

LIFESPAN OF TWO LONG-LIVED BIVALVES, *ARCTICA ISLANDICA* AND *PANOPEA GENEROSA*

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ABSTRACT

The aim of this paper is to compare the life span of the two long-lived bivalves *Arctica islandica* from the northern Atlantic, and *Panopea generosa* from the Pacific Ocean. Both these species are burrowing clams supporting commercial fisheries for human consumption. Shell length, longevity, age at sexual maturity, and recruitment are compared. The reliability of ageing methods and factors controlling growth line formation are discussed.

INTRODUCTION

There are principally two methods of defining the life span of marine bivalves. One is the analyses of age structure of the population. The maximal age achieved by 5% of the population investigated is determined. Other indicators of the life span are calculated according to the parameters of growth equations of the molluscs; age of the largest individual and age of reaching the size comprising a specific share, usually 95%, of the theoretically maximum (Zolotarev 1980). Assessment of the life span according to the age reached by a certain part of the population is of course lower than the age assumed for the oldest individual but in the present paper the values of maximal age as an indicator of life span of the species mentioned is used. Shells of many bivalves and gastropods reliably reflect their age. Study of the outer surface and peculiarities of the inner structure of the shell can be used in sclerochronology to analyze life-history patterns, such as growth rate and age, as well as to reconstruct marine environmental climatic conditions through the life span of the animal. Bivalve molluscs have historically been aged by examining the external valve surfaces for dark growth „rings“ that form as an annual periodic event. These rings have been

associated with factors having probable effect on the metabolism of growth such as environmental conditions (temperature etc.) or intrinsic conditions (spawning). Using the outer growth rings only the first 10-15 annual increments can be separated as a rule and therefore in species with a very long life history incomplete or conflicting age estimates may result from this method. In some bivalve species, internal narrow dark growth lines (annuli) alternating with broad light growth-increment deposits are seen in the broken edge of valves. The annuli have continuity with rings on the external valve surface. Diamond saw-blade equipment has facilitated sectioning bivalve shells for an examination of the accretion of shell layers from the beginning of their formation at the umbo to the ventral margin. However, simply cutting the valves may not show well defined annuli due to variations in the microstructure of the shell deposits. Therefore a technique involving preparation of the cut valve surface has been developed, the so called “acetate peel replicate technique” (Ropes 1985). This technique which relies on differential solubility of dense and loose growth zones to acid, is both labour-intensive and time-consuming but is the only known method producing accurate

age data for old bivalves. To prepare a bivalve for ageing the flesh is removed and the shell is cleaned and dried. One valve (either the right or the left one) from each individual is embedded in resin (Bioplastic) and cross-sectioned with a diamond saw-bade on a line from the umbo to the ventral edge of the shell (through the hinge tooth). The cut face is polished and etched with hydrochloric acid. A replicate is then made from the etched surface with cellulose acetate. The acetate peel is then examined microscopically and internal growth lines counted. The lines in the hinge tooth are most often counted, as erosion from outside forces does not occur here. Age determination studies using the acetate peel replicate method have increased estimates of longevity for virtually every bivalve species examined, with life spans commonly greater than 20 yr. and often exceeding 50 yr. (Zolotarev 1980). Bivalves such as *Arctica islandica* (Linnaeus, 1767) (Thompson *et al.* 1980, Ropes *et al.* 1984, Steingrímsson and Thorarinsdóttir 1995), *Tindaria callistiformis* (Turekian *et al.* 1975), *Crenomytilus grayanus* (Zolotarev 1980) and *Panopea generosa* (Gould, 1850) (Shaul and Goodwin 1982) (syn. *P. abrupta* (Conrad 1849) have exceptional longevity of over 100 years.

