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**Development of an ageing methodology, and first estimates of  
growth parameters and natural mortality for rubyfish  
(*Plagiogeneion rubiginosum*) off the east coast of the North Island (QMA 2)**

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(QMA 2)

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## EXECUTIVE SUMMARY

Paul, L.J., Horn, P.L., & Francis, M.P. 2000: Development of an ageing methodology, and first estimates of growth parameters and natural mortality for rubyfish (*Plagiogeneion rubiginosum*) off the east coast of the North Island (QMA 2).

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This report covers part of the work required under Specific Objectives 1 and 2 of Project INS9802, namely: "To determine age and growth of ... rubyfish in QMA 2 ...", and "To estimate [the] natural mortality rate of ... rubyfish ...".

Otoliths, scales, and fin spines were examined to determine the most suitable ageing procedure. All showed growth-related structures (zones, annuli, or rings), with variable but generally poor agreement between them. Within-reader and between-reader variability of counts was high. Fin spines showed 5–7 large growth zones, with an abrupt change to very narrow rings. Otolith sections showed 5–7 large inner growth zones, a transition region where zones were usually difficult to distinguish, and an outer region of very narrow zones. Otolith reading, although difficult, was used to estimate ages. Dark zones (usually narrow) in transmitted light were counted, and assumed to be annual. There was finer dark banding within zones, 5–15 in the first 5–7 zones, 2 or more in the outermost narrow zones.

The outermost zones in otoliths from large fish (45–53 cm) were sometimes very narrow and difficult to count even with high magnification.

Otolith zone counts were affected by microscope magnification. The finer zones in the outer part of the otolith were not adequately discriminated at x50 magnification. The individual age estimates for rubyfish had low precision, but there was little overall systematic bias within or between readers (at magnifications of x80 or greater), suggesting that the growth curves derived from averaged age estimates are relatively robust. The main area of concern is the estimation of ages of young fish (less than about 20 years old); these fish are the most difficult to age, and there was evidence of systematic bias within and between readers for them.

Our attempts to validate the otolith ageing technique using marginal increment analysis failed, because of our inability to classify the marginal composition in younger fish, or to measure the very narrow marginal increment in older fish. Validation is therefore a high priority for this species, considering that our age estimates (maximum age 88.5 years with many over 50 years) suggest that rubyfish are among the longest-lived commercially fished species in New Zealand.

A randomisation test revealed a significant difference between the growth curves for males and females but the difference was small and possibly spurious. We therefore suggest that the von Bertalanffy growth curve for the combined sexes best describes the growth of adult rubyfish:

$$L_t = 48.68 (1 - e^{-0.045[t+16.53]})$$

A lack of young fish in our samples led to an unrealistically low estimate of  $t_0$ . Furthermore, our age estimates and the fitted von Bertalanffy growth curve suggest that early growth of rubyfish is relatively rapid. We speculate that the apparent absence of young rubyfish from trawl catches, and their rapid early growth, result from young fish inhabiting different areas from old fish.

Several techniques were used to estimate the natural mortality rate ( $M$ ). A Chapman-Robson estimate of the total mortality rate was 0.035, suggesting that  $M$  was less than this. Two empirical methods (the Pauly and Hoenig methods) produced  $M$  estimates of 0.05–0.10. We consider the most plausible estimate of  $M$  to be 0.03, although this is based on unvalidated ages, and it is not known if the samples adequately represented the population age structure.

## 1. INTRODUCTION

Rubyfish were first recorded in New Zealand commercial fish catches in 1983, when a near-bottom trawl fishery for alfonosinos (*Beryx* spp.), bluenose (*Hyperoglyphe antarctica*), and to a lesser extent gemfish (*Rexea solandri*) developed along the east coast of the North Island between southern Wairarapa and East Cape (in QMA 2). Rubyfish were initially only recorded as a bycatch, landings reaching 250 t by 1990, but from 1992 rubyfish became a targeted species and catches rose to 735 t in 1995–96 (Annala *et al.* 1999). In the two subsequent years landings declined to 463 and 380 t, but it is not known whether targeted fishing effort declined. About three-quarters of the rubyfish catch is taken in QMA 2. Much smaller quantities are taken as bycatch in trawl fisheries targeting gemfish, hoki, barracouta, and jack mackerel elsewhere around the North Island (Paul 1997).

A preliminary unstandardised CPUE analysis of the main rubyfish fishery showed a decline during the early 1990s, with effort moving progressively from southern to northern grounds in the region (Paul 1997). It could not be determined whether this reliably represented a decline in stock size, as the middle depth fishery for alfonosino, bluenose, and gemfish is complex. Limited quotas for these species have required the fleet to move between grounds with a different mix of species, and the same vessels also participate in the deeper water fishery for orange roughy (*Hoplostethus atlanticus*). However, the apparent decline did signal the need for further examination not only of this mixed-species fishery, but of the rubyfish itself, since very little was known of its biology.

A precise and reliable ageing technique is fundamental to any study of fish population dynamics. The most common application of an ageing technique is the derivation of growth curves and estimation of growth rates. This in turn enables age-structured population models to be applied. Other important applications of ageing techniques are the estimation of ages at maturity and recruitment, longevity, population age structure, natural and fishing mortality rates, and recruitment strength and variability. An ageing technique also provides the opportunity for detecting density-dependent changes in various population parameters over time, such as growth rate and age-specific fecundity. The ability to age fish is a requirement for most fish population models, and also for monitoring population responses to exploitation.

This study was undertaken as MFish Project INS9802. Its main objective was to develop an ageing technique for rubyfish, and to apply it to samples of fish from QMA 2 (east coast North Island) in order to estimate some of the biological parameters necessary for a stock assessment: growth rate, longevity, and natural mortality rate. A separate study, MFish Project INS9801, is directed at establishing the size and age structure of commercial landings of rubyfish from this region.

The species was introduced into the Quota Management System from 1 October 1998, with a TACC of 577 t (75% in QMA 2). This TACC is close to the mean landing of 583 t in the four years 1991–92 to 1994–95, but landings in the two subsequent years declined to 463 and 380 t (Annala *et al.* 1999).

## 2. BACKGROUND BIOLOGICAL INFORMATION

Paul (1997) reviewed the very limited information on *Plagiogeneion rubiginosum* and its New Zealand fishery. The species is recorded from the eastern South Atlantic to Australasia, but when Parin (1991) described three additional species of *Plagiogeneion* from the Indian Ocean he suggested that some early records of *P. rubiginosus* (emended to *rubiginosum*) may have been based on misidentifications. The depth range is listed as 50 m to over 700 m (Heemstra & Randall 1977, Amaoka *et al.* 1990, Anderson *et al.* 1998), although beyond New Zealand this may incorporate some records of the other species. Anderson *et al.* (1998) listed the mean depth as 359 m.

Rubyfish occur in subtropical water around New Zealand, so extend to the northern South Island and along the northern slope of the Chatham Rise, but are absent from the southern South Island and the Campbell Plateau (Anderson *et al.* 1998). Although widespread they are seldom taken during research bottom-trawl surveys, and information from the pattern of commercial catches suggests they probably occur a little distance above the seafloor, and in schools or looser aggregations above or near submarine banks and ridges. It is target-fished in depths of 150–500 m, centred on 200–300 m (Paul 1997).

Clark & King (1989) presented some length frequency data by sex, and recorded that the fish were feeding on midwater crustaceans (amphipods, euphausiids, decapods), salps, and myctophid fishes, but there is otherwise little biological information on New Zealand fish. Small fish (under 25 cm) are infrequently caught.

