Behaving in the Dark: Locomotor, Chromatic, Postural, and Bioluminescent Behaviors of the Deep-Sea Squid *Octopoteuthis deletron* Young 1972

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Abstract. Visual behaviors are prominent components of intra- and interspecific communication in shallow-water cephalopods. Meso- and bathypelagic cephalopods were believed to have limited visual communication, other than bioluminescence, due to the reduced illumination at depth. To explore potential visual behaviors in mesopelagic squid, we used undersea vehicles to observe 76 individuals of *Octopoteuthis deletron*. In contrast to predictions, we found this species capable of a variety of visually linked behaviors not previously reported for a deep-ocean cephalopod. The resultant ethogram describes numerous chromatic, postural, locomotor, and bioluminescent behavioral components. A few common body patterns—the whole appearance of the individual involving multiple components—are characterized. The behaviors observed from individual squid were compared using a Nonmetric Multi-Dimensional Scaling (NMDS) ordination, onto which hydrographic and observation parameters were mapped. Observation length, specimen collection, and contact with the vehicle affected which behaviors were performed. A separate NMDS, analyzing the body patterns, indicated that these sets of behavioral components could be visualized as groups within the NMDS ordination. While the functional roles of the behaviors described are not yet known, our findings of numerous behaviors in *O. deletron* clearly indicate that bioluminescence is not the sole method of visual communication by deep-sea squid.

Introduction

Shallow-water squids, octopuses, and cuttlefishes are renowned for their inter- and intraspecific visual communica-

tion (Packard and Sanders, 1971; Packard and Hochberg, 1977; Hanlon and Messenger, 1988, 1996). These cephalopods assess their surroundings with well-developed vision, though in most species vision is monochromatic (Messenger, 1977; Kito *et al.*, 1992; Shashar *et al.*, 1998; Sweeney *et al.*, 2007). Individuals are capable of polyphenism consisting of near instantaneous changes in appearance through a broad range of camouflage and communication methods (Packard and Sanders, 1971; Packard and Hochberg, 1977; Hanlon and Messenger, 1988; Roper and Hochberg, 1988; Hanlon *et al.*, 1999a; Barbato *et al.*, 2007). An individual's overall appearance, or body pattern, is composed of the following component types: chromatic, textural, postural, and locomotor. Chromatic expression is achieved by pigmented chromatophores, underlying reflective leucophores and iridophores, and polarizing elements (Mirow, 1972a, b; Messenger, 1974; Packard and Hochberg, 1977; Cloney and Brocco, 1983; Packard, 1988; Mathger and Hanlon, 2007). Skin texturizing is accomplished with dermal muscles (Packard and Hochberg, 1977); this component type is present in octopuses and cuttlefishes but absent from squids. Postural components are the positions of muscular, flexible limbs and body (Packard and Sanders, 1971). Locomotor components and maneuvers are movements of the whole body or its constituents (Roper and Hochberg, 1988). Variations of bioluminescence, or biologically derived light, expressed by an individual can also be considered a type of body patterning component (Herring, 2000).

Body patterns used in inter-specific communication enable cephalopods to achieve search image impedance by using polyphenism to hinder recognition (Hanlon *et al.*, 1999a); perform deimatic behavior to startle potential predators (Edmunds, 1974); and implement effective predation—for example, *Sepia officinalis* may use the dynamic Passing Cloud body pattern to distract prey prior to attack

(Hanlon and Messenger, 1988). There are multiple ways in which polyphenism is used to camouflage the individual. In *background resemblance* the individual approximates a random sample of the visual background (Endler, 1981). The juxtaposition of colored areas in *disruptive coloration* attract a predator's attention away from the animal's outline (Cott, 1940; Chiao *et al.*, 2007). *Counter-shading* is used to cancel shadows on a body surface caused by uneven illumination (Cott, 1940). Finally, in *masquerade* the animal resembles an inedible or non-prey entity (Endler, 1981; Hanlon *et al.*, 1999a).

Body patterning may be used in intraspecific communication to attract and court mates, repel or deceive sexual competitors, coordinate movements within a shoal, and warn conspecifics of predators (Moynihan and Rodaniche, 1982; Hanlon and Messenger, 1996; Hunt *et al.*, 2000).

Species that experience diverse environmental encounters may benefit from a varied communication repertoire. Body patterning diversity in cephalopods is thought to be influenced by activity patterns (diel *vs.* nocturnal), social behavior, habitat complexity, predators, and reproductive mode (Hanlon and Messenger, 1988). Cephalopods that are either asocial or nocturnally active, use simple reproductive modes, or dwell in homogeneous environments may display fewer body patterns than other cephalopods (Hanlon and Messenger, 1988). In the deep ocean, most species are asocial, the water is a nearly homogenous visual substrate, and both intra- and interspecific interactions are infrequent due to low animal densities (Childress, 1995; Herring, 2000). In addition, below 200 m, more than 99% of surface illumination has been attenuated, and this "twilight" environment makes visual communication less viable than in well-lit habitats (McFall-Ngai, 1990). Consequently, limited body patterning has been predicted for deep-ocean cephalopods (Hanlon and Messenger, 1996; Nixon and Young, 2003).

The characteristic distribution of light in the deep sea has led to convergence in camouflage tactics across taxa (Johnsen, 2001; Marshall, 1979; Johnsen, 2001, 2005; Warrant and Locket, 2004). In the relatively well-lit euphotic and upper mesopelagic zones, individuals are often counter-shaded, transparent, have highly reflective silvered sides, and/or have laterally flattened bodies to minimize their silhouette (Johnsen, 2001). Below 30 m depth, red wavelengths are completely absent from ambient light. At these depths, non-transparent individuals often have red, purple, brown, or black body coloration, which appears black in the absence of red light (McFall-Ngai, 1990). In the mesopelagic (200–1000 m), light down-welling from the surface is many times greater than that reflected laterally or from below, and predators looking upward may decipher the silhouette of potential prey (Gleadall and Shashar, 2004). In an apparent response to this vulnerability, many deep-sea animals possess downward-directed photophores that counter-illuminate their bodies, diminishing or canceling their silhouette (Young, 1977, 1983).

Camouflage by deep-sea animals centers almost exclusively on the few successful tactics presented above: transparency, silvering, counter-illumination, and red coloration. There has been no *a priori* reason to expect deep-sea cephalopods to be different, despite the multitude of capabilities known for shallow-dwelling cephalopods (Moynihan and Rodaniche, 1982; Hanlon and Messenger, 1996). Consistent with this reasoning, most deep-sea cephalopods have been found to possess silvered eyes and digestive glands that are counter-illuminated, and bodies that are transparent or of dark, usually red, coloration (Chun, 1910; Voss, 1967; Herring, 1988).

Octopoteuthis deletron Young 1972 is a solitary mesopelagic squid that is found in the eastern North Pacific from Alaska to Baja California, off Peru, and perhaps off Japan (Young, 1972). Individuals attain a mantle length of 17 cm; possess large, elliptical fins; and have long arms with hooks in place of suckers along most of the length (Young, 1972). Members of the family Octopoteuthidae lose the tentacles at an early life-stage, leaving just the eight arms to function in prey capture (Young, 1972). Individual *O. deletron* possess a variety of photophores, the most conspicuous of which are single organs that occupy the terminus of each arm (Young, 1972; Vecchione *et al.*, 2002). This species also has a number of ventrally directed photophores: a series along the core of the four ventral arms; an arm base organ on arm pairs II, III, and IV; a pair of small medial head organs; a photophore posterior to each eye; a pair of visceral photophores situated ventral to the ink sac; and a single posterior "tail" organ (Young, 1972). Counter-illumination by ventral photophores has been observed from the congener *Octopoteuthis neilseni* (Young and Vecchione, 2006).

Materials and Methods

Observations were made during dives of two remotely operated vehicles (ROVs) operated by the Monterey Bay Aquarium Research Institute (MBARI). The ROV *Ventana*, a 40-hp electro-hydraulic vehicle, ranges to 1500 m. Illumination is provided by six 400-W DSPL HID Daylight lamps. The ROV *Tiburon* is an electric vehicle that ranges to 4000 m; it has four 400-W DSPL HMI lights for illumination. Both of these arrays produce illumination in the daylight range (5500–5600 °K). One important difference between these vehicles is that hydraulic power produces more noise than electric power; the ROV *Tiburon* is quieter in the water. Each ROV dive is recorded on Panasonic D5 high definition videocassettes or Sony Digital Betacam standard definition videocassettes, or both. Since 1988, MBARI has archived more than 15,000 hours of video footage from over 3200 ROV *Ventana* dives and over 1150 ROV *Tiburon* dives in the Monterey Submarine Canyon and surrounding waters. Organisms encountered are annotated by scientists and video-lab staff using MBARI-designed Video Annotation Reference System software, and the annotations are synchronized with hydrographic parameters (Robison,

1993). Video sequences used in this study were viewed directly from ROV dive tapes on a Sony HR Trinitron monitor or a Sony MEU-WX2 Multiformat Engine and LMD-232W LCD monitor. Monitor settings maintained animal coloration according to ROV illumination produced *in situ*. All sequences were viewed multiple times at normal and slow playback speeds. Each unique behavior was defined, categorized as one of four component types (chromatic, postural, locomotor, or bioluminescent), and recorded as present or absent from the observation sequence of each individual. A few of the common body patterns, or combinations of components, were also described.

