent pursuit (Hunt & Seibel 2000). As one moves deeper it should be easier to hide within a cloud of ink, especially if this ink is chemically noxious or bad-tasting (Norman 2000). Secondly, based upon decreases in metabolic rates of animals as temperature and oxygen concentrations decrease with depth, thus the occurrence of more lethargic species (see Moiseev 1991), I expected animals to release clouds in which to hide rather than wasting energy jetting away.

## MATERIALS AND METHODS:

The archival video database at the Monterey Bay Aquarium Research Institute (MBARI) allows one to analyze footage obtained since the 1987 inception of the institute and subsequent dives of the Remotely Operated Vehicles (ROV) Ventana & Tiburon. The entirety of each dive performed by MBARI's two ROVs is recorded on High Definition (HD) and/or digital-beta videocassettes. With close to 2500 Ventana dives and over 500 ROV Tiburon dives, there are over 10,000 hours of video from the waters of Monterey Bay. Annotations of the animals encountered as well as their activities are made during the dives using the Video Information Capture with Knowledge Inferencing (VICKI) software. Video lab staff also review each tape, annotating all animals with VICKI as well.

The Video Information Management System (VIMS) database, designed by MBARI software engineers, allows for the retrieval of specified sequences containing information of interest. For the current project, I searched for the following combinations in order to retrieve appropriate video sequences: ink, inking, squid species, squid species & ink, and squid species & inking. The program is capable of returning the following information for each annotation: date of recording, time, location, ship, ROV, tape number, time-code, chief scientist, available frame-grabs, and depth.

Each sequence was reviewed multiple times at full speed and in slow-motion. Notes were taken for each by recording the time code at which the animal or ink was first observed, describing characteristics such as position, posture, coloration, behavior and type of ink release. Time codes were recorded throughout when aspects changed notably. Ink-type data were summarized in Excel, categorized into 100 m depth intervals, to look for common inking patterns of each species and whether inking patterns varied over the range reviewed or within species ranges.

On several dives we were able to collect live specimens, including one of each of the following: *Chiroteuthis calyx*, doratopsis (juvenile *C. calyx*), *Cranchia* sp., *Galiteuthis phyllura*, *Histioteuthis heteropsis*, *and Octopoteuthis deletron*. These were transported to a cold-box in the sea-water lab facility at MBARI and transferred into kreisels. Specimens were left undisturbed for at least 24 hours prior to video footage being taken with a Canon L1 Hi-8 recorder equipped with low-light intensifier. Either a flashlight with red filter or low intensity red overhead lights were used during recording. Each specimen was recorded for ten minutes without the presence of the observer in order to get an idea of behavior within the kreisel, under low-light. Then the specimens were recorded for an additional ten minutes while a soft poker was used to nudge the specimen in an attempt to induce inking.

## RESULTS

### ROV VIDEO SEQUENCES

### General Observations

Ink release was observed from the surface down to 1100m (Table 1-3), a point beyond which few species occur with regularity. The frequency of inking did not decrease with increasing depth; all squid species continued to ink throughout their depth range (Table 1-3). Also, no pattern of change in frequency of ink type was found with changing depths (Table 1-3). Any possible pattern observed was due to differences in species ranges since each species favors one or two types of ink-release (Table 1-3).

Five types of ink release were observed from video sequences; pseudomorphs, clouds, continuous trails, trails of pseudomorphs, and mantle fill. The most common use of ink is as a decoy through the release of pseudomorphs (Table 1). The animal releases a condensed ink burst of similar size and shape to itself and subsequently jets away, commonly as the animal changes trajectory. This type of ink release was demonstrated by all of the species studied here, although, infrequently for some. Clouds or smoke-screens are more diffuse and spread-out compared to pseudomorphs and were observed second most frequently (Table 2). Also relatively common was the use of ink trails (Table 3), due to the frequent occurrence of *Gonatus onyx*, a species that favors this type of inking behavior. Pseudomorph trails are very infrequent as are mantle fills, although the latter is probably due to the infrequency of observing the species which commonly utilize such inking behavior (Table 3).

Each species typically favors one, possibly two, types of ink release. Most species, however, have been observed releasing more than one type of ink, and a few can release up to four types. Ink releases are usually associated with a particular behavior. The release of a pseudomorph is typically followed by the animals quick escape, whereas with the release of a cloud or ink trail the individual usually remains within it or nearby.