Mel'nikov & Ivanin (1995) presented growth data on *P. rubiginosum* in the west Indian Ocean, but conceded that their fish may have been one of Parin's new species. Their work was based on scale-reading, which they found difficult beyond 7–8 years because of crowded rings at the edge; they reported ages up to 9 (males) or 10 (females). Scale-reading generally under-estimates ages, particularly if ring-crowding is observed, and these ages can only be regarded as approximations.

### 3. METHODS

#### 3.1 Fish sampling

The fish aged during this study were obtained during a market sampling programme for alfonsino (*Beryx splendens*), bluenose (*Hyperoglyphe antarctica*), and rubyfish caught by commercial trawlers in QMA 2. Between October 1998 and September 1999, 18 samples of rubyfish were measured, and these were randomly subsampled for age. A total of 765 otolith samples was obtained. From the first few hundred of these, 90 were randomly selected for ageing. Because of difficulty in interpreting these otoliths, anal fin spines (in addition to otoliths) were then collected from 12 fish. A further six fish were obtained for an investigation of the utility of several other structures (scales, spines, etc.) in ageing rubyfish. Otoliths from 135 more fish were then chosen to complete the main sample for ageing, being taken selectively from the largest fish in the total market sample collection (as at June 1999) in order to cover the higher age range as well as possible.

Fish were measured as fork length, to the nearest cm below, and sex and maturity stage recorded.

#### 3.2 Otoliths

The otoliths were extracted and stored dry in coded paper envelopes. An examination of whole otoliths immersed in oil, with reflected light, showed a confused pattern of light and dark zones on the concave (distal) surface; the otoliths from large fish were also sufficiently thick to suggest that the outermost growth zones might be restricted to the proximal side of the otolith and only visible in cross-section. A trial of the 'break and burn' procedure was undertaken on four otoliths; each was broken across the centre, the larger half smoothed and polished back to a straight transverse section, which was heated by a low flame until light brown and viewed with reflected light. Again, the pattern of light and dark zones was very confused. At magnifications between x20 and x40 the zones were variable in width and colour, and the darker zones merged and subdivided in such a way that zone counts were highly subjective. At higher magnification the distinction between 'dark' and 'light' became unclear, with markings of intermediate coloration.

Both these procedures were considered unsatisfactory, but some trial thin sections, viewed with transmitted light, appeared more promising.

Thin sections were prepared following the standard NIWA procedure (*see* Stevens & Kalish 1998). The straightest dorso-nuclear otolith prism was marked on its distal surface with a fine pen. Otoliths were embedded in sets of three in an epoxy resin mould, with their marks in alignment. The mould was then sectioned using a dual-bladed diamond saw. After being attached to a microscope slide with a thermoplastic cement, the sliced sections were ground thinner and polished smooth. Three thickness categories were used. From an initial sample of 12 otoliths, pairs of sections were prepared at about 400 and about 200  $\mu\text{m}$  ('thick' and 'thin'). An intermediate thickness of  $300 \pm 100 \mu\text{m}$  was chosen for subsequent samples. The section surfaces were coated with high-refraction immersion oil and viewed with transmitted light at various magnifications (*see* Section 3.5). Bright- and dark-field illumination were tried, the former proving to be more suitable.

### 3.3 Scales

Scales were collected from a subsample of fish with a view to comparing their structure with that of the otoliths. Although scales are generally less reliable than otoliths, particularly in long-lived fish, the likely maximum age of rubyfish was not known at the time of sampling. The only study on age determination in *Plagiogeneion* (Mel'nikov & Ivanin 1995) had used scales, and had at least implied that the species studied (its identity is now uncertain) was relatively short-lived. The scales were taken from midbody, below the lateral line, and stored dry with the corresponding otoliths. They were later cleaned of mucus and adhering skin fragments, and mounted between two microscope slides, 4–6 scales per fish. They were read in transmitted light using a binocular microscope at various magnifications, and the images of a few scales were obtained using a library microfiche reader/printer at x23 magnification. Some scales from other body regions were also examined (*see* Section 3.4).

### 3.4 Fin spines and other structures

From a subsample of six fish a series of bony structures (the first large dorsal and anal fin spines, the largest pelvic and pectoral spines, a pectoral fin ray, a branchiostegal ray, the cleithrum, and operculum, and a vertebra) were removed and stored dry. For the spines and rays, segments from near their base were embedded in an epoxy resin mould, and sectioned using a dual-bladed diamond saw. After being attached to a microscope slide with a thermoplastic cement, the sliced sections were ground to a thickness of about  $300 \pm 100 \mu\text{m}$  and polished. They were viewed under transmitted light using both bright- and dark-field illumination, using a range of magnifications. The operculae and vertebrae were cleaned, and examined in reflected light using a range of magnifications.

From these six fish, otoliths and scales were also collected; the otoliths included sagittae and lapillae, and the scales were taken from three body regions ("standard" midbody, above the lateral line, and between the lateral line and anal fin).

### 3.5 Age reading

Three readers were involved at different stages of this study. (1) Reader 1 (LJP) and reader 2 (CÓM) undertook the first age reading of 90 fish, using otolith thin sections viewed in transmitted light. (2) Readers 1 and 2 read otolith 'thick' and 'thin' sections, and fin spine sections, from the sample of 12 fish, using transmitted light. (3) Readers 1 and 2 read the various hard structures from six fish. (4) Reader 3 (PLH) read the 'thick' and 'thin' otolith sections and the fin spines from the 12 fish sample, and then 27 otolith sections of the 90 fish sample. (5) Reader 1 read the final sample of 135 otolith thin sections. To this stage, reader 1 had used a binocular microscope at x50 magnification, reader 2 a compound microscope at x80 or x100 magnification, and reader 3 a compound microscope at x80 magnification. It became apparent that a magnification of at least x80, with good optics and

lighting, was required to properly define the outermost very small (potentially annual) growth zones in the largest otoliths. (6) Reader 1 re-read the main samples (12+90+135 fish) at x100 magnification, compound microscope, and reader 3 read these samples at x80 magnification, compound microscope. (7) Reader 1 made a further reading of the main samples at x100 magnification.

In final readings, otolith sections were assigned four levels of clarity: 1, good; 2, reasonable; 3, poor; 4, almost unreadable and/or an estimate based on zone spacing.

The whole sample of 237 otolith sections was read three times by reader 1 (at x50, and x100 magnification twice) and once by reader 3 (at x80 magnification). The readings by reader 1 were labelled  $R_{1,1}$ ,  $R_{1,2}$  and  $R_{1,3}$  respectively, and the single reading by reader 3 was labelled  $R_3$ . Otolith zone counts were assessed for ageing bias and precision (between readers, and among readings by reader 1) using age-bias plots, and plots of the coefficient of variation ( $cv$ ) against age, as recommended by Campana *et al.* (1995). Because of the wide age range and small sample size, we grouped the fish into 5-year intervals for these plots. The two plots show the means (and their standard errors), and the  $cvs$ , respectively, of the zone counts made by reader  $y$  for each "age" as determined by reader  $x$ . For example, for all of the rubyfish otoliths that were judged by reader 3 to have 21–25 zones, the mean, standard error and  $cv$  were calculated from the zone counts made by reader 1 for the same fish, and plotted on the X-axis at the mean of the ages estimated by reader 3.

The final age estimate for each rubyfish was taken as the mean of the  $R_{1,3}$  and  $R_3$  readings. A growth curve was fitted to the length-at-age data using the von Bertalanffy growth model:

$$L_t = L_\infty \left( 1 - e^{-K[t-t_0]} \right)$$

where  $L_t$  is the expected length at age  $t$  years,  $L_\infty$  is the asymptotic maximum length,  $K$  is the von Bertalanffy growth constant, and  $t_0$  is the theoretical age at zero length.