The resulting presence/absence data matrix was used to explore (a) behavioral similarities between individuals and (b) behavioral components that were observed simultaneously (body patterns). For both analyses a Non-metric Multi-Dimensional Scaling (NMDS) ordination calculated using a Bray-Curtis coefficient dissimilarity matrix and 100 restarts was performed in Primer-E 6.0 (Clarke and Warwick, 2001). The placement of samples in an NMDS ordination is based on the rank dissimilarity between two samples; samples that are more similar are more closely spaced in the ordination. We used a Kruskal 1 fit scheme to allow equal dissimilarities to be represented by unequal distances
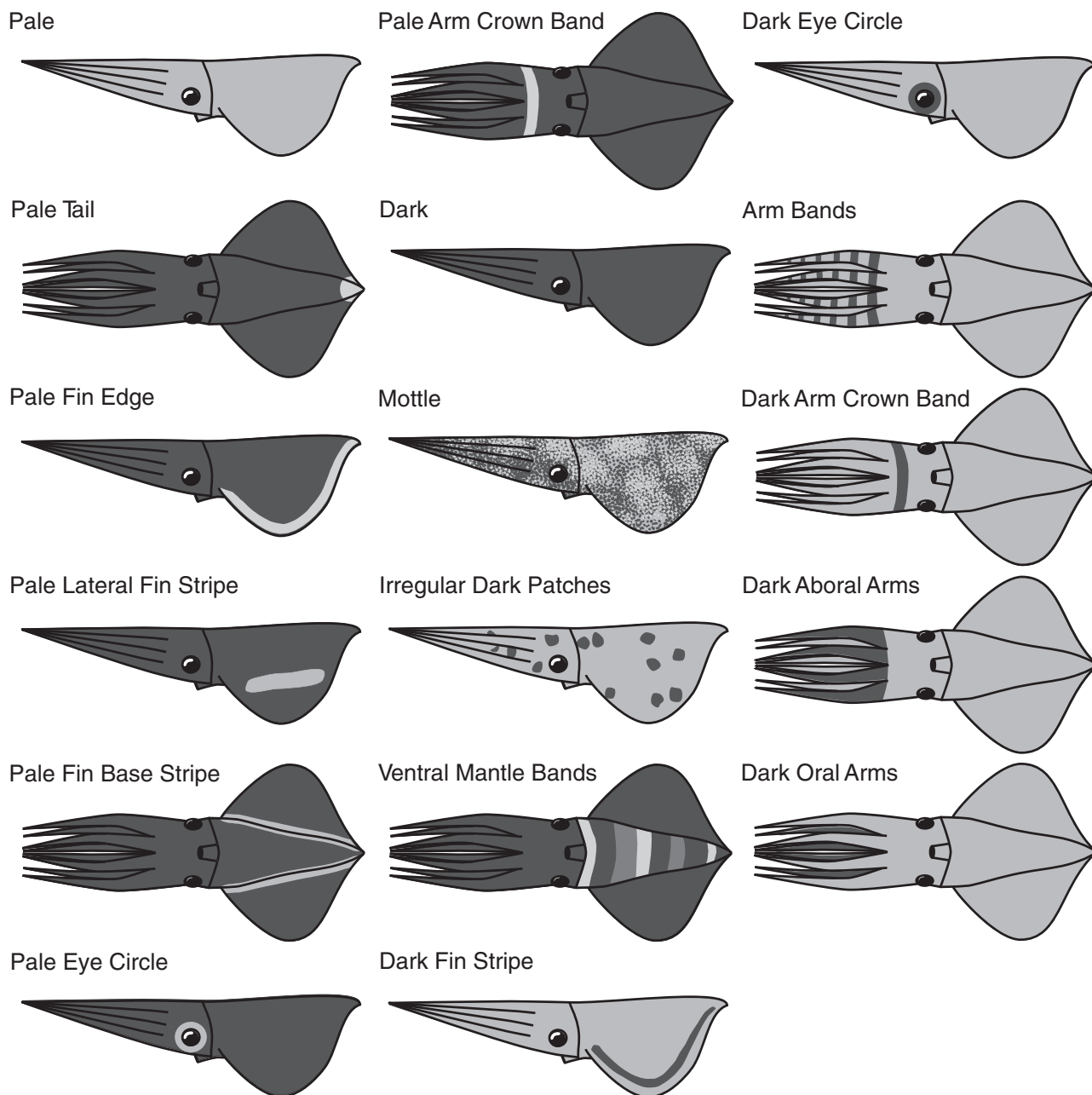

Figure 1. Light and dark chromatic behavioral components of *Octopoteuthis deletron*.

Table 1

Chromatic, postural, locomotor, and bioluminescent behavioral components and body patterns of Octopoteuthis deletron

Component type†	*n*¶	Description
Light chromatic components		
1. Pale Fin Edge*	51	Translucent or white along the entire length of both fin edges
2. Pale Tail*	48	White area at the posterior end of the ventral mantle; it may extend onto the posterior fins
3. Pale Arm Crown Band	17	Transverse area of white or gray across the base of the four ventral and/or the four dorsal arms
4. Pale Lateral Fin Stripe	15	Elongate pale area in the central region of the fin along anterior-posterior body axis, expressed dorsally or ventrally
5. Pale*	12	Whole body or any of the mantle, fins, funnel, head, and/or arms white to gray; very small individuals translucent
6. Pale Eye Circle	12	White or gray coloration partially or entirely surrounding the eye
7. Pale Fin Base Stripe	11	Pale region on the mantle and/or fin where fin and mantle meet, expressed dorsally or ventrally
Dark chromatic components		
1. Dark	61	Whole body or any of the mantle, fins, funnel, head and/or arms red or pink
2. Mottle*	28	Pale and red/pink creating irregular pattern on whole body or any of the mantle, fins, funnel, head, and/or arms
3. Dark Arm Crown Band*	21	Red band across the base of the four ventral and/or four dorsal arms
4. Dark Oral Arms	16	Some or all oral arms colored red/pink while the aboral arms pale
5. Ventral Mantle Bands*	16	Variable number of pale, medium red, and/or deep red bars spanning laterally across the ventral mantle
6. Arm Bands*	13	Regularly spaced red rings of a pale or pink arm
7. Dark Eye Circle	12	Red or pink surrounding the eye partially or entirely
8. Dark Fin Stripe	6	Red stripe along fin contours inward of the fin edge
9. Irregular Dark Patches*	6	Sparse, irregularly spaced red/pink patches over the whole pale individual or mantle, fins, funnel, head, and/or arms
10. Dark Aboral Arms	3	Some or all aboral arms colored red/pink while the oral arms pale
Postural components		
1. Dorsal Mantle Up*	67	Body horizontal with dorsal mantle upward
2. Dorsal Arm Curl*	63	Arms curling toward the dorsal mantle
3. Fins Out*	45	One or both fins are held straight out to either side
4. Tail Down*	38	Body vertical with posterior mantle downward
5. Fins Curled Ventrally	28	One or both fins wrap around the body, overlapping
6. Straight Arms	28	Arms point away from the head
7. Fins Curved Ventrally*	23	One or both fins curve ventrally
8. Tail Up	22	Body vertical with posterior mantle upward
9. Arm Tips Inward	18	Arms straight with arm tips curving toward oral region, sometimes crossing
10. Lateral Arm Spread	15	Arms spread to either side
11. Arm Keels Prominent	10	Skin flanges on aboral side of arms raised
12. Arms Curled*	10	Some or all arms coiled to form a single loop or a few whorls
13. Splayed Arms	9	Arms progressively farther from the other arms along the length
14. Compact Arms	7	The arms are intertwined and usually held close to the head
15. Central Arm Space	5	Arms curve outward then recurve orally so the tips are surrounded by the arms
16. Ventral Arm Curl	3	Arms curling toward ventral mantle
17. Dorsal Mantle Down	2	Body horizontal with ventral mantle upward (body upside-down)
Locomotor components		
1. Fins Flapping	59	Movement of the entire fins or the edge only
2. Hovering	51	Neutral buoyancy used to hold station in the water column; fins may be used for stabilization
3. Jolt*	50	A sudden, quick change in posture following previous quiescence or movement at moderate speeds
4. Arm Spread*	48	All eight arms briefly spreading into a wide circle, then returning to previous or new posture
5. Ink Release	43	Thick or diffuse clouds, pseudomorphs, long ropes, short strings, diffuse puffs, or alternating with defecation
6. Backward Jetting*	36	Rapid posterior first movement using the siphon; often accompanied by Full Fin Flaps
7. Full Fin Flap	24	Fins touch dorsally then quickly swing to touch or overlap ventrally; occurs once or multiple times consecutively
8. Grasp	23	Contact between oral side of arms and submersible, usually with Arms Spread
9. Backward Gliding*	22	Posterior first movement using only the siphon
10. Forward Jetting*	22	Rapid anterior first movement using the siphon; often accompanied by Full Fin Flaps
11. Arm Autotomy	13	Clean breaks along the arm or regenerated arm-tips as evidence of previous autotomy
12. Eye Blink	18	Skin around right or left eye covers then uncovers the lens
13. Rotating*	17	Revolutions around the vertical or horizontal body axis, while individual is stationary or moving
14. Backward Swimming*	15	Posterior first movement using the siphon and Fins Flapping
15. Flip*	14	Individual quickly turning the body 180°–360° from its original position
16. Forward Swimming	10	Anterior first movement using the siphon and Fins Flapping
17. Flicking Arm Tip/s	9	One or more distal arms were whipped back and forth
18. Writhing Arms	9	Arms wrapped around or immediately in front of the head and weaved in and out of each other
19. Arms Unroll	6	Arms held together, straightening along their length from a curved orientation such as Dorsal Curl
20. Bite	4	Attempt to grip submersible with beak
21. Forward Gliding	4	Anterior-first movement using only the siphon
22. Expose Arm Hooks	2	Hooks extended out of surrounding soft tissue