Distribution of Arctica islandica and Panopea generosa:

The ocean quahog, *Arctica islandica* is a boreal sublittoral species and one of the largest bivalve species inhabiting the marine waters of Europe and North America. It is generally found buried in silt and mud bottoms at depths as shallow as 4 to as deep as 280 m (Merill and Ropes 1969). The stock size of ocean quahogs off the west, north and east coasts of Iceland has been estimated at about 1,000,000 tonnes (Thorarinsdóttir and Einarsson 1996, Eiríksson 1988). Since 1976 *A. islandica* has been the focus of important commercial fisheries for human consumption in eastern North America

(Murawski and Serchuk 1989) but in Iceland it has only supported a minor inshore fishery for bait, however. Recently, an interest arose in investigating the potential of the stock to support large scale commercial exploitation for human consumption (Thorarinsdóttir and Einarsson 1996). The pacific geoduck *Panopea generosa* is a burrowing clam occurring from Alaska to Baja California. The species is found deep in the sediment in the lower intertidal zone down to a depth of 60 m. It supports important catches taken by divers at depths of 6-20 m (Shaul and Goodwin 1982). The total standing crop in water depths of 10-30 m in Puget Sound in Washington was estimated to be 127,000 tonnes (Shaul and Goodwin 1982).

Shell-length and longevity:

Arctica islandica has a maximum shell length of 140 mm and its maximum longevity amounts to 225 years (Ropes 1985). The average size in the commercial catches off the coast of Iceland is 75 mm which is reached in 30-40 years and shell length-frequency distributions have shown that most of the clams were in the size class 75-80 mm shell length (Thorarinsdóttir and Einarsson 1996). The oldest individual from Icelandic waters was 202 years old (Steingrímsson and Thorarinsdóttir 1995). In Icelandic waters shell growth slows down greatly at about 60 mm shell height and by the age of 15-20 years, and after that growth is extremely slow (Steingrímsson and Thorarinsdóttir 1995). A distinct change from fast to slow growth has been observed in the North Sea at the age of 10-15 years (Witbaard and Duineveld 1990). The growth rate in this species is one of the slowest that has ever been measured in bivalves (Turekian *et al.* 1975, Michael *et al.* 1994). The mortality rate has been found to range from 0.015-0.05 on the Scotian Shelf in Canada (Rowell and Chaisson 1983) and 0.01-0.03 off the east coast of the United States (Anon. 1995). *Panopea generosa* has a maximum shell length of 206 mm and the

average adult size of 158 mm is reached in 10 years after which the growth is extremely slow (Goodwin 1976). The average length in populations off Washington State varied from 124-171 mm (Goodwin 1976). The mean age in samples from Canada varied from 20-60 years and the oldest individual aged was 146 years old. Mortality rates calculated from age frequencies were found to range from 0.003-0.05 (Harbo *et al.* 1983, Breen and Shields 1983).

Age at sexual maturity and recruitment:

Age at sexual maturity in *Arctica islandica* shows a wide range and may be dependent upon growth rate and locality. Off the coast of Long Island ocean quahogs attain maturity at 5 -10 years of age (Ropes *et al.* 1984), off the coast of Nova Scotia as early as 7 years (Rowell *et al.* 1990) and at even older age in Icelandic waters (Thorarinsdóttir unpublished data). There are indications that the recruitment of *Arctica islandica* populations is very sporadic. Age-frequency distributions from a population off Northwest Iceland showed three modes at approximately 20 years intervals which indicates that strong recruitment events have only occurred approximately every twenty years during the last fifty years or so (Steingrímsson and Thorarinsdóttir 1995). Length-frequency distributions of a population, sampled over a 10 year period off the Atlantic coast of the United States, did not show any sign of recruitment (Murawski *et al.* 1982). Moreover it appears that no significant recruitment of *Arctica islandica* has taken place in this population during the last 20 -30 years (Anon. 1993). In Canada *Panopea generosa* recruits to the fishing stock at 4 years of age (Harbo *et al.* 1983). In many localities in Canada recruitment is considered low and juveniles are scarce (Harbo *et al.* 1983, Sloan and Robinson 1984). In a population in British Columbia individuals under the age of 10 years comprised only 5% of the populations investigated (Breen and Shields 1983).

