Bomb signals in old Antarctic brachiopods

Sir — Skeletal check-marks are commonly used to assess the age and growth of organisms. They are usually assumed to be formed annually. By using radiocarbon bomb signals to calibrate growth checks in shells of Antarctic brachiopods, we show that they were laid down with a sub-biennial periodicity. The data also indicate that low Southern Ocean ^{14}C signals are probably not caused by upwelling deep water, but are more probably due to reduced atmospheric supply and long-term radiocarbon deposition in ice.

Articulate brachiopods dominate the macrofossil record from Cambrian times. They are sessile filter-feeders, present in all oceans of the world, and are classified as 'low-energy lifestyle' organisms[1]. Growth-rate investigations, which are performed rarely, are typically based on analyses of bands in their calcium carbonate shell valves[2]. All species with carbonate skeletons incorporate ^{14}C from the environment. Radiocarbon concentrations in oceans are low compared with atmospheric and terrestrial levels, because their dissolved carbon pool is around 60 times the atmospheric pool. Variability in oceanic signals has been used to indicate areas of upwelling water[3], and coral and bivalve mollusc skeletal signals to assess ^{14}C records in latitudes to 42 °N (ref. 4).

Antarctic ^{14}C levels are especially low, posing problems when dating marine material. Age corrections up to 1,400 years are necessary for recent material, whereas around 400 years is typical elsewhere[5].

We obtained age estimates for the brachiopod *Liothyrella uva* from Signy Island, Antarctica (60°43' S, 45°36' W), by counting alpha growth checks in shell valves (G_c) and from measured increments (G_i) in a 2-year mark–recapture growth study. The G_i ages were 1.84 times older than G_c values (*a* in the figure), and this factor was significantly different from 2 ($t=15.8$, $P<0.001$). Ten brachiopods were then aged using $G_c \times 1.84$, and samples were cut from the oldest parts of their shell valves. Shell samples thus obtained were deposited between 1945 and 1985, and contained enhanced ^{14}C from the mid-1950s onwards (*b* in the figure). The ^{14}C increase occurred within 1–2 years of the first radiocarbon bomb signals found in nearby Antarctic peninsula ice-cores[6]. The ^{14}C signals peaked around 1962 and declined thereafter, although another peak possibly occurred between 1975 and 1980, following enhanced ice-core activity in 1972–74 (ref. 6).

Shell-activity data are, therefore, 2–5 years later than terrestrial signals, peaks are less precise, and the time required for the signal to return to background levels is much longer. This reflects the large carbon pool and long residence time in Antarctic circumpolar water, and contradicts the hypothesis that upwelling deep water with low radiocarbon content causes reduced signals in polar oceans[3], which would cause signals to decay more rapidly (upwelling is also unlikely from oceanographic considerations — Signy lies within the strongly stratified Weddell–Scotia confluence[7]). Lower marine signals in polar latitudes are, therefore, more probably due to reduced atmospheric ^{14}C supply and long-term radioisotope incorporation in ice.

The close correlation of shell age with ^{14}C signal confirms that growth checks were not formed annually, and indicates either entrainment to a biennial environmental cycle that occasionally breaks down, or an endogenous cycle with a periodicity of less than 2 years. Using the × 1.84 conversion of growth rings to age gives a maximum of 52 years for *L. uva* (2 years' periodicity gives 56 years). Temperate and tropical brachiopod ages are generally 2–15 years. Ages >50 years were calculated recently for *Magellania fragilis*[2], a Weddell Sea species, assuming annual growth checks. Periodicities approximating 2 years would predict ages of 90–100 years.

