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Validation of the Use of Thin-sectioned Otoliths for Determining the Age and Growth of Golden Perch, *Macquaria ambigua* (Perciformes: Percichthyidae), in the Lower Murray–Darling Basin, Australia

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Abstract

Golden perch, *Macquaria ambigua*, from the Murray–Darling Basin were aged by using transverse thin sections of their sagittal otoliths. Samples from 889 fish were obtained from riverine and lacustrine habitats and from wild and stocked populations. Error in the precision of age estimates (calculated as the mean percentage error of the independent age estimates of four readers) was 5·6% (3·9% after allowing for discrepancies in relation to the annual mark on the edge of the otolith). Validation was accomplished by using a combination of analysis of the progression of modes in length–frequency distributions, qualitative and quantitative marginal-increment analysis, and analysis of age estimates of fish from populations with a known stocking history. The technique was validated for fish up to 8 years of age (455–545 mm total length, 1695–3988 g total weight), and the greatest recorded age was 16 years (530–600 mm total length, 2607–4050 g total weight). Annual marks become visible in otolith sections in most fish of all ages in October, and 1 October was designated as the birth date. A description of our method of reading sections of golden perch otoliths, including recognition of false annual marks, is given. Otolith length, width and thickness increased linearly with fish length and with $\log_{10}$(fish age), whereas otolith weight increased linearly with fish age and exponentially with fish length. The continuous growth of the otoliths and the consistency in the appearance of annual marks support the accuracy of estimates up to the maximum recorded age. The mean length-at-age and the parameters of the length–weight relationship were estimated. The von Bertalanffy growth parameters were also estimated ($L_\infty = 507$ mm, $t_0 = 0\cdot420$ years, $K = 0\cdot454$). No significant differences were found in growth rates or length–weight relationships between males and females. However, growth (particularly in weight) was highly variable among sites and years, and slow-growing 5-year-olds may be shorter than fast-growing 1-year-olds. Ages were estimated for a sample of 86 golden perch caught between 1949 and 1951 but a comparison of growth rates between these and more recent collections was inconclusive.

Introduction

Golden perch, *Macquaria ambigua* (Richardson 1845), is found throughout the Murray–Darling, Lake Eyre, Bulloo and Fitzroy–Dawson drainage systems except in upper tributaries, and it has been widely introduced to other coastal systems in Queensland, New South Wales and Victoria (Brumley 1987; Allen 1989). Individuals may grow up to 76 cm in length and 23 kg in weight but are commonly less than 5 kg (Lake 1967*a*). Golden perch requires a rise in water level at some stage during the summer months (November to late February) in order to spawn, and females will resorb their eggs if the spawning stimuli fail to occur (Lake 1967*b*). Spawning occurs in an all-or-nothing fashion: all oocytes are shed in a single spawning act (Mackay 1973). Golden perch is a major target species of inland recreational and commercial fisheries and is hatchery-reared for commercial enterprises and government-sponsored stocking programmes (Rowland *et al.* 1984; Cadwallader 1985).

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The ability to determine the age of a fish accurately is one of the most useful features available in fish biology and fishery science (Bagenal 1974). There have, however, been no comprehensive studies on the age or growth of golden perch. Llewellyn (1966) reported the lengths and weights of a small number of known-age fish (presumably pond-reared) and illustrated the scales and a section of the second anal spine of these fish. He also reported that annual rings can be seen in golden perch otoliths and, although stating that their scales were difficult to interpret and often vague, concluded that the age of golden perch was best determined by a combination of scales and transverse sections of spines.

Data on the age and growth of other Australian freshwater members of the family Percichthyidae or other fish of the Murray–Darling drainage basin are similarly sparse (Anderson 1992). Harris (1985) has validated the use of sections of sagittal otoliths to age Australian bass, *M. novemaculeata*, reporting a maximum age of 22+ years. He found whole otoliths unsatisfactory and demonstrated that scale reading gave a marked underestimate of age in all but the younger fish (up to age 5). Cadwallader (1984) used both scales and whole otoliths to age Macquarie perch, *M. australasica*, and reported both to be equally reliable as indicators of age. Although reporting fish up to 9 years old on the basis of scale reading, he validated the technique only up to age 4. Unvalidated age estimates for *M. australasica* from scales have previously been used by Cadwallader and Rogan (1977) and K. A. Bishop and R. D. J. Tilzey (unpublished data). The use of sectioned otoliths to age Murray cod, *Maccullochella peeli*, has been validated by Gooley (1992), and age and growth estimates for *M. peeli* and trout cod, *M. macquariensis*, the other percichthyid species found in the Basin, are reviewed by Anderson *et al.* (1992). Recently, Penn and Potter (1990) validated the use of otoliths to age the nightfish, *Bostockia porosa*, a small percichthyid from Western Australia, and reported a maximum age of 6 years.

Otoliths are widely accepted as one of the more reliable methods for ageing fish, and for fish with thick otoliths it is necessary to section the otoliths through their centres (Bedford 1983). Beamish (1979*a*) has suggested that the examination of sections of otoliths should become a routine approach in any attempt to age fish by using otoliths.

In the present paper, the age structures of several golden perch populations, including stocked and natural propulations from lacustrine and riverine habitats, are reported, using samples collected over a 40-year period. The validity of the ageing technique using thin-sectioned otoliths is assessed, and the technique for reading the sections is described to allow other readers to employ the technique.

Materials and Methods

Sources of Fish

Fish were obtained from several sources, using a combination of regular and ad hoc surveys, donated material, and the opportunistic collection of samples from fish caught by anglers and professional fishermen (Fig. 1; Table 1). Populations sampled included those comprised exclusively of stocked fish (Wimmera River near Horsham, Loddon River near Kerang, Campaspe River downstream of Lake Eppalock, Green Lake near Horsham, and Lake Nagambie and Tahbilk Lagoon near Nagambie), stocked populations that may also contain fish from other sources (Reedy and Middle Lakes near Kerang, Broken River downstream of Benalla, Lake Cullulleraine near Mildura, and Lake Burrinjuck and Googong Reservoir near Canberra), and wild populations (Barmah Forest). All these populations were sampled with gill-nets (mesh size 38–203 mm) and single-wing fyke nets (minimum opening dimension 200 mm, mesh size 25 mm). Samples from the Wimmera River at Horsham included a large proportion of fish caught by anglers in an annual fishing competition held in March. Samples from the population of golden perch established by stocking in Googong Reservoir in the Australian Capital Territory (ACT) and from the population in Lake Burrinjuck in New South Wales (NSW) were provided by the ACT Parks and Conservation Service and the NSW Department of Agriculture and Fisheries, respectively. In addition to these recent collections, otoliths collected from golden perch caught in the Barmah Forest area (Moira Lakes) and at unspecified locations on the Murray and Nurrumbidgee rivers by J. T. O. Langtry between 1949 and 1951 (here termed the historical collection) were also obtained for comparison.

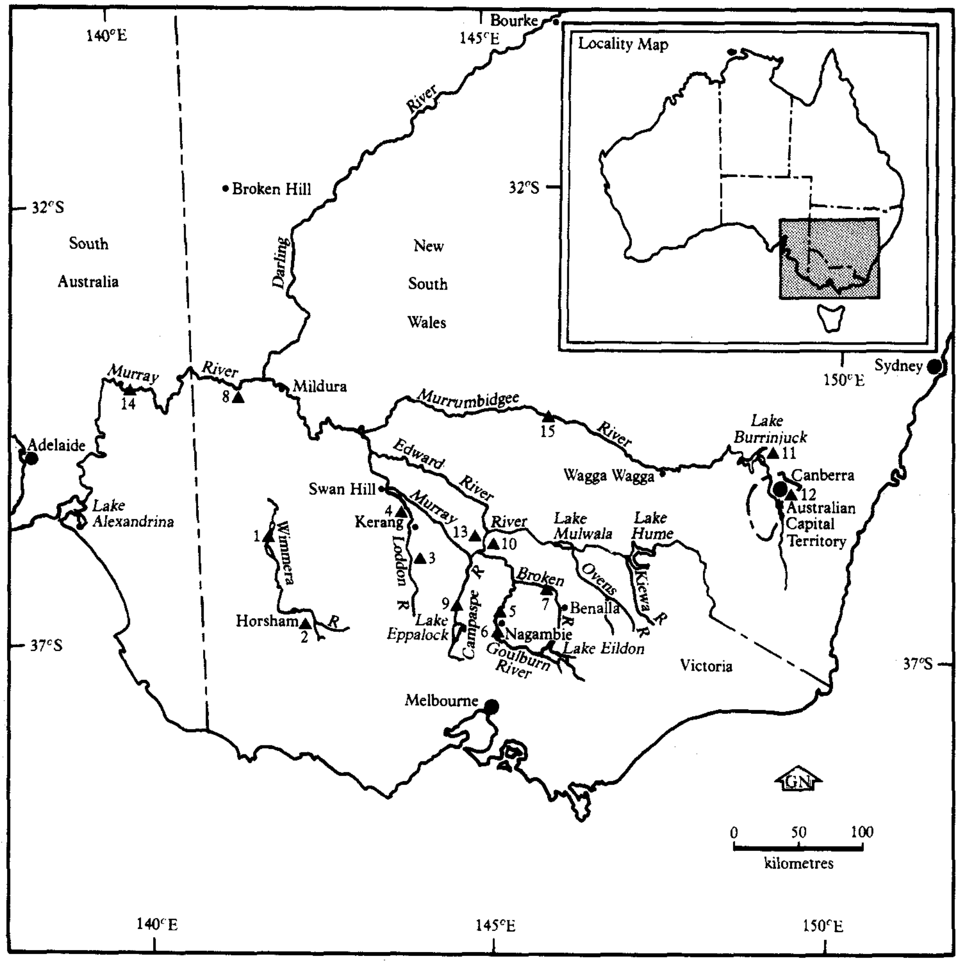

Fig. 1. South-eastern Australia, showing sampling localities and major rivers of the Murray–Darling Basin. Numbers refer to sites as listed in Table 1.

Measurements of total fish length (millimetres), total fish weight (grams) and sex were obtained when possible.

Collection, Treatment and Description of Otoliths

Sagittal otoliths were dissected from specimens, using a technique similar to that described by Harris (1985) for *M. novemaculeata*, and stored dry in jars or envelopes.