Ink release behavior, however, is not stereotyped. For example, an individual can release a pseudomorph and remain by it for several seconds before leaving the area, and in many cases individuals have been observed to release a combination of ink-types when one is not doing the trick. These are all incorporated with numerous variations of body color and posture in order to deceive other organisms from discovering the presence of a squid.

One interesting aspect not predicted was the variation in color of ink from different species. For example, the ink of *G. onyx* appears a dark olive-yellow, while that of *L. opalescens* is almost black. Cranchiids use a diffuse grayish-green ink. Adult *C. calyx* possess ink of a greenish hue, while the ink of juveniles can be similar, or appear white. *H. heteropsis* releases either whitish-grey or grey-brown ink whereas *Onychoteuthis borealjaponicus* has only been observed to release yellowish-green ink.

### *Chiroteuthis calyx*

One commonly encounters this species in the fishing posture (Hunt 1996; Fig. 1); the main body is horizontal while the mantle is tilted upwards, the arms are spread outward then curved downward from the body. The fourth pair of arms support the retractable feeding tentacles within grooves along their inner surface (Moiseev 1991; Hunt 1996); the tentacles are fully extended when the animal is undisturbed but can be held at varying lengths. Adult *C. calyx* are often discovered in the fishing posture within a diffuse cloud of ink; rarely have they been observed releasing the ink. This species is a 'sit-and-wait' predator, slow to move, or even retract their tentacles until they have been watched for some time and possibly pursued. When approached too closely, the animal will commonly assume a horizontal position, holding the arms in an outstretched 'V'. The webs of the arms are spread and red in color, and the tips of the arms curl back and touch at the ends (Fig 2). The arms resembles the outline of an elongated heart. This species reddens its arms and dorsal mantle when disturbed, and a greatly perturbed individual will turn red around and between the eyes, the arms and mantle also deepening in color.

Adult *C. calyx* have been observed to release pseudomorphs on occasion, usually when the individual has had direct contact with the ROV during sampling or attempted sampling. In this case the ink release is followed by jet-produced escape. In other cases pseudomorphs occur along with diffuse clouds and the animal remains within or nearby.

Juveniles of this family, called the doratopsis stage (Vecchione, et al 1992), occur at shallower depths than adults (Roper & Young 1975). Doratopsis individuals have more elongated bodies, as well as an extension of the gladius equal in length to the body and out-stretched tentacles. They are usually either in the horizontal or vertical position when approached, but then typically assume a vertical position, with the 'tail' pointing downwards. Doratopsis ink more readily than adults, releasing anywhere from one to 30 pseudomorphs of the same length and thickness as the body while moving down in the water column. We often see doratopsis remaining motionless among several pseudomorphs they have released horizontally (Fig. 3). Although less common, juveniles also release clouds of ink in which they remain in a straight or bent horizontal position.

### *Cranchia* spp.

Cranchiids are transparent squids (Hunt 1996), relying on their invisibility and color/posture changes for defense instead of inking. Only a few instances of *Cranchia* spp. releasing ink have been observed. One involved the release of a pseudomorph, with the individual then jetting away. The other involved the release of a cloud, which the individual remained within. Both instances occurred between 400-600m.

### *Galiteuthis phyllura*

This species is also a cranchiid, and the most commonly observed member of this family within Monterey Bay. As described above, it also takes quite a lot of jostling to make a *Galiteuthis phyllura* ink. Usually, changes in posture and skin coloration are used. The cranchiids are known for their 'cockatoo' posture (Moiseev 1991; Fig. 4). Here the arms are held together at 90° to the body axis, either straight or curved outwards distally. In addition, this species will expand the sparse mantle chromatophores and those located around and between the eyes and along the arms to make them red. When the animal is highly disturbed the deep-red arms are pulled back to so that they surround the body like an inverted umbrella, revealing the buccal mass and beak.

The inking behavior cranchiids display, however, is mysterious. Instead of spewing ink out of the funnel, the animal allows its mantle to fill with the substance so it becomes opaque. Individuals either pinch their collars closed and hold the ink in or release the ink in small, diffuse trails as they respire.