Table 1 (*Continued*)

Component type†	*n*¶	Description
Bioluminescent components		
1. Arm-tip Chrom. Contracted/Expanded*	38	Asynchronous on-and-off control of arm-tip bioluminescence
2. Chronic Arm-tip Chrom. Contracted*	32	Continuous bioluminescence of more than 1 min
3. Acute Arm-tip Chrom. Contracted*	27	Brief simultaneous flashes of the arm-tip photophores
Body Patterns		
1. Dark, Pale Tail, Pale Fin Edge, Dorsal Mantle Up, Dorsal Arm Curl, Fins Out or Fins Curved Ventrally (sometimes with Arm-tip Chromatophores Contracted/Expanded or Chronic Arm-tip Chromatophores Contracted)		
2. Dark, Jolt, Arm Spread, Forward Jetting or Backward Jetting, Acute Arm-tip Chromatophores Contracted (sometimes with Flip)		
3. Tail Down, Backward Gliding or Backward Swimming, Dark or Mottle on dorsal mantle, Ventral Mantle Bands, Dark Arm Crown Band, Arms Curled (sometimes with Rotating)		
4. Pale, Irregular Dark Patches, Arm Bands		

† All 59 components were used in the first NMDS ordination (Fig. 4); those denoted by an asterisk (*) were used in the second NMDS analysis (Fig. 5). (Chrom. = chromatophores).

¶ The number of individuals (*n*), among 76 specimens observed, which demonstrated the component or maneuver. Variations are given within the text.

in the ordination (Clarke and Gorley, 2006). Shared presence between samples increases the similarity between individuals; however, shared absence between samples does not increase similarity. Individual squid were treated as the samples, with behavioral components as the variables in the first NMDS analysis. This ordination indicates similarities between individuals with respect to the behaviors each performed. For each individual, ancillary data—encounter depth, temperature, salinity, oxygen, beam transmission, length of observation, year, month, observing vehicle, contact or no contact with vehicle, and whether or not the individual was collected—were mapped onto the ordination to assess potential correlations with observed behaviors. We were unable to quantify individual size and sex from the video and therefore could not map these factors onto the ordination. In the second NMDS analysis, behaviors were treated as the samples and individuals as the variables, to explore which behavioral components were commonly observed together. This analysis could not be calculated using the full data set because the format of the data matrix cannot indicate which behaviors were performed simultaneously. We therefore performed the analysis with a subset of behaviors that constituted the body patterns we defined, including only those behaviors that were unique to one body pattern. Our goal was to validate the body patterns by visualizing them in the ordination.

Undersea vehicles have provided invaluable *in situ* observations of mesopelagic nekton and zooplankton (Barham, 1963, 1966; Alldredge *et al.*, 1984; Widder *et al.*, 1989; Moiseev, 1991; Vecchione and Roper, 1991; Seibel *et al.*, 2005, Bush and Robison, 2007). Disturbances caused by vehicle presence have yet to be quantified (Hunt *et al.*, 2000; Widder *et al.*, 2005). However, we assume that although encounter with an ROV is unfamiliar, it will not result in novel behaviors (Hunt, 1996). Furthermore, because animals likely enter defensive mode when confronted

with unfamiliar stimuli, we believe that the behaviors observed represent, but are not limited to, defensive behaviors (Vecchione and Roper, 1991; Hunt, 1996; Hunt *et al.*, 2000, Bush and Robison, 2007).

Results

Seventy-six individuals of *Octopoteuthis deletron* were encountered during 64 ROV dives from 1992 to 2007. Observations were obtained between 0711 and 2129 Pacific Standard Time, and a total of 8.7 observation hours were accumulated. Individual observation length varied from a few seconds to more than 37 minutes. Encounter depths were between 344 and 1841 m; most individuals (93%) were found between 344 and 787 m (Appendix Fig. 1). Our observations provided no evidence of diel vertical migration (Appendix Fig. 2). The range of hydrographic parameters where *O. deletron* occurred was temperature, 2.3–7.8 °C; oxygen concentration, 0.14–1.36 ml/l O_2; practical salinity, 34.0–34.5; and beam transmission, 76.4%–92.4%. Collected specimens (*n* = 9) measured 4–15 cm in mantle length and represented immature and mature individuals of both sexes.

Ethogram

Octopoteuthis deletron has a broad repertoire of behavioral components with which it can respond to external stimuli. Here we describe all behavioral components that were performed by more than one individual. In most cases, the few components that were observed from only one individual can be classified as incomplete expressions of the components described here. The total number of components observed was 59, and they are organized into five categories. There are seven light chromatic components (Fig. 1, Table 1), 10 dark chromatic components (Fig. 1, Table 1), 17 postural components (Fig. 2, Table 1), 22 locomotor components and maneuvers (Table 1), and three
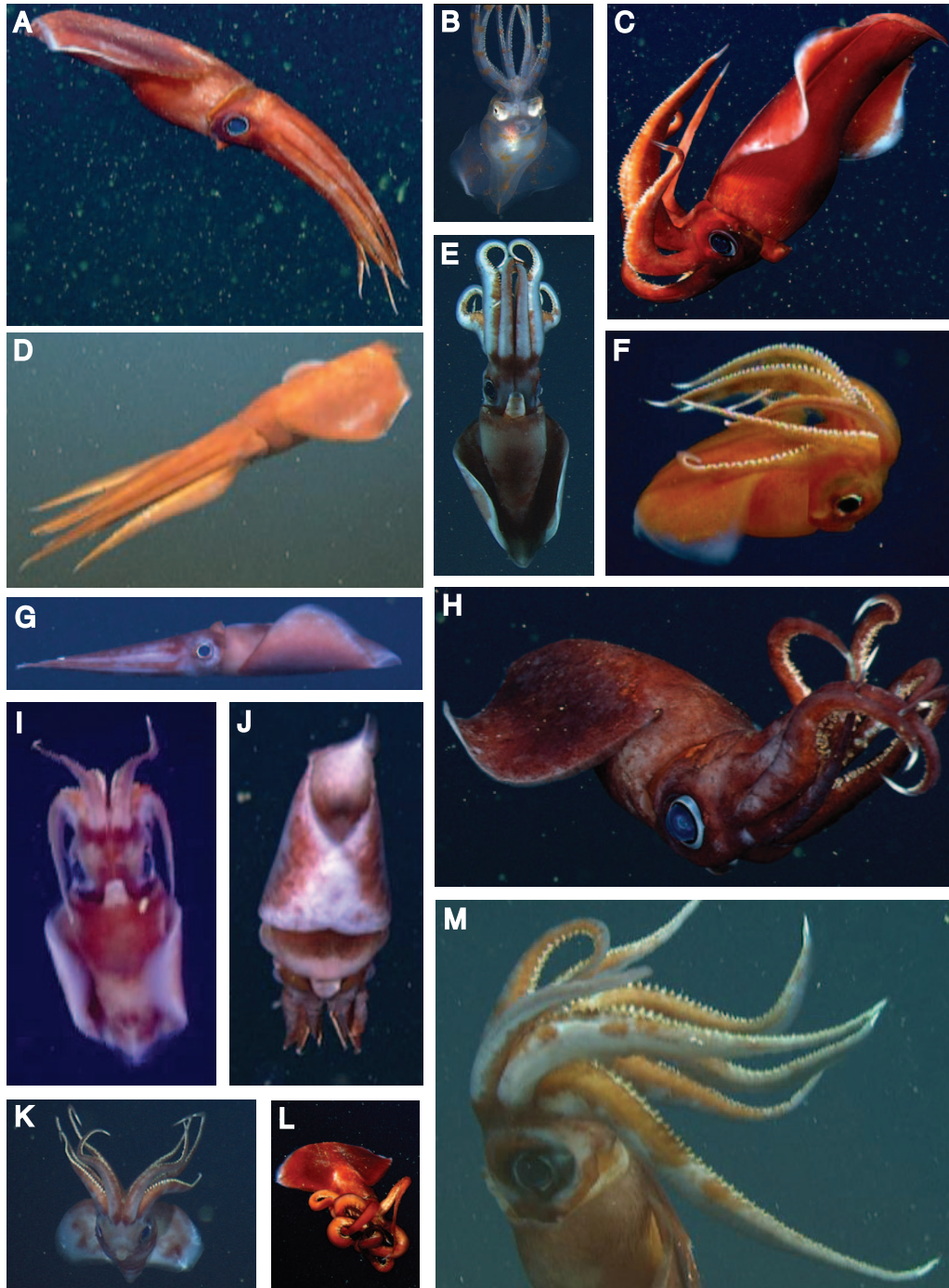
Figure 2. Postural components of *Octopoteuthis deletron*. (A) Dorsal Mantle Up, Fins Out, Ventral Arm Curl. (B) Tail Down, Fins Out, Central Arm Space. (C) Tail Up, Fins Out, Dorsal Arm Curl. (D) Dorsal Mantle Up, Fins Out, Arm Keels Prominent, Straight Arms. (E) Tail Down, Fins Curved Ventrally, Arms Curled. (F) Dorsal Mantle Up, Fins Curved Ventrally, Dorsal Arm Curl. (G) Dorsal Mantle Down, Fins Curved Ventrally, Straight Arms. (H) Dorsal Mantle Up, Fins Out, Arm Tips Inward. (I) Tail Down, Fins Curved Ventrally, Dorsal Arm Curl. (J) Tail Up, Straight Arms, Fins Curled Ventrally. (K) Tail Down, Fins Out, Lateral Arm Spread. (L) Dorsal Mantle Up, Fins Out, Compact Arms. (M) Tail Down, Dorsal Arm Curl, Splayed Arms. All images are frame-grabs taken directly from ROV dive footage and are unmodified except for cropping. All images © MBARI.

