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Economy of arm autotomy in the mesopelagic squid *Octopoteuthis deletron*

Stephanie L. Bush[1,2,3,*]

[1]Midwater Ecology Lab, Monterey Bay Aquarium Research Institute, Moss Landing, California 95039, USA
[2]Department of Integrative Biology, Valley Life Sciences Building, University of California, Berkeley, California 94720, USA
[3]*Present address:* Department of Biological Sciences, Center for Biotechnology and Life Sciences, University of Rhode Island, Kingston, Rhode Island 02881, USA

ABSTRACT: Remotely operated vehicles (ROVs) were used to observe and collect the mesopelagic squid *Octopoteuthis deletron* Young, 1972. I documented numerous individuals with shortened, blunt-ended arms and regenerating arm-tips, which may be indicative of arm autotomy, i.e. the jettisoning of a body part as a defense. To test the hypothesis that *O. deletron* is capable of arm autotomy, laboratory investigations and an *in situ* experiment using ROVs attempted to induce autotomy. I looked for autotomy fracture planes in histologically sectioned arms. *O. deletron* is capable of arm autotomy, but it requires traction to occur. *O. deletron* has numerous places where an arm can sever; arm breakage always occurred immediately proximal to the point of interaction, minimizing tissue loss, and demonstrating 'economy of autotomy'. Despite the fact that this species can autotomize an arm anywhere along its length, only a few well-defined fracture planes were found in our histological sections, indicating that autotomy probably occurs via loss of tensile strength during a defensive interaction. In *O. deletron*, an autotomized arm usually thrashes and the terminal arm photophore bioluminesces—whether a steady glow, flashing on and off, or both—which could be an important part of predator distraction associated with autotomy in dark, mesopelagic waters. *O. deletron* is the first squid reported to autotomize its arms, the only cephalopod known to be capable of economy of autotomy, and is one of very few species known to use attack autotomy, whereby a predator is grasped by a body part that is subsequently autotomized.

KEY WORDS: Cephalopod · Autotomy · Economy of autotomy · Attack autotomy · Bioluminescence · Defense · Mesopelagic

INTRODUCTION

Anti-predator behaviors are categorized as primary or secondary defenses according to when they are enacted. Primary defenses operate regardless of predator presence and are often permanent features of an organism's morphology or ecology—such as cryptic coloration or nocturnal activity—thereby decreasing the likelihood of detection (Edmunds 1974, Endler 1981). Secondary defenses are performed when an organism has perceived a potential predator (Edmunds 1974). These defenses decrease the chance of a successful attack and include startle, counter-attack, protean (erratic) behavior, playing dead (thanatosis), fleeing, and autotomy.

Autotomy is the defensive loss of a body part that is instigated by nervous control and occurs at a fracture plane (Fleming et al. 2007). The jettisoned body part, which often moves vigorously after autotomy, draws a predator's attention away from the potential prey organism, increasing its probability of escape (Edmunds 1974). Autotomy is typically a last-resort defense in predator–prey interactions since it involves the loss of tissue (Wilkie 2001, Maginnis 2006, Fleming et al. 2007).

*Email: stephanie_bush@mail.uri.edu

The loss of a body part or parts through autotomy may result in a number of costs, including decreases in: locomotor efficiency, sexual recognition and selection, ability to escape, foraging and prey handling, and fecundity (Maginnis 2006, Fleming et al. 2007, Wrinn & Uetz 2008, Lawrence 2010). In addition, the energy expenditure required to regenerate lost tissue can reduce fitness (Naya et al. 2007). Autotomy nonetheless occurs in a wide range of vertebrate and invertebrate taxa, and these multiple independent evolutionary occurrences point to the effectiveness of defensive autotomy (Maginnis 2006, Fleming et al. 2007).

An autotomy fracture plane can be either a structurally weak anatomical breakage point, or a potential breakage site that experiences a loss of tensile strength during autotomy (Wilkie et al. 1990, Wilkie 2001, Fleming et al. 2007). A fracture plane allows for a clean break that minimizes trauma and speeds healing (Wilkie 2001). Most species require external resistance, such as a predator's grip, for autotomy to occur (Fleming et al. 2007). Some organisms require a force equivalent to their own mass or more to autotomize (Fleming et al. 2007). The threshold for breakage varies between species, individuals, and even limbs within an individual (Fleming et al. 2007).