### *Gonatus onyx*

*Gonatus onyx* has four inking strategies, each with commonly associated behavior. The two principal types of ink released are continuous ink-trails (Fig 5) and pseudomorphs. The former is utilized by adult individuals only, who are solitary and inhabit a deeper range than juveniles. Ink-trails can be one long release of ink, or a few shorter ones, as well as straight, curved, or in various configurations and have tapered ends. Very rarely have we observed this type of ink released, the individual having already produced it when approached by the ROV. The animal might be located above, below, or at either end of the ink trail and maintains its position. Upon further approach the individual turns a deep red and changes to a J-pose (see Moiseev 1991; Hunt & Seibel 2000), the body vertical and arms curled upwards toward the dorsal mantle, if it was not already in this posture. Alternatively, the animal will turn white and bolt mantle-tip first downwards. This behavior is also sometimes, but not always, associated with the release of a pseudomorph.

Pseudomorphs can be the sole type of ink released. Their use is much more common in *G. onyx* juveniles as they make quick jet-escapes, also found by Hunt & Seibel (2000). Juveniles occur in groups within a shallower depth range (Roper & Young 1975), and have never been observed to release ink trails. They do sometimes release a series of up to 8 pseudomorphs as they jet away. A similar type of discontinuous ink-trail has been recorded only once from an adult *G. onyx*. Interestingly, the animal remained next to the release just as if it were a continuous trail and only departed upon pursuit.

The last type of ink release demonstrated by this species is a cloud (Fig. 6), a release of a huge amount of ink which blocks the animal from view as it hides inside. This behavior has only been observed for adult and sub-adult *G. onyx*, but not for juveniles. It was only observed when the animal was relatively close to the ROV, and in several cases bumped into the ROV as it was jetting past.

### *Histioteuthis heteropsis*

This species is most commonly encountered in the J-pose, with the distal portion of the arms curled back toward the dorsal mantle or to the sides of the body (Fig. 7). The animal will usually use its fins and funnel to maintain position, moving slowly away when approached. If the individual is followed it will move to a vertical posture and begin downward movement at moderate speed. In some cases we have found individuals in this vertical posture, with arms together and pointed down. There is somewhat of a bend in the body such that the large, left eye is directed upwards and the smaller eye somewhat downwards. *Histioteuthis heteropsis* will sometimes ink without prolonged disturbance, however, usually only inks when approached closely, bumped, or provoked for a lengthy amount of time. Ink can be released from either the J-pose, usually a cloud, or the straightened pose, usually a pseudomorph. Like other species the former is released and the animal remains either within or near it, while the latter is followed by jet escape.

### *Loligo opalescens*

These are fast-moving, schooling squid, commonly seen by the ROV in shallow water as they utilize the bright lights to hunt. At times, large groups will jet by and only one individual will ink, while at other times individuals will hang out in front of the camera and/or around the detritus samplers (sometimes inadvertently swimming inside) and suddenly ink at some unseen disturbance. As indiscriminately as their timing of inking is their form of inking (Fig. 8); they may release a pseudomorph, a cloud, a squiggly trail, various forms in between. They are somewhat consistent in that the release of a pseudomorph or trail is usually followed by quick jet-escape, while individuals usually maintain their position next to cloud-like releases.

*Octopoteuthis deletron*

Individuals are usually in a horizontal position with arms spread and curled back over the dorsal mantle when first observed (Fig. 9). Upon approach animals begin using the funnel to jet downwards, increasing the pace by adding beats of the enormous fins when pursued. This species also makes subtle color changes, from a deep red to a less striking red with a frosty grey on the arms and along the edges of the fins. Inking is usually only observed when the animal is bumped, for example upon attempted collection. In most cases, clouds are released and the individuals remain near the release. Surprisingly, we have also observed this species in the J-pose next to ink trails. Very rarely does *O. deletron* release pseudomorphs.

*Onychoteuthis borealjaponicus*

While much larger, this species resembles *L. opalescens* in that individuals usually occur in groups. They are also similar with respect to inking behavior, in that ROV encounters with this species result in only some individuals releasing ink, a mixture of pseudomorphs and clouds within the same time period. In the few instances where solitary individuals were encountered, either a pseudomorph or cloud was released, in most cases. Again, usually individuals remained near clouds and bolted from pseudomorphs, but in some cases the opposite was true (Fig 10). In one sequence, as a group of *O. borealjaponicus* moved past the ROV, an individual attached itself to a $CO_2$ release apparatus. It continued to release small amounts of ink and finally detached itself, spreading its arms to reveal its beak before moving on.