Golden perch otoliths resemble those of other *Macquaria* species, and terminology used by Harris (1985) to describe otoliths of *M. novemaculeata* is used here. Golden perch otoliths are large, ovoid and laterally concavo-convex, with a deep groove on the convex proximal surface. They tend to be more elongate than those illustrated for *M. australasica* (Cadwallader 1984) and to have a more prominent rostrum than that illustrated for *M. novemaculeata* (Harris 1985). Larger otoliths, especially, have very irregular or scalloped margins.

The lengths of both otoliths from each fish were measured as the shortest distance between the anterior and posterior ends, and the dorsal-ventral widths were measured at the widest point with dial calipers to the nearest 0·05 mm. Each otolith was weighed to the nearest 0·01 g on a Mettler PE3600 digital balance.

Table 1. Range of sampling dates and number of *M. ambigua* for each sampling locality
Site numbers refer to localities illustrated in Fig. 1. Map numbers and grid references are from the 1 : 100 000 National Mapping Series

Locality	Site No.	Map No., Grid reference	Sampling dates First	Sampling dates Last	Number of fish
Wimmera River	1	7324, 180 686	11.iii.86	10.iii.91	371
Green Lake	2	7825, 055 660	8.ii.84	18.iii.88	14
Loddon River	3	7626, 625 435	19.ii.84	21.ii.91	159
Reedy and Middle Lakes	4	7626, 605 475	21.iii.87	26.iii.87	31
Lake Nagambie	5	7924, 345 275	31.viii.84	18.xii.87	17
Tahbilk Lagoon	6	7924, 305 225	8.xii.87	10.xii.87	7
Broken River	7	8025, 855 682	1.iii.88	8.ii.90	6
Lake Cullulleraine	8	7229, 545 075	20.iii.89	24.iii.89	18
Campaspe River	9	7824, 800 410	11.i.89	18.i.89	9
Barmah Forest	10	7926, 260 300	11.i.90	15.i.91	35
Lake Burrinjuck	11	8628, 270 490	21.xi.87	21.iv.88	18
Googong Reservoir	12	8727, 055 755	18.xi.88	18.xi.88	25
Moira Lakes	13	7826, 140 200	23.x.51	28.xi.51	65
Murray River	14		11.x.49	2.vii.51	14
Murrumbidgee River	15		9.x.49	4.xi.49	7

The left otolith was used for age determination whenever possible. It is rare for there to be different ring patterns on the two sagittal otoliths from the same fish (Williams and Bedford 1974). Embedding and sectioning of otoliths and mounting of sections generally followed the technique of Bedford (1983), using a saw similar to that described by Augustine and Kenchington (1987). Otoliths were embedded in clear polyester resin in 8-mm-thick blocks (about 62 mm square) after their nuclei had been aligned over a fine groove cut into the base of the mould. Several serial sections of otoliths (about 0·5 mm thick) were cut on either side of the nucleus, using a Gemmasta lapidary saw with a diamond-impregnated blade (10·2 cm in diameter and 0·1 mm thick; cf. Augustine and Kenchington 1987). The use of clear embedding-grade resin allowed for accurate positioning of otoliths in each block and alignment of otoliths with the saw blade. The cut sections were examined, and those closest to the nuclei were selected. These were washed, dried and mounted on microscope slides under coverslips, using further polyester resin.

Age Determination

The reading of the age of fish by using patterns on scales or otoliths is not a simple and unequivocal process (Panella 1974). Lack of consistency in the application of terms to whole or sectioned otoliths, and different methods of illumination and sample preparation, add to the problem. It is therefore clear that, in order for others to be able to use a technique and to obtain results that are consistent, the method of reading must be adequately described and the terminology must be precisely defined in terms of what was seen and read.

Thin sections of golden perch otoliths clearly show a concentric pattern of light (translucent) and darker brown (opaque) bands or zones when viewed with transmitted light (Figs 2 and 3). Counts of the opaque bands were used to estimate ages as described below. All otoliths were viewed separately by four readers, who independently counted annual bands without knowledge of fish size or of locality or date of collection. Otoliths were read after all samples had been collected, using transmitted light under either a dissecting or a compound microscope.

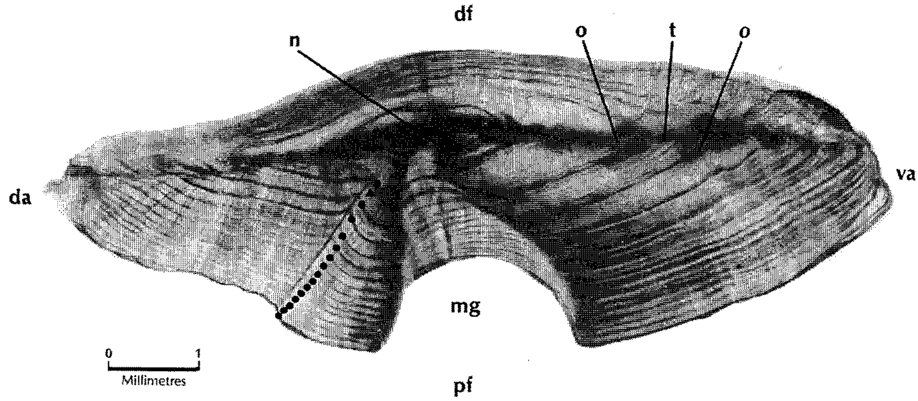

Fig. 2. Transverse section through the nucleus of the left sagittal otolith of an *M. ambigua* individual estimated to be age 16, showing the major features of such sections when viewed with transmitted light (fish length 533 mm, fish weight 2607 g, collected from the Murrumbidgee River). Dots, annual marks; triangle, false annual mark; da, dorsal apex; df, distal (outer) face; mg, medial groove (sulcus); n, nucleus; o, opaque material along dorsal-ventral axis; pf, proximal (inner) face; t, translucent band through opaque material adjacent to an annual mark; va, ventral apex.

The appearance of bands varied on different parts of sections, and there were subsidiary bands within the main opaque and translucent patterns. To resolve the complex finer detail visible on the sections and to define a consistent reading method, we worked initially with a small sample of known-age material derived from stocked populations. Thus, each of the four readers was 'calibrated' and trained to a consistent reading method before all samples were examined.

In young fish bands were most easily counted along the dorsal-ventral axis, but in older fish they were more clearly defined across the proximal (inner) face on either side of the medial groove. Bands could usually also be traced across the distal (outer) margin of the section and across the sulcus or medial groove, but the latter was sometimes difficult because of the abrupt flexure of the ring at the edge of the groove. Sections of *M. ambigua* otoliths differ from those of *M. novemaculeata* (as illustrated by Harris 1985) in that more deposition occurs along the distal face in young fish and the first four or five bands are discernible across this outer face as well as across the proximal face (Fig. 3*D*). Sections of *M. ambigua* otoliths also exhibit deposits of opaque material along the dorsal-ventral axis (Fig. 2), where the counted bands reach their maximum diameter.

A band was counted as an annual mark when it was completely discernible on both sides of the medial groove (see Figs 3*C* and 3*D*). The presence of an associated brown zone near the medial groove was also a key criterion for recognizing annual bands. Other criteria used to distinguish annual bands were their clarity across the distal margin of the section (for the first few bands only) and their clarity across the medial groove.

There was often a complex series of finer dark and light bands, particularly among the first few annual bands (Figs 3*A* and 3*C*), and some experience was required to identify and exclude the false bands. The position of the first annual band varied considerably, and its recognition was aided by the frequent presence of a narrow and translucent band that was sharply delineated where it crossed the opaque zone along the dorsal-ventral axis of the section. Two or more such translucent bands may be present within the first or second annual bands, but the association of one such band with a darker ring traceable through the proximal face of the section, and the other criteria mentioned above, allowed consistent identification of the first annual mark. At least one additional distinct ring was usually visible within the first annual mark (presumably formed during larval or juvenile stages of development), and false annual marks were also common between the first and second annual marks. Each reader also measured the diameter of the innermost band counted (with an eyepiece micrometer).

