

A note on the age at sexual maturity of humpback whales

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ABSTRACT

The conclusion of researchers in the 1950s that humpback whales reached sexual maturity at about age five was largely influenced by their interpretation of baleen tracings, and to achieve consistency with these tracings the accumulation rate of ear plug laminations (growth layer groups: GLGs) was assumed to be two per year. However, ovulation and natural mortality rates calculated by these researchers under the same assumption produced estimates that are difficult to reconcile with other biological data or with more recent estimates using individual re-sighting data. Such disparities are reduced or disappear when an annual accumulation rate is used, in which case their ear plug data would have indicated a mean age at sexual maturity of 9–11 years. Recent estimates of the age of female humpback whales at first calving using longitudinal studies of photo-identified individuals have produced conflicting results, some (from southeastern Alaska) being compatible with the earlier age-determination studies, others (from the Gulf of Maine) suggesting a much younger age.

KEYWORDS: HUMPBACK WHALE; GROWTH; AGE DETERMINATION; AGE AT SEXUAL MATURITY; PHOTO-ID

INTRODUCTION

The potential for using laminations in the ear plug of mysticetes for age determination was discovered in the mid 1950s (Laws and Purves, 1956; Purves, 1955). Prior to this, biologists had relied heavily on the pattern of transverse ridges and grooves in baleen plates, a technique first suggested by Scoresby (1820) but only taken up seriously by Ruud (1940; 1945) and Tomilin (1945). While counting the ear plug laminations was more straightforward than trying to interpret the ridging on baleen plates, and problems of wear did not arise, there was still a need for calibration of the rate of lamina accumulation. This was really only established (for fin whales, *Balaenoptera physalus*) in 1967 (Roe, 1967), and for sei whales (*B. borealis*) in 1974 (Lockyer, 1974), in both cases at one growth layer group (GLG, or one dark plus one light lamination) per year.

Chittleborough published his classic works on the biology of southern humpback whales (*Megaptera novaeangliae*) between 1954 and 1965, thus overlapping the period of the discovery of ear plug age determination but pre-dating its calibration. His finding (Chittleborough, 1959), and that of Nishiwaki (1959), that humpback whales reached puberty around age five, later received some support from longitudinal studies of individual humpback whales first sighted as calves in the Gulf of Maine, in which 12 females reached sexual maturity between the ages of five and seven (Clapham, 1992). Despite this apparent confirmation of Chittleborough and Nishiwaki's findings, scepticism has remained, largely because their conclusions flew in the face of conventional thinking about the age of other rorquals at puberty (generally taken to be at around age ten). There have even been moves to organise a humpback whale ear plug reading exercise, ideally involving Chittleborough himself, to attempt to reconcile the apparent paradox (Bannister *et al.*, 2000).

This note was prompted by a paper received for review (since published as Gabriele *et al.*, 2007), in the course of which some of the original publications were revisited.

REVIEW OF PAPERS

Chittleborough (1959)

This paper presents the results of reading ear plugs from 657 humpback whales and also includes photographs of 12

plugs from eight whales, bisected for reading, as well as the resultant counts. Apart from two examples of unreadable plugs, a comparison of the photographs with Chittleborough's counts makes it clear that what he considered a lamination was identical to what would be called a GLG today and his description in the text of the laminations and how he interpreted them confirms this. It seems extremely unlikely that Chittleborough interpreted plugs any differently from the majority of present-day readers, and he gives the number of laminations at puberty in 290 females as ranging from 5–14 with a mean of close to nine.

Chittleborough's conclusion that the age at puberty was five (and the rate of lamination accumulation thus two per year) was based on the results of his interpretation of tracings from baleen plates. Illustrations of such tracings that he gives show how difficult their interpretation must have been, particularly as there did not seem to be any neonatal baseline from which to start counting. Although wear at the tip was supposed to make the allocation of ages to whales more than six years old unreliable, there seems no objective means of establishing when wear started and how fast it occurred. The omission of the portion of the baleen plate below the gum must also have influenced age readings. Perhaps because of these difficulties, there has never been adequate calibration of this technique for age determination. Stable isotope analyses of bowhead and right whale baleen has shown that (for balaenids at least) annual periodicity in baleen growth can be identified (Best and Schell, 1996; Schell *et al.*, 1989) and could theoretically provide a means for calibrating baleen growth in humpback whales. In comparable analyses of minke whale baleen, however, only one or two periods could be identified, even in the largest animals (my interpretation of figures in Hobson *et al.*, 2004). The latter authors concluded that if minke whale baleen grows at the same rate as bowhead baleen (17–25cm year⁻¹), then the baleen plate may represent only the last year of life. They did not mention that at the southern right whale rate of baleen growth (25–60cm/year), the plates would represent even less than that.

Nishiwaki (1959)

By plotting the total number of ovarian corpora against the number of ear plug laminations in about 100 females,

Nishiwaki showed that the first ovulation occurred around an age of 9–12 laminations in the ear plug, concluding that sexual maturity is reached when 11 laminations have accumulated. He then simply stated ‘Since two laminations are formed in a year, the whale just reaching to the sexual maturity is five years old or slightly old than that’. No supporting data or reference is given for the conclusion that lamina formation is bi-annual.

Dawbin (1959)

Two marked humpback whales caught in Cook Strait, New Zealand, had been at large for 12 months and 18 months respectively, but baleen and ear plugs were only recovered from the latter animal. This whale was estimated at 36ft in length at marking (so clearly not a calf) but proved to be only 34ft 7in when killed. Despite the obvious error in size-estimation at marking, it was estimated to be at least in its second year and therefore when killed would have had a minimum age of three years. Baleen tracings showed three zones and there were five distinct and two indistinct laminations in the ear plug, while histological analysis of the testes indicated that the whale was still sexually immature. This was taken as supporting evidence of a bi-annual rate of lamina accumulation. However as the whale’s age was actually unknown, and the baleen tracing analysis only consistent with the minimum age assigned, the evidence is inconclusive.