A test was made for a significant difference between male and female growth curves using a randomisation test based on Kimura's (1980) method (A. Dunn, NIWA, pers. comm.). For each of 500 simulated data sets, selected randomly with replacement from the original data, rubyfish were allocated randomly to each sex. The null distribution was generated by calculating, for each data set, the difference between the residual sum of squares obtained from fitting the full data (via Kimura's method) and that obtained by fitting the sexes (again via Kimura's method). The probability that growth curves fitted separately to the two sexes represented an improvement over fitting a single growth curve to the pooled data was determined by comparing the actual difference in residual sum of squares with the simulated null distribution.

### 3.6 Natural mortality

Estimates of the natural mortality coefficient ( $M$ ) were obtained using the Chapman-Robson (1960) estimator, and two other techniques that are based on observed empirical relationships between  $M$  and other more easily measured parameters: maximum age in the population (Hoenig 1983) and growth rate and water temperature (Pauly 1980).

Chapman & Robson (1960) developed an estimator of the total mortality rate ( $Z$ ) that uses information from a random, aged sample of the population:

$$Z = \log_e \left( \frac{1 + \bar{a} - 1/n}{\bar{a}} \right)$$

where  $a$  is the mean age above the recruitment age and  $n$  is the sample size. Dunn *et al.* (1999) showed that this estimator usually performed better than other catch curve methods. For a fished population,  $M$  will be less than  $Z$ . We estimated  $Z$  from a sample of 838 rubyfish collected randomly from QMA 2 catches during 1998–2000 under MFish projects INS9801 and INS1999/01. The sample

included the 237 fish that were aged by reader 1 ( $R_{1,3}$ ) in the present study; the remaining fish were also aged by reader 1 to produce a consistent set of ages.

Hoenig (1983) compared published estimates of mortality rates and life spans for fishes, cetaceans, and molluscs. He found a significant negative relationship between the two variables that explained (for fishes) 68% of the variability in  $M$ :

$$\log_e M = 1.46 - 1.01[\log_e(t_{\max})]$$

where  $t_{\max}$  is the maximum age reached by the species. The oldest fish in our aged samples was used as a minimum estimate of  $t_{\max}$ . We also applied a commonly used "rule-of-thumb" based on Hoenig's equation:

$$M = -(\log_e p)/A$$

where  $p$  is the proportion of the population that reaches age  $A$  (or older) in an unexploited stock (Annala *et al.* 1999).

Pauly (1980) examined the relationship between reported values of  $M$ , the von Bertalanffy growth parameters ( $K$  and  $L_{\infty}$ ), and the mean annual temperature at the position where the fish were caught ( $T$ ). He obtained a multiple regression equation that explained 72% of the variance in  $M$ :

$$\log_{10} M = -0.0066 - 0.279 \log_{10} L_{\infty} + 0.6543 \log_{10} K + 0.4634 \log_{10} T$$

Our previous experience with this formula has shown that the estimate of  $M$  is not particularly sensitive to the value of  $T$  used. Nevertheless, it is difficult to estimate the mean annual temperature for a species, so we applied sensitivity tests to determine the effect of a range of plausible temperature estimates.

## 4. RESULTS

### 4.1 Otoliths

Entire otoliths immersed in oil and burned cross-section surfaces, both viewed in transmitted light, showed a confusing pattern of dark and light zones that could not be identified as paired hyaline and opaque growth zones. These reading procedures were not investigated further.

Thin sections, about  $300 \pm 100 \mu\text{m}$ , viewed in transmitted light at a magnification of at least  $\times 80$ , showed a clearer pattern of light and dark zones, but these could not be easily recognised as the paired hyaline and opaque growth zones normally seen in otoliths. The initial response of all three readers was that these otoliths would be extremely difficult to interpret (which led to the efforts of readers 1 and 2 to investigate alternative structures – see Sections 4.2 and 4.3). There were two categories of "growth increments", which in the following account are termed **bands** (narrow dark lines or marks) and **zones** (a set of closely-spaced bands).

There was considerable variation in the pattern and clarity of zonation in the otolith sections from different fish. In some otoliths there was a reasonably clear pattern of alternating dark and light zones extending from a very dark nuclear region out to the margin, particularly in the region of the (medial) sulcus (Figures 1, 2). In some otoliths these zones were also recognisable along the dorsal and ventral axes, although the dark zones were usually subdivided and split into bands, in the pattern often seen along these long axes of fish otoliths. In other otolith sections the zonation was extremely obscure, with apparently split dark zones extending from the nucleus out to the edge. However, in most otoliths

at least some pattern could be recognised in the way the dark and light zones alternated, and in the way the dark zones were split into finer bands. This is shown diagrammatically in Figure 3.

In the sulcal area the dark zones became more narrowly spaced with increasing distance from the nucleus. This was most marked out to zones 10–15; from about zone 20 or 30 the distance between successive dark zones narrowed only very slightly. In some otoliths the innermost dark zones were either narrower than the intervening lighter zones, or about equal to them; as such, they appear to represent the hyaline and opaque zones seen in otoliths of other species viewed under similar lighting conditions. Under high magnification (over x20) these dark zones are each made up of a series of fine bands. In other rubyfish otoliths these alternating dark and light zones were difficult to distinguish, and most of the inner portion of the otolith comprised a large number of fine bands. Most of these fine bands were uniform in thickness and spacing, but some were a little thicker than others, and/or followed by a slightly greater width of light material. This grouping of fine bands into zones gave a similar appearance to the pattern of the more typical dark and light zones of otoliths, although the intervening light zones were much narrower than usual.

Zone 1 is difficult to define, but appears to comprise the outer edge of the dark nucleus plus 5–10 fine bands immediately outside it; sometimes these appear to merge into a single band away from the sulcus, sometimes they remain as multiple bands.

Zones 2 to 5, and often 6 to 8, comprise 5–15 bands each; the bands in each zone are either equal in appearance, or the bordering few are thicker, darker, and sometimes appear to have been merged. These first zones are much more widely spaced, and almost always much broader, than the subsequent zones. The outermost of these zones, either zone 5, 6, 7, or 8, is often darker in general appearance than adjacent zones. In most sections, the outermost edge of these broad zones continues dorsally and ventrally (i.e., away from each side of the sulcus) as either a narrower but dark set of fine bands, or as what appears to be a structural crack in the otolith. In difficult-to-read sections, this latter feature is a useful pointer to the positions of these zones.

From zones 6–8 to zones 15–25 (the outer limit is highly variable) the fine bands within each dark zone diminish in number to between 2 and 5, and the bands at the inner and outer margin of each zone are usually darker. Beyond this, each dark zone comprises 1–4 (often 2) bands.

In the sulcal region, the early zones (1 to 15–20) are usually clearest in the wedge-shaped section through the collicular crest which forms the dorsal edge or rim of the sulcus (Figure 3, B). The later zones are clearest along the opposite, ventral edge of the sulcus. On otoliths classified as 'good' or 'reasonable', recognisable zones are present on both edges. Whenever possible, complete counts were made on each side of the sulcus, and the clearest count recorded; occasionally it was possible to trace a prominent zone across the sulcus, but this tended to be a region of discontinuity.

On both edges of the sulcus, the outermost dark zones (those comprising 1–4 fine bands) were split, or at least their component bands became more widely separated, when they reached the edge of the sulcus (Figure 3, D). This made the spacing of bands within and between these zones more equal, and the zones more difficult to distinguish. It was necessary to make the zone counts a little distance in from the edge.