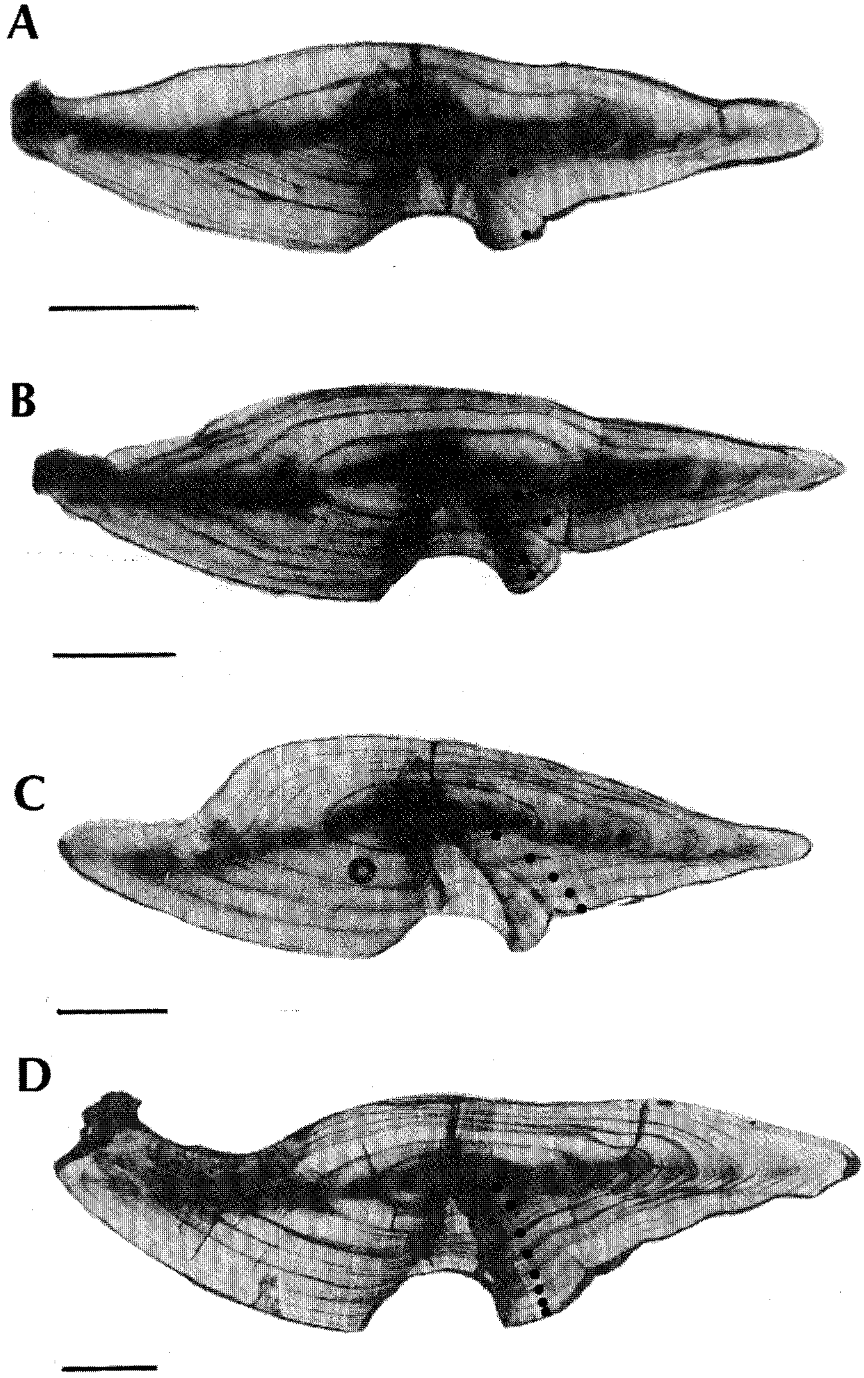

Fig. 3. Transverse sections of left sagittal otoliths of *M. ambigua* of various ages, viewed with transmitted light: (*A*) fish age 2 from the Loddon River, collected 2 November 1990, length 230 mm, weight 170 g; (*B*) fish age 3 from Tahbilk Lagoon, collected 8 December 1987 (stocked February 1985), length 295 mm, weight 390 g; (*C*) fish age 5 from Googong Reservoir, collected 18 November 1988, length 331 mm, weight 504 g; (*D*) fish age 8 from the Wimmera River, collected 11 march 1991, length 470 mm, weight 1695 g. Dots, triangles and letters are as defined in Fig. 2.

Standard texts on age determination techniques (e.g. Bagenal and Tesch 1978; Jearld 1983) recommend that ages be adjusted around a designated birth date to ensure that fish of the same brood are always allocated to the same age group. However, it is also important that readers be unaware of the date of sample collection and the size of fish to avoid biasing age determinations. In particular marginal-increment analyses that aim to establish the time of formation of annual marks will be biased, and arguments concerning validation will be somewhat circular, if readers know collection dates and use them (consciously or not) in deciding whether an annual mark is present at the edge of the structure under examination. As age adjustment must be done after all reading is completed, it is necessary to know whether the outermost annual mark recorded was at the edge (i.e. whether the estimates for fish caught before the birthday need to be increased or whether the new annual mark has already been formed and included in the age estimate). Neither standard texts nor published papers describe a means of meeting these potentially conflicting requirements and objectively recording such items. The technique described here for *M. ambigua* should prove to be applicable to other ageing studies. Each reader recorded whether the outermost band counted was regarded as being newly formed or near the edge of the section (recorded as C) or as being due or not completely formed (recorded as N). Sections in which the outermost band was not on the edge and another band was not yet due were recorded as Z. The outermost band counted was regarded as being remote from the section edge (and was recorded as Z) when the marginal growth increment exceeded about 25% of the previous increment between bands. Bands were regarded as being due (N) when marginal growth exceeded about 75% of the previous increment.

Precision of Estimates

A verification procedure was adopted to resolve discrepancies between readers and hence to improve the precision of age estimates.

Discrepancies between readers' counts were often due to differences either in the placement of first annual marks or in whether a ring was counted at the edge of an otolith. The measurements of inner-ring diameters and the position of the outermost band allowed the sources of discrepancies to be identified. Ages agreed by three or more readers were regarded as verified ages. When only one reader disagreed with an age determination, that reader would reexamine the otolith without reference to any previous results. When two or more readers were in disagreement, all readers would reread the otolith, again without reference to previous determinations.

Disagreements due solely to the counting of an annual mark at the edge were often resolved by an adjustment made with reference to the date of capture and the assigned birthday, determined as described below. Otoliths for which an agreed age could not be assigned were regarded as not verified and were excluded from subsequent analyses.

The independent reading of all otoliths by four readers allowed calculation of the precision of the resulting age estimate, using the formula of Beamish and Fournier (1981) for the average percentage error (apE):

$$\mathrm{apE} = \frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij}-X_j|}{X_j}\right],$$

where N is the number of fish aged, R is the number of times fish were aged, X_{ij} is the ith determination of the jth fish, and X_i is the average age of the jth fish. This index was calculated firstly for the initial determinations of the four readers prior to attempts to resolve age-reading discrepancies and again after adjustments were made for the time of annual-mark formation.

Determination of Birthday

Using a conventional birth date regardless of minor variation in the time of annual-mark formation ensures that fish hatched in the same season are members of the same age group (Jearld 1983). Assigning a 'birthday' is also important for standardizing age estimates in terms of years and months. The most appropriate 'birthday' was determined as the time when new annual bands were recognized as being completed at the edges of sections.

This time of formation was determined from the pooled data set by plotting the percentage of fish in each two-week time period throughout the year for which three or more readers recognized a ring at the edge of the otolith. Ages for otoliths collected in the months around this date were adjusted where necessary as follows. Bands that had been counted at the edges of otoliths collected prior to the 'birthday' were deducted from the verified age estimate. Conversely, the estimated (verified) ages for otoliths collected after this date that showed no band at the edge were increased by one.

Marginal Increments and Otolith Dimensions

Because of the difficulty in precisely locating the nucleus in all sections, increments between the edges of annual bands were measured as the maximum distance between bands on the dorsal–ventral axis. This could be done reliably only for the first four annual bands. The total dorsal–ventral width and the maximum distal–proximal thickness of each section were also measured, using an eyepiece micrometer. Marginal increments were expressed as a percentage of the increment between the two previous annual bands; e.g. for the increment outside band 4,

$$\frac{(\text{total width} - \text{diameter of band 4}) \times 100}{\text{diameter of band 4} - \text{diameter of band 3}}.$$

The divisor was the diameter of the first band when only one band was present.

Validation of Age Estimates

The validity of the ageing method was assessed by a combination of techniques: modal progression of dominant size classes, qualitative and quantitative marginal-increment analysis, and examination of the estimated age structure of populations with a known stocking history. The collection of frequent samples of golden perch from the Loddon River near Kerang provided evidence of modal progression of clearly defined size classes over a period of 16 months. A comparison of the age estimates for these fish with the expected age increments over this period is a test of the validity of the technique. The timing and periodicity of formation of bands was also tested by using these data. Samples from the Wimmera River over an eight-year period show progression of strong size classes. Comparison of the expected age increments with the age estimates for these fish again provides a test of the validity of the estimated ages.

To demonstrate that the bands counted did indeed form once a year, mean monthly marginal increments for fish from all sites were calculated, firstly for the combined age groups and then separately for ages 1 to 4 to examine potential differences between age groups. Similarly, a qualitative assessment of the timing and periodicity of band formation in fish of all ages was provided by the distribution of the percentage of otoliths with a ring at the edge, both for the whole sample (as used in the determination of the 'birthday') and for different age groups separately (to show any differences with fish age).

The accuracy of the technique was tested by sampling from populations with a known stocking history, which allowed for comparisons of age estimates with the expected ages or known maximum ages. Samples from the Loddon, Wimmera and Campaspe Rivers, Tahbilk Lagoon, Googong Reservoir and Lake Burrinjuck were used for this purpose. Fish are usually stocked in February or March of the year following that in which they were bred. Thus, for example, the 1982 stocking in the Wimmera River was of fish of the 1981 year class.

Plots of the mean diameters of annual marks for each age support the concept of annual marks as consistently recognizable features in the otoliths.

Data Analysis

Length–weight relationships and von Bertalanffy growth curves were determined by using the nonlinear curve-fitting routines of SYSTAT (Wilkinson 1987), with least-squares estimation as the loss function. When fitting the growth curves age was expressed as a decimal number with the fractional part representing the proportion of a year between the 'birthday' (see above) and the date of capture. Growth curves for subgroups were compared by using a test of the *F*-ratio of regression and residual mean squares (Zar 1974), where the regression mean square was derived from the difference between the sum of squares from the combined data set and the total of the subgroup sums of squares. Comparisons were made between the sexes and between the recent and historical collections. The general form of the relationship between otolith dimensions and estimated age and fish length were also determined by using SYSTAT routines. Logarithmic relationships, where determined, used base-10 logarithms.

Results

Otoliths from a total of 879 golden perch were collected, sectioned and aged. Annual marks were relatively widely spaced for the first 2 or 3 years of life, then became more closely and regularly spaced (see Figs 2 and 3). A small number of otoliths displayed an unusual granular pattern in which annual marks were usually nevertheless distinguishable but difficult to locate precisely for measurements. Some otoliths were unreadable because of errors in the cutting of sections (sections being cut either too thickly or off-centre). However, only 15 were rejected from subsequent analysis because of a failure by at least three readers to agree on an age estimate.

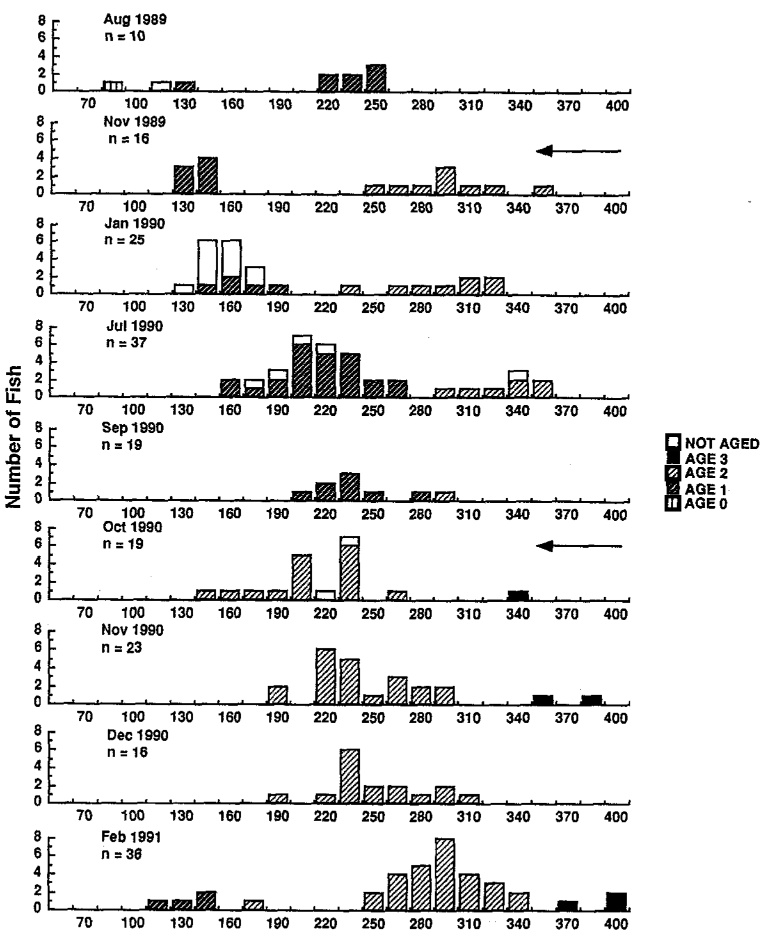

Fig. 4. Length-frequency distributions (15-mm size classes) for *M. ambigua* collected from the Loddon River, showing estimated ages of fish. Arrows indicate first samples taken after the assigned birth date (1 October).