Among cephalopods, some shallow-water octopuses autotomize and regenerate arms (Ward 1998, Norman & Finn 2001, Norman & Hochberg 2005, Hochberg et al. 2006, Huffard 2007). *Ameloctopus litoralis* autotomizes at a pre-formed fracture plane near the base of the arm (Norman 1992, Norman & Finn 2001). Other octopuses also have a specific section along the arm (e.g. between Suckers 4 and 7 in *Abdopus* 'sp. Ward'), where autotomy occurs, but no fracture plane is evident prior to this (Norman & Finn 2001). In *Abdopus capricornicus*, an autotomized arm can thrash for more than an hour post-autotomy (Norman & Finn 2001). Though the rate of regeneration likely depends upon temperature, nutrient availability, and the animal's life-stage, arm regeneration was reported to take 10 wk for *Abdopus* 'sp. Ward' and, where known, 2 to 3 mo for its congeners (Ward 1998, Norman & Finn 2001, Norman & Hochberg 2005). The males of pelagic octopuses in the family Argonautoidea jettison their spermatophore-laden mating arm (hectocotylus) and pass it to a female during mating (Naef 1923, Roper et al. 1984, Norman et al. 2002). While this is not performed in a defensive context and therefore not considered autotomy, members of the argonautoid genus *Tremoctopus* are able to jettison portions of their web (Thomas 1977). Given the evolutionary distance between near-shore, benthic, and pelagic octopuses that autotomize or jettison body parts, this behavior must have evolved multiple times among cephalopods (Norman & Finn 2001, Strugnell et al. 2006). Autotomy has not been previously reported in squids, cuttlefishes, Vampyromorpha, or nautiluses.

Squids of the deep-sea genus *Octopoteuthis* have feeding tentacles as paralarvae, but lose them at an early life-stage as they begin an ontogenetic descent into deeper water (Young 1972, Sweeney et al. 1992). Each of the squids' 8 arms has 2 series of hooks that alternate along the length, with a few small suckers between these hooks and a large, terminal photophore (Young 1972). These photophores are approximately equal in size among the arms of an individual and increase in length along with arm growth. Net-caught specimens commonly have blunt-ended arms of unequal lengths or regenerating arm tips (Young & Vecchione 2009). An arm cut off of a moribund *O. neilseni* immediately began to thrash, and the arm-tip photophore was luminescent (Young & Vecchione 2009). Additionally, an *O. megaptera* observed *in situ* by a ROV was missing a few of its arm-tips (Vecchione et al. 2002). These observations led to the hypothesis that *Octopoteuthis* spp. are capable of arm autotomy (Young & Vecchione 2009). However, arm loss due to physical damage from nets or sub-lethal predation could not be ruled out, and no cases of arm autotomy were observed directly. I tested the hypothesis that *O. deletron*, which inhabits mesopelagic depths (300 to 1000 m) in the eastern North Pacific (Young 1972), is capable of arm autotomy by undertaking *in situ* observation and experimentation, laboratory manipulations, and histological sectioning.

MATERIALS AND METHODS

Submersible observations

I made direct *in situ* observations and reviewed video footage from previous dives of 3 ROVs ('Ventana', 'Tiburon', and 'Doc Ricketts') owned and operated by the Monterey Bay Aquarium Research Institute. Footage was primarily obtained within or just outside Monterey Bay, California; however, additional observations were made off the coast of Oregon. Each vehicle was equipped with a high-resolution, broadcast-quality video system that allowed us to make detailed observations of an organism at a distance of 5 to 10 m. An onboard variable ballast system allowed the ROV to be trimmed to neutral buoyancy. These features allowed us to examine *Octopoteuthis deletron* individuals for breaks along each arm. Regeneration was observed as partial regrowth from a blunt end, photophores that were smaller than those of other arms, or distal hooks that were disproportionally smaller than proximal hooks. While cephalopod species descriptions include an arm formula describing the relative length of arm pairs, due to collection damage, no arm formula was reported for *O. deletron* (Young 1972). Therefore, relative arm length was not used to determine whether autotomy, regeneration, or both had occurred in the absence of relatively smaller portions of an arm, hooks, or photophores.

Laboratory observations

Each ROV had a number of collection devices designed to minimize disturbance to specimens of interest. *Octopoteuthis deletron* individuals were collected for laboratory observations at sea and ashore. I used arm touching, holding (without pressure), pinching (with pressure), pulling, dragging arm hooks along pieces of Velcro, and electric shocks from a 6V battery to attempt to instigate autotomy. The bioluminescence output of a terminal photophore was measured (n = 1, QE65000 Spectrometer, Ocean Optics Inc.).