bioluminescent components (Fig. 3, Table 1). We report the number of individuals observed performing each behavior rather than the total number of times it was observed,

because individual observation times were not standardized. Components were not always completely expressed. Video sequences demonstrating some of the behavioral compo-
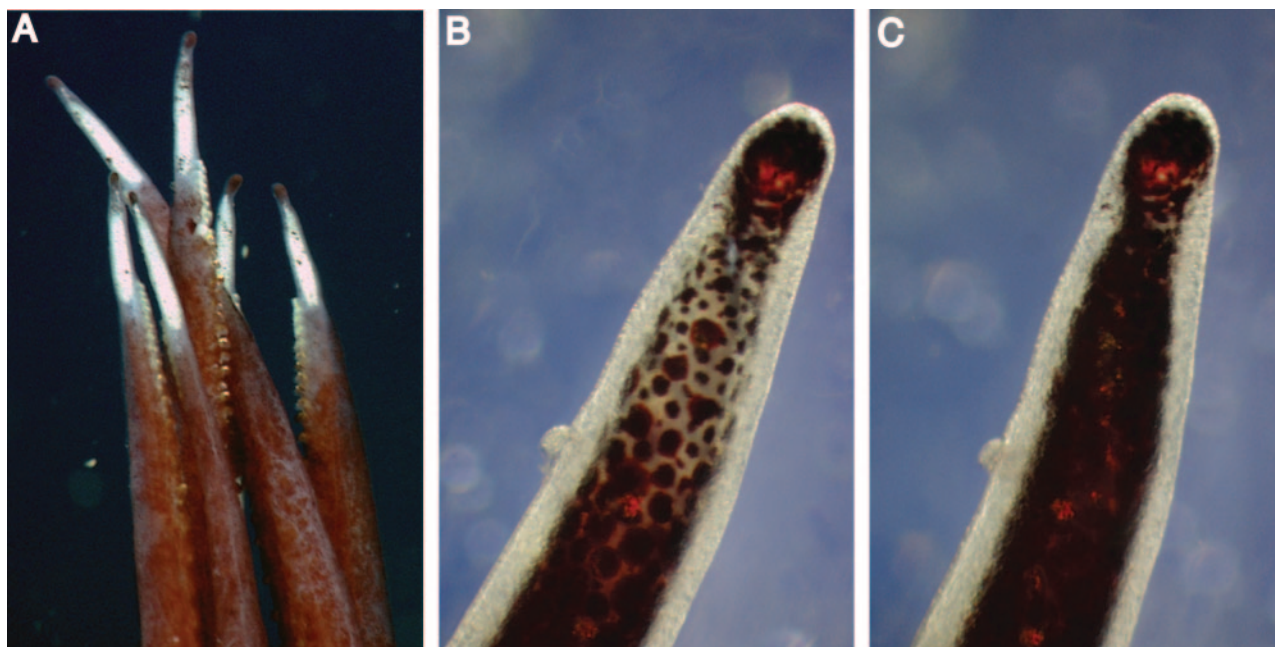
Figure 3. Different stages of arm-tip photophore bioluminescence in *Octopoteuthis deletron*. (A) Chromatophores contracted. A frame-grab taken directly from ROV dive footage. Image © MBARI. (B) Chromatophores partially expanded. (C) Chromatophores fully expanded. (B) and (C) are laboratory images taken with a microscope. All images are unmodified except for cropping.

nents, including the range of expression, can be viewed on MBARI's website (see Bush *et al.* 2008). Similar components described for previously studied squids are noted in the text as follows: components in single quotes are from published ethograms where each component has been explicitly defined; components in double quotes are from other published works. A brief description of four common body patterns is included.

Light chromatic components. **Pale** ($n = 12$) is a white or gray appearance of juveniles and adults. Very small individuals are translucent when expressing Pale. An individual may express Pale over the entire body or any combination of the mantle, fins, head, funnel, and/or arms. This component is similar to the following: 'clear' of *Doryteuthis plei* (Hanlon, 1982), *Loligo forbesii* (Porteiro *et al.*, 1990), *Loligo reynaudii* (Hanlon *et al.*, 1994), *Doryteuthis pealeii* (Hanlon *et al.*, 1999b), *Doryteuthis opalescens* (Hunt *et al.*, 2000), and *Sepioteuthis australis* (Jantzen and Havenhand, 2003); 'all clear' of *Alloteuthis subulata* (Lipinski, 1985); 'all light' of *Sepiola affinis* (Mauris, 1989); "clear" of *Gonatus onyx* (Hunt and Seibel, 2000); and "all white" of *Mastigoteuthis hjorti* (Vecchione *et al.*, 2002). **Pale Tail** ($n = 48$) consists of a small white posterio-ventral mantle area. It may extend onto the posterior fins. On occasion the tail photophore can be seen within the Pale Tail. In a few cases, a small red spot covers the tail photophore, making it conspicuous when surrounded by the Pale Tail. **Pale Fin Edge** ($n = 51$) is translucent or white along the entire edge of both fins. It is expressed in *S. affinis* during 'dark fins'

(see fig. 1 in Mauris, 1989), "colored fin centers" in *Chiroteuthis calyx* and *Galiteuthis phyllura* (Hunt, 1996), and "accentuated white fin edges" of *M. hjorti* (Vecchione *et al.*, 2002). Pale Fin Edge and Pale Tail are commonly expressed together. **Pale Lateral Fin Stripe** ($n = 15$) is an elongate pale area on the centro-lateral fin along the anterior-posterior axis. It may be expressed on the dorsal or ventral side. **Pale Fin Base Stripe** ($n = 11$) is a pale region along the mantle and/or fin where they meet. It is expressed either dorsally or ventrally, and is sometimes restricted to a central spot. **Pale Eye Circle** ($n = 12$) is a white or gray area partially or entirely surrounding the eye. This is similar to 'golden ocular epaulettes', restricted to the dorsal eye, of *S. australis* (Jantzen and Havenhand, 2003). **Pale Arm Crown Band** ($n = 17$) is a transverse white or gray area at the base of the four ventral arms and/or four dorsal arms. The Pale Arm Crown Band can be restricted to four ventral spots, one at each arm base, located over the arm base photophore.

Dark chromatic components. In **Dark** ($n = 61$), the mantle, fins, funnel, head, and/or arms are red or pink. In general, smaller individuals produce a lighter shade of red or pink; however, the shade can vary within an individual. Dark in *O. deletron* is similar to 'all dark' of *D. plei*, (Hanlon, 1982), *A. subulata*, (Lipinski, 1985), *S. affinis*, (Mauris, 1989), *L. forbesii* (Porteiro *et al.*, 1990), *L. reynaudii* (Hanlon *et al.*, 1994), *D. pealeii* (Hanlon *et al.*, 1999b), and *D. opalescens* (Hunt *et al.*, 2000); "solid orange" of *G. onyx* (Hunt and Seibel, 2000); "all-red" of *M. hjorti* (Vecchione *et al.*, 2002); 'dark mantle' and 'all dark'