Validation of Age Estimates

Length-frequency distributions for fish from the Loddon River near Kerang (Fig. 4) showed two distinct size classes between August 1989 and December 1990. In November 1989, they were assigned ages 1 and 2, which are consistent with the expected ages of fish from stockings made in February of 1988 and 1989. No fish were stocked in 1986 or 1987. These two size classes show progressive increase in length through to February 1991. Three features of these length–age distributions support the validity of the age estimates. Firstly, the age estimates are consistent within each size class on all sampling occasions; secondly, there is a consistent difference of one year between adjacent groups, which would be expected if size class corresponds to year class; and thirdly, age increments were recorded for each size class once a year after October in both 1989 and 1990. Only two fish of the total of 182 fish aged (1·1%) were assigned ages that were anomalous with their size classes (one fish 130 mm long, August 1989, and one fish 175 mm long, February 1991). In February 1991, the two main size groups were joined by a third smaller group (age 1), which is consistent with the third group being from a later stocking made in March 1990. It is important to recall that all samples were examined without reference to locality or date of capture or to fish size.

Age estimates for golden perch collected from the Wimmera River near Horsham in March each year between 1984 and 1991 include fish up to age 8 (Fig. 5). Between 1984 and 1987, the 1981 year class (from 6000 fish stocked in early 1982) predominated in the catch and is traceable as progressively older fish through successive years until March 1988, when a 6-year-old fish was caught. This progression of ages provides support for the technique being valid up to age 6. The 1982, 1983 and 1985 year classes (of 10 000, 20 000 and 4000 fish, respectively) were represented by very few fish in the distributions. (There was no stocking of the 1984 year class.) The 1986 year class (from 4000 fish) was caught as 1-year-old fish in 1988 and then in succeeding years as small numbers of progressively older fish. The 1987 year class (10 000 fish stocked) was caught over three successive years, commencing in March 1989 as 1-year-old fish. These fish dominated the catch as 2-year-olds in March 1990 and remained a strong year class at age 3 in March 1991. In 1991, age-2 fish from the 1988 year class (10 000 fish stocked) dominated the catch. For the pooled sample from the Wimmera River, only one fish from the 369 aged (estimated as age 6 when it was caught in 1986) was assigned to a year class for which there was no known stocking.

Golden perch were first stocked into the Campaspe River downstream of Lake Eppalock in 1987 (fish of the 1986 year class). Otoliths for nine golden perch (length range 102–160 mm, weight range 16–60 g) caught in January 1989 were all read as age 1, consistent with this known stocking history. Prior to this stocking, a single angler report in 1983 was the only known post-1975 record of golden perch being found in this stretch of river (Brumley 1987).

Similarly, a stocking of 10 000 golden perch of the 1984 year class into Tahbilk Lagoon (from which golden perch were previously unrecorded) was followed by the capture of seven fish in December 1987. These were all estimated as age 3, the expected age of fish derived from this stocking.

Age estimates were made from the otoliths of 24 fish from Googong Reservoir, which was known to have been stocked with the 1980, 1983 and 1986 year classes. Of these fish, 19 were aged (Fig. 6*A*) as belonging to one of these three year classes (age 2, 5 or 8 when caught in November 1988). However, five fish were estimated as age 4 and did not correspond to any known stocking. These fish either have been incorrectly aged or are derived from sources other than known legal stockings. These five fish all showed similar patterns of annual marks in their otoliths that are distinct from those from the age-5 or age-2 fish, suggesting a growth history different from that of either of these year classes. As discussed below, some of the age-5 fish are very small for their age, and it is possible that, in impoundments such as Googong Reservoir or in other habitats in which growth is very slow, the normal pattern of annual-mark formation is disrupted and fish age may consequently be underestimated. However, illegal or accidental stockings of three other species of fish have been known to occur in Googong Reservoir (Murray cod, *Maccullochella*

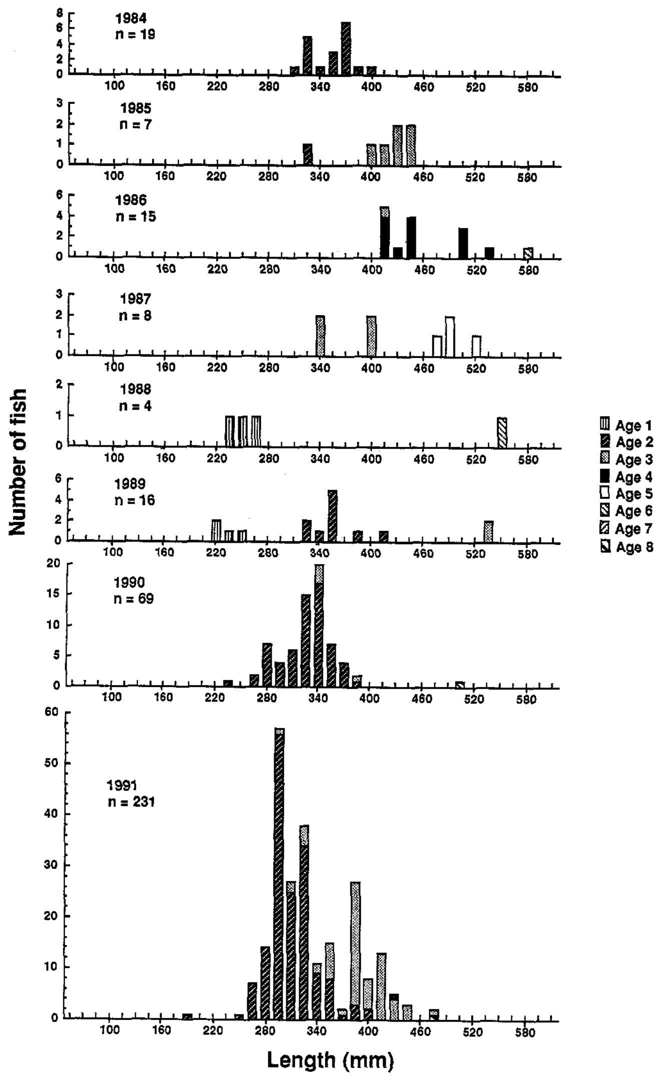

Fig. 5. Length–frequency distributions (15-mm size classes) for *M. ambigua* collected from the Wimmera River in March of each year, showing estimated ages of fish.

peelii; common carp, *Cyprinus carpio*; and European perch, *Perca fluviatilis*), and golden perch are believed to have been stocked into private impoundments within the catchment of Googong Reservoir (K. Kukolic, ACT Parks and Conservation Service, personal communication). Thus, it is quite feasible that the apparently incorrectly aged golden perch may be derived from one of a range of other possible sources.

The golden perch population in Lake Burrinjuck includes a combination of stocked fish and naturally bred fish, although successful breeding is believed to be an irregular event (J. Burchmore, NSW Department of Fisheries, personal communication). Otoliths from 18 fish, collected between November 1987 and April 1988, were aged (Fig. 6*B*). Of these fish, 12 were assigned to the 1979 year class, corresponding to the largest stocking made in this impoundment. The other six fish were aged as belonging to year classes for which

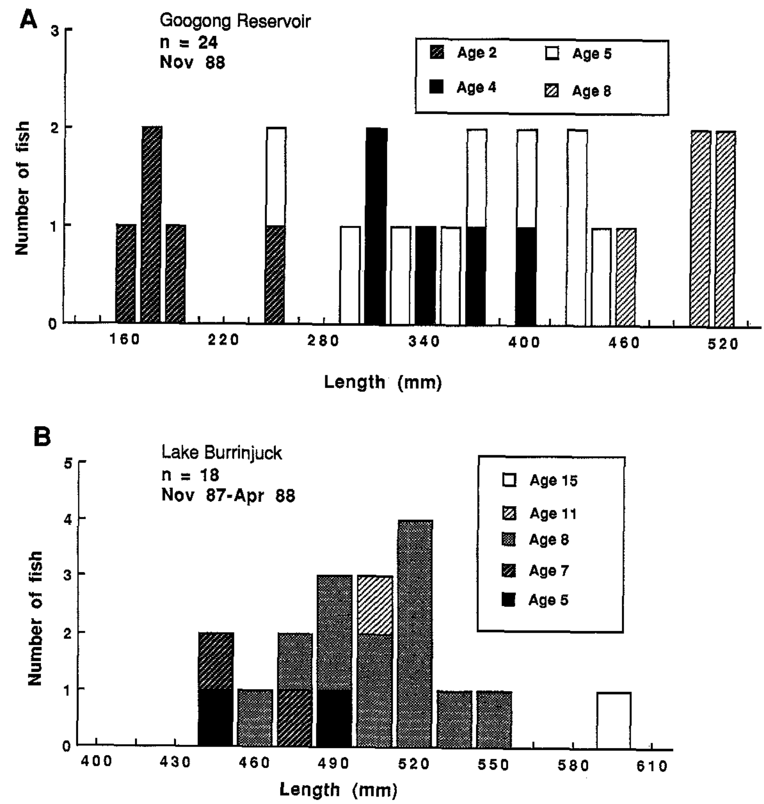

Fig. 6. Length-frequency distributions (15-mm size classes) for *M. ambigua* collected from (*A*) Googong Reservoir and (*B*) Lake Burrinjuck, showing estimated ages of fish.

there has been no known stocking, but four of these fish were assigned to year classes sufficiently different from known stockings as to be highly unlikely to be derived from them. Thus, two fish may have been incorrectly aged, differing by only one year from the known ages of stocked fish.