Zones were sometimes equally (occasionally more) clearly recognisable on the proximal side of the otolith about one-third of the distance from the sulcus to either the dorsal or ventral edge, and some counts were also made here. However, at these positions the zones sometimes merged in a way that made it unclear whether two zones had merged or one zone had split (Figure 3, E). This generally occurred where the otolith width decreased (*see* otolith shapes, Figures 1, 3), and it was concluded that this represented a merging of zones where the otolith was compressed. In several otoliths where the outermost zones were poorly defined, counts were made in the sulcal region to a zone that

extended clearly across to these dorsal or ventral positions, and then continued the count to the edge from here.

A feature visible in the outermost zones of some otoliths, on either or both sides of the sulcus, was a thickening of about every fifth dark zone (Figure 3, F). That is, the pair (or more) of fine bands constituting this particular zone were more prominent than those in the adjacent dark zones. This pattern is similar to the pattern often seen in the innermost zones, approximately zones 1–12, where a relatively darker band was interpreted as delineating the edge of a zone. However, apart from some initial trial counts (*see* Section 4.5.1), this apparent grouping of some outer zones was ignored in the final readings, and each small zone was counted. While it could be argued that this introduces an inconsistency in the interpretation of growth structures across the otolith section, with the narrow innermost structures being grouped, and the narrow outermost ones being counted individually, the reading procedure and nomenclature are consistent. The broad inner zones, and the narrow outer zones, all comprised several bands; the inner zones 5–15, the outer zones as few as two. The relatively darker bands which demarcate the edges of the zones in the inner region are almost always present, but the superficially similar dark bands in the outer region were only sometimes visible, and then for short and irregular distances.

The most difficult part of the otolith zone sequence to interpret was that immediately beyond the first series of 5–7 dark zones, out to a position between zones 15 and 20. In some otoliths the zones here decreased quite suddenly in width, and in others they decreased more gradually. In the clearest otoliths the decrease in zone width was usually reasonably gradual. This latter observation was used when interpreting the most difficult otolith sections, and instead of counting *all* apparent zones some grouping was made in this region. If all zones seen were true zones, the count should have been higher. That is, some counts were conservatively low, perhaps by 3–8 zones. This difficulty, and possible bias, was greatest in sections where the total zone count fell between these values (5–20). When the narrow zones of older fish were visible outside this region of the otolith, the intervening region was more easily interpreted. The change from broad to narrow growth zones can be likened to the 'transition zone' in orange roughy (Tracey & Horn 1999) and oreos (P.J. McMillan, NIWA, pers. comm.), although whether it is fully comparable requires further investigation.

In general, the more zones an otolith section had, the easier it was to interpret. However, in a small proportion of the sections with over 60 zones, the outermost zones became very closely spaced and difficult to resolve even at x100 magnification.

As is clear from the preceding account, some subjectivity was involved in identifying and counting zones. In particular, it was difficult to count through a 'transition region' (zones 5–15) where there was sometimes a sudden large reduction in zone width, sometimes a moderate reduction, and where sometimes the zones and their spacing became gradually narrower without an obvious change in appearance. A few sections from large otoliths were clear to exceptionally clear, and a zone count could easily be made; these sections showed that the zones being counted with difficulty in the poorer sections were similar in appearance and spacing, and differed only in clarity. These clear sections gave counts of at least 80 zones.

## 4.2 Scales

The scales showed moderately clear growth checks or annuli (Figure 4) and counts could be made, though with difficulty. The fine circuli were always parallel to the scale margin, which meant that the annuli did not intersect them and cause thickening and/or breaks, as often occurs in ctenoid scales. The annuli were created by a slightly wider spacing between circuli. In the outermost zones, 3–6 circuli made up the growth zone between annuli. In the scales from larger fish (over 40 cm) the outer annuli were crowded, although the outermost one or two annuli were not particularly close to the

scale's edge. Trial counts extended up to 30 annuli, though they were recorded with considerable uncertainty. Scales from different parts of the body were essentially similar, although the largest – from the central body – gave slightly clearer counts of the outer annuli.

### 4.3 Fin spines and other structures

Fin spines, rays, and branchiostegal elements all had a banded pattern, most strongly developed in the dorsal and anal fin spines (Figure 5), probably because they provided a relatively larger cross-section. These spines had a central cavity, possibly filled with oil vacuoles and vascular tissue. The first 5–7 rings were wide and dark, with the first (innermost) of these the least well developed. They were usually visible right around the spine section. The outermost of these wide rings (usually ring 5) was often wider and darker than the others. Subsequent rings outside this were also clear but extremely narrow, and visible only on the broadest part of the spine section, e.g., where it was expanded into a ridge extending along the spine. The larger this expansion, the more narrow rings could be seen, with the outermost ones extremely closely spaced. Around most of each spine the outermost wide ring (usually #5) was at or close to the edge, and the subsequent sequence of very narrow rings was partially obscured by edge artefacts (adherent tissue, leached protein, etc.) resulting from the preparation procedure. Readers 1 and 2 counted 7–17 rings from five fish 33–43 cm in length, and 12–22 from a 49 cm fish. Reader 3 counted up to 15 rings, and considered there were more, but beyond adequate resolution at x80 magnification. Agreement between the different spines in the counts made by readers 1 and 2 was moderately good (*see* Table 1), but because the number of narrow rings depended on the presence and extent of a ridge expansion in the section, and the outermost rings were at the limits of resolution and potentially truncated at the section's edge, they were considered to be unreliable indicators of age. Their value lay mainly in demonstrating an apparent and possibly major change (decrease) in growth rate about the time rings 5, 6, or 7 were formed.

**Table 1: Comparative readings of zones or rings in several structures from six rubyfish, readers 1 and 2**

Length (mm)	336		347		363		404		430		490	
	M		M		F		F		M		M	
Reader	1	2	1	2	1	2	1	2	1	2	1	2
Otolith, sagitta	9	8	11	10	8	6	16	11	15	14–15	22	15–20
Otolith, lapilla	10	7–8	11	10	8	7–8	8	x	12	10–11	11	9–10
Scale above LL	7	7	8	5?	8	6	7	7	9	9	13	10
Scale, centre	10	6–7	9	8	9	7	8	9	10	9	13	12–13
Scale, rear	8	x	8	10	8	8–9	8	8	11	9–10	13	12–13
Spine, dorsal	8	8	10	9	8	7–8	11	10–11	12	14–17	12	11–14
Spine, anal	8	8	10–13	9–12	7	6	11	10–11	13	13–14	11	12–14
Spine, pectoral	7	7–8	9	8–12	5	5–6	12	10	x	10–12	10	10–16
Spine, pelvic	8	8–9	12	8–11	7	5–6	11	10	13	13–15	12/22	12–16
Vertebra	x	6–8	x	8?	x	8?	x	10	x	12?	x	x
Cleithrum	x	x	x	8–9	x	x	x	x	x	x	x	12
Branchiostegal	x	x	x	x	7	6	x	9	10	12	12	11
Operculum	x	x	x	8–9	x	7	x	10	x	12	x	11–13

Notes:

1. All readings were considered subjective and had some uncertainty. A question mark (?) indicates the best single estimate but with greater uncertainty. A range (–) indicates that several equally good estimates were made within the range. A slash (12/22) indicates two equally probable estimates were made. A cross (x) indicates that no zones could be seen and a reading was not made.

2. Reader 1 re-read these six sagittal otoliths after reading the main sample of 200+ otoliths, with reasonably comparable results. These paired readings (the second in brackets) for the six fish are: 9 (9), 11 (11), 8 (8) 16(16), 15 (18), 22 (20).

