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Abstract

In the majority of the shallow-water cephalopod species, senescence is a short stage of their lifespan, which takes place at the end of sexual maturity. Senescence is not a disease, although senescent cephalopods can be frequently mistaken with diseased animals. Senescence is accompanied by physiological, immunological and behavioural changes, which are briefly exposed in this chapter. A suppressed immune system may increase susceptibility to parasite infection in senescent cephalopods. High prevalence of infection by *Aggregata octopiana* was observed in *Octopus vulgaris* and *Aggregata* sp. in *Octopus maya*. In both cases, the infection was found in post-spawned females and was infecting different organs. Cestode larvae *Prochristianella* sp. were found in the buccal mass of post-spawned *O. maya* females.

Keywords

Senescence • Physiological changes • Immunological changes • Parasitology

16.1 Introduction

In the majority of the shallow-water cephalopod species, senescence is a short stage of their lifespan, which takes place at the end of sexual maturity (Tait 1986, 1987; Anderson et al. 2002). After mating, female octopuses adopt an ‘extreme pattern of maternal care’ (Wang and Ragsdale 2018). The mother abstains from food and exclusively takes care of the eggs, which will cost its own life; death usually occurs by the time of the offspring hatching (Wells 1978; Hanlon and Messenger 1996; Anderson et al. 2002). The senescence is reached still while the female breeds the eggs or soon after their hatching, while in males it usually begins after mating (Pascual et al. 2010).

Generally, males die approximately the same time as the females (Hanlon 1983; Mangold 1983; Van Heukelem 1983), but in some species, males may live longer than females, such as *Enteroctopus dofleini* (Hartwick 1983) or *Octopus vulgaris* (Mangold 1983).

The physiological process by which senescence occurs is not completely understood (Tait 1986, 1987; Anderson et al. 2002). Optic gland secretions, probably activated by environmental factors (e.g. light, temperature) and nutrition (Van Heukelem 1979), are involved in gonad maturation and in the inhibition of feeding (Tait 1986, 1987; Wodinsky 1977). Although a relatively small amount of information is available regarding the mechanisms that lead to senescence, it has been hypothesized that in species with terminal spawning (see Rocha et al. 2001 for a review of the reproductive strategies), the levels of hormonal secretions are high which would trigger the inhibition of feeding and lead to death. In species with intermittent spawning, the levels of hormonal secretions are lower, which would initiate spawning without inhibiting food intake and growth (Jackson and Mladenov 1994). Moreover, an attractive genetic mechanism of ageing, and therefore, senescence,

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was hypothesized by Guerra (1993) for all living cephalopods, except *Nautilus* species.

When sexual maturity occurs, the digestive gland ceases to function properly, leading to a gradual decrease in food intake until its cessation, consequently stopping growth (Mather 2006). A reduction of digestive enzymes in the posterior salivary glands and digestive gland observed in post-spawning octopuses is also assumed to contribute to starvation, body weight loss, and consequently, death (Sakaguchi 1968). Signs of degeneration in the nervous system and deterioration in the long-term memory process can also occur in senescent cephalopods (Chichery and Chichery 1992a).

16.2 Other Signs of Cephalopod Senescence

Senescence is accompanied by physiological, immunological and behavioural changes, which may include: (i) reduced or loss of appetite and feeding; (ii) retraction of the skin around the eyes; (iii) cloudy eyes; (iv) loss of coordination; and (iv) occurrence of skin lesions (Chichery and Chichery 1992a, b; Dumont et al. 1994; for reviews also see Anderson et al. 2002; Mather 2006).

Probably, one of the most remarkable consequences in senescent cephalopods is the loss of body weight as a consequence of starvation. A loss of body weight was observed in both male and female senescent octopuses: *Enteroctopus doffeini* (Cosgrove 1993; Anderson et al. 2002); *Octopus cyaneae* (Van Heukelem 1976); *Octopus maya* (Roumbedakis et al. 2018); *Octopus mimus* (Cortez et al. 1995); *Octopus vulgaris* (O'Dor and Wells 1987; Hernández-García et al. 2002) and *Octopus rubescens* (Anderson et al. 2002). According to these studies, in males the total loss of body weight varied between 4.3 and 32.1%, while in females larger percentages were observed, varying between 25 and 71%.

A decrease in both gonadosomatic and hepatosomatic indexes associated with the deterioration of general physiological condition occurs in post-spawned cephalopods (Tait

1986, 1987; Pollero and Iribarne 1988; Castro et al. 1992; Cortez et al. 1995; Zamora and Olivares 2004; Estefanell et al. 2010; Roumbedakis et al. 2018). Changes in gonads and the digestive gland appearance are also observed: ovaries and digestive glands became pale and opaque and oviductal glands darken (Fig. 16.1a–c), a reduction in size also occurs.