of *S. australis* (Jantzen and Havenhand, 2003); and "red coloration" of *Taningia danae* (Kubodera *et al.*, 2007). In **Mottle** ($n = 28$), the mantle, fins, funnel, head, and/or arms are covered in an irregular pattern of pale and red or pale and pink. **Irregular Dark Patches** ($n = 6$) are small, unevenly spaced red or pink patches on a pale body. This component is observed only in small individuals and is similar to the 'irregular dark patches' of *A. subulata* (Lipinski, 1985), 'fin and mantle spots' of *L. forbesii* (Porteiro *et al.*, 1990), and 'fin spots' of *L. reynaudii* (Hanlon *et al.*, 1994) and *D. pealeii* (Hanlon *et al.*, 1999b). **Ventral Mantle Bands** ($n = 16$) consists of a variable number of pale, medium red, and/or deep red bands that span the breadth of the ventral mantle. They can occupy the entire mantle along the anterior-posterior axis or only part of its length, and each band may vary in width. The 'bands' of *L. reynaudii* (Hanlon *et al.*, 1994) and *D. pealeii* (Hanlon *et al.*, 1999b) are similar, except that in the shallow-water squids they are expressed both dorsally and ventrally. **Dark Fin Stripe** ($n = 6$) consists of red along the contours of the fin inside of the edge. Similar components in other species include 'stitchwork fins' of *D. plei* (Hanlon, 1982); 'dark fin line' and 'lateral mantle stripe' of *L. forbesii* (Porteiro *et al.*, 1990); 'fin stripe' of *L. reynaudii* (Hanlon *et al.*, 1994), *D. opalescens* (Hunt *et al.*, 2000), and *S. australis* (Jantzen and Havenhand, 2003); 'mantle margin stripe' of *D. pealeii* (Hanlon *et al.*, 1999b); "fin highlights" of *C. calyx* and *G. onyx* (Hunt, 1996; Hunt and Seibel, 2000); and "red fin edges" of *M. hjorti* (Vecchione *et al.*, 2002). **Dark Eye Circle** ($n = 12$) is red or pink that surrounds the eye partially or entirely. This component is more extensive than, but similar to, "eyebrow patches" of *C. calyx*, *G. phyllura*, and juvenile *G. onyx* (Hunt, 1996; Hunt and Seibel, 2000) and 'shaded eye' of *S. australis* (Jantzen and Havenhand, 2003). **Arm Bands** ($n = 13$) are regularly spaced rings along the arms, consisting of alternating pale or pink with red. They occur on some or all arms; for example, arms IV could have Arm Bands while the others do not. One band may occur across either the ventral or dorsal four arms near the base, but distal to the arm crown. The **Dark Arm Crown Band** ($n = 21$) is a transverse band across the base of the four ventral and/or four dorsal arms over the arm base photophores. Dark Arm Crown Band sometimes manifests as four red spots. Some or all of the aboral arms in **Dark Aboral Arms** ($n = 3$) are colored red or pink while the oral arms remain pale. The similar components 'dark arms' of *L. forbesii* (Porteiro *et al.*, 1990) and 'dark head and arms' of *L. reynaudii* (Hanlon *et al.*, 1994) do not include pale coloration of the oral arms. Some or all of the oral arms in **Dark Oral Arms** ($n = 16$) are colored red/pink while the aboral arms remain pale. This component is similar to 'white arms' of *D. pealeii* (Hanlon *et al.*, 1999b), though the latter is without the pale aboral arms.

Postural components. In **Dorsal Mantle Up** ($n = 67$, Fig. 2A, D, F, H, L) the body is horizontal with dorsal mantle upward. This is common to many squids—for example the "horizontal" of *Octopoteuthis megaptera* (Vecchione *et al.*, 2002). In **Dorsal Mantle Down** ($n = 2$, Fig. 2G) the ventral mantle is upward; *i.e.,* the individual is upside-down. In **Tail Up** ($n = 22$, Fig. 2C, J) the body is vertical, with the posterior mantle pointed upward. This component is equivalent to the mantle portion of the "head down posture" of mastigoteuthids (Roper and Vecchione, 1997; Young *et al.*, 1998; Vecchione *et al.*, 2002). In **Tail Down** ($n = 38$, Fig. 2B, E, I, K, M) the body is vertical with the posterior mantle downward. An equivalent "oblique body" occurs in *O. megaptera* (Vecchione *et al.*, 2002). In **Fins Out** ($n = 45$, Fig. 2A–D, H, K–L) one or both fins are held out to the side as in the "rigid fins" of *O. megaptera* (Vecchione *et al.*, 2002). The fins can be flapping while in Fins Out (see Locomotor components and maneuvers, below). **Fins Curved Ventrally** ($n = 23$, Fig. 2E–G, I) occurs when one or both fins bend toward the ventral mantle. It is equivalent to 'fins curved ventrally' of *D. opalescens* (Hunt *et al.*, 2000). In **Fins Curled Ventrally** ($n = 28$, Fig. 2J) one or both fins wrap closely around the body, one overlapping the other when both are curled. The fins can touch the mantle or not. The fins were never observed to pulse in this posture as *Mastigoteuthis magna* was observed to do, the latter creating a slow jet-propulsion (Roper and Vecchione, 1997). **Straight Arms** ($n = 28$, Fig. 2D, G, J) point away from the mantle and are either (a) held together along their entire length (Fig. 2G) as in "aligned arms" of *Histioteuthis heteropsis* (Hunt, 1996) and 'rigid arms' of *S. australis* (Jantzen and Havenhand, 2003), (b) lined up next to one another in a plane (Fig. 2D) similar to 'arm plane' of *D. opalescens* (Hunt *et al.*, 2000), or (c) spaced slightly apart so arms do not touch distally (Fig. 2J). One or two arm-tips can stick out from the rest of the arms while in Straight Arms, similar to 'two raised arms' of *L. forbesii* (Porteiro *et al.*, 1990), and 'raised arms' of *D. opalescens* (Hunt *et al.*, 2000), and *S. australis* (Jantzen and Havenhand, 2003). **Dorsal Arm Curl** ($n = 63$, Fig. 2C, F, I, M) involves the arms curving toward the dorsal mantle. The variations of this posture include (a) arms held together pointing above the head, *i.e.,* perpendicular to the anterior-posterior axis; (b) arms curved back closely over the head (Fig. 2C); (c) arms curved over the dorsal mantle (Fig. 2F); (d) arms curved over the dorsal mantle, held side-to-side in a plane; (e) arms curved over the dorsal mantle, some or all arms distally curved back toward the head (Fig. 2I); and (f) arms spread from above the head to over the mantle, either straight or with curved tips. Equivalent components are the "cockatoo" posture of cranchiid squids (Vecchione and Roper, 1991), "J-curl" of *G. onyx* (Hunt and Seibel, 2000), 'J-curl' of *D. opalescens* (Hunt *et al.*, 2000), "arms flexed dorsally" of *O. megaptera* (Vecchione *et al.*, 2002), and 'upward curl' of *S. australis* (Jantzen and Havenhand, 2003). **Ventral Arm Curl** ($n = 3$, Fig. 2A) has the arms curved toward the ventral mantle. The 'downward curl' of *L. forbesii* (Porteiro *et al.*, 1990),

'drooping arms' of *D. pealeii* (Hanlon *et al*., 1999b), 'downward curling' of *D. opalescens* (Hunt *et al*., 2000), and 'downward curl' and 'drooping arms' of *S. australis* (Jantzen and Havenhand, 2003) are all comparable. In **Splayed Arms** (*n* = 9, Fig. 2M) the arms are progressively farther from the other arms along their length. This can occur while the arms are positioned in any direction relative to the mantle. Usually the arms spread from the base; however, the arms may be held together proximally and medially, with only the distal arms extended outward. The 'PI posture' of *S. affinis* (Mauris, 1989); 'splayed arms' of *L. forbesii* (Porteiro *et al*., 1990), *L. reynaudii* (Hanlon *et al*., 1994), and *D. opalescens* (Hunt *et al*., 2000); and 'splayed arms' and 'flared arms' of *D. pealeii* (Hanlon *et al*., 1999b) are similar. **Arm Tips Inward** (*n* = 18, Fig. 2H) involves the arms held out from the head with the arm tips curving toward the oral region, sometimes crossing. The following modifications were observed: (a) one arm pair (pair I) was S-curved or C-curved above the other arms, or (b) one pair (pair IV) remained straight. In **Arms Curled** (*n* = 10) some or all of the distal arms are coiled to form a single loop or a few concentric whorls. One variation (Fig. 2E) consists of four or six arms curled and the resultant rings spread in a plane and lined up end to end, similar to the "Elk" posture of *G. onyx* (Hunt and Seibel, 2000). **Arm Keels Prominent** (*n* = 10, Fig. 2D) occurs when the skin flanges on the aboral arms are raised in one or more arm pairs. Keels on the third arm pair may function as airfoils for stabilization and lift modification during locomotion in *Lolliguncula brevis* (Bartol *et al*., 2001). We observed Arm Keels Prominent while individuals were stationary. **Central Arm Space** (*n* = 5, Fig. 2B) occurs when (a) the arms curve outward proximally then inward distally or (b) the arms are held together at the base, curved outward medially, then inward distally. In both cases, the tips curl orally and are surrounded by the arms. In **Lateral Arm Spread** (*n* = 15, Fig. 2K) the arms are spread to the sides in a few different conformations: (a) a 'V' in front of the head with arms straight or distally curved inward, (b) arms curve to either side then extend posteriorly along the mantle, (c) spread in a 180° arc away from the head, or (d) each dorsal arm meets with the corresponding ventral arm—*i.e.,* LI with LIV, LII with LIII, RI with RIV, and RII with RIII—to form four pairs that spread away from the head. Similar postures are 'PB2' of *S. affinis* (Mauris, 1989) and 'downward V curl' of *L. reynaudii* (Hanlon *et al*., 1994). In **Compact Arms** (*n* = 7, Fig. 2L) each arm is curved or curled and intertwined with the other arms, which commonly cover the head.