Although growth rings were present in most structures, and gave similar counts to the otolith sections originally investigated, they were no clearer than in the latter, and were considered not to be clear enough to be used for routine ageing.

#### **4.4 Otolith marginal increments**

Because samples of rubyfish otoliths were to be collected between October 1998 and at least September 1999, it was intended to carry out a marginal increment analysis to validate the otolith ages. This proved not to be possible. The inner dark growth zones (5–10) are either made up of many fine bands, or are diffuse without clear edges, particularly in the transition zone from broad to narrow growth increments. They also tend to undulate, and it was impossible to determine with any degree of certainty their distance from the otolith margin. The outer growth zones are more regular but very narrow, and it was not possible to quantify the marginal increment. It was difficult, in most otoliths, to even determine whether the margin was dark or light.

#### **4.5 Development of an otolith ageing methodology**

##### **4.5.1 First otolith readings**

The first set of readings was made by readers 1 and 2 on a sample of 90 otoliths. Both readers considered them difficult to interpret; on the four-stage readability scale most were assessed as 3 (poor) or 4 (almost unreadable). The readings were made independently and then discussed. Two interpretations were considered: (1) after 5–7 broad and widely-spaced growth zones there was a series of very narrow growth zones, and (2) the latter very narrow zones should be grouped, between 2 and 6 (often 4) comprising a true growth zone, sometimes indicated by slightly more prominent narrow dark zones at these intervals.

Using interpretation (1), counts of up to 75 growth zones could be made; however, some subjectivity was required in combining fine bands into the 5–7 inner growth zones, counting across an obscure transition area between the broad and narrow zones, and then choosing when to count the narrow bands as single zones instead of components of zones. Such high “ages” also seemed surprising for a semi-pelagic, although relatively deepwater, fish.

Subjectivity was also required when using interpretation (2). The grouping of the outer fine bands into possible “zones” of 2–6 bands occurred in a minority of the otoliths, and seldom across the whole sequence of bands/zones in the sulcal region where they were clearest. In many otoliths the slightly darker bands in the outer region were only just discernible, and in the otoliths generally considered “clearest” these relatively darker bands were not visible. Reader 1 made a count from 81 of the 90 otoliths, but considered most to be highly subjective and unreliable. Reader 2 obtained a count from 58 otoliths, and also considered these counts unreliable. These counts are compared in Figure 6. Agreement between readers was poor ( $r = 0.35$ ), with reader 2 almost always counting more zones (Figure 6A). When zone counts are plotted against fish length (Figure 6B) a plausible growth pattern is shown up to “age” 23 (after allowing for the between-reader variation), although it does imply a rapid growth rate in years 1–4.

##### **4.5.2 First otolith readings compared with fin spines**

The zone counts obtained by subjectively grouping the outermost narrow “bands” into “zones” of 2–4 bands mostly lay between 5 and 18. This was in the range of counts obtained from other structures (see Table 1), and seemed plausible for this kind of fish. The variation in zone counts between

readers 1 and 2 could be simply the result of the first attempts to age a new species with inherently difficult otoliths.

A second set of samples from 12 fish was then investigated, using otolith sections which were "thick" (about 400  $\mu\text{m}$ ) and "thin" (about 200  $\mu\text{m}$ ), and anal fin spine sections cut from three places (near the top, in the centre, and near the bottom). All were read by readers 1, 2, and 3 (Table 2). When possible, readers 1 and 2 made two otolith zone counts, "high" and "low", using the interpretations (1) and (2) described in Section 4.5.1. Reader 3 considered interpretation (2) too subjective and made only the high counts of interpretation (1).

**Table 2: Comparative readings of zones in thick and thin otolith sections, using two reading interpretations, and of rings in anal spine sections, from 12 rubyfish, readers 1, 2, and 3**

Fish	Reader	Otolith				Spine		
		Thick		Thin		Top	Centre	Bottom
		1 (High)	2 (Low)	1 (High)	2 (Low)			
43, F	1	40	12	26	13	17	11	16
	2	x	12	x	13-15	12	11-13	11-12
	3	32	x	33	x	14	12	15
44, F	1	38	12	29	13	16	17	16
	2	22	15	x	14	12-14	13-14	13-14
	3	35	x	35	x	16	15	15
44, F	1	29	10	34	10	14	17	20
	2	22	15	x	15	13-14	15-17	13-15
	3	34	x	34	x	15	19	20
44, M	1	28	13	39	13	12	17	18
	2	x	14	34	x	x	11-13	14-15
	3	40	x	42	x	x	18	18
44, M	1	20	10	29	9	13	17	18
	2	x	16	26	x	12-14	16-17	16-17
	3	23	x	32	x	x	16	17
44, M	1	30	12	39	11	16	18	23
	2	22	x	24-28	x	12-15	15-17	13-19
	3	36	x	36	x	x	18	17
44, F	1	30	13	33	11	10	16	21
	2	33	12	x	17	10-13	12	11-15
	3	50	x	49	x	16	15	14
45, F	1	32	9	42	11	12	16	10
	2	28	x	x	12	9-11	11-12	9-14
	3	40	x	42	x	15	15	15
45, F	1	44	12	47	11	20	23	21
	2	30+	12	31	14	16-18	16/22	14-18
	3	41	x	41	x	23	25	24
46, M	1	49	12	41	14	10	20	18
	2	35	x	28	17	14-15	14/22	14-15
	3	41	x	44	x	x	16	15
47, M	1	31	14	63	14	11	13/24	18
	2	x	15+	35/42+	x	x	12/20	15-17
	3	53	x	69	x	x	17	18
48, F	1	56	14	51	13	20	28	22
	2	x	x	32	x	20-22	16-21	17-21
	3	62	x	60	x	x	23	22

Note: (See notes to Table 1.)

There was moderate agreement among readers in the zone counts from otolith sections, particularly the high counts by readers 1 and 3. The low counts by readers 1 and 2 were sometimes similar, but sometimes considerably different, or were considered impossible to obtain. Both the thick and thin

sections could be read, with better agreement among the latter, which were also subjectively judged easier to interpret. The spine sections gave more variable results, both for different parts of the spine, and among the three readers.

The counts by reader 3 were generally higher than those by reader 1 (Figure 7A). They were made at a higher magnification (x80 cf. x50). After further comparative readings of these and other otolith sections at various magnifications, this was considered likely to explain the difference, even though the original x50 readings had been regarded as satisfactory. All subsequent readings were made at x80 or x100.

#### 4.6 Second otolith readings

Although rubyfish otolith sections were considered difficult to interpret and ambiguities and uncertainties remained, the assumptions and interpretations made by readers 1 and 3 resulted in sufficiently similar counts for the investigation to continue. For most otoliths, considerable subjectivity was involved in making counts through the transition region, immediately outside what were considered to be 5–7 broad, widely spaced dark growth zones. However, in the few otolith sections where all or most zones were clear, the growth zones in this region appeared to be reasonably normal; the spacing between zones did decrease quite rapidly, but not abruptly. This pattern was used to interpret those otoliths with an obscure sequence of zones in this region. From beyond this transition zone (i.e., from growth zones 15–20) to the edge the narrow dark zones were relatively straightforward to count.

Thin otolith sections from 27 fish were then read independently by readers 1 and 3, and the results showed close agreement (Figure 7, B).

#### 4.7 Final otolith readings

Four readings were used for the final analyses: three by reader 1 (at x50, and x80 twice), and one by reader 3.

