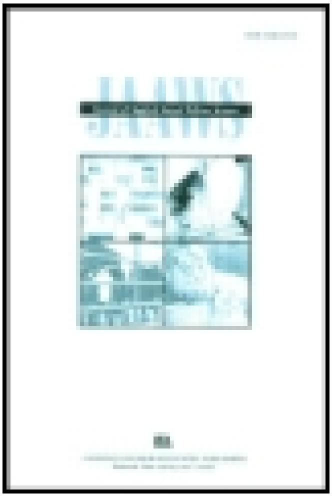

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Octopus Senescence: The Beginning of the End

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Senescence is a normal stage of an octopus's life cycle that often occurs before death. Some of the following symptoms typify it: lack of feeding, retraction of skin around the eyes, uncoordinated movement, increased undirected activity, and white unhealing lesions on the body. There is inter- and intraspecific variability. Senescence is not a disease or a result of disease, although diseases can also be a symptom of it. Both males and females go through a senescent stage before dying—the males after mating, the females while brooding eggs and after the eggs hatch. There are many aspects of octopus senescence that have not yet been studied. This study discusses the ecological implications of senescence.

A public aquarium or scientist frequently calls one of us about a sick octopus. For example, a large male giant Pacific octopus (GPO), *Enteroctopus dofleini,* held in captivity for 6 months is not eating and is losing weight. The octopus is acting strange—not going into his lair and moving around the tank in the open much of the time. As time progresses, his skin develops lesions, and this nonhu-

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man animal loses coordination. People notice, and, inevitably, they start asking about the welfare of the animal. We have seen this pattern before. For example, at The Seattle Aquarium a GPO named Clyde (in honor of the cephalopod biologist Dr. Clyde Roper) weighed 18 kg when he was collected. He thrived in captivity for 5 months and grew to a size of 32 kg but then stopped eating. He lost 10 kg over 2½ months, 32% of his body weight, before dying. He crawled all over his tank, even into stinging sea anemones that he normally avoided. His eyes were prominent and seemed larger than normal. This animal had the symptoms of octopus senescence, a precursor to his death.

To understand octopus senescence, it is necessary first to understand the life history of octopuses. We are familiar with the reproductive patterns typical of mammals; they can reproduce several times during their life span; that is, they are iteroparous. Almost all octopuses are semelparous, meaning they reproduce once and then die (Mangold, 1987). Salmon, cicadas, and century plants are other examples of semelparous organisms (Stearns, 1992).

Many animals have life spans that last many years. In general, mollusks other than cephalopods are smaller but often live for many years (Morton, 1967). Powell and Cummings (1985) reported several gastropods and bivalves who live for more than 50 years. However, cephalopods "live fast and die young," a motto O'Dor and Webber (1986) borrowed from the Hell's Angels and applied to cephalopods. Even the GPO, who frequently reach a size of 50 kg, only live about 3 years (Hartwick, 1983). The very small sepiolid *Idiosepius pygmaeus* lives for only 80 days (Lewis & Choat, 1993). Most other octopuses only live a year (Hanlon & Messenger, 1996), although this depends on size at maturity and temperature at which the species lives. Animals who mature at large sizes and live in colder water tend to have longer life spans (Wood & O'Dor, 2000).

Octopuses are born, grow rapidly, mature, mate, and—if female—brood eggs. Then they die. Males generally die about the same time as the females (Hanlon, 1983a; Mangold, 1983a; Van Heukelem, 1983), but male GPOs (Hartwick, 1983) and *O. vulgaris* (Mangold, 1983b) may live longer than females. Death may be prolonged into a senescent state, but for most species it is inevitable once an octopus has reproduced. In the wild, a senescent octopus who is not camouflaged and who is moving around inordinately is likely to quickly become part of the food chain.

Senescence occurs at the end of a mature octopus's natural life span and often lasts for a period of a month or more. However, there are other reasons octopuses may experience senescence-like symptoms that are animal welfare issues. Poor water quality (lack of dissolved oxygen, low pH, pollutants), incorrect temperature, collecting stress, and disease (Budelmann, 1998) also can cause these symptoms and even death in captive octopuses.