Mature and spent females of the deepwater squid *Moroteuthis ingens* showed advanced tissue breakdown with individuals having a tin mantle wall with inelastic, gelatinous appearance. Histological examination of the mantle wall revealed that tissue breakdown was due to a drastic histolysis of muscle tissue and to a lesser extent, collagen fibres (Jackson and Mladenov 1994). These features are considered by these authors in relation to the processes contributing to terminal maturation in *M. ingens*. Thus, because all the examined individuals had empty caecums, senescence and post-spawning death may be associated with starvation, as found in captive *Illex illecebrosus* (Rowe and Mangold 1975). Moreover, O'Dor and Wells (1978) noted that the tissue breakdown and death in *Octopus vulgaris* is not simply due to starvation and the energy demand of a developing ovary, because males also cease eating, show similar tissue degeneracy and die at approximately the same time as their mates. Therefore, they concluded that tissue degeneracy and death should be under the control of the optic hormone and that this hormone acted to inhibit protein synthesis. Nevertheless, it is probably that a developing ovary also produces a hormone that increases the release of muscle amino acids into the blood (O'Dor and Wells (1978).

The information on the effects of senescence in males is much scarcer than in females. Tait experience (2013) with a senescent male Caribbean Reef Octopus (*O. briareus*) showed that its behaviour at the end of their life cycle is markedly different than that of females. Senescent males tend to be quite active, often at odd/uncharacteristic times of the day. Like females, males will generally refuse food offerings when they have approached the end of their life cycle. The male also exhibited a decline in his ability to control his chromatophores. The movement of both the male



Fig. 16.1 Physiological changes in the gonad and in the digestive gland of post-spawning *Octopus maya*. **a** Gonad of a female octopus immediately after spawning; and **b** 40 days after spawning; **c** digestive gland of a female octopus 40 days after spawning

and the female are significantly less coordinated than in early stages of experimentation.

Parallel to body deterioration, a possible reduction in the immunological responses can occur during senescence (Pascual et al. 2010). However, studies evaluating the immunocompetence and health status of senescent cephalopods are rare (e.g. Roumbedakis et al. 2018). Although an immunological compensation through the cost of using energy reserves in female octopuses in the first period after spawning (i.e., until at least 40 days post-spawning) can occur (Roumbedakis et al. 2018), there is some evidence of an impairment of the immune system in senescent cephalopods. For instance, arm regeneration may not occur in injured senescent cuttlefish (Féral 1988) and host defence against parasite infection may be impaired in senescent octopuses (Pascual et al. 2010). The presence of ‘unhealed wounds’ in senescent female octopuses may be possibly related to an impairment of the immune responses (Wang and Ragsdale 2018).

Behavioural changes are also observed in senescent cephalopods. A recent study with sexually matured female *Octopus bimaculoides* described four stages of reproductive behavioural stages: (i) non-mated; (ii) feeding; (iii) fasting; and (iv) declining (Wang and Ragsdale 2018). The most remarkable characteristics commonly observed in senescent animals (e.g. skin lesions, retraction of skin around the eyes, missing arm tips or suckers) were seen in the fourth stage. The authors also identified that multiple signalling systems of the optic glands are involved in these behaviours.

16.3 Parasitology and Senescence

Senescence is not a disease, although senescent cephalopods can be frequently mistaken with diseased animals. For that reason, in order to be able to differentiate these conditions, it is important to recognize its signs (Anderson et al. 2002). Senescence-like symptoms due to poor animal welfare (e.g. changes in water quality parameters) can also occur (Budelmann 1998). Skin lesions caused by hits against the tank walls also are a common cause for bacterial infections (Hanlon and Forsythe 1990), which may eventually become a more likely occurrence due to the loss of coordination in senescent cephalopods.