Sea-ice dynamics in the Weddell Sea have a 7–9-year cycle[8]. Poor phytoplankton years also occurred at Signy Island on four occasions between 1972 and 1982 (ref. 9). However, these were not at approximately 2-yearly intervals, and no known sea-ice cycle approximates 2 years. Other long-term cycles identified include 4–6-year periodicities in life-history traits of phocids around the Antarctic Peninsula, which were suggested as being related to the El Niño–Southern Oscillation. However, the trends in these data were weak, and different biological cycles occurred in different phases with the El Niño signal[10]. A clear environmental signal of shorter periodicity has yet to be identified in this area. Alter-

natively, approximately biennial growth checks could result from endogenous cycles. Several Antarctic benthic invertebrates have reproductive cycles of >1 year (ref. 11), and reduced overall resource supply may underpin such extended cycles. Clearly, care is needed in interpreting shell check-marks and ageing cold water species, without independent dating. Whether the underlying causes of near-biennial growth bands are taxon-specific or environmentally modulated also requires elucidation.

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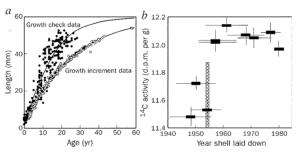11. Clarke, A. Invert. Reprod. Dev. **22**, 176–184 (1992).

Mating success of male birds

Sir — Widemo and Owens[1] examined the amount of variation in mating success on mating arenas (leks) among male birds of the ruff *Philomachus pugnax*, and concluded that the skew in male mating success decreases with increasing average lek size. Such a relationship has important implications for our understanding of the evolution of lekking as a mating system and sexual selection in general[1-3].

Widemo and Owens' conclusion was challenged by Mackenzie *et al.*[2] on the basis that the skew index[4,5] used to quantify the amount of variation in mating success between males is expected to decrease with lek size under a null version of the model in which mating occurs entirely at random. Although it is true that the skew index decreases with increased lek size under random mating (dashed line, *a* in the figure), this decrease is much less pronounced than the exponential decrease suggested by Mackenzie *et al.*[2] (solid line, *a* in the figure). The drop in skew observed by Widemo and Owens in larger leks is therefore not simply an artefact of the relationship between the skew index and lek size.

Two other possible factors could

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a, Brachiopod shell length compared with age from external shell check-marks (G_c) and from growth increments (G_i) from a field mark–recapture study. Shell check-marks were analysed twice in 113 individuals by both authors independently (size range, 3–55 mm length; total, *n* = 205).

For G_i data, 286 *L. uva* (size range: 4–54 mm length) were collected, measured and returned to the collection site. They were remeasured after 2 yr. General von Bertalanffy functions were fitted to both data sets (G_c data: $K = 0.086$, $D = 1.582$, $t_0 = -1.834$, $R^2 = 0.873$; G_i data: $K = 0.040$, $D = 0.991$, $R^2 = 0.996$; L_∞ was set to 60.0 mm to cover the whole size range) using the SIMPLEX iterative nonlinear fitting algorithm. The difference between the two functions fitted a linear model (age (G_i) = –0.785 + 1.842 × age (G_c); $r^2 = 0.997$; *n* = 113). After removing handling effects, by comparison with 6-month-duration trials (data not shown) at the same locality, mortality in the G_i experiment was <2% yr^{-1}. Growth rates in shorter-duration trials were also not significantly different from the 2-yr experiment. *b*, Shell ^{14}C activity (decompositions min^{-1} g^{-1}, ± s.d.) versus age. The oldest 5–8 mm (corresponding to approximately the first 3–4 yr of life, calculated from G_i data in *a*) of the brachial valves of 10 *L. uva* 12–57 mm long were analysed by accelerated mass spectroscopy. They had 8–25 growth rings (15–46 yr old, using the × 1.84 factor). Horizontal bars, 3–4-yr period of shell deposition; horizontal lines, 95% confidence interval for sample ages; hatched vertical bar, earliest enhanced radioisotope signals in Antarctic Peninsula ice-cores. ^{14}C data for samples before the ice-core signal were significantly lower than later ones (ANOVA, $F = 76.5$; 2, 6 d.f.; $P < 0.001$). Shell-activity levels correspond to ^{14}C ages of 890–1,340 yr.