The physiological processes by which senescence occurs are fairly well known (Tait, 1986, 1987). The process is driven by secretions from the optic gland (Tait, 1987; Wodinsky, 1977) that elicit ripening of the reproductive organs, inactivation of the posterior salivary and digestive glands, and cessation of appetite, which normally causes death by starvation after reproduction. Activation of the optic gland appears to be affected by environmental factors such as light, temperature, and nutrition that, thus, ultimately control reproduction and life span (Van Heukelem, 1979). The behavioral aspects of senescence have been less remarked on but have been casually known for millennia. Aristotle stated, "[T]he females after giving birth … become stupid, and are not aware of being tossed about in the water, but it is easy to dive and catch them by hand" (cited in Balme, 1991, p. 323).

The purpose of this article is to document the indicators of senescence, both physical and behavioral, that we have observed in several cold, temperate, and tropical octopuses. We hope that knowledge of the senescence phenomenon will help aquarists and researchers understand what is happening to their animals as they grow old. We cite what is known about octopus senescence. Such knowledge is perforce limited, and we draw on our own observations to expand the knowledge of its occurrence.

SYMPTOMS OF SENESCENCE

Four conditions or activities are all indicators of octopus senescence. These are (a) loss of appetite and lack of feeding leading to weight loss, (b) retraction of the skin around the eye, (c) undirected or uncoordinated activity, and (d) the occurrence of white lesions on the skin.

Many researchers and aquarists have noted the loss of appetite in both male and female octopuses at this stage, and it is fairly well documented (Cortez, Castro, & Guerra, 1995; Hanlon, 1983a, 1983b; Joll, 1983; Mangold, 1983a; Tait, 1986, 1987; Van Heukelem, 1977, 1979; Wodinsky, 1977). It has been posited that such fasting is what inevitably leads to the animal's death by starvation (Tait, 1987).

The eyes of octopuses stay the same size while the body shrinks as the animal loses weight. This causes the skin around the eyes to retreat, making the eyes more visible.

The increased activity at the start of senescence is undirected activity (particularly in males). It is not hunting, foraging, or performing other activities with a purpose. O'Dor and Wells (1978) showed that both starved and senescent female octopuses used dissolution of muscle tissue as fuel, which kept the metabolic rate at an unnaturally high level. A study on activity patterns of *Octopus vulgaris* at the Konrad Lorenz Institute showed that senescent males were statistically more active than normal males (Meisel, 2002). The undirected activity of senescent males should not be confused with perseverating activity ("pacing") of bored octopuses—this may be alleviated with proper environmental enrichment (Anderson & Wood, 2001; Dickel, Boal, & Budelmann, 2000; Wood & Wood, 1999) as it is in other animals (Shepherdson, 1998). This undirected activity may be related to mate searching. It is not known whether senescent males can still successfully mate a female, whether they still have spermatophores, or whether they have the "mental capacity" to mate.

The occurrence of white lesions on a senescent octopus has been the subject of controversy and discussion (Budelmann, 1998; Reimschuessel & Stoskopf, 1990). A young octopus, in good condition and in good water quality, can sustain an injury that may cause such lesions. However, Hanlon (1983a) remarked that the skin deteriorates during the 2- to 4-week senescence of both male and female *O. briareus.* "Skin damage usually leads to infection only in old animals" (Mangold, 1983b, p. 359). Van Heukelem (1977) stated that the healing processes of octopuses are shut off during senescence, so skin injuries may become secondarily infected with *Aeromonas, Vibrio,* and *Staphylococcus* bacteria (Reimschuessel & Stoskopf, 1990).

MALE SENESCENCE

A male octopus's senescent condition begins after maturity. A male may mate more than one female and may mate the same female more than once (Mangold, 1983b). There is evidence that both sexes are promiscuous and that there is sperm competition among males (Cigliano, 1995; Mangold, 1987). Males may use their spatulate ligulas on their third right arms to remove another male's stored sperm in a female (Hanlon & Messenger, 1996). A male's supply of spermatophores (sperm packets he passes into the female) may be limited. Whether they can make more and how long it would take them to do so if they can is unknown, but "mating is highly unlikely to exhaust males (referring to *Octopus vulgaris*)" (p. 358), according to Mangold (1983b).

Other octopus species have a very limited number of spermatophores at any one time, which may limit their chance to mate successfully. GPOs have only 10 spermatophores (Mann, Martin, & Thiebsch, 1970), and the deep-sea octopus *Bathypolypus arcticus* typically has only 3 or 4 (O'Dor & Macalaster, 1983) available for use. Although it has been reported that there is permanent production and release of spermatophores in male *Octopus vulgaris* (Mangold, 1983b), it is not known if this is true for other species or if it occurs after the onset of senescence.