LABORATORY

Low-light observations and review of videotape taken in the laboratory revealed that I was unable to induce inking. There was only one instance of inking, in which I thought a cranchiid was dead because it was lying on the bottom of the kreisel, but jetted away when prodded. On analysis of the video I realized that this individual had released a pseudomorph prior to jetting away. The animals all reacted more strongly to light and to my presence than they did to the prodding, however, neither caused them to ink.

## DISCUSSION:

Just as in shallow water species, deep-sea squids use ink as a decoy method or for mimicry of something other than a squid (Hunt 1996). However, at depths below 200 m they can no longer rely upon color vision and probably rely upon the play of shadows at such depths (Robison 1999). Shadows still occur at depths to which no sunlight penetrates because of the frequency of bioluminescence in the deep-sea (Robison, 1995). If a predator relies upon locating a shadow the size and shape of a squid and a squid releases a pseudomorph, one can visualize a predator lunging for its prey and getting a mouthful of ink instead. On the other hand, the use of ink clouds creates larger shadows in which the animal is able to hide or remain next to so that either the outline of the squid is canceled or predators simply avoid something creating such a large shadow.

A novel use of ink not discussed in any previous literature is that of an ink trail. In a habitat where siphonophores are some of the most common animals, a few of the squid species seem to utilize this to their advantage. Adult *G. onyx*, for example, most commonly release long trails of olive-green ink, which would create a shadow resembling the stinging body of an elongate organism such as *Apolemia* spp. This form of shape mimicry is also evident from juvenile *C. calyx*, whose long body, tail extension, and release of long, thin ink pseudomorphs causes them to be confused with shorter siphonophores such as *Nanomia bijuga* (see Robison 1999).

The most puzzling use of ink is that of the cranchiids, who allow their mantle to fill with ink (Hunt 1996; Norman 2000). These animals are transparent and only their eyes and ink sacs create shadows for predators looking from below (Robison 1999). If the use of ink is for cancellation of these shadows then one would speculate that the ink sac would be lost completely over time. Additionally, these animals have developed photophores to cancel out the shadows created by these organs (Robison 1995). They are surely slow to ink, so this behavior is truly a last effort of defense. One possible explanation is that these animals are trying to draw attention to themselves by puffing up, holding their arms in odd positions, and filling up with ink.

## CONCLUSIONS:

I have shown that no inking behavior or pattern dominates at any particular depth and that the frequency of ink-types does not change throughout the water column. I suggest that ink release is indeed used as a visual defense in deep-sea squids. Several species occur well below depths of sunlight penetration, and they continue to ink with similar frequencies at all depths. At these depths neither the animal nor the ink can be seen. I suggest that there is sufficient down-welling light and/or light from bioluminescence that enables squids to use ink to modify or create shadows that deter or confuse predators (Young & Roper 1975; Robison 1995). Each type of ink release lends support to this idea: pseudomorphs can still act as a shadow decoy, ink clouds cancel out the shadow of a squid with a much larger one, and filling the mantle in cranchiids may cancel out shadows created by non-transparent organs. Also, ink trails and long, thin pseudomorphs resemble stinging siphonophores such as *Apolemia* spp., deterring possible predators.

An alternative hypothesis is that ink contains yet-to-be discovered chemical components that is either confusing or noxious to predators. Previous studies have shown that animals become confused when they encounter the ink of shallow-water cephalopods (Moynihan & Rodaniche 1982). A deterring or noxious chemical component to cephalopod ink would explain its use at any depth, no matter what the light regime. Such a component might be paired with any of the ink-types to deter predators. A squid releasing a cloud of ink has provided a large area of possible chemical deterrence and perhaps hides within or near it as this provides the greatest safety. Pseudomorphs are more concentrated, thus a higher dose to the predator that accidentally attacks it. But this type of ink release, of course, covers less area, thus reducing chances that the predator will fall for the decoy and not chase the true individual. Unfortunately, this hypothesis suggests an extra metabolic cost to the already costly behavior of inking, occurring in a place where animals have low metabolic rates. The production and storage of these proposed chemicals poses many interesting questions.

