

Ageing and longevity in the Decapoda (Crustacea): A review

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Abstract

Ageing and longevity is a neglected field of crustacean biology. Information on longevity is available for less than 2% of the extant species of the Decapoda. Maximum ages reliably determined range from 40 days to 72 years corresponding to a life span difference of a factor of 650. The shortest-lived decapods are planktonic dendrobranchiate shrimps, and particularly long-lived species with life spans of decades are found in the Astacidea. Most decapods seem to live for 1–10 years. High geographical latitude, the deep sea and freshwater caves promote longevity. The majority of the Decapoda is indeterminately growing and presumably characterized by negligible senescence. The adults of the determinately growing decapods like some brachyuran crabs suffer from mechanical senescence and are unable to regenerate lost appendages. The decapod crustaceans have developed many effective anti-ageing mechanisms including moulting, detoxification of free radicals, removal of cellular waste, renewal of tissues by life-long stem cell activity, regeneration of appendages, detoxification of environmental pollutants and isolation of pathogens and diseased tissue areas by melanisation and encapsulation. Age related diseases including cancer are virtually unknown. The present compilation of data on longevity and senescence in decapods is the first one that covers the whole spectrum of a higher invertebrate taxon. It is hoped to provide an interesting source of information for carcinologists and biogerontologists. Further improvement of knowledge on ageing and longevity in the Decapoda would be beneficial for crustacean aquaculture, fisheries and ecological modelling. Some decapods even have good potential to become models for general ageing research.

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1. Introduction

The Decapoda are among the better investigated animal groups, which is mainly due to their ubiquity in aquatic ecosystems, their historical role as biological models and their importance as human food. The Decapoda comprise more than 14,750 extant species that are morphologically and physiologically highly diverse and inhabit a broad variety of marine and freshwater habitats (Martin and Davis, 2001; De Grave et al., 2009). Some of them are even terrestrial.

Decapod species have been used as research subjects since the times of Aristotle, the father of zoology (384–322 BC). A most remarkable example in this context is Thomas Huxley's book "The crayfish: an introduction to the study of zoology", which used the freshwater crayfish *Austropotamobius pallipes* (Lereboullet, 1858) to discuss a multitude of general biological questions (Huxley, 1880). Nowadays, species from various clades of the Decapoda serve as experimental animals for research on structural–functional relationships, development, neurobiology, sociobiology, behaviour, etc. (Vogt, 2002; Wiese, 2002; Scholtz, 2004; Duffy and Thiel, 2007). The use of decapods for human consumption goes back to ancient times but increased considerably in recent times because of aquaculture and diversification of fishing

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practices. In the year 2008, capture fisheries and aquaculture production of shrimps, lobsters, spiny lobsters, crayfish and crabs amounted to 10.23 million tonnes and had a value of 41.44 billion US\$ (FAO, 2010).

Despite the long-lasting and intense familiarity of humans with decapods and the increasing popularity of decapods in sea-life centres and hobby aquarist circles, knowledge of their ageing and longevity is very limited. This may mainly be because age determination is more complicated in the Decapoda than in other popular and commercially important animal groups like mammals (Spinage, 1973), fishes (Das, 1994) and molluscs (Abele et al., 2009). In reviews and books on biogerontology there is usually no mentioning of decapods, sometimes with the exception of a short annotation saying that lobsters can reach ages of 100 years (Finch, 1990; Osiewacz, 2003; Masoro and Austad, 2006; Kirkwood, 2008; Bodnar, 2009). Age information is not only of academic interest but forms the basis for the calculation of growth rate, mortality rate, productivity, population dynamics and stock management, ranking it among the most influential biological variables (Sheehy, 1990a; Campana, 2001).

This review attempts to give an overview on the state of the art of ageing and longevity in decapod crustaceans. It first deals with methods of age determination, then with life span ranges in different suborders and the dependency of longevity on geographic latitude and habitat. Thereafter, it addresses anti-ageing strategies of decapods, the relationship of growth type and senescence format and age-related diseases. Finally, the article emphasizes the benefits of ageing research in Decapoda for carcinology and ecology and identifies the potential of decapods for general biogerontological research.

2. Methods of age determination

Age determination in the Decapoda is severely hampered by the lack of permanent age information bearing structures like the scales and otoliths of fishes (Skurdal et al., 1985), the bivalve shells (Schöne et al., 2005) or the genital plates of sea urchins (Flores et al., 2010), which show annual or even daily growth rings. Therefore, age determination in decapods often relies on less direct age indicators and associated growth models. Methods of age determination include the observation of specimens in captivity, tagging and recapture, length-frequency distribution analyses in wild populations and analysis of data on moult increment and intermoult duration (Hartnoll, 2001). An alternative approach uses the continuous deposition of the age pigment lipofuscin in specific areas of the brain (Maxwell et al., 2007). Currently, this approach is tentative.

2.1. Rearing in captivity

Determination of the age in captivity is the most exact and reliable ageing technique. Such data are only available for

some rather short-lived decapods that are reared in aquaculture or kept as laboratory models, exhibition animals or pets (Wickins and Lee, 2002; Lukhaup and Pekny, 2008; Brown et al., 2010). However, since laboratory collected data are often the result of a protected life under optimal conditions they are of limited value for ecology and fisheries. They rather show the upper possible limits of longevity in a species.

2.2. Tagging and recapture

Another direct and exact method of age determination is mark and recapture. In order to ensure life-long retention of the mark, the tags ideally have to be placed underneath the cuticle. Otherwise, they are lost during moulting. There are several internal markers available for decapods, among them passive integrated transponders (microchips), coded microwire tags, visible implant alphanumeric tags and visible implant elastomeres (Weingartner, 1982; Hartnoll, 2001; Davis et al., 2004; Buřič et al., 2008). The latter two are placed under transparent parts of the cuticle and are readable from outside. However, after a few moults when the cuticle becomes thicker and more calcified readability is often impaired (Davis et al., 2004). Therefore, the most suitable tags for ageing of long-lived decapods are passive integrated transponders and coded microwire tags.

Alphanumeric tags are thin sheets made of soft plastic. They have a size of 2.5 mm × 1 mm and carry a code composed of letters and numbers (Buřič et al., 2008). Elastomeres consist of a silicon based material and a curing agent, which are mixed immediately before use and injected as a fluid. There are several fluorescent and non-fluorescent dyes available, which allow numerous combinations, particularly if different colours are placed at various sites of the animal (Davis et al., 2004). Elastomere tags are mostly used to mark batches but can also be used for individual tagging. The microchips used so far had a length of 12 mm, a diameter of 2.1 mm and a weight of 0.1 g (Bubb et al., 2002), restricting its use to larger specimens. The code of the microchip is externally readable from a distance of 15–25 cm by an electronic reader (Hartnoll, 2001). Meanwhile, transponder size has been reduced to 7 mm × 1.5 mm and 32 mg. Coded microwire tags are ferromagnetic steel rods of 0.5–1 mm × 0.25 mm carrying a number code etched into them. Unfortunately, these tags have to be excised from the animal before being read. Tagged animals are identified using magnetic detectors, either manually or in processing lines, and the excised tag code is then read under a low power microscope. This method also allows tagging of juveniles, for instance 1st benthic stage spiny lobster *Panulirus argus* (Latreille, 1804) (Sharp et al., 2000) or 1.5 months old European lobster *Homarus gammarus* (Linnaeus, 1758) of carapace lengths of 5–8 mm (Linnane and Mercer, 1998).

There are some more methods available to tag decapod crustaceans like radiotelemetry, externally glued number tags, external anchor tags and cauterization but these

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