##### 4.7.1 Comparison between readers

The first two otolith readings by reader 1 ( $R_{1,1}$  and  $R_{1,2}$ ) were strongly positively correlated ( $R^2 = 88\%$ ), but there was a clear systematic bias: for nearly all fish the second reading produced a higher zone count than the first (Figure 7A; note that the figure shows the mean  $\pm 1$  standard error; the 95% confidence limits of the mean are twice the range indicated by the error bars). We attribute this bias to the use of low magnification (x50) for the first reading and high magnification (x100) for the second reading. The greater resolution provided by the higher magnification enabled more fine zones to be discriminated. For this reason, the first reading by reader 1 is not considered further in this report. The second and third readings by reader 1 (both at x100 magnification) showed no overall systematic bias, but for fish less than 20 years old, the third reading produced slightly lower zone counts than the second (Figure 7B). There were some major outliers in the comparison between the second and third readings, indicating that the repeatability of zone counts was poor for some otoliths. These differences were not investigated, but may result from different interpretations of the difficult 'transition zone' (see Section 5.1), and/or the choice of the line along which to count zones (in most cases counts in two or more parts of an otolith were similar, but sometimes additional and plausible zones could only be seen in one small outermost area).

Otolith readings by readers 1 and 3 were also highly correlated ( $R^2 = 93\text{--}94\%$ ) (Figure 8), and there was little bias apart from the tendency noted above for the third reading of reader 1 to assign low ages to fish less than 20 years old. This was considered to result from accumulated experience of reading rubyfish otoliths of all ages. Those from fish older than 20 and with clear narrow zones in the outermost (20+) part of the otolith, in particular, provided a clearer perspective of the broad early zones (to about 7) and the spacing of zones across the difficult 'transition zone'. When the younger otoliths were re-read, split zones, and sets of bands within a zone, earlier counted separately, were more frequently grouped.

Ageing precision was low and variable for rubyfish younger than 40 years, both within and between readers (cvs mostly 15–25%; Figure 9). For older fish, precision was better (most cvs around 10%, ignoring the first reading of reader 1).

## 5. GROWTH RATE

Based on the mean of the zone counts of  $R_{1,3}$  and  $R_3$ , the estimated ages of the sampled fish ranged from 8.5 to 88.5 years (Figure 10). Males and females had similar age and length ranges, but females tended to be slightly larger at a given age than males. A randomisation test showed that von Bertalanffy growth curves fitted separately to the two sexes were significantly different ( $P = 0.006$ ) (Figure 10, Table 3). However, the differences between the estimates of  $L_\infty$  and  $K$  for the two sexes were negligible, and the main difference was in the values of  $t_0$  (–17.2 for males and –18.5 for females). The estimates of  $t_0$ , the theoretical age at which length is zero, are clearly unrealistic. They are derived from extrapolations of the von Bertalanffy growth curves beyond the range of the data, as a result of the lack of data for fish younger than 8 years.

**Table 3: von Bertalanffy growth parameters and standard errors for rubyfish**

Parameter	Estimate $\pm$ std error		
	Males	Females	Both sexes
$L_\infty$	48.60 $\pm$ 0.66	49.05 $\pm$ 0.60	48.68 $\pm$ 0.42
$K$	0.043 $\pm$ 0.005	0.043 $\pm$ 0.005	0.045 $\pm$ 0.004
$t_0$	–17.15 $\pm$ 2.77	–18.48 $\pm$ 3.29	–16.53 $\pm$ 2.02

## 6. NATURAL MORTALITY

The greatest mean age obtained in this study was 88.5 years, though reader 1 aged one fish at 100 years. Using longevitys of 80, 88.5, and 100 years, Hoenig's regression and rule-of-thumb methods produced estimates of  $M$  around 0.05 (Table 4). The estimates are not particularly sensitive to the value of longevity used. However, they are based on unvalidated maximum ages and should be regarded as preliminary.

**Table 4: Rubyfish mortality rate estimates for three longevitys using Hoenig's regression method and a rule-of-thumb approximation to it**

Estimation method	Longevity (years)		
	80	88.5	100
Hoenig's (1983) regression	0.052	0.047	0.041
Hoenig's rule-of-thumb ( $p = 0.01$ )	0.058	0.052	0.046

Using the von Bertalanffy growth parameters for both sexes combined, and a mean water temperature of 10.4 °C (based on bottom temperatures measured on research trawl survey shots that caught

rubyfish), Pauly's method produced an  $M$  estimate of 0.13. For temperatures between 8 and 12 °C (the temperature range over which most trawl shots catching rubyfish were made),  $M$  was in the range 0.11–0.14.

The sample of aged fish from QMA 2 that was used to estimate  $Z$  contained 830 fish, only eight of which were less than 7 years old. Taking 7 years as the age at recruitment, the mean age in the sample was 27.8 years and the sample size was 830 fish. The Chapman-Robson estimate of  $Z$  was 0.035. Increasing the age at recruitment in one year increments to 12 years progressively reduced the estimate of  $Z$  to 0.029.

## 7. DISCUSSION

Otolith zone counts were affected by microscope magnification. The finer zones in the outer part of the otolith were not adequately discriminated at x50 magnification, although this was not obvious to reader 1 during his first reading. We recommend that all rubyfish otoliths be read at magnifications of x80 or greater. We only briefly investigated heated otolith cross-sections, and did not explore the possibility of ageing by baked and embedded cross-sectioned otoliths, but believe these techniques are unlikely to be successful because of the high magnification and carefully controlled lighting required to discriminate the outermost growth zones.

The individual age estimates for rubyfish had low precision, and a comparison of estimates between and among readers revealed some extreme outliers. The repeatability of zone counts for any particular individual is therefore low. However, there was little overall systematic bias within or between readers (at magnifications of x80 or greater), suggesting that the growth curves derived from averaged age estimates are relatively robust. The main area of concern is the estimation of ages of young fish (less than about 20 years old); these fish are the most difficult to age, and there was evidence of systematic bias within and between readers for them.

Our attempts to validate the otolith ageing technique using marginal increment analysis failed because of our inability to classify the marginal composition, or to measure the marginal increment. Validation is therefore a high priority for this species, considering that our age estimates (maximum age 88.5 years with many over 50 years) suggest that rubyfish are the third longest-lived commercially fished species in New Zealand (after orange roughy and oreos).

A randomisation test revealed a significant difference between the growth curves for males and females. However, the difference was biologically trivial (equivalent to a horizontal displacement of the curves by 1.3 years). Given the small sample sizes (112 and 123 for males and females respectively) and the poor ageing precision, we believe the difference may be spurious. We therefore suggest that the von Bertalanffy growth curve for the combined sexes best describes the growth of adult rubyfish:

$$L_t = 48.68 (1 - e^{-0.045[t+16.53]})$$

A lack of young fish in our samples led to an unrealistically low estimate of  $t_0$ . Furthermore, our age estimates and the fitted von Bertalanffy growth curve suggest that early growth of rubyfish is particularly fast (Figure 10). This is supported by the fin spine sections (Figure 5) with 5–7 well spaced rings followed by a sequence of very narrow rings, as well as by the wide spacing of the first otolith zones. Commercial fishers rarely catch small rubyfish, which probably reflects their unavailability to trawl gear as well as a selective effect of mesh size (though small fish should be caught occasionally even in large mesh sizes). We speculate that the apparent absence of rubyfish from trawl catches, and their rapid early growth, result from young fish inhabiting different areas (and perhaps depths) from old fish. Schools of small rubyfish have in fact been encountered a short

distance above the seafloor in areas away from the main grounds, and are avoided (anecdotal information from fishers to NIWA). Small rubyfish have seldom been caught during research trawl surveys, but samples of small (13–34 cm) fish measured from two adjacent stations in depths of 135 and 150 m during a 1990 survey off the central west coast had length modes at 15–16 cm and 19–20 cm which might have represented early age groups.