Histology

One, 4, or 8 arms from 15 *Octopoteuthis deletron* specimens were sectioned to look for fracture planes (n = 82 arms). As controls, arms were sectioned from 1 *Chiroteuthis calyx*, 1 *Gonatus* sp., and 1 *Vampyroteuthis infernalis*, none of which are thought to autotomize their arms. All material was preserved in 10% formalin and arranged in cassettes for paraffin embedding, longitudinal sectioning, staining with hematoxylin and eosin, and slide-making. Each slide was scanned under a dissecting or compound microscope for fracture planes, such as a weak point within the longitudinal muscles as in *Ameloctopus litoralis* (Norman 1992), and instances of regeneration not visible from gross morphological assessments.

In situ experimentation

In a previous study, I observed several individuals grabbing (counter-attacking, n = 23 of 76; Bush et al. 2009) the ROV, though none of these instances resulted in arm autotomy. I hypothesized that autotomy during counter-attack requires grasping by the arm hooks to provide resistance and that the arm hooks are unable to attach to the metal components of the ROV. I tested this hypothesis by mounting a 200 mm laboratory bottle-brush onto the swing arm of a ROV ('Ventana' or 'Doc Ricketts'). The vehicle was manipulated to touch an *Octopoteuthis deletron* individual (n = 7) lightly on the arm/s or mantle in order to instigate a counter-attack. Control tests were performed with 7 *Chiroteuthis calyx*, 9 *Galiteuthis phyllura*, 9 *Gonatus* spp., 1 *Histioteuthis heteropsis*, 1 *Japetella diaphana*, 15 *Taonius borealis*, and 1 *Vampyroteuthis infernalis*. All of these species co-occur with *O. deletron* at mesopelagic depths off Central California, and none are thought to autotomize arms.

RESULTS

Submersible observations

I observed 84 individual *Octopoteuthis deletron* during ROV dives from June 2003 to October 2010 and reviewed recorded footage of 21 individuals from previous dives (total n = 105). Some observations were limited by viewing distance; therefore, I was only able to make clear determinations for 62 individuals. Of these, 17 (27%) had from 1 to 8 blunt-ended, foreshortened arms. These 17 individuals had

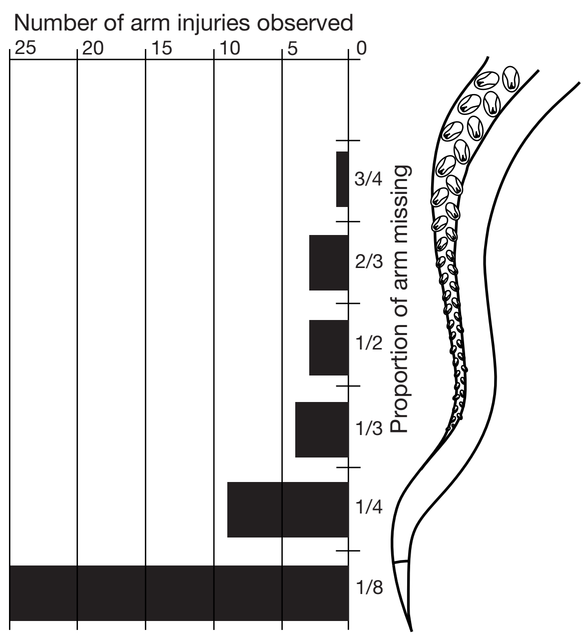

Fig. 1. *Octopoteuthis deletron.* The number of arm injuries observed (n = 47) plotted by the proportion of arm missing. The proportion missing was determined by comparing the relative length of the injured arm to the lengths of the uninjured arms. We assumed that uninjured *O. deletron* arms are approximately equal in length

a total of 47 arm injuries (Fig. 1). Any of the arms could have an injury, and no arms were found to have more injuries relative to other arms. It was not possible to determine if specimens with multiple injuries obtained them during one or more interactions. Injuries occurred from just proximal to the terminal photophore to the loss of three-fourths of the arm (Fig. 1). Loss of the arm tip, including the terminal photophore, was the most common type of injury (n = 25 of 47 injuries, 53%; Figs. 1 & 2A). In contrast, only 1 individual was missing three-fourths of an arm (Fig. 2B). One arm was encountered slowly sinking through the water column; the squid itself was not seen. The arm was missing a small, irregularly shaped portion of flesh next to a cleanly severed end (Fig. 2C). Nine (of 62, 14.5%) individuals were actively regenerating arms (Fig. 3A to C).