Parasitological studies in senescent cephalopods are rare, however, they may provide important insights into host–parasite interactions. In senescent female cephalopods, the transmission of parasites through the food chain (e.g. trematodes digenea, cestodes, nematodes) might be reduced or inexistent, due to the reduction or lack of feeding in this period. Moreover, senescent cephalopods parasitized may eventually not properly activate immunological reactions, as observed in *Octopus vulgaris* infected with *Aggregata* (Pascual et al. 2010), in which low host reaction and no

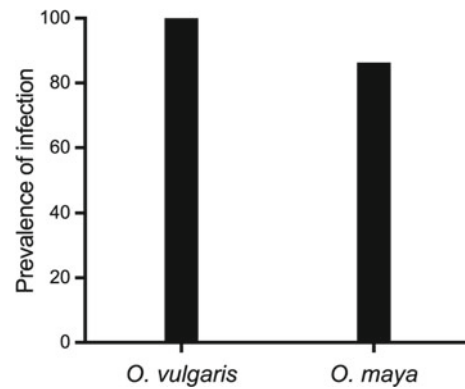


Fig. 16.2 Prevalence of infection of *Aggregata* spp. in post-spawned female octopuses: *Octopus vulgaris* ($n = 4$; compiled from Pascual et al. 2010) and *O. maya* ($n = 22$; original data)

signs of inflammation were observed. A suppressed immune system may increase susceptibility to parasite infection in senescent cephalopods.

As commonly observed in adult octopuses, post-spawned female octopuses also present high prevalence of infection by *Aggregata* spp. (Apicomplexa, Aggregatidae) (Fig. 16.2). In post-spawned female *O. vulgaris*, large numbers of sporogonial stages (infective forms) of *Aggregata octopiana* were highly spread in host tissues, probably to ensure the completion of parasite’s life cycle (Pascual et al. 2010). In post-spawned female *O. maya* infections by *Aggregata* sp. were observed in the caecum (Fig. 16.3a), intestine, and gills of the hosts (Roumbedakis et al. 2017).

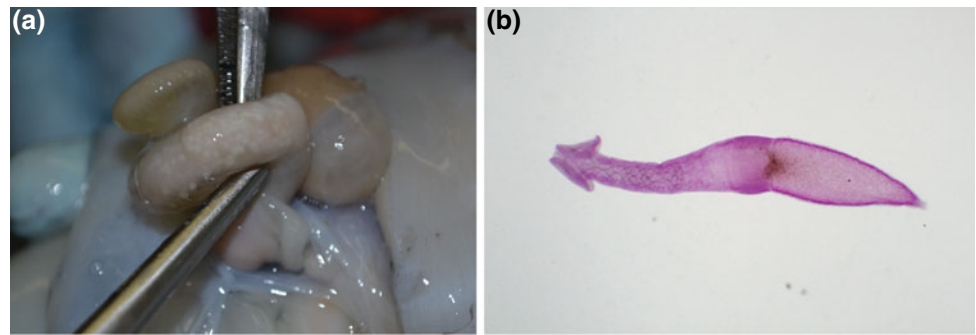
In addition, post-spawned female *O. maya* was also parasitized with cestode larvae *Prochristianella* sp. (Cestoda, Trypanorhyncha). This parasite was found in the buccal mass of the female octopuses (Fig. 16.3B), with 90.9% of prevalence and mean intensity of infection of 155.4 ± 107.73 .

Both parasites, the coccidian *Aggregata* sp. and the thrypanorhynch cestode *Prochristianella* sp., are transmitted by the food chain. In this study, female octopuses were captured in the wild and acclimatized in the laboratory for approximately 1–2 months until sampling, which occurred immediately after or until 40 days after spawning. In the beginning of the acclimation period octopuses fed on frozen crabs or on an artificial diet and then feeding was gradually reduced until the spawning. This suggests that these animals were already infected with both parasites before capture.

16.4 Concluding Remarks

The degenerative process and death are so rapid in the majority of cephalopods that quantitative and qualitative changes are very important. For this and other reasons (e.g. excellent adaptation of some species to confinement

Fig. 16.3 Parasites of post-spawning female *O. maya*. **a** Caecum infected with the coccidian *Aggregata* sp. **b** Trypanorhynch cestode *Prochristianella* sp. collected from the buccal mass



conditions, and their capacity to tolerate well surgical operations) cephalopods are an excellent material for the study of mechanisms regulating ageing in laboratory models, and therefore in bio-gerontology. As pointed out by Nussey et al. (2012), the recent emergence of long-term field studies presents irrefutable evidence that senescence is commonly detected in nature. These authors found such evidence in 175 different animal species. The bulk of this evidence comes from birds and mammals, but senescence was also evidenced in other vertebrates and insects. It could surprise the absence of the cephalopods in this comprehensive review, but this may be due to the fact that senescence has hardly been observed in nature in these organisms. Parasitological studies in senescent cephalopods are rare, however, they may provide important insights into host–parasite interactions. For the above reasons, we consider that both the study of senescence in cephalopods and the relationship between this critical period of the life cycle and the pathological processes caused by infections is still in its infancy, and should be a field of research to be developed.

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