DISCUSSION

Reports of bivalves of very high age as *A. islandica* and *P. generosa* have raised questions on the reliability of the ageing methods used, but evidence supporting the hypothesis that the internal growth bands are in fact formed annually has been derived from many studies. Bennett *et al.* (1982) analysed shells of *A. islandica* and *P. generosa* for natural radionuclides to determine growth rate and age. The quantities of unsupported ^{210}Pb and ^{228}Ra present in the shell were consistent with the growth bands being annual. Turekian *et al.* (1975) used the radionuclide ^{228}Ra as a chronometer to test annual banding in *A. islandica*. Six samples from a specimen having 22 growth bands were analyzed and predicted an age of exactly 22 years for this clam. Thompson *et al.* (1980) recovered young individuals of known age and found out that the number of bands was consistent with the hypothesis of annual banding. Studies measuring oxygen and carbon isotopes in the shell material made by Witbaard *et al.* (1994) have supported the hypothesis as well. The pulse of ^{14}C around 1960, resulting from atmospheric nuclear-bomb testing was recorded in the shell at a location in concurrence with that expected from band counting. On the contrary, Owen and Richardson (1996) studied deposition of growth lines in *A. islandica* from a shallow inshore site. They concluded that formation of growth lines in *A. islandica* are not universally formed annually but are results of both periodic and aperiodic events such as unsynchronised burrowing or disturbance. In shallow water, storms, low tides and abrupt temperature changes can disturb growth which is not necessarily the case in deeper waters. Factors controlling growth line formation in bivalves are not fully understood although water temperature, food availability, spawning, disturbance and anaerobic metabolism caused by deep burrowing of the bivalves have been suggested as possible factors. In

A. islandica Jones (1980) found that growth line deposition coincided with spawning in late summer or fall. Anaerobiosis resulting from deep burrowing and valve closure has also been proposed to explain growth line formation in *A. islandica* (Lutz and Rhoads 1977). In *P. generosa* forming of dark growth lines have been connected to negligible shell growth occurring during winter (Shaul and Goodwin 1982). The clams are inactive with retracted siphons during the winter which indicates a period of anaerobic metabolism causing dissolution of the calcium carbonate and concentration of the organic material in the shell, forming a growth line (Shaul and Goodwin 1982). Both these species grow relatively fast in the first years of life subsequently the growth slows down and the mortality rate becomes extremely low. The recruitment is as well considered low in both species. However, these species start spawning at a relatively low age compared to the longevity and there is no obvious indications of reproductive senility (Thompson *et al.* 1980, Sloan and Robinson 1984). The potential to reproduce for many years may be an evolutionary strategy in response to uncertain larval and juvenile survival. Both *A. islandica* and *P. generosa* are now seen as potentially valuable tools for evaluating long term environmental changes. Witbaard *et al.* (1994) observed cyclic variation in stable isotopes of oxygen coinciding with growth bands in *Arctica islandica*. This variation agreed with annual temperature variations suggesting that growth bands are a reflection of seasonal temperature -determined differential growth rate. Weidman and Jones (1993) have produced a shell-derived time history of nuclear bomb ^{14}C for the period 1939-1990 from annual growth bands in *A. islandica* from Georges Bank. In the Pacific geoduck shell growth has been correlated with environmental changes as annual standardised growth index was calculated for the years 1907-1980. Changes in growth were observed around 1919 and 1962

coinciding with annual temperature increase in these years (Campbell and Noakes 1991). An European freshwater bivalve *Margaritana margaritifera* was for many years regarded as having the highest longevity among invertebrates (Comfort 1979) but now *A. islandica* is considered to have the longest life span. This is probably the result of applying a method of determining age that has higher resolving power than that used before. We may assume that in future investigations the maximum age of many species of bivalves will prove to be even higher.

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