Locomotor components and maneuvers. While **Hovering** (*n* = 51), an individual maintains its position in the water column, either remaining motionless or using the fins for stabilization. Neutral buoyancy has been described for *O. megaptera* and many other deep-sea cephalopods (Vecchione *et al*., 2002; Seibel *et al*., 2004). **Fins Flapping** (*n* = 59) consists either of synchronized flapping of the edges or entire fins, or of sinusoidal waves along the length of the fins. An analogous movement is "fin undulations" of *M. magna* (Roper and Vecchione, 1997). In a **Full Fin Flap** (*n* = 24), the fins touch dorsally along the lateral edge, and then quickly swing all the way around the mantle to touch or overlap ventrally. This component may occur once or multiple times sequentially and generally accompanies Jetting or a Jolt (see below). Comparable locomotion occurs as "dorsoventral beat" of *M. magna* (Roper and Vecchione, 1997), "flapping of fins" in *O. megaptera* (Vecchione *et al*., 2002), and "cycle of fin movement" in *T. danae* (Kubodera *et al*., 2007). **Backward Gliding** (*n* = 22) *sensu* Hunt *et al*. (2000) is gradual posterior-first movement using only the funnel, with fins held rigid. **Forward Gliding** (*n* = 4) *sensu* Hunt *et al*. (2000) is gradual anterior-first movement using only the funnel for propulsion, while the fins are held rigid. Speed for Backward and Forward Gliding is less than half a body length per second. **Backward Swimming** (*n* = 15) is posterior-first movement using the funnel and Fins Flapping. **Forward Swimming** (*n* = 10) is anterior-first movement involving both the funnel and Fins Flapping. **Backward Jetting** (*n* = 36) is rapid posterior-first movement *via* funnel pulses. **Forward Jetting** (*n* = 22) is anterior-first movement involving rapid expulsion from the funnel. Speeds of two or three body lengths per second are typical for Backward and Forward Jetting. Full Fin Flaps usually accompanied Forward and Backward Jetting. No matter the form of locomotion, whether gliding, swimming, or jetting, forward or backward, the movements we observed were typically downward (deeper) in the water column and only rarely upward. Movement toward greater depths has also been observed in *G. phyllura*, *G. onyx*, and *C. calyx* (Hunt, 1996; pers. obs.). **Rotating** (*n* = 17) is more than one body revolution around the vertical or horizontal axis. It can occur while the individual is stationary or moving. Rotation around the anterior-posterior body axis has been observed in *H. heteropsis* (Hunt, 1996). A **Jolt** (*n* = 50) is a sudden, quick change in posture or movement. Either just the arms are flung forward in a Jolt, once or a few times, and then returned to their previous orientation, or the whole body moves. A Jolt may immediately follow a mechanical disturbance from the ROV (*n* = 9), without physical contact with the vehicle. **Arm Spread** (*n* = 48) involves all eight arms spreading into a wide circle, and then returning to the previous or a new posture. It can be a slow maneuver but is usually rapid. Most often the arms are straight while spread, but they can curve orally, clockwise, or counterclockwise distally. Somewhat analogous maneuvers occur as 'peristaltic arm flare' in *S. australis* (Jantzen and Havenhand, 2003), "arms swept up" of *Vampyroteuthis infernalis* (Hunt, 1996; Robison *et al*., 2003), and "spreading all arms" of *T. danae* (Kubodera *et al*., 2007). A **Flip** (*n* = 14) involves the individual quickly rotating the body forward, end-over-end, 180°–360° from its starting position. It is often preceded by a Jolt and can be concurrent with Arm Spread. It is com-

parable to the "somersault" of *T. danae* (Kubodera *et al.*, 2007). **Ink Release** is observed in several forms: (a) a cloud (*n* = 25), either diffuse or of interconnecting ink blobs, (b) a single pseudomorph (*n* = 9) or two or more consecutive pseudomorphs (*n* = 2) that hold their shape, (c) a diffuse puff (*n* = 6), (d) a long slender rope (*n* = 2), (e) a short, thin string (*n* = 2), and (f) alternating with defecation (*n* = 1). Seven individuals released more than one of the above ink types. Several squid (*n* = 8) inked within the collection device; therefore the release type could not be determined. Commonly, as we approached a cloud we found the individual either within or adjacent to the ink. Pseudomorphs usually occurred as the squid jetted away from encounter. The ink is viscous and may remain intact for several minutes (Bush and Robison, 2007). **Arms Unroll** (*n* = 6) begins with the arms held together, straightening in unison along their length from a curved posture such as Dorsal Arm Curl. **Eye Blink** (*n* = 18) consists of the skin surrounding the left or right eye closing over the lens, then opening; it happens either once or a few consecutive times. **Writhing Arms** (*n* = 9) occurs as the arms wrap around or immediately in front of the head and weave in and out of each other. It was observed separately from the stationary Compact Arms postural component. During **Flicking Arm Tip/s** (*n* = 9), one or more distal arms are whipped back and forth. This sometimes accompanies Writhing Arms. Individuals **Grasp** (*n* = 23) parts of the vehicle, usually with Arms Spread and followed by Forward or Backward Jetting. The similar component "attacking" occurs in *T. danae* (Kubodera *et al.*, 2007). **Bite** (*n* = 4) occurs when captured individuals are seen moving around in the clear collection apparatus opening and closing the beak against the container. Individuals can **Expose Arm Hooks** (*n* = 2) by pushing them out of the surrounding soft tissue. **Arm Autotomy** was observed in the laboratory; evidence of previous autotomy was seen as shortened arm stubs of individuals *in situ* (*n* = 13). This has been reported for other deep-sea cephalopods: "missing arm tips" in *O. megaptera* (Vecchione *et al.*, 2002) and in *O. neilseni* (Young and Vecchione, 2006), and "regenerated light organs" of *V. infernalis* (Robison *et al.*, 2003).

Bioluminescent components. Chromatophore layers surrounding the photogenic tissue control the bioluminescent output of arm-tip photophores. We assumed that arm-tip photophores were luminescent when we could see the pale, reflective photogenic tissue as the chromatophores contracted (Fig. 3). The number of bioluminescent components is probably underestimated here because close observations in which we could clearly see the arm-tip photophores were limited. **Arm-tip Chromatophores Contracted/Expanded** (*n* = 38) is intermittent bioluminescence. The eight photophores are not synchronized and may flash at variable rates. This component is commonly coupled with the following postural components: Dorsal Arm Curl, Arm Tips Inward, Central Arm Space, Writhing Arms, Arms Curled, and/or

Flicking Arm Tips. Similar behaviors have been reported as "responses 1 and 3" of *Pterygioteuthis microlampas* and *Pterygioteuthis giardi* (Young *et al.*, 1982), the "flashes" of *T. danae* (Roper and Vecchione, 1993), and the "flash" of *V. infernalis* (Robison *et al.*, 2003). **Chronic Arm-tip Chromatophores Contracted** (*n* = 32) signifies continuous bioluminescence of more than 1 min and was observed with Arms Straight, Dorsal Arm Curl, Arm Tips Inward and/or Central Arm Space. **Acute Arm-tip Chromatophores Contracted** (*n* = 27) is brief, simultaneous bioluminescence of the eight arm-tip photophores, most commonly occurring during Arm Spread. The "bright flashes" and "short flash" of *T. danae* (Roper and Vecchione, 1993; Kubodera *et al.*, 2007), and "arm tips glowing" of *V. infernalis* (Robison *et al.*, 2003) are comparable. For many individuals, a combination of Arm-tip Chromatophores Contracted/Expanded and Chronic Arm-tip Chromatophores Contracted occurs. For example, arms I terminal photophores are in Chronic Arm-tip Chromatophores Contracted, whereas the other six photophores are in Arm-tip Chromatophores Contracted/Expanded.

Body patterns. We have not made an exhaustive list of the body patterns that *O. deletron* is capable of, but we present a few of the most commonly observed. The first pattern involves Dark with Pale Tail and/or Pale Fin Edge, and the postural components Dorsal Mantle Up, Dorsal Arm Curl, and Fins Out or Fins Curved Ventrally. In many cases Arm-tip Chromatophores Contracted/Expanded or Chronic Arm-tip Chromatophores Contracted were also performed. A second body pattern consists of Dark coloration with Jolt, Arm Spread, Forward or Backward Jetting, and Acute Arm-tip Chromatophores Contract; Flip is sometimes included. In the third pattern, individuals paired Tail Down with Backward Gliding or Backward Swimming, Rotating, Dark or Mottle on the dorsal surface, Ventral Mantle Bands, Dark Arm Crown Band, and Arms Curled. In a fourth body pattern, small individuals frequently demonstrated Pale (translucent) with Irregular Dark Patches over the mantle and fins and Arm Bands.

Non-Metric Multi-Dimensional Scaling ordination

The dataset for the NMDS analyses consisted of 76 individuals each with observed/not observed scores for the 59 behaviors described above. The first NMDS arranged individuals (data points) in two dimensions on the basis of the behaviors each squid performed in common with every other individual. Close data points indicate that the two individuals they represent performed more behaviors in common than individuals farther apart in the ordination. The stress of an NMDS solution refers to the ease with which the data can be arranged into the given number of dimensions. Stress for our 2-dimensional solution is 0.19; stress for the 3-dimensional solution is 0.14. Kruskal (1964) indicates that stress values from 0.10–0.20 are fair to poor

in terms of explaining variation of the data. Despite these high stress values, we present the 2-dimensional solution to show which of the factors affected the behaviors performed. Individuals encountered at similar depths do not cluster in our ordination (data not shown), indicating that depth is not correlated with observed behaviors. The same is true of salinity, temperature, oxygen concentration, beam transmission, observation year, month, and vehicle (data not shown). However, individuals that were observed for longer than 10 minutes are clustered in the ordination and surrounded by individuals that were observed for 10 minutes or less (Fig. 4A). Longer observation time led to more behaviors observed (Appendix Fig. 3,) and therefore more behaviors in common. Individuals that contacted the ROV performed more behaviors in common than individuals that did not contact the ROV, and individuals that were collected performed more of the same behaviors than individuals that were not collected (Fig. 4B–C).