Otolith Dimensions

Continued growth with age (rather than with fish length) in at least one otolith dimension is essential for bands to be formed consistently each year and for age estimates to remain accurate when fish growth begins to slow down. Otolith length, width and thickness increased linearly with the logarithm of estimated age, whereas otolith weight and fish age were approximately linearly related (Fig. 7). The fitted curves and line tend to overestimate otolith length, width and weight for both the oldest and the youngest ages. Thus, although the rate of increase in all otolith dimensions slowed in fish older than age 6, all continued to increase with age. The relationships between otolith dimensions and fish length differed greatly from those between otolith dimensions and fish age. Otolith width and thickness increased linearly with fish length, whereas for otolith length the line of best fit was slightly curved and otolith weight increased exponentially with fish length (Fig. 8). The fitted line and curve overestimated otolith width and weight for smaller fish but otherwise fitted the data well. It is clear from these relationships that otolith length, width and thickness, although linearly related to fish length, all continued to increase with age even for the older slower-growing fish. Otolith thickness continued to increase at a rate faster than that of the

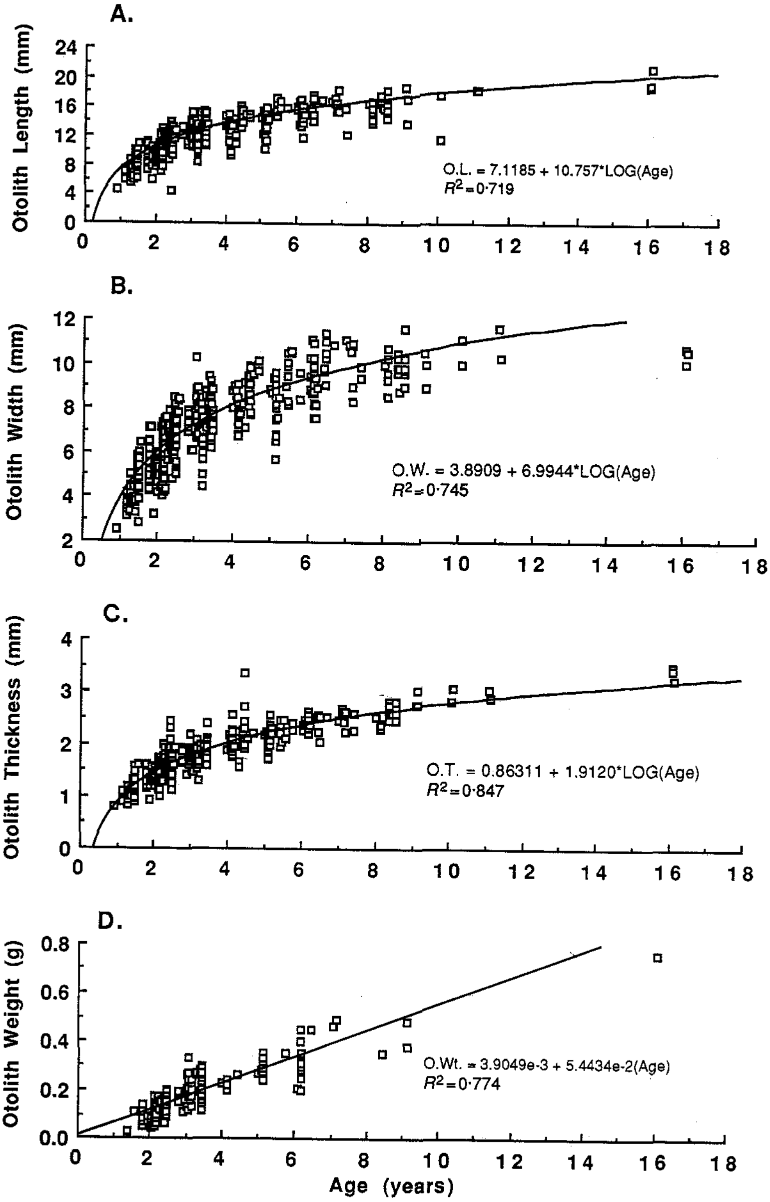

Fig. 7. Scatter-plots of otolith (*A*) length, (*B*) width, (*C*) thickness and (*D*) weight versus estimated age for *M. ambigua*. Equations for lines of best fit have been determined by least-squares regression (logarithms are base 10).

other two dimensions. This growth in thickness represented the deposition of new material over the proximal face of the otolith (rather than just at the margins), and increased otolith thickness consequently contributed most to the recorded linear increase in otolith weight with age.

If estimated ages accurately reflect true ages, it is to be expected that the mean diameter of each successive annual mark will increase with age. The average annual-band diameters for ages up to 4 do show such an increase, although the annual increment decreased with

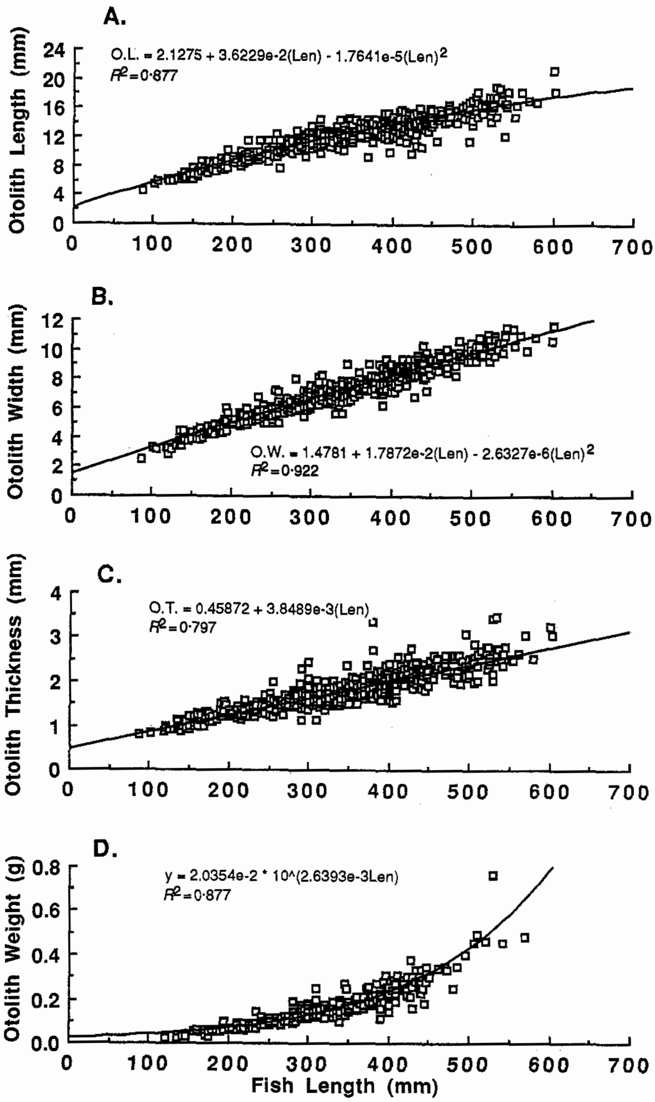

Fig. 8. Scatter-plots of ololith (*A*) length, (*B*) width, (*C*) thickness and (*D*) weight versus fish length for *M. ambigua*. Equations for lines of best fit have been determined by least-squares regression.

increasing age (Fig. 9). The standard deviation and range of diameters increase with age, reflecting increased variability in fish size with age: the diameter of the largest first annual band was greater than the diameter of the smallest fourth annual band. Band diameter was measured in the same dimension as otolith width (on the dorsal–ventral axis), and this variability in band diameter corresponds with the large variability in otolith width with age.

Time of Band Formation

The pooled data set, combining fish from all sites, shows that one annual mark was formed each year and that this was usually first recorded in samples collected in October

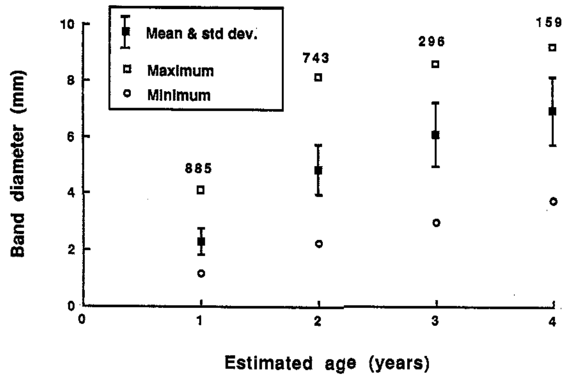

Fig. 9. Mean (±1 standard deviation) and range of band diameters for the first four bands on transverse sections of otoliths of *M. ambigua* from the pooled data set. Numbers above data points indicate sample sizes.

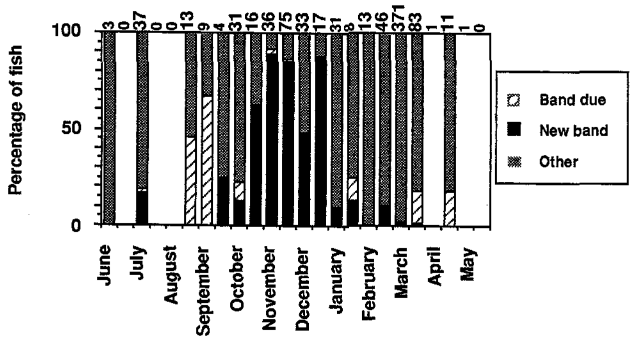

Fig. 10. Time of formation of bands as indicated by the percentage of *M. ambigua* otoliths collected in each two-week period for which either a new band was counted at the edge by three or four readers (new band), a new band was expected but not yet counted (band due), or banding was recorded otherwise (other). All sites and ages have been combined; numbers above histograms indicate sample sizes.

or November (Fig. 10). There was some individual difference among readers in the time at which bands were first recognized at the edge, and even for agreed edge bands the time of formation varied between July and March.

To validate the technique for all ages, it is necessary to demonstrate that band formation is annual in older as well as young fish. Marginal-increment ratios, calculated from the measurements of band diameters up to age 4, clearly show a consistent pattern (Fig. 11). Growth beyond the last band was at a minimum in October or November for each age, although there are fewer data for older fish.