Male and female octopuses both go into senescence, but females typically brood fertile eggs during this time, an activity with a clear and necessary reproductive purpose. Unlike in females, senescence in male octopuses occurs without as clear a sign that they are at the end of their lives. The best sign that males are becoming senescent is their lack of appetite. They stop eating, and their bodies begin to deteriorate. They can survive a surprisingly long time without eating. At The Seattle Aquarium, male GPOs ($N = 7$) stopped eating a mean of 48 days (range = 14 to 76 days) and lost a mean 17.4% of their body weight (range = 4.3% to 32.1%) before dying. Gabe's (1975) male GPO died 54 days after mating.

At the Konrad Lorenz Institute, senescence was monitored in three male *O. vulgaris*. They stopped eating a mean of 131 days (range = 79 to 188 days) before dying. They did not stop eating suddenly but gradually ate less and less. Two of the *O. vulgaris* had small white lesions for 248 and 257 days before their deaths; these lesions increased in number and size prior to death. An *O. macropus* died 165 days after his last mating. During this time, he rarely ate the food given, and was never seen during the day, but was very active at night, mostly swimming and jetting.

Undirected activity of a senescent male octopus is likely to get him in trouble by exposing him to predators. Senescent males are much more likely to escape from captivity because of their increased activity (personal observation), and senescent male GPOs and *Octopus rubescens* are frequently found crawling out of the water onto the beach. Senescent males have been found even in river mouths, going upstream (personal observation).

A study on the biorhythms of *O. vulgaris* showed that a senescent male animal spent 80% of his time active, compared to three subadult males who spent an average 41% of their time active (Meisel, 2002).

Undirected movement of senescent male octopuses is also frequently observed with uncoordinated activity. They look as if they have forgotten how to crawl or swim properly; they lose their balance and appear to "trip" over their own arms, and they do not seem to control their own bodies. Senescent octopuses may even eat their own arms. Again, this is different from the bacteria-caused disease that causes autophagy in previously healthy octopuses of any age (Budelmann, 1998).

In a study of visual control of arm movements in *O. vulgaris,* it was possible to see the progression of one animal toward senescent behavior (U. Griebel, personal communication, May 1, 2002). The animals were presented a transparent plexiglas T-maze. The octopuses had to learn to look first and then make the right choice for the reward. Before senescence, one male performed 68% of the right choices; afterward, however, he fell back to chance level (48%). Not only did the animal's performance decrease, but so did his willingness to perform the trials.

FEMALE SENESCENCE

Although the term *senescence* typically is used in referring to the condition in male octopuses, females also may develop signs of senescence. Senescence in females is especially apparent in those who are brooding eggs, have survived after the eggs hatched, or are removed from their eggs. While brooding eggs, females do not leave them, and they reduce or stop feeding (Mangold, 1987). They guard the eggs from predators and clean and oxygenate their eggs (Cosgrove, 1993; Gabe, 1975). To provide the energy to do this, they metabolize their own bodies. In the wild, female GPOs lost 50% to 71% of their body weight while brooding eggs (Cosgrove, 1993). In captivity, female *Octopus mimus* lost 25% of their body weight (Cortez et al., 1995); *O. cyanea,* 36% (Van Heukelem, 1976); and *O. vulgaris,* 50% (O'Dor & Wells, 1987). At The Seattle Aquarium, female GPOs lost a mean of 49.5% of body weight, whereas female *O. rubescens* lost a mean 50.3% of their body weight before dying.

If a female survives after her eggs have hatched, she will be senescent. She probably will not eat, she may not shelter in a den, and she will not behave like a healthy octopus because she is dying. There are a few exceptions to this general pattern. Several female GPOs have been reported to continue to eat during the first part of egg guarding as have a few *Octopus vulgaris* (Mangold, 1983b). Tait (1987) exclaimed, "There is no such thing as a 'typical octopus!'" (p. 24). There are a few species like *O. chierchiae* who lay more than one batch of eggs and continue to feed and grow between batches of eggs (Rodaniche, 1984). However, the typical pattern is for females to die when their eggs hatch. They already show some symptoms of senescence similar to males while they are brooding, and those who survive past brooding act in the same way as senescent males.