Chittleborough (1960b; 1962)

The recapture of two marked humpback whales and the collection of ear plugs and reproductive organs (and in the one case baleen plates) from them were used to provide evidence in confirmation of a bi-annual rate of lamina accumulation. The whales were a male 36.75ft long and a female 39ft long at death, and both had been at large for almost five years after marking. The male had 12 laminations in the ear plug and the testes weighed 1kg each. The size, number of laminations and testes weight were all consistent with an individual approaching puberty, but the age from baleen plate tracings was given as ‘at least 5 years’ (as Chittleborough (1959) stated that ages of six or more were impossible to separate using baleen tracings, this qualification is quite significant). The female had ten laminations in the ear plug and one corpus albicans in the ovaries. Chittleborough posited that the whale must have become mature one year earlier, but there is no indication that the whale was lactating and so it is possible that the whale had become mature at least two years previously (i.e. it had completed one full reproductive cycle). It is important to note that, despite the title of one of the papers, neither of these was an individual of known age, and both were described at marking as yearlings approximately 30ft long. Estimates of whale length at sea can be very inaccurate (errors of 15% or more in either direction were observed for Antarctic minke whales (Best, 1984)), and the reasons for their assignment as yearlings are unknown (but would certainly not include individual identification). As evidence of a bi-annual rather than annual rate of lamina accumulation, the data from these whales must be considered equivocal.

OTHER IMPLICATIONS OF ASSUMING A BI-ANNUAL RATE OF EAR PLUG LAMINA ACCUMULATION

Chittleborough (1959), Nishiwaki (1959) and Symons and Weston (1958) regressed the number of ovarian corpora

against age as determined from ear plug laminations for humpback whales off Australia, the Ryukyu Islands in the North Pacific, and Antarctic Area I respectively. The regression coefficient so obtained for the Australian data was 0.558 ovulations per lamination, for the Antarctic data 0.59 per lamination, and although the coefficient for the Japanese data was not given, it can roughly be estimated from the illustrated slope of the regression as 0.50. Under the assumption of a bi-annual rate of lamina formation, these translate into annual ovulation rates of between 1 and 1.18 per year. If these are compared with annual pregnancy rates of 0.37 (Chittleborough, 1965) and 0.40 (derived from data in Nishiwaki, 1959), it suggests that only one in 2.5–3 ovulations was successful, and that presumably a high proportion of females must have undergone a post-partum ovulation. However, examination of the ovaries of females killed in Tonga shortly after parturition failed to reveal such a phenomenon (Chittleborough, 1965), implying that the frequency of ovulation at the start of each reproductive cycle must be much higher than the 1.2 observed (Chittleborough, 1959). Chittleborough’s explanation of this discrepancy was that some of the ovulations at the start of the reproductive cycle must have been ‘missed’ because their corpora lutea had regressed so much they were not recognised as being from the current cycle. However, if the rate of lamina accumulation was assumed to be annual rather than bi-annual, the ovulation rates would be halved and it would be unnecessary to postulate major ovulation failure (or ‘missing’ corpora albicantia).

Chittleborough (1965) also estimated the natural mortality rate of humpback whales assuming two ear plug laminations accumulated per year. For the Area IV population off Western Australia, coefficients for adult males and females were estimated as 0.086 (SE 0.14) and 0.087 (SE 0.129) respectively, while for the Area V population off East Australia, an estimate of 0.097 was considered to be representative of natural mortality in adult males (Chittleborough, 1960a; 1965). More recently, estimates of annual survival in humpback whales have been obtained from re-sightings of naturally marked individuals. In the Gulf of Maine (North Atlantic), Buckland (1990) estimated annual survival as 0.951 (95% CI: 0.929, 0.969), and Barlow and Clapham (1997) non-calf survival at 0.96 (SE 0.008). In the central North Pacific, Mizroch *et al.* (2004) estimated adult survival at 0.963 (95% CI: 0.944, 0.978). Although the populations, time periods and methods involved are all different, the Northern Hemisphere estimates imply substantially lower annual mortality rates than those calculated by Chittleborough. However, if an annual rather than bi-annual rate of lamina accumulation had been adopted, the mortality rates for Australian humpback whales would have been halved and would essentially be not significantly different from those for the Northern Hemisphere.

CONCLUSIONS

This review indicates that it was an assumption of a bi-annual rate of lamina accumulation, rather than a different interpretation of what constituted a growth layer group in the ear plug, that led to estimates in the late 1950s of the age of humpback whales at sexual maturity of around five years. In this assumption, researchers were mainly guided by the results of baleen plate tracings, a technique that seemed to involve a high degree of subjectivity in its interpretation, was only applicable to animals in the first few years of life and

was never calibrated adequately. Estimates of ovulation and natural mortality rates made under the assumption of a bi-annual rate of lamina accumulation now seem too high to be biologically feasible.

The conclusions of the 1950s studies on the age of humpback whales at sexual maturity were seemingly supported by later longitudinal studies of individually identified animals in the Gulf of Maine (Clapham, 1992). However, further such studies in southeastern Alaska have revealed ages at first calving in humpback whales of 8–16 (average 11.8) years, more consistent with the results of age determination studies assuming an annual rate of lamina formation in the ear plug (Gabriele *et al.*, 2007). The reasons for this discrepancy between the two photo-identification studies remain to be resolved.

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