Similarly, when the percentage of fish for which at least three readers recognized a completed band at the otolith edge is plotted separately for fish of ages 1 and 2 combined, ages 3 and 4 combined, and ages 5 and over combined, the pattern of band formation is similar (Fig. 12), indicating that bands are formed annually in all age groups. October or November (but also December and January for older fish) show a peak in the number of fish with a ring at the edge. Recognition of a newly formed band is dependent on the

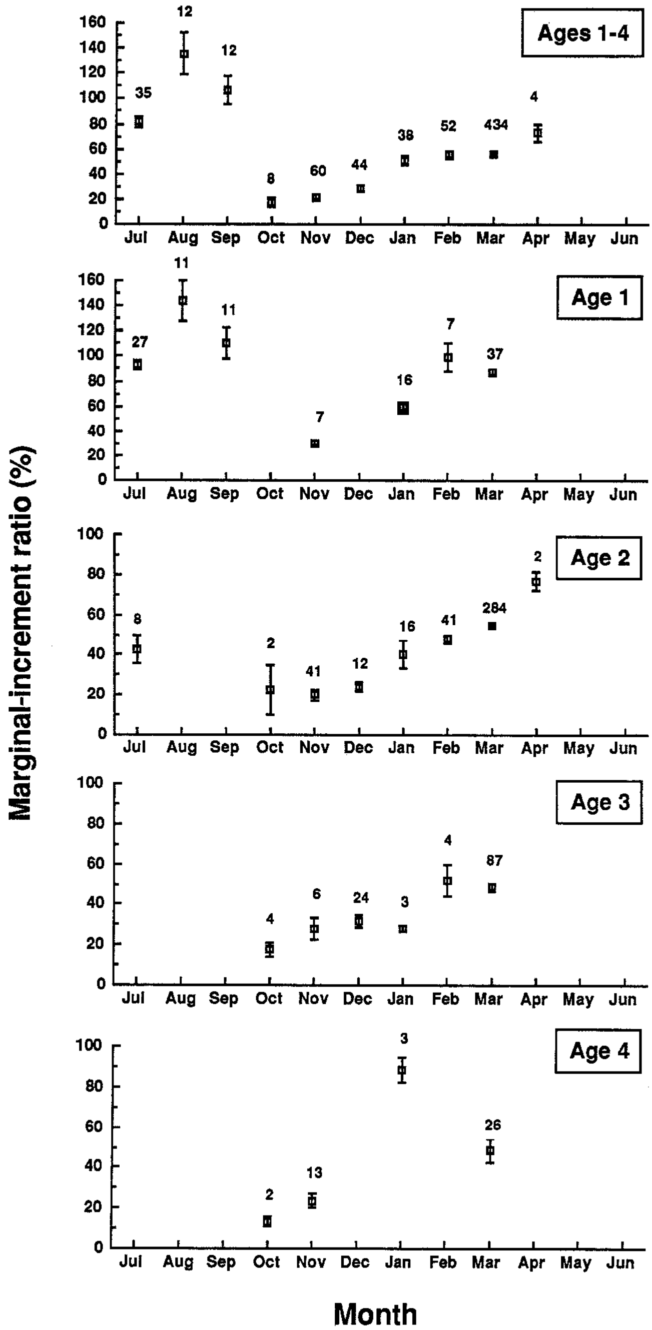

Fig. 11. Mean (± 1 standard error) marginal-increment ratio (as a percentage of the previous growth increment) by month for *M. ambigua* of ages 1–4, combined and separately. Numbers above data points indicate sample sizes; only samples containing two or more fish have been used.

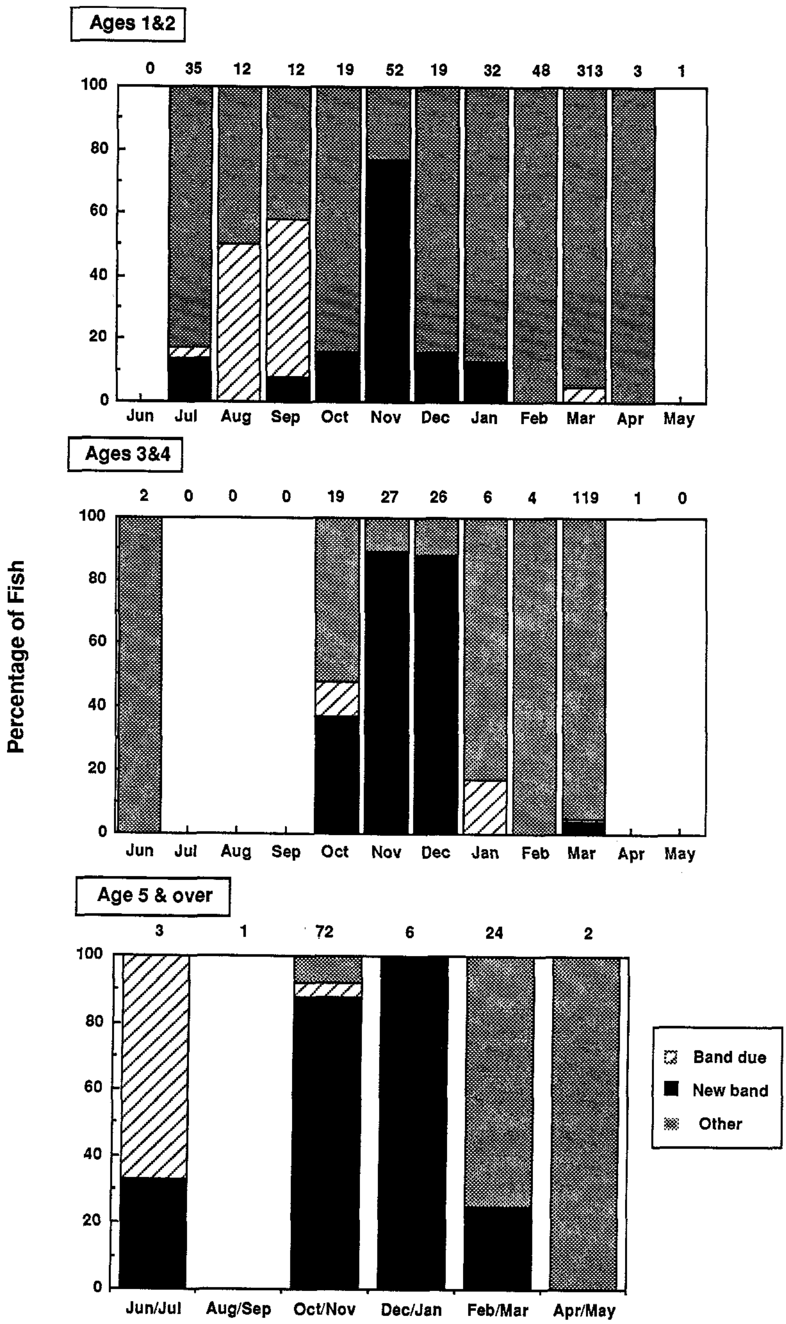

Fig. 12. Time of formation of bands for *M. ambigua* of ages 1 and 2 combined, ages 3 and 4 combined, and ages 5 and over combined as indicated by the percentage of otoliths collected in each time period for which either a new band was counted at the edge by three or four readers (new band), a new band was expected but not yet counted (band due), or banding was recorded otherwise (other). All sites have been combined; numbers above histograms indicate sample sizes; only samples containing two or more fish have been used.

change in the optical density of the section edge. The tendency for new bands to be recorded later in the growing season in older fish may result from their decreased annual increments delaying recognition of the changes in the edge pattern.

Precision of Age Estimates

The average percentage error in the precision of the age estimates, calculated from the initial age estimates of the four readers, was 5·6%. After age estimates were adjusted to allow for discrepancies between readers that were attributable solely to the counting or noncounting of newly forming annual marks, the average percentage error was reduced to 3·9%. The method of calculating this error yields larger error values for discrepancies of a given magnitude in younger fish than in older fish (although younger fish are usually easier to age). For the golden perch used in the present study, 73% were estimated to be age 3 or younger.

Length–Weight Relationships

The length–weight relationship for the total data set ($n=881$) was calculated as

$$W=(3\cdot 34\times 10^{-7})L^{3\cdot 66},$$

where W is the fish weight (grams) and L is the fish length (millimetres) (Fig. 13*C*). Inspection of scatter-plots of the data for males and females separately revealed almost complete overlaps, and curves fitted to the separate data sets differed little.

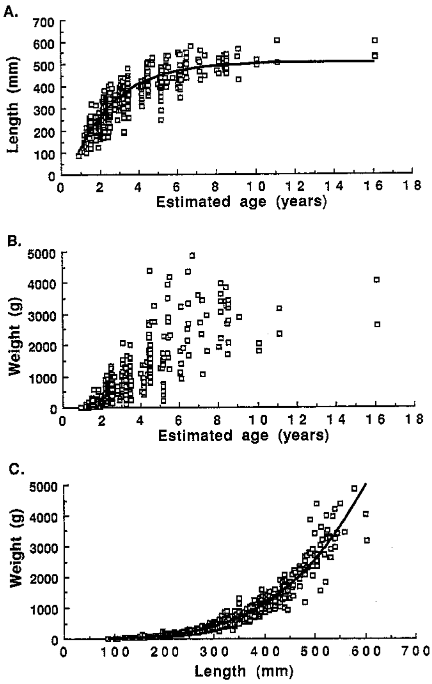

Fig. 13. Growth in (*A*) length and (*B*) weight with estimated age, and (*C*) the length–weight relationship, for *M. ambigua*. All sites, sexes and years have been combined. For the parameters of the fitted curves, see Table 2.