The second NMDS, in which we used a subset of behaviors to test the validity of the four body patterns we defined (Table 1), is composed of four clusters of behaviors (Fig. 5; 2D stress = 0.15; 3D stress = 0.09). All of the components included in this analysis are likely part of one or multiple body patterns other than the four described in the current study. This is probably the reason for the poor fit of the NMDS solution to the data. Nevertheless, each cluster corresponds to one of the body patterns, indicating that they are natural elements of *O. deletron*'s behavior.

Discussion

In contrast to predictions that the body patterning of deep-sea cephalopods is limited to transparency, silvering, red coloration, counter-illumination, and bioluminescence (Hanlon and Messenger, 1988, 1996; Nixon and Young, 2003), we have seen that *Octopoteuthis deletron* can exhibit numerous behavioral components. In fact, the total number of components now described for *O. deletron* (59) is comparable to that for other squids for which ethograms are available: 16 components (chromatic only) in *Doryteuthis plei* (Hanlon, 1982), 59 mentioned for *Sepioteuthis affinis* (Mauris, 1989), 28 in *Loligo forbesii* (Porteiro *et al.*, 1990), 36 in *Loligo reynaudii* (Hanlon *et al.*, 1994), 56 in *Doryteuthis pealeii* (Hanlon *et al.*, 1999b), 39 in *Doryteuthis opalescens* (Hunt *et al.*, 2000), and 48 in *Sepioteuthis australis* (Jantzen and Havenhand, 2003). It is unclear what, if any, benefits are conferred by these numerous behavioral capabilities. However, possibilities include interspecific communication, such as attracting prey or deterring predation, and/or intraspecific communication—for example, species recognition and mate attraction.

Octopoteuthis deletron may use variable body patterning and positioning as a primary defense to cause search image impedance and avoid detection by a predator. Deep-sea cephalopods are known prey of teleosts, marine mammals,
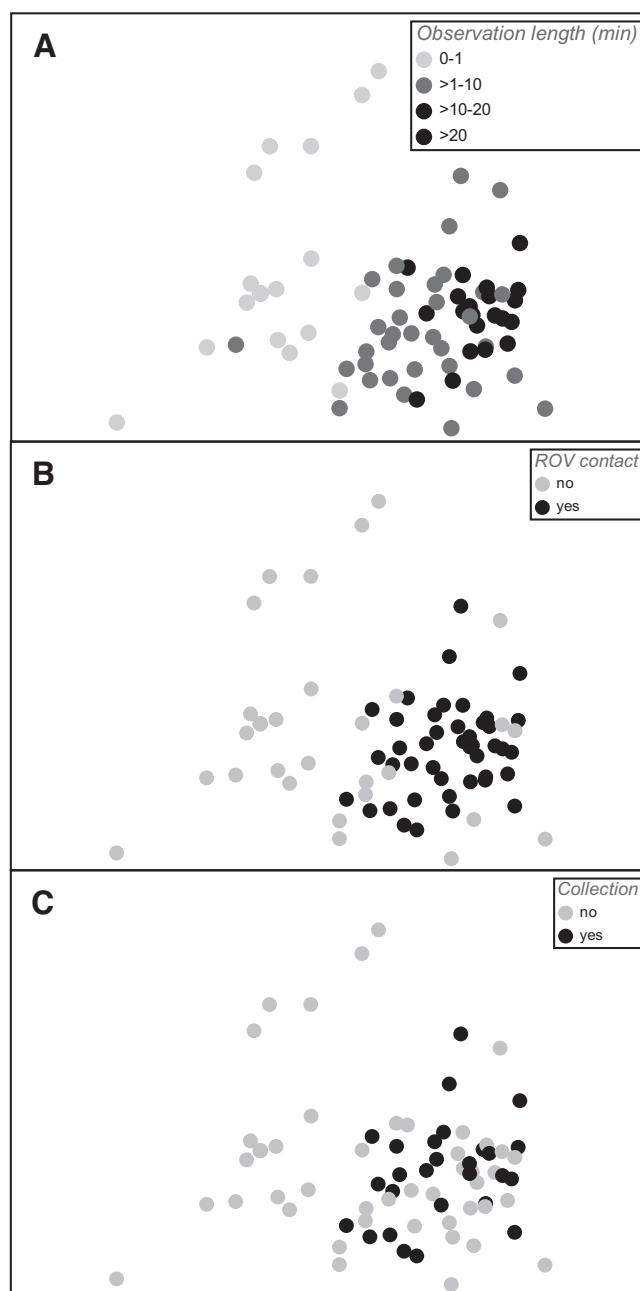

Figure 4. Non-metric Multi-Dimensional Scaling ordination of individual *Octopoteuthis deletron* behavior sets. Observation length (min), ROV contact, and collection correlated with behaviors observed. (A) Observation length (min). (B) ROV contact. (C) Collection.

sharks, and other cephalopods (Clarke, 1994, 1996; Klages, 1996; Markaida and Hochberg, 2005). Some of these predators forage visually, despite the limited light conditions of meso- and bathypelagic depths (Levenson and Schusterman, 1999; Fristup and Harbison, 2002; Southall *et al.*, 2002; Watwood *et al.*, 2006), and they probably form search images to increase hunting efficiency (Edmunds, 1974). Shallow-water cephalopods are capable of quickly changing their appearance to counteract visual search images (Hanlon
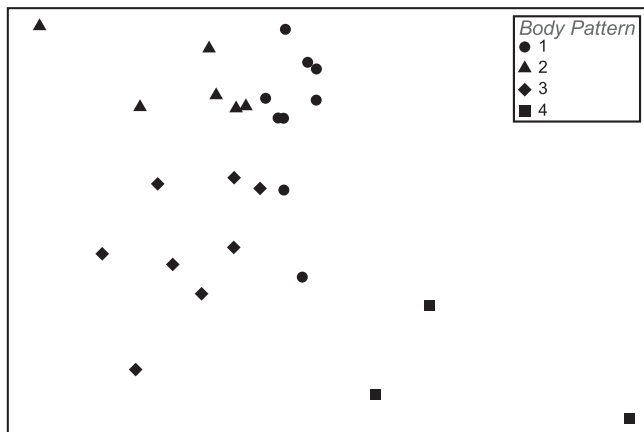
Figure 5. Non-metric Multi-Dimensional Scaling ordination calculated from the subset of behavioral components that comprise the four body patterns (Table 1).

and Messenger, 1996; Huffard, 2006), and it is likely that *O. deletron* uses complex postural and bioluminescence body patterning toward this end. Locomotor components and maneuvers may serve to impede the hydrodynamic signature of squid. Many deep-sea fish have well-developed lateral lines that can detect even the smallest movements of their prey (Marshall, 1979). Pinniped vibrissae are sensitive to prey movements and can be used to track prey from hundreds of meters away (Dehnhardt *et al.*, 2001). *O. deletron*'s extensive locomotor components and maneuvers may prevent detection by confusing such hydrodynamic search images.

Disruptive coloration and illumination may be used to obstruct the body outline and prevent detection. *Octopoteuthis deletron*'s chromatic components that comprise interspersed white and red areas may serve a disruptive function. The red body coloration appears black while the white areas are discernible, breaking up the body outline. This effect was observed when encountered individuals were at the farthest limits of the vehicle's lights—the red blended with the dark background, but the white areas were conspicuous. Similarly, the body pattern consisting of a uniform Dark or Mottle dorsal side, with Ventral Mantle Bands and ventral Dark Arm Crown Band may confuse predators as the Rotating squid appears and disappears. Ventral photophores may produce disruptive illumination (Herring, 1977). The combination of disruptive illumination and disruptive coloration, whereby dark or light chromatic components and bioluminescence accentuate each other, may be an effective cryptic strategy.

Secondary defenses are enacted once an individual is aware of a predator's presence or has been detected by a potential predator (Edmunds, 1974). Some components may be used to alert, blind, startle, or confuse predators once concealment has failed. Arm-tip photophore bioluminescence is conspicuous and may communicate to predators that the squid is alert and aware of its presence, thereby

forestalling an attack (Young *et al.*, 1982). Young *et al.* (1982) predicted that bright bioluminescent displays might temporarily blind the sensitive eyes of predators, allowing an animal to elude a potential predator. The commonly observed Arm Spread, with all eight photophores simultaneously bioluminescent (Acute Arm-tip Chomatophores Contracted), was frequently followed by Forward or Backward Jetting. This sequence may startle or bewilder a predator and allow escape. Downward movement is a common response of mesopelagic micronekton, including many squids, that serves to move an individual away from a disturbance and into darker water (pers. obs.).

The maneuvers Grasp, Bite, and Arm Autotomy probably constitute a last-resort defensive attempt to cause physical injury to a predator or to sacrifice a diversionary body part (Edmunds, 1974; Herring, 1977; fig. 9.10 by R. Young, in Hanlon and Messenger, 1996). The hooks and beaks likely irritate or injure predators, causing them to release the individual. An autotomized arm with bioluminescing arm-tip photophore may distract a predator while the squid retreats.