For any subsequent work on ageing, fin spine samples should be examined from fish less than about 25 cm, as well as otoliths. Spines might prove suitable for ageing juvenile fish. The change from broad to very narrow rings at 5–7 may indicate the attainment of maturity, but is so abrupt that it may alternatively, or in addition, reflect a major change in the fish's life history, such as a change from a pelagic to a demersal habitat. It seems likely to mark a sudden decrease in growth rate.

This sudden change is not as clearly shown in the otolith, but otolith growth is known to be a less sensitive indicator of a fish's somatic growth than are hard parts which are more directly a part of the body (scales, fin spines, etc.) and which must grow in direct proportion to the body. The obscure 'transition zone' on most otoliths, however, does suggest that changes are occurring at this time.

The estimates of  $M$  obtained using Hoenig's (1983) and Pauly's (1980) methods must be interpreted cautiously, because the data sets used by the two authors to develop their regressions contained only a few fish species with longevity greater than 25 years and  $M$  values less than 0.1. Furthermore, there is much unexplained variability in the data used for both studies, suggesting that estimates predicted from the regressions may be quite inaccurate. Pauly's method produced estimates of  $M$  more than double those of Hoenig's method.

The Chapman-Robson estimate of  $Z$  (0.035) was lower than either of the two empirically based estimates of  $M$ . The sample used to estimate  $Z$  is probably representative of the catch, because samples were collected over a lengthy time period (about 9 months) from scattered localities throughout QMA 2. However, it is not known how representative the sample is of the population. Fish younger than 7 years were poorly represented in the samples, but this should not affect the estimate, which is based only on recruited year classes. Increasing the age at recruitment had little effect on the estimate of  $Z$ . Given that the QMA 2 rubyfish stock has been exploited for more than 7 years,  $M$  is likely to be lower than  $Z$ . We consider the most plausible estimate of  $M$  to be 0.03. However, this  $M$  estimate is based on unvalidated ages, and possibly unrepresentative samples.

Rubyfish appear to be a long-lived species, but our age estimates are unvalidated. It is possible that the individual otolith markings we have interpreted as growth zones should be grouped in some way when counted, but when we attempted to do this our interpretation became highly subjective. After initial misgivings about the zone counts, which increased rapidly over only a small increase in fish length, implying extremely slow adult growth, we became more confident when the few very clearest otoliths showed a pattern of light and dark zones which is typical of teleost otoliths, and provided plausible zone counts from 60 to at least 80. These otoliths, in thin section, looked very similar to otoliths from other species known to be long lived. Our high counts from the otoliths which were not as clear were made under the assumption that their zones were structured in a similar way. That is, that all growth zones were multi-banded, with 5–15 bands in the early zones and 2 or more in the outermost zones. We considered the presence of some more widely spaced darker bands (usually at the outer edge of what we recognised as a zone) to be an artefact, as they were present only in some portions of some otoliths.

## 8. ACKNOWLEDGMENTS

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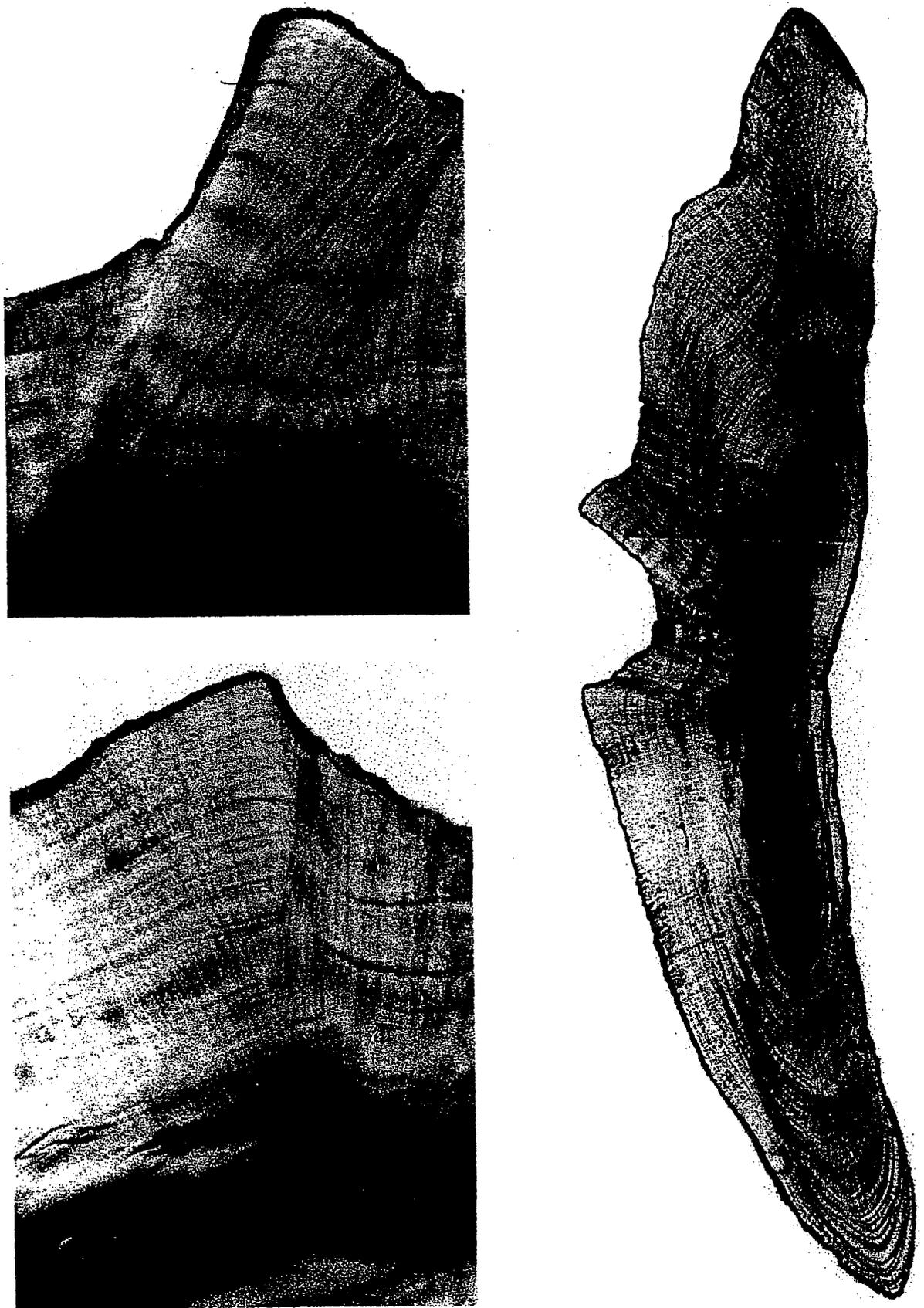


Figure 1: Otolith thin section from a 33 cm female rubyfish, photographed in transmitted light. Right, entire section (x29). Upper left, the dorsal edge of the sulcal region (x72). Lower left, the ventral edge of the sulcal region. The three final readings from this otolith were 10, 11, or 12 dark zones.