While this study has allowed for the explanation of some aspects of inking in deep-sea squids, not surprisingly, there are many questions that remain. As long as MBARI continues to gather ROV footage, more data on this subject can be collected and analyzed, hopefully with the result that more can be learned about the inking behavior of some of the less common species occurring in the Monterey Bay. Another direction that I would like to see this work head in is towards the testing of ink from several species chemically. This is difficult since one has to know what chemicals to look for prior to testing. I believe that also carrying out behavioral experiments with other deep-sea organisms in the laboratory, testing how organisms react to direct exposure to squid ink, would be beneficial.

## ACKNOWLEDGEMENTS:

Thank you to my mentors; Bruce Robison, Kim Reiseinbichler, Rob Sherlock, and Karen Osborn for letting me work on a cephalopod project and for their unfailing and indefatigable help and information. Thank you to George Matsumoto, without whom there would be no one to keep all of the interns in line, busy, and making the most of their time here at MBARI. Thanks to the staff of the video lab for putting up with my endless assistance requests and my hours watching stacks of tapes. None of my study would have been possible without the crew and pilots of both the Pt. Lobos/Ventana and Western Flyer/Tiburon courteously and determinedly chasing and collecting specimens for me. Finally, to Derek Greenwood for constant support, help, and keeping me sane at the end.

## REFERENCES:

Budelmann, B U. 1994. Cephalopod sense organs, nerves and the brain: adaptations for high performance and life style. Pgs. 13-31. In: Physiology of Cephalopod Molluscs. Gordon & Breach Pub. Grp.

Hanlon, R T & J B Messenger. 1996. *Cephalopod Behavior*. Cambridge University Press.

Hunt, J C. 1996. *The behavior and ecology of midwater cephalopods from Monterey Bay*. PhD Disseration, UCLA.

Hunt, J C, & B A Seibel. 2000. Life history of *Gonatus onyx* (Cephalopoda: Teuthoidea): ontogenetic changes in habitat, behavior and physiology. *Marine Biology*. **136**: 543-552.

Lucero, M T, Farrington, H, W F Gilly. 1994. Quantification of L-Dopa and Dopamine in squid ink: implications for chemoreception. *Biol. Bull*. **187**: 55-63.

Moiseev, S I. 1991. Observations of the vertical distrbution and behavior of nektonic squids using manned submersibles. *Bull. Mar. Sci*. **49(1-2):** 446-456.

Moynihan, M. 1985. *Communication and non-communication in cephalopods*. Indiana University Press, Bloomington.

Moynihan, M, & A F Rodaniche. 1982. The behavior and natural history of the Caribbean reef squid Sepioteuthis sepioidea. *Advances in Ethology*. **25**: 1-150.

Nolen, T G & P M Johnson. 2001. Defensive inking in *Aplysia* spp.: multiple episodes of ink secretion and the adaptive use of a limited chemical resource. *J. Exp. Bio*. **204**: 1257-1268.

Norman, M. 2000. *Cephalopods: a world guide*. Conch Books. Hackenheim.

Robison, B.H. (1995). Light in the ocean's midwaters. *Scientific American*, **273**: 60-64.

Robison, B. 1998. Shape change behavior by mesopelagic animals. *Mar. Fresh. Behav*. Physiol. **32**: 17-25

Roper, C F E, & R Young. 1975. Vertical distribution of pelagic cephalopods. *Smithsonian Contributions to Zoology*. **209**: 1-33

Tett, P. 1990. *The Photic Zone*. Pgs. 5987. In: Light and Life in the Sea. Ed. Herring, Campbell, Whitfield & Maddock. Cambridge University Press, Cambridge.

Young, R, & C F E Roper. 1975. Bioluminescent countershading in midwater animals: evidence from living squid. *Science*. **191**: 1046-1048

Vecchione, M, Robison, B H, & C F E Roper. 1992. A tale of two species: tail morphology in paralarval chiroteuthis (Cephalopoda: Chiroteuthidae). *Proc. Biol. Soc. Wash*. **105(4)**: 683-692

Wells, M J. 1994. The Evolution of a Racing Snail. Pgs. 1-12. In: Physiology of Cephalopod Molluscs. Gordon & Breach Pub. Grp.