Body patterning could also be used for prey acquisition. Bioluminescent flashes, such as Arm-tip Chromatophores Contracted/Expanded, or Flicking Arm-tips during bioluminescence might attract crustaceans, fish, or cephalopods within reach by mimicking their prospective prey (Herring, 1977). Bioluminescent lures occur in anglerfishes and stomiatoid fishes, and photophores in some chiroteuthid, histioteuthid, cranchiid, and enoploteuthid squids, cirrate octopuses, and *V. infernalis* have been proposed as lures (Herring, 1977; Marshall, 1979; Hunt, 1996; Robison *et al.*, 2003).

The same chromatic components that effectively hide *O. deletron* from its predators could allow it to remain undetected as it hunts its own prey. In the deep sea, the roles of predator and prey are sometimes suddenly interchangeable. Many species are capable of capturing and consuming individuals almost as large as themselves, so the effectiveness of remaining undetected may determine who obtains a meal and who becomes a meal.

Complex body patterning behaviors may also be important in intraspecific communication. Deep-sea animals are often widely dispersed and may have specific mechanisms to assist in species recognition, mate selection, and reproductive behavior (Herring, 2000). While long distance attraction probably involves chemosensory tactics, photophores are likely key tools for species recognition at closer range (Herring, 1977, 2000). Photophore arrangement is often species-specific, and some species also have sexually dimorphic photophore positions (Young, 1975; Herring, 1977, 2000). However, coloration, postures, locomotion, and maneuvers may be important in these interactions as well, or as a means to orchestrate bioluminescent displays used to communicate with conspecifics (fig 9.10 by R. Young, in Hanlon and Messenger, 1996). Cephalopods also

have a lateral line analog that could be used to detect and recognize potential mates by their particular locomotion or maneuvers (Budelmann and Bleckman, 1988).

Several non-communication possibilities exist to explain the behaviors of *O. deletron,* including physiology, locomotor efficiency, ontogeny, and phylogeny. Previous authors have predicted that physiological limitations during locomotion may cause certain color patterns, or may limit others due to connections between locomotor muscles and chromatophore muscles (Hunt, 1996; Huffard, 2006). However, in the current study we found no cases of chromatic components linked with locomotion. Hunt (1996) hypothesized that some postures were designed for maximum hydrodynamic efficiency during locomotion and therefore had no role in signaling. However, we observed many postures, maneuvers, and chromatic components in stationary individuals. Juvenile *O. deletron* occur in the upper few hundred meters of the water column (Okutani and McGowan, 1969). The behaviors we observed could be remnants of these juvenile stages that are no longer useful at mesopelagic depths. Although we observed only a few juveniles, they appeared to have a smaller behavioral repertoire than adults (analyses not performed). Finally, *O. deletron*'s behaviors may reflect those of their ancestors, which recent phylogenies indicate were also deep-water species (Lindgren *et al*., 2004; Strugnell *et al*., 2006; Lindgren and Daly, 2007). It is possible that ancestral deep-sea cephalopods also had varied repertoires of body patterning. We conclude that the behaviors we observed in *O. deletron* are unlikely to be vestigial given that they are metabolically costly and those used in intraspecific communication might attract predators. We assume that behaviors with no current utility will be lost over evolutionary time.

Non-metric Multi-Dimensional Scaling was successfully used to display similarities between individuals on the basis of the behaviors observed from each and to assess observer-defined body patterns. Although these analyses did not explain the majority of variation in our data sets, we did demonstrate that hydrographic data such as depth and oxygen apparently did not affect which behaviors an individual performed, but the length of our observations and the interactions of the squid with the ROV did affect an individual's behavior. This information is essential to obtaining further observations and interpreting the function of the behaviors defined in this study. Lastly, although the format of our data matrix did not allow determination of body patterns from the NMDS, we have shown that it may be used to support those previously defined.

Acknowledgments

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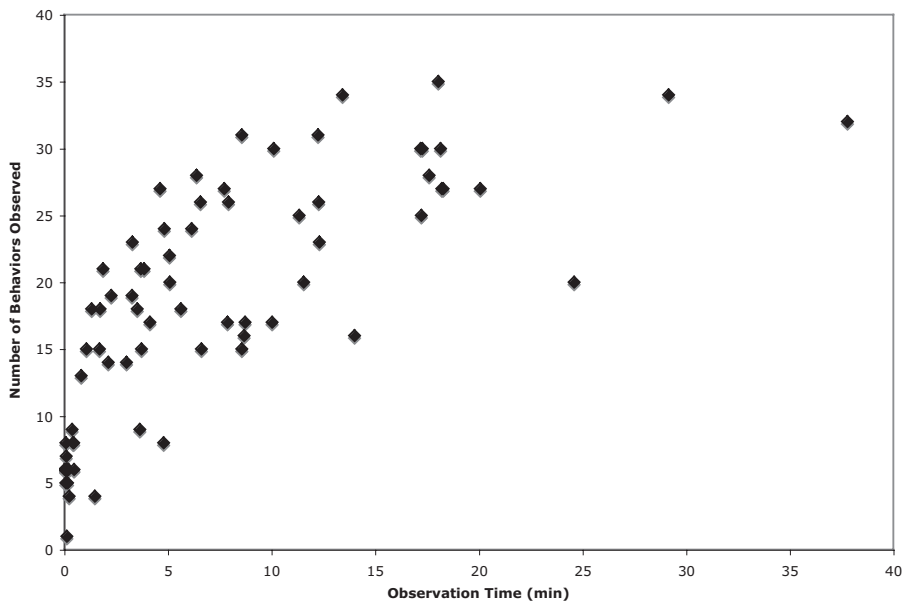
Appendix
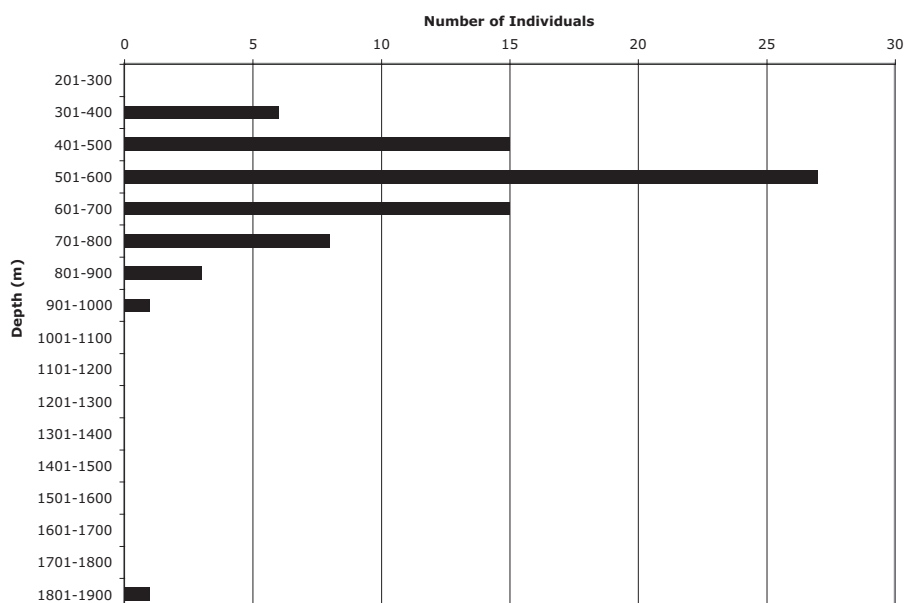
Appendix Figure 1. *Octopoteuthis deletron* encounter depths.
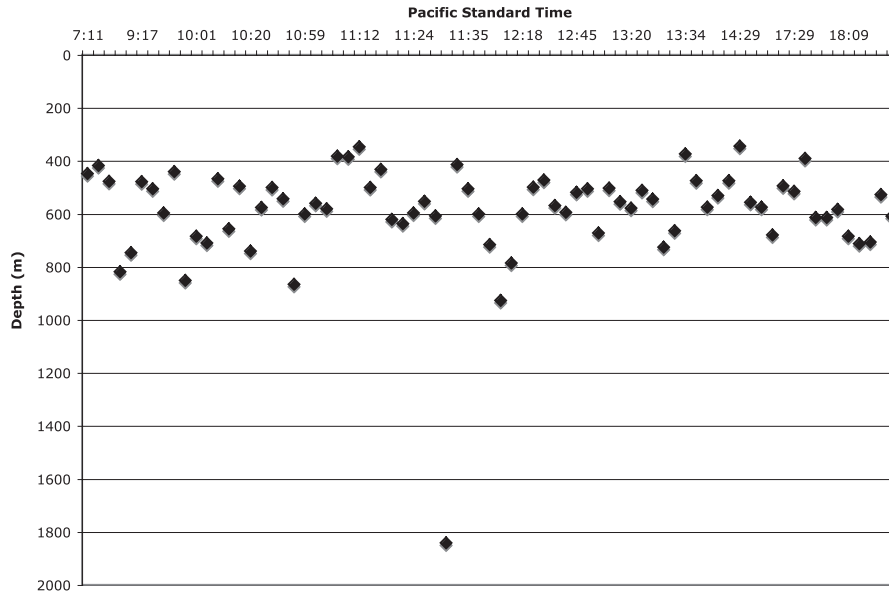
Appendix Figure 2.   Encounter depth compared with time of day (Pacific Standard Time).

Appendix Figure 3.   Number of behaviors performed by individual *Octopoteuthis deletron* compared to the amount of time (min) each individual was observed.