Growth

The growth in length of golden perch with age is well described by the von Bertalanffy growth curve (Fig. 13*A*), but there was much variability about the fitted curve. The increase in average fish length with age is fastest in the first four years, is slower between age 6 and age 10, and all but ceases after this. The von Bertalanffy growth function was fitted to the data for males and females separately (Table 2), but the F-ratio test indicated that there

Table 2. Mean ($\pm$1 standard error) and range of lengths and ages, and parameters of the von Bertalanffy growth function ($\pm$1 standard error) for females, males, all fish, and recent (post-1960) and historical (pre-1960) collections of *M. ambigua*

Group	n	Length (mm)			Age (years)			Growth parameters		
		Mean	Minimum	Maximum	Mean	Minimum	Maximum	L_∞ (mm)	K	t_0 (years)
Females	133	405·6 ($\pm$8·05)	120	604	4·94 ($\pm$0·217)	1·39	16·1	544 ($\pm$21·6)	0·317 ($\pm$0·044)	−0·111 ($\pm$0·218)
Males	72	364·5 ($\pm$10·4)	135	600	4·27 ($\pm$0·284)	1·39	16·1	527 ($\pm$23·1)	0·326 ($\pm$0·31)	0·071 ($\pm$0·054)
All fish	874	327·0 ($\pm$3·06)	86	604	3·12 ($\pm$0·059)	0·90	16·1	507 ($\pm$4·61)	0·454 ($\pm$0·012)	0·420 ($\pm$0·030)
Recent	796	31 ($\pm$3·0)	86	600	2·88 ($\pm$0·51)	0·90	16·1	501 ($\pm$9·71)	0·461 ($\pm$0·035)	0·435 ($\pm$0·107)
Historical	78	435·7 ($\pm$6·61)	323	604	5·75 ($\pm$0·273)	2·08	16·1	589 ($\pm$47·8)	1·47 ($\pm$0·052)	−3·71 ($\pm$1·70)

were no significant differences between the sexes ($F = 1 \cdot 96$, $P > 0 \cdot 05$). The parameters of the von Bertalanffy growth function for the combined data set were $L_\infty = 507$ mm, $K = 0 \cdot 454$ and $t_0 = 0 \cdot 420$ years (Table 2). The longest fish recorded was 604 mm (weight 3174 g and estimated to be age 10) from the Murray River in November 1949. The parameters of the von Bertalanffy growth function indicated a larger maximum size but lower K and t_0 values for the historical collection than for the recent collection. The F-ratio test indicated that these differences were highly significant ($F = 12 \cdot 0$, $P < 0 \cdot 001$), but the biological significance of these data must be interpreted with caution. The recent collection is much larger and includes a much larger number and proportion of smaller and younger fish (Table 2), differences which will themselves tend to produce differences in the growth curves between the samples of the types described. An examination of the differences in mean length-at-age for recent and historical collections (Table 3) shows no consistent trend.

The variability in length-at-age is clearly seen in the plot of mean length versus age for the pooled data set (Fig. 14). Fish may reach 300 mm in length as 1-year-olds or may be less than this length at age 5. The slow-growing 5-year-olds present in the samples are mainly derived from Googong Reservoir in the ACT (five of six 5-year-old fish less than 380 mm were from this impoundment).

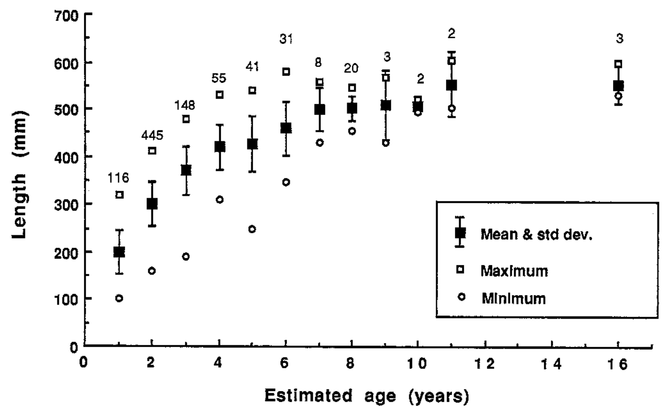

Fig. 14. Mean (±1 standard deviation) and range of lengths versus estimated age for *M. ambigua*. All sites, sexes and years have been combined; numbers above data points indicate sample sizes.

Growth in length with age for golden perch from the Loddon and Wimmera Rivers (two sites for which sufficient data are available) show mean values for fish from the Wimmera River that are consistently higher than those for fish from the Loddon River (Fig. 15).

The growth in weight with age is more variable than is growth in length, and for the younger age classes the range of values recorded for any one age spanned more than an order of magnitude (Fig. 13*B*). Thus, fast-growing 1-year-old fish may be heavier (and longer) than slow-growing 5-year-olds. The heaviest fish recorded was 4870 g (length 580 mm and estimated to be age 6) from the Wimmera River in June 1986.

Discussion

The combined results of the age estimates for *Macquaria ambigua* from the Loddon, Wimmera and Campaspe Rivers, Tahbilk Lagoon, Googong Reservoir and Lake Burrinjuck indicate that the technique provides accurate age estimates (and is therefore valid, *sensu*

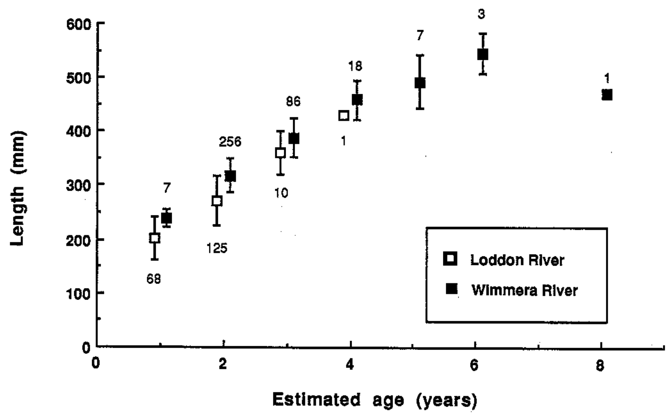

Fig. 15. Mean length (±1 standard deviation) versus age for *M. ambigua* from the Loddon and Wimmera Rivers, calculated separately. All sexes and years have been combined; numbers above and below data points indicate sample sizes.

Beamish and McFarlane 1983) for fish up to age 8. Regular sampling of the Loddon River population showed a consistency between age estimates and progression in size of discrete size classes. In addition, monitoring over a 16-month period showed that only a single annual band was formed each year. The longer-term sampling of the Wimmera River documents a progression of strong year classes of increasing age and agreement between estimated ages and known years of stocking. Age estimates for samples from Tahbilk Lagoon, the Campaspe River and Googong Reservoir also show close correspondence with expected ages based on the known stocking histories. Only 11 of a total of 605 fish (1·8%) were apparently incorrectly aged. For these fish, the assigned ages did not correspond with year classes known to have been stocked or were anomalous with the estimated ages of other fish of the same size group. Because of the possibility that fish may have entered waterbodies from sources other than known legal stockings, many of these fish may in fact have been aged correctly and the accuracy of the technique may consequently be better than indicated. Conversely, because the estimated ages of some of the stocked fish did not match their known ages when caught, errors in the age estimates may be larger than indicated.

The consistent appearance of annual bands in otoliths and the confirmation of their consistent formation in October or November for all age classes examined support the validity of the technique and the accuracy of the older age estimates. There is no qualitative change in the appearance of bands after the first two years' growth that would suggest that the process of band formation, which has been validated as being annual up to age 8, alters after this time. The measurements of otolith growth provide further evidence in support of this contention. Even for fish near the asymptotic length, when growth is slowest, annual marks are distinct and, apart from those in the first few years, relatively evenly spaced. False annual marks are found within the first two years' growth, but the method of reading described allowed for their consistent identification by all readers, and the age estimates correspond closely with the known stocking histories of the waterbodies.

Beamish and McFarlane (1983) stress the need to validate (i.e. demonstrate accuracy for) all recorded ages, but this was not achieved in the present study. Underestimations of the true age of older fish have been recorded for several species, particularly where fish survive for long periods after increases in length become minimal. Frequently, scales have been found to fail to form annual marks because of slow growth (e.g. Baccante and Sandhu 1981), whereas for the same species otolith sections provided accurate age estimates regardless of growth rates (Erickson 1983). Otolith sections also may produce age estimates greatly exceeding those based on whole otoliths (Beamish 1979*b*; Boehlert and Yoklavich 1984; Hoyer *et al.* 1985). We did not attempt to use scales for ageing *M. ambigua*, but we believe that the technique we employed is the most accurate available for this species. Harris (1985) found that sectioned otoliths provided consistent and accurate ages for *M. novemaculeata* but that scales and whole otoliths did not. Llewellyn (1966) reported that flooding and drought caused false annual marks or subsidiary checks in the scales of Australian inland fish species. In contrast, we found that false annual marks, although a regular feature of golden perch otoliths in the first two years' growth, were subsequently far less common and were easily recognizable.

We have demonstrated that the otoliths of *M. ambigua* continued to grow and lay down annual marks after growth in fish length essentially ceased. All otolith dimensions continued to increase well beyond this age (about age 10), and annual increments remained sufficiently large to allow successive annual marks to be clearly distinguished. For fish older than 10 years, this growth was most evident in otolith thickness, and occurs in the proximal rather than the distal face of the otolith; and it is on the proximal face that annual marks are most clearly formed. It has been shown in several species that otolith growth becomes 'uncoupled' from somatic growth as the latter slows and that otolith growth continues in an incremental manner independent of somatic growth (Reznick *et al.* 1989; Secor and Dean 1989; Campana 1990; Casselman 1990). It is this dependence on time rather than solely on somatic growth that makes otolith growth such a useful measure for age-determination purposes. We are therefore confident of the accuracy of our age estimates up to the maximum recorded age of 16 years, but final validation of the technique for older ages would be prudent.

The age estimates for fish of known age indicate a high level of accuracy for the technique (error less than 5%). Harris (1985) reported an error rate of 17% for known-age *M. novemaculeata*. No other estimates of the accuracy of age estimates for other Australian percichthyid species of fish have been published. The estimate of precision (5% average percentage error) also indicates that the technique is highly reproducible. The value is especially low considering that the estimate is based on independent readings by four readers rather than on repeat readings by one or two readers.

In addition, the otoliths of *M. ambigua* frequently exhibited false annual marks, but these were consistently recognized by readers. The factors causing these marks to be formed are unknown. Harris (1985) reported the formation of migration checks in the otoliths of about 10% of juvenile *M. novemaculeata*, produced during upstream recruitment migration from breeding grounds in an estuary. Davis (1977) reported subsidiary checks in the dorsal spines of *Tandanus tandanus* from a tributary of the Murray River, which he attributed to breeding. Neither explanation seems applicable to the marks observed in the otoliths of *M. ambigua*.