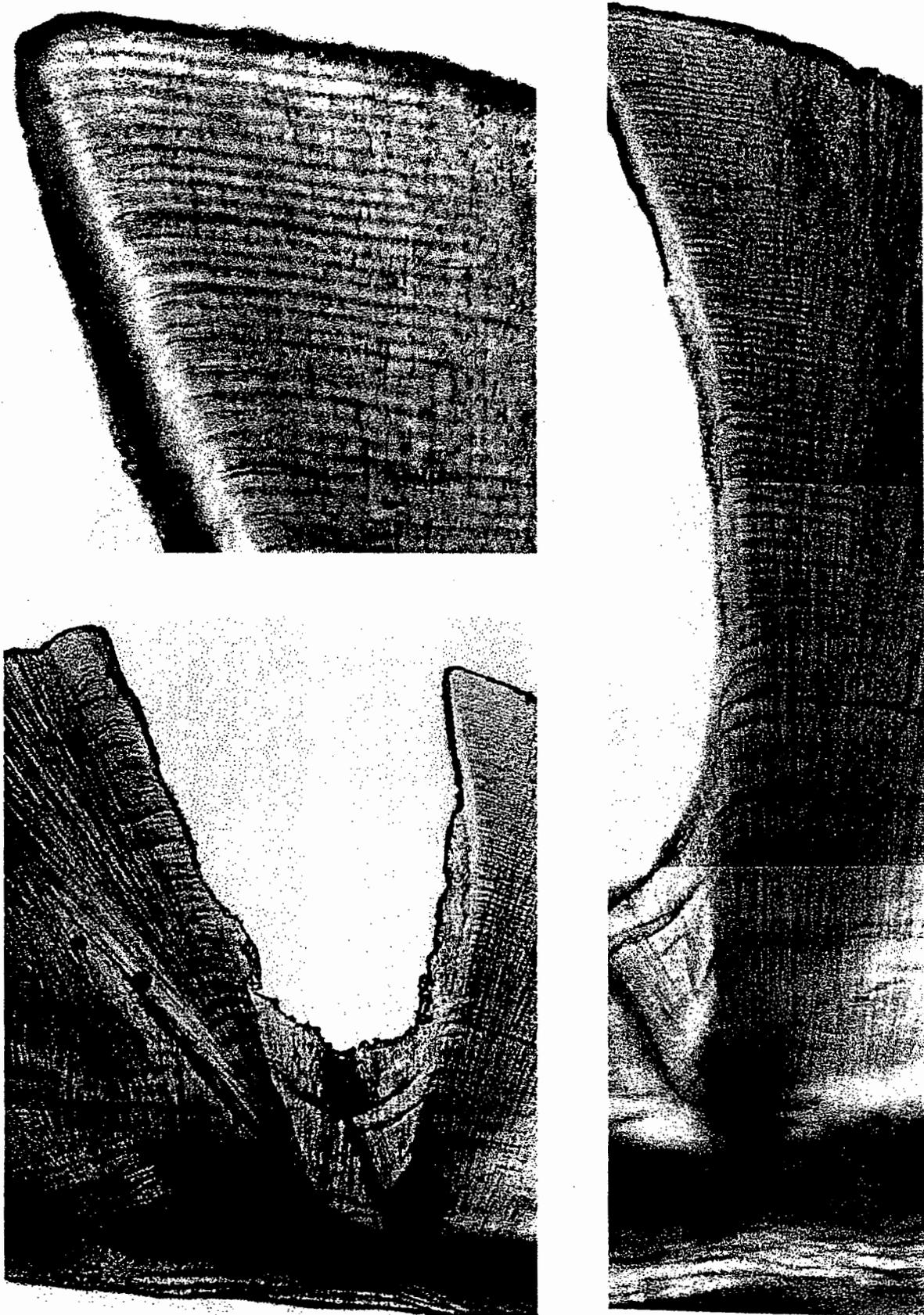


Figure 2: Otolith thin section from a 45 cm female rubyfish, photographed in transmitted light. Lower left, sulcal region (x32). Right, ventral edge of the sulcal region (x80). Upper left, outer portion of the ventral edge of the sulcal region (x160). Three readings gave 58, 72, or 75 dark zones.

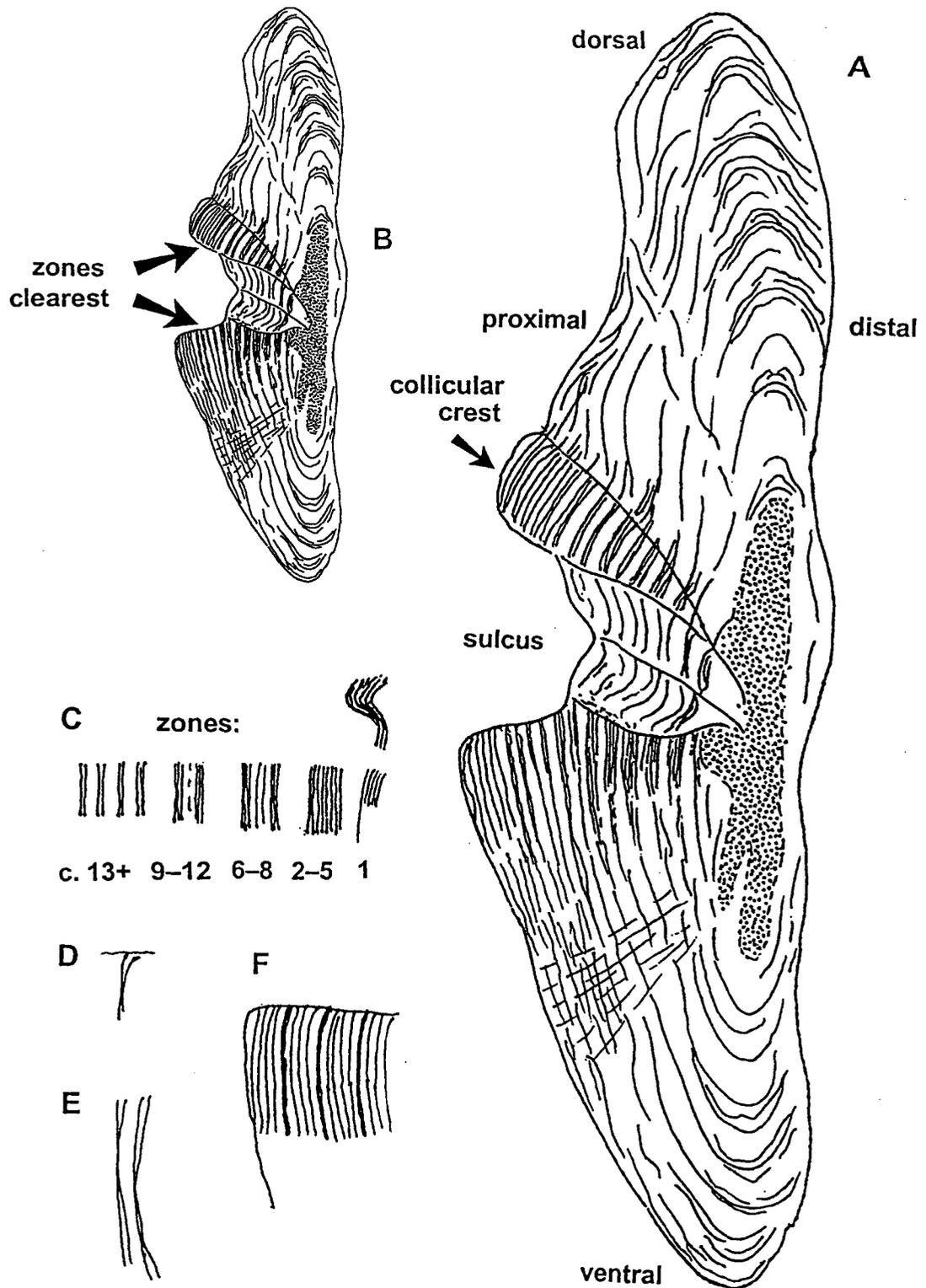