During 1 *in situ* observation, 2 arms of an individual were accidentally severed by ROV collection equipment during attempted specimen capture. These arms thrashed for 15 and 32 s before going out of the camera's view. In a separate observation, an individual released 2 pseudomorphs (a type of ink release that approximates the size of the squid; see Bush et al. 2009) and autotomized an arm that thrashed rapidly for 9 s before going off-screen.

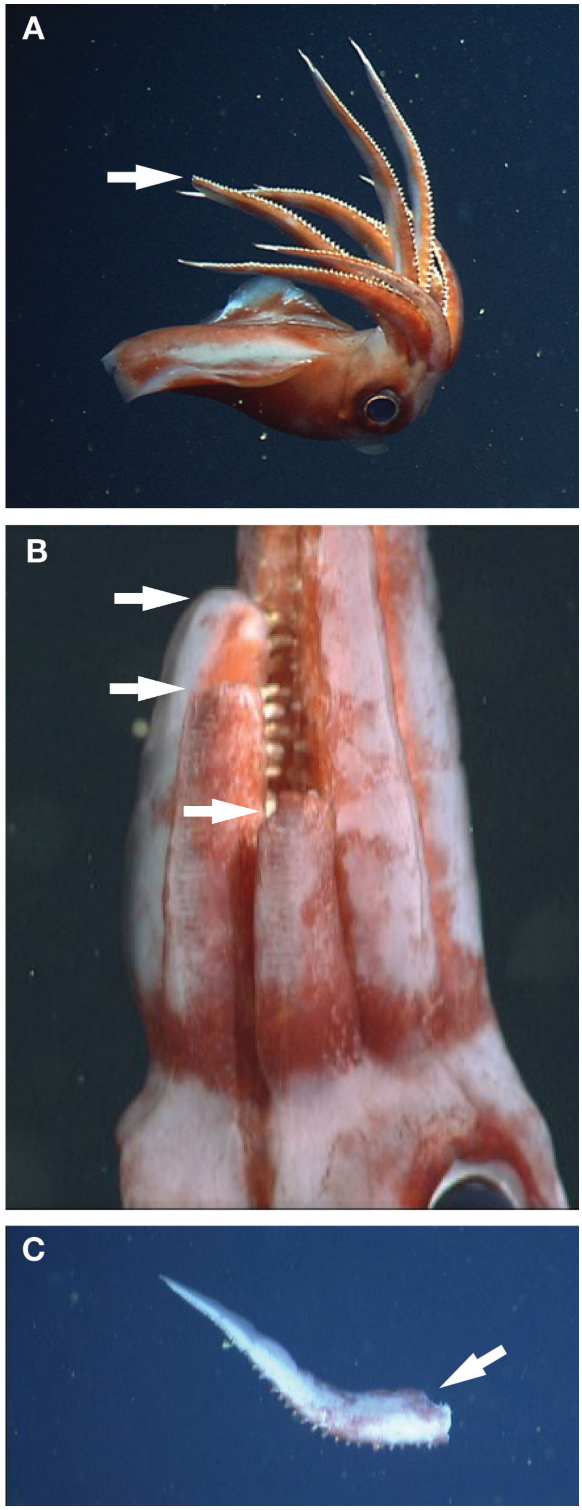

Fig. 2. *Octopoteuthis deletron.* (A) An individual missing the terminal photophore of Arm LII (arrow). (B) An individual with 3 arms autotomized at different lengths (arrows). (C) Arm found sinking through the water column. Arrow points to the irregularly shaped location that was missing tissue, proximal to the clean break, which was possibly a result of autotomy

Laboratory observations

Of the 11 individuals tested, 7 (64%) autotomized 1 or more arms. Four individuals partially autotomized an arm, whereby a split occurred from either the oral or aboral side, but did not fully sever; 1 of these individuals later fully autotomized the arm at the same spot. An *Octopoteuthis deletron* arm partially or completely autotomized only at the point of stimulation. Autotomy never occurred within the terminal photophore. Autotomy requires voluntary nervous control which was only elicited when resistance occurred. Two autotomy mechanisms were induced: (1) an arm is grabbed by an external source (i.e. a potential predator), providing the traction for autotomy and (2) the arm hooks grasp an object (i.e. a potential predator) and their attachment provides the traction for autotomy.