Most cephalopods held in captivity who do not have a chance to mate will not spawn normally (Boyle, 1991). Most researchers do not keep adult octopuses together as they are cannibalistic (Hanlon & Forsythe, 1985); under such conditions, females are much more likely to lay infertile eggs or not lay eggs. Egg-bound females do not appear to have a longer life span (Boyle, 1991). We have observed that the unmated females of some species (*Enteroctopus dofleini, Octopus briareus, O. vulgaris,* and *Bathypolypus arcticus*) lay infertile eggs and also become senescent. They stopped eating; laid scattered, infertile eggs (unlike the dense egg mass of a normal female); or laid and brooded infertile eggs. If they are not brooding, they often are more active, out in the open, and noticeably physically deteriorating.

DISCUSSION

The life history stage of senescence prior to dying is typical for many cephalopods but not other mollusks. Senescence is likely part of an adaptive program that is hormonally regulated in this class (Tait, 1986). Hormonal control of octopuses' life cycles has been fairly well studied (Mangold, 1987), and senescence is a direct result of such control (Tait, 1986). Wodinsky (1977) found that removal of optic glands in female *Octopus filosus* made them cease brooding, start feeding again, and live longer than normal. This experiment has not yet been performed on male octopuses. If it were, it might be possible to grow a "supermale" who lives longer and grows larger than normal. Such features would be valued by public aquariums where octopuses are popular display animals (Carlson & Delbeek, 1999).

Many aquarists have observed and remarked on the increased activity of some senescent male octopuses (Anderson, 1987; Anderson & Martin, 2002). Such activity may lead to a greater propensity to escape an enclosure. We do not know if senescent males still (a) can mate, (b) possess viable sperm and spermatophores, and (c) can produce more spermatophores—and, if so, for how long once they have reached senescence. Their activity during senescence may be related to an increased urge to mate. Because senescent males will soon die, they may have little to lose, and their best strategy to pass on their genes may be to seek further opportunities to mate by being more active.

At the end of life, the brooding behavior of females is clearly a necessary component of reproduction for octopuses. Female octopuses likely must balance energy allocated to both producing eggs and maintaining enough energy to brood their offspring until they hatch. In an uncertain world, the potential loss of an entire brood likely has a much stronger effect on evolutionary strategy than the lost chance for producing a few more eggs. This would select female octopuses to err slightly on the side of having too much energy resources, which would lead them to survive occasionally past the brooding period. However, we have observed that brooding females who are removed from their eggs act senescent but still are able to brood if replaced back on them.

A few species of octopuses are iteroparous (Rodaniche, 1984) as are *Nautilus* (Ward, 1987) and many other species of mollusks (Morton, 1967). However, most octopuses are constrained to a semelparous life cycle that may end in senescence. Such a pattern may be adaptive. Semelparity has the benefits of producing more offspring and producing them quickly, both of which increase fitness (Stearns, 1992). Young octopuses are particularly capable of efficient assimilation of ingested food and very fast growth rates (Mangold, 1983b). Therefore, they are able to reach maturity quickly. Thus, senescence and death at a young age are the costs of such a strategy.

There is still much we do not know about octopus senescence, and there are many opportunities for future research. The onset and duration of senescence need to be documented in other species. The condition of naturally dying animals, state of internal organs, number of spermatophores in males, ability to mate, and the correlation with hormonal systems need to be further researched. The factors that cause some females to continue eating after egg-laying or egg-hatching need to be studied.

There are implications for aquarium husbandry of senescent octopuses. It is important for those who keep octopuses and work with them to understand that these cephalopods are short-lived animals and that the senescence stage is a significant part of their life cycle. It is critical to recognize the symptoms of senescence and be able to differentiate them from other husbandry problems related to diseases, infections, injuries, and the effects of poor water quality. Research on octopus physiology, growth, and behavior will be confounded if senescent animals are used in experiments.

Senescent octopuses in the wild probably do not live long due to the added risk of predation, but senescence may be extended in the laboratory or public aquarium (the so-called laboratory artifact). Senescent animals are acting normal for their life stage, but this behavior is not normal relative to the rest of their lives. Octopus keepers need to realize this and make amends for it. Senescent male octopuses may make good public aquarium displays (Anderson, 1987). They are active and do not require much, if any, food. However, octopus keepers need to realize that such activity and lack of appetite of a large, old octopus is the beginning of the end.

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