## Appendix A-Tables

**Table 1.** Occurrence of pseudomorph release of each species categorized by 100 m depth intervals.

| **Species** | **0-100 m** | **101-200** | **201-300** | **301-400** | **401-500** | **501-600** | **601-700** | **701-800** | **801-900** | **901-1000** | **1001-1100** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **C. calyx** | | | | II | IIII | II | I | | | | |
| ***Cranchia* spp.** | | | | | I | | | | | | |
| **Doratopsis** | | IIIIIII | IIIIIIII | IIIIIIIIIIIIII | IIIIIIII | I | | | I | | |
| **G. phyllura** | | | | | I | | | | | I | |
| **G. onyx** | | I | | II | III | I | II | II | | IIII | |
| **H. heteropsis** | | | | I | II | | | I | | | |
| **L. opalescens** | IIIIIIIII | I | I | II | | | I | | | I | |
| **O. deletron** | | | | I | | | | | | | |
| **O. borealjaponicus** | | | | IIIIIIII | | | | | | | |

**Table 2.** Occurrence of cloud release of each species categorized by 100 m depth interval.

| Species | 0-100 m | 101-200 | 201-300 | 301-400 | 401-500 | 501-600 | 601-700 | 701-800 | 801-900 | 901-1000 | 1001-1100 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| C. calyx | II |  |  |  | IIIIII | IIII |  |  |  |  |  |
| *Cranchia* spp. |  |  |  |  |  | I |  |  |  |  |  |
| Doratopsis |  |  | II | IIIIII |  | I |  |  |  |  |  |
| G. phyllura |  |  |  |  | I |  |  |  |  |  | I |
| G. onyx | I | II |  | I | I |  | I |  | I | I |  |
| H. heteropsis |  |  |  |  |  |  |  |  |  |  |  |
| L. opalescens | I | I |  |  |  |  |  |  |  |  |  |
| O. deletron |  |  |  | I |  | II | I |  |  | I |  |
| O. borealjaponicus |  |  |  | IIIIIIII |  | I |  |  |  | I |  |

**Table 3.** Other ink releases for each species categorized by 100 m depth intervals.

| Ink type | Species | 0-100 m | 101-200 | 201-300 | 301-400 | 401-500 | 501-600 | 601-700 | 701-800 | 801-900 | 901-1000 | 1001-1100 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Trail | G. onyx |  | III | I | II | IIII | II | IIIIII | IIIIIIIIIIIIII | IIIIIIIII | IIIIIIIII |  |
| Pseud trail | G. onyx |  |  |  | I | I |  | I |  |  |  |  |
| Trail release | G. phyllura |  |  |  |  | I | I |  |  |  |  |  |
| Blob release | G. phyllura |  |  |  | I |  |  |  |  |  |  |  |
| Mantle fill | G. phyllura |  |  |  | I | II | I |  |  |  |  | I |
| Cloud trail | L. opalescens | II |  |  |  |  |  | I |  |  |  |  |
| Cloud trail | O. deletron |  |  |  |  |  | I | I |  |  |  |  |
| Trail | O. borealjaponicus |  |  |  | I |  |  |  |  |  |  |  |

## Appendix B- Figures

**Figure 1.** Adults *Chiroteuthis calyx* in fishing posture.

**Figure 2.** Defensive 'arm-tip touch' pose of *C. calyx*.

**Figure 3.** Juvenile *C. calyx* (doratopsis) having released a series of pseudomorphs.

**Figure 4.** *Galiteuthis phyllura* in 'cockatoo' posture.

**Figure 5.** Adult *Gonatus onyx* in J-pose below a long ink trail.

**Figure 6.** Adult *G. onyx* hiding within a cloud of ink.

**Figure 7.** *Histioteuthis heteropsis* in typical J-pose with arms curled back.

**Figure 8.** A group of *Loligo opalescens* with releases of both small clouds and pseudomorphs.

**Figure 9.** *Octopoteuthis deletron* in defensive pose within a diffuse ink cloud.

**Figure 10.** *Onychoteuthis borealjaponicus* jetting through a thick ink cloud.