One individual grasped the textured bottom (rubber topped with fabric) of its holding container with the arm hooks, somersaulted, and released ink as it autotomized part of all 8 arms. All the severed arms thrashed while the terminal photophores bioluminesced steadily for ~10 s. The autotomized sections measured 9 to 22 mm in length (mean = 15.9 mm). In

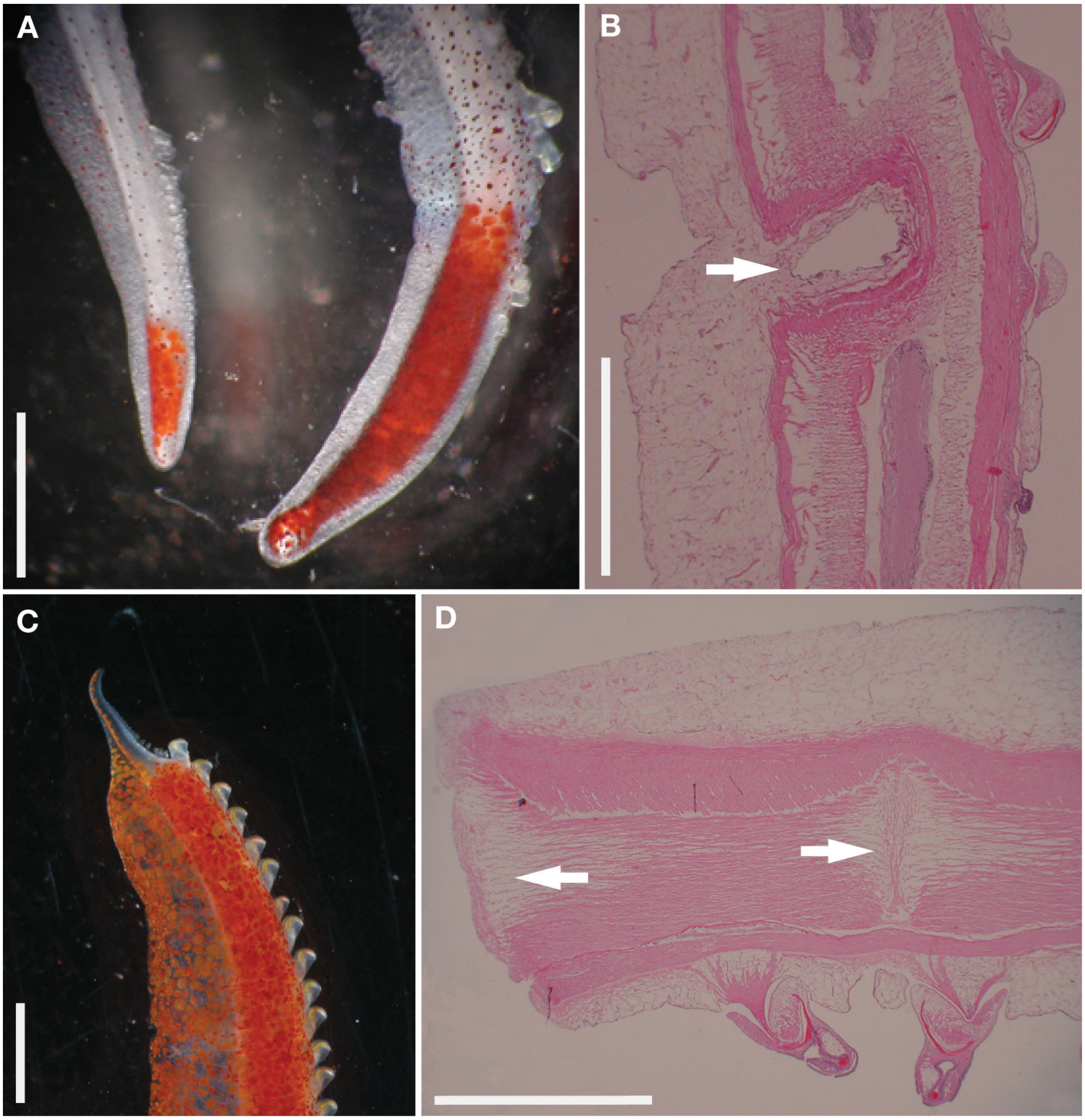

Fig. 3. *Octopoteuthis deletron*. (A) A regenerating photophore (left) next to a full-sized photophore (right). (B) An example of damage, possibly from a partial autotomy, that has been regenerated (arrow). (C) A previously autotomized arm beginning to regenerate. No terminal photophore is yet present, chromatophores have developed only on the aboral side, and hooks have just begun to form at the proximal end. (D) Two fracture planes (arrows) of an *O. deletron* arm. The fracture plane on the left is where the arm autotomized; the fracture plane on the right is a point where the arm began to, but did not completely autotomize. Scale bars = 5 mm

