BIAS IN ESTIMATES OF MAXIMUM LIFE SPAN, WITH AN EXAMPLE OF THE EDIBLE COCKLE, *CERASTODERMA EDULE*

by

J. J. BEUKEMA

(Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands)

ABSTRACT

The assessment of maximum life span in a natural population of a species ("ecological longevity") meets with several difficulties. Using as an example a long-term data series of a tidal-flat population of the edible cockle, *Cerastoderma (Cardium) edule*, it is shown that the age of the oldest individual found depends on the sampling effort (both size of area sampled and duration of sampling period), on the numbers of cohorts studied and on their size. All of these factors enhance the number of (old) specimens examined and, thus, the chance that a very old individual is encountered. Even in a relatively short-living species such as the cockle, low-effort or low-density estimates were biased by one or more years.

It is argued that the available data on longevity may all be considered underestimates and thus should be used with caution. An example of incautious use is discussed.

KEY WORDS: longevity, *Cerastoderma edule*, long-term cycles, marine benthos.

INTRODUCTION

The concept of longevity or maximum life span is hard to define. In fact, no operational definition can be given. Increased rates of mortality at high age point to the reality of a "physiological longevity" (i.e. maximum life span under optimal, and thus controlled, conditions), but an exact time cannot be measured, only approached. The estimation of "ecological longevity" (i.e. maximum life span under natural conditions) is even less precise. In most natural populations, numbers of animals belonging to one cohort will decrease exponentially without a clear indication of senescence, i.e. any significantly higher mortality rates at old ages cannot be assessed. Even if age determinations in old individuals are sufficiently precise, their numbers will usually be too low to determine exactly their mortality pattern. So, longevity is usually defined simply as "the oldest individual encountered during a study of a population of a certain species".

Though such a definition is undoubtedly practical, some inherent difficulties go with its use. A higher searching effort for old individuals (by increasing sample size, studying more populations, populations of
larger size or during a longer period) will almost certainly yield even older individuals and thus raise the estimate of longevity. The records available in the literature, therefore, will have to be considered preliminary underestimates. The magnitude of this bias is generally unknown. Some authors appear to have used longevity estimates without realizing this bias. Such lack of caution appears evident in a paper by Powell & Cummins (1985), suggesting a relationship between molluscan longevity and long-term cycles in marine benthic communities.

Their paper induced me to study in a specific species the problem of the estimation of longevity. A long series of field data on the edible cockle, *Cerastoderma edule* L., appears to be suitable for this purpose: its populations can be dense, are easy to sample quantitatively and the ages of individual specimens can be determined readily and adequately.

**METHODS**

A 20-year data set on the cockle (*Cerastoderma edule* L.) was obtained by frequent (twice annual) sampling during 1968-1988 of 15 fixed stations scattered over a 50-km² tidal-flat area in the western part of the Dutch Wadden Sea. At each station, an area of generally 0.9 m² was sampled, mostly by sieving 50 cores of 180 cm² each along a transect of 1 km. The total area sampled per half year thus usually amounted to 13.5 m², and therefore, the numbers of cockles from each cohort observed on the tidal flats were expressed per 13.5 m². If the total area sampled was (slightly) different from 13.5 m², the number was recalculated to represent the number per 13.5 m².

Ages of cockles in this area are relatively easy to determine by counting the year marks on the shells. Two other factors contributed to the precision of the assessment of ages:

1. the age composition of the sub-populations at each station was always known from foregoing samplings (cockles hardly change places);
2. At any station, only few cohorts were present at a time. This was caused by two factors: a high year-to-year variation in reproductive success with (almost) complete failure in certain years (Beukema, 1982b) and high mortality rates, amounting to an average of about 75% per year (mean instantaneous death rate $z = ab. 1.4 \text{ a}^{-1}$; Beukema, 1982a) and after severe winters locally approaching 100% (Beukema, 1979; 1985). Errors in age determination, therefore, will have been rare simply by the presence of only one or two year classes at a time at any station. See Beukema (1982a) for further details on methods and on the cockle population.