The birthday allocated to golden perch in the present study may not apply to other populations and, in particular, may vary with latitude, being earlier in the more northern (and generally warmer) parts of the species' range and later in cooler regions. However, 1 October should prove to be a suitable date for populations over most of the range of the species. *M. ambigua* occurs over a 15° range in latitude, but no studies of populations at different latitudes in Australia are available. Davis (1977) reported that, for a population of *T. tandanus* in northern New South Wales, annual marks in the dorsal spines were found in June or July. Harris (1985) selected 30 November as the birthday for *M. novemaculeata* from the Sydney Basin, and Jones (1974) also estimated 30 November as the appropriate birthday for *M. ambigua* from the lower Murray River. Annual mark formation in *Maccullochella peeli* from Lake Charlegrark and elsewhere in the southern regions of the Murray–Darling Basin has also been set at 1 October (Anderson *et al.* 1992; Gooley 1992).

The maximum length and weight recorded in the present study (604 mm and 4·87 kg) are well below previously reported maxima for *M. ambigua* (760 mm and 23 kg; Lake

Table 3. Mean lengths-at-age (and standard errors) and von Bertalanffy growth parameters for *M. ambigua* for all fish in the present study, for the recent and historical collections, and from previous studies

Source	Mean length (mm) at age (years)										Growth parameters		
	1	2	3	4	5	6	7	8	9	10	L_∞ (mm)	K	t_0 (years)
Allfish	200	301	370	420	427	459	500	502	510	508	507	0·454	0·420
	(4·39)	(2·16)	(4·07)	(6·42)	(9·06)	(10·2)	(16·1)	(5·83)	(42·0)	(13·0)			
Recent	202	302	369	426	428	497	490	504	—	—			
	(4·38)	(2·16)	(4·32)	(8·08)	(15·5)	(16·9)	(25·6)	(5·89)	—	—			
Historical	—	333	381	403	427	443	517	470	510	508			
	—	—	(10·0)	(5·82)	(6·66)	(11·1)	(3·46)	—	(42·0)	(13·0)			
Jones (1974)	162	281	368	425	463	499	528	562	588	—	—	0·33	—
Reynolds (1976)	170	300	380	430	470	—	—	—	—	—	—	0·53	—

1967*a*), and the oldest estimated age of 16 years that we recorded may also be well short of the age to which this species may live.

The average length at age 1 exceeds that reported by Jones (1974) and Reynolds (1976) (Table 3), but for ages 2 to 4 average lengths-at-age are similar. For older ages, the mean lengths-at-age in our study are less than those calculated by Jones (1974) for fish from the lower Murray River. Populations of *M. peeli* from the lower Murray River have also been found to grow more slowly than do populations higher in the catchment (Anderson *et al.* 1992).

It is evident from the data presented here that growth in *M. ambigua* is highly variable among different waters. This variability is evident in the plots of length and weight versus age (Fig. 13) and is also a source of the variability apparent in the plot of band diameter against age (Fig. 9). Attempts to elucidate any differences in growth rate between the recent and the historical collections are confounded by differences in the number and size range of fish in the two samples and in particular by the lack of smaller fish (minimum length 323 mm) in the historical sample. Because of the variability in growth, a generalized age-length key could not be developed for this species that could confidently be applied across the species' range, but the ageing technique described should nevertheless allow accurate ages to be determined for individual populations and growth to be reliably assessed.

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References

Allen, G. R. (1989). 'Freshwater Fishes of Australia.' (TFH Publications: Neptune City, New Jersey.)

Anderson, J. R. (1992). Age determination for native freshwater fish in the Murray–Darling Basin. In 'Australian Society for Fish Biology Workshop on the Measurement of Age and Growth in Fish and Shellfish'. (Ed. D. A. Hancock.) Bureau of Rural Resources Proceedings No. 12 (in press). (Canberra: Australia.)

Anderson, J. R., Morison, A. K., and Ray, D. (1992). Age and growth of Murray cod, *Maccullochella peeli* (Perciformes: Percichthyidae), in the lower Murray–Darling Basin, using thin-sectioned otoliths. In 'Age Determination and Growth in Fish and Other Aquatic Animals'. *Australian Journal of Marine and Freshwater Research* **43**, 983–1013.

Augustine, O., and Kenchington, T. J. (1987). A low-cost saw for sectioning otoliths. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **43**, 296–8.

Baccante, D., and Sandhu, J. (1981). Annulus formation and growth characteristics of tagged walleye in a lightly exploited lake. Ontario Fisheries Technical Report Series No. 9. (Ministry of Natural Resources: Ontario.)

Bagenal, T. B. (1974). Introduction. In 'Ageing of Fish: Proceedings of an International Symposium'. (Ed. T. B. Bagenal.) p. v. (Unwin Brothers: Old Woking, England.)

Bagenal, T. B., and Tesch, F. W. (1978). Age and growth. In 'Methods for Assessment of Fish Production in Fresh Waters'. (Ed. T. B. Bagenal.) pp. 101–36. (Blackwell: Oxford.)

Beamish, R. J. (1979*a*). Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths. *Journal of the Fisheries Research Board of Canada* **36**, 141–52.

Beamish, R. J. (1979*b*). New information on the longevity of Pacific ocean perch (*Sebastes alutus*). *Journal of the Fisheries Research Board of Canada* **36**, 1395–400.

Beamish, R. J., and Fournier, D. A. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 982–3.

Beamish, R. J., and McFarlane, G. A. (1983). The forgotten requirement for age validation in fisheries biology. *Transactions of the American Fisheries Society* **112**, 735–43.

Bedford, B. C. (1983). A method of preparing sections of large numbers of otoliths embedded in black polyester resin. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **41**, 4–12.

Boehlert, G. W., and Yoklavich, M. M. (1984). Variability in age estimates in *Sebastes* as a function of methodology, different readers, and different laboratories. *California Fish and Game* **70**, 210–24.

Brumley, A. R. (1987). Past and present distributions of golden perch *Macquaria ambigua* (Pisces: Percichthyidae) in Victoria, with reference to releases of hatchery-produced fry. *Royal Society of Victoria Proceedings* **99**, 111–16.

Cadwallader, P. L. (1984). Use of scales and otoliths to age Macquarie perch *Macquaria australasica* (Pisces: Percichthyidae). Fisheries and Wildlife Service, Victoria, Arthur Rylah Institute for Environmental Research, Technical Report Series No. 12. 35 pp.

Cadwallader, P. L. (1985). Freshwater fisheries production in Australia. *Australian Fisheries* **44**, 12–15.

Cadwallader, P. L., and Rogan, P. L. (1977). The Macquarie perch, *Macquaria australasica* (Pisces: Percichthyidae) of Lake Eildon, Victoria. *Australian Journal of Ecology* **2**, 409–18.

Campana, S. E. (1990). How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 2219–27.

Casselman, J. N. (1990). Growth and relative size of calcified structures of fish. *Transactions of the American Fisheries Society* **119**, 673–88.

Davis, T. L. O. (1977). Age determination and growth of the freshwater catfish, *Tandanus tandanus* Mitchell, in the Gwydir River, Australia. *Australian Journal of Marine and Freshwater Research* **28**, 119–37.

Erickson, C. M. (1983). Age determination of Manitoban walleyes using otoliths, dorsal spines, and scales. *North American Journal of Fisheries Management* **3**, 176–81.

Gooley, G. J. (1992). Validation of the use of otoliths to determine the age and growth of Murray cod, *Maccullochella peelii* (Mitchell) (Percichthyidae), in Lake Charlegrark, western Victoria. In 'Age Determination and Growth in Fish and Other Aquatic Animals'. *Australian Journal of Marine and Freshwater Research* **43**, 1091–102.

Harris, J. H. (1985). Age of Australian bass, *Macquaria novemaculeata* (Perciformes: Percichthyidae), in the Sydney Basin. *Australian Journal of Marine and Freshwater Research* **36**, 235–46.

Hoyer, M. V., Shireman, J. V., and Maceina, M. J. (1985). Use of otoliths to determine age and growth of largemouth bass in Florida. *Transactions of the American Fisheries Society* **114**, 307–9.

Jearld, A., Jr (1983). Chapter 16. Age determination. In 'Fisheries Techniques'. (Eds L. A. Nielson and D. L. Johnson.) pp. 301–24. (American Fisheries Society: Bethesda, Maryland.)

Jones, W. (1974). Age determination and growth studies of four species of fish from the River Murray. B.Sc.(Hons) Thesis, Zoology Department, University of Adelaide.

Lake, J. S. (1967*a*). Freshwater fish of the Murray–Darling river system: the native and introduced fish species. New South Wales State Fisheries Research Bulletin No. 7. 48 pp.

Lake, J. S. (1967*b*). Rearing experiments with five species of Australian freshwater fishes. I. Inducement to spawning. *Australian Journal of Marine and Freshwater Research* **18**, 137–53.

Llewellyn, L. C. (1966). Age determination of native inland fish of New South Wales. *Fisherman (Sydney)* **2**(4), 14–19.

Mackay, N. J. (1973). Histological changes in the ovaries of the golden perch, *Plectroplites ambiguus*, associated with the reproductive cycle. *Australian Journal of Marine and Freshwater Research* **24**, 95–101.

Panella, G. (1974). Otolith growth patterns: an aid in age determination in temperate and tropical fishes. In 'Ageing of Fish'. (Ed. T. B. Bagenal.) pp. 28–39. (Unwin Brothers: Old Woking, England.)

Penn, L. J., and Potter, I. C. (1990). Biology of the nightfish, *Bostockia porosa* Castelnau, in a south-western Australian river. *Australian Journal of Marine and Freshwater Research* **41**, 627–45.

Reynolds, L. F. (1976). Fish tagging in the River Murray. *SAFIC* **8**, 11–15. (South Australian Fisheries Dept: Adelaide.)

Reznick, D., Lindbeck, E., and Bryga, H. (1989). Slower growth results in larger otoliths: an experimental test with guppies (*Poecillia reticulata*). *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 108–12.

Rowland, S., Dirou, J., and Selosse, P. (1983). Production and stocking of golden and silver perch in NSW. *Australian Fisheries* **42**(9), 24–8.

Secor, D. H., and Dean, J. M. (1989). Somatic growth effects on the otolith–fish size relationship in young pond-reared striped bass, *Morone saxatilis*. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 113–21.

Wilkinson, L. (1987). 'SYSTAT: The System for Statistics.' (SYSTAT Inc.: Evanston, Illinois.)

Williams, T., and Beford, B. C. (1974). The use of otoliths for age determination. In 'Ageing of Fish'. (Ed. T. B. Bagenal.) pp. 114–23. (Unwin Brothers: Old Woking, England.)

Zar, J. H. (1974). 'Biostatistical Analysis.' (Prentice-Hall: Englewood Cliffs, New Jersey.)

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