addition to these longer arm sections, 8 shorter sections (1 from the medial portion of each arm, 2.1 to 4.0 mm length; mean = 2.98 mm) were also jettisoned, but these did not move. There were also 119 arm hooks that had separated from arm tissue and were either attached to or lying on the container bottom. The bioluminescence was bright enough to be seen under full laboratory lighting. The maximum spectral output (measured from a different specimen) peaks at 465 nm.

Histology

Evidence of regeneration was observed at different points along arms from 8 of 15 individuals (53 %; Fig. 3A to C). In addition, several arms (n = 14 of 82, 17 %) were partially separated in 1 or more places, usually from the oral (hook-bearing) side of the arm. These may have been the result of partial autotomies such as those that occurred in laboratory observations. Fracture planes were found within 5 to 8 mm of the point at which autotomy had occurred in 2 arms (1 from each of 2 individuals; Fig. 3D). No other fracture planes were found. No regeneration, evidence of autotomy, or fracture planes were found in any other species examined.

In situ experimentation

When touched by the bottle-brush, an *Octopoteuthis deletron* would sometimes move quickly away from the stimulus, stop, and then maintain its position. In other cases, counter-attacks by the squid were elicited, in which the squid jetted away from the stimulus, paused with the arms spread to their widest extent, then jetted toward the stimulus, and grasped it. Usually the chromatophores overlying the terminal photophores were all contracted when the arms were spread widest, exposing the photogenic tissue (i.e. the photophores were presumably bioluminescent). Most touches by the bottle-brush were to the arms, and when a counter-attack was elicited it was as described above. In cases where the squid was touched on the posterior mantle, the individual flipped around to orient the arms toward the bottle-brush and then counter-attacked. Not every touch by the bottle-brush elicited a counter-attack, and not all counter-attacks resulted in arm autotomy; however, all instances that resulted in arm autotomy were preceded by a counter-attack. Five out of the 7 *O. deletron* I tested *in situ* autotomized 1 (4 individuals) or 2 arms (1 individual, Video 1 in the supplement at www.int-res.com/articles/suppl/m458p133_supp/) onto the bottle-brush. One of these individuals counter-attacked and autotomized an arm after being touched by the bottle-brush once; however, counter-attack and autotomy were not instigated in other individuals until they were touched by the bottle-brush 10 to 18 times. While some of the 43 individuals of other squid species held onto the bottle-brush, they never counter-attacked or autotomized an arm.

After autotomy, 3 of the 5 *Octopoteuthis deletron* jet-escaped, each releasing an ink pseudomorph. The other 2 individuals remained still after autotomy, 1 hovered within its own ink cloud. Terminal photophores on all the autotomized arms were white (i.e. bioluminescent) while visible on the ROV camera feed screen. Some of the autotomized arms (n = 4) remained attached to the bottle-brush by the hooks near the site of autotomy. In 2 cases, the distal, free end thrashed, in 2 others it did not thrash. Twice an autotomized arm (1 each from 2 individuals) detached from the bottle-brush soon after autotomy; 1 thrashed for 47 s, while the other thrashed for 10 s before going out of sight.

DISCUSSION

Like many animal species, *Octopoteuthis deletron* has a series of defenses that escalate from primary to secondary (Edmunds 1974). Primary defenses include crypsis and polyphenism, while the secondary defenses of deflection, jet-escape, ink release, and startling with bioluminescence come into play when primary defenses fail (Edmunds 1974, Herring 2002, Bush et al. 2009). *O. deletron* is the first squid species reported to autotomize its arms, and each of the 8 arms is capable of doing so. Multiple arms can be autotomized at once, presumably enhancing the distraction of a potential predator and increasing the likelihood of the squid's escape. Additionally, if 1 or a few arms are autotomized, the other arms can still be autotomized during another defensive interaction. The fact that fracture planes were only observed in 2 of 15 individuals likely indicates that autotomy in *O. deletron* occurs at potential, instead of preformed, sites of weakness.

The ability to regenerate the arms may allow autotomy to be used as a defense repeatedly given sufficient time. A specimen with all arms autotomized was collected by ROV and kept alive in the laboratory for several days. A few of the arms regenerated up to 2 mm of tissue after 9 d at 4 to 6°C (H. J. Hoving & M. Powers pers. comm.). The habitat temperature of this species is ~2 to 8°C (Bush et al. 2009), and, though I do not know typical growth rates for *Octopoteuthis deletron*, if this rate is representative, it indicates that regeneration may be relatively rapid.

Defensive autotomy has numerous costs, such as reduced growth and decreased fecundity, as the animal must allocate energy to regenerating the autotomized tissue (Maginnis 2006, Fleming et al. 2007, Lawrence 2010). Previous studies have shown preferential investment in regeneration of autotomized tissue over contributions to nutrient reserves, and increased metabolic rates during regeneration (Lawrence & Larrain 1994, Naya & Bozinovic 2006). Deep-sea species must balance these requirements with the demands of living in a habitat where food is limited and potentially hard to find, and an organism must maintain neutral buoyancy or swim constantly (Herring 2002, Robison 2004). Additionally, *Octopoteuthis deletron* has been proposed to use the terminal photophores as lures for potential prey or to signal to conspecifics, so the loss of these photophores resulting from arm autotomy could make prey enticement or mate attraction and signaling less effective (Bush et al. 2009). Similarly, subduing and handling prey may be less effective without 8 fully intact arms (Ramsay et al. 2001).

To counteract some of these costs, *Octopoteuthis deletron* demonstrates 'economy of autotomy' — breakage occurs just proximal to where the arm is grasped or where the arm hooks hold onto an object (Bustard 1968). Economy of autotomy is relatively uncommon among animals that autotomize, though it occurs in some clams, seastars, brittlestars, crinoids, and lizards (Delage & Herouard 1903, Gilmour 1963, Bustard 1968, McVean 1975). Economy of autotomy has the clear advantage of minimizing tissue loss, and thereby reducing the associated costs of this defense, while still allowing escape (Delage & Herouard 1903, Fleming et al. 2007). *O. deletron* is the first cephalopod species reported to be capable of economy of autotomy.

Attack autotomy was first documented in crabs, which grip potential predators with the claw, and then autotomize it (Robinson et al. 1970, McVean 1975). *Octopoteuthis deletron* is the only other species known to perform attack autotomy, which likely startles or distracts the predator as the squid grabs it, and then the autotomized arm or arms may begin to thrash and bioluminesce. After autotomization, individuals sometimes moved rapidly away. However, escape is energetically expensive and may stimulate environmental bioluminescence, allowing a predator to follow the squid (Widder et al. 1989, Seibel et al. 2000, Robison et al. 2003). Perhaps for these reasons, *O. deletron* has been observed to remain motionless after *in situ* autotomy, sometimes within an ink cloud. The latter has been observed in a number of other deep-sea squids (Vecchione et al. 2002, Bush & Robison 2007).

The movement of the thrashing arms will stimulate additional bioluminescence in the surrounding water, and probably increase the predator's attention (Widder et al. 1989). The use of bioluminescent appendages or secretions as a defensive distraction has been observed in many deep-sea animals, including jellies, polychaetes, crustaceans, and the cephalopod *Vampyroteuthis infernalis* (Herring 2002, Robison et al. 2003, Osborn et al. 2009, Haddock et al. 2010). Likely there are additional species to be discovered using similar tactics.

Mesopelagic animals face many challenges in their large, 3-dimensional habitat where both food and mates may be few and far between (Herring 2000). The use of bioluminescence to signal to potential mates or attract prey is common in the deep sea (Herring 2000). This will also attract predators, however, and, once detected, a midwater animal has nowhere to hide and must avoid being attacked by distracting the predator or attempting escape. The posture in which *Octopoteuthis deletron* is typically first observed by a ROV — with the body horizontal and the arms positioned 90° to the body axis or reaching backward over the mantle (arms parallel to the body axis; see Bush et al. 2009), while the photophores luminesce on and off — may divert attention away from the head and body to the sacrificial arms, giving *O. deletron* an effective defensive strategy against a diversity of predators (Clarke 1996, Croxall & Prince 1996, Klages 1996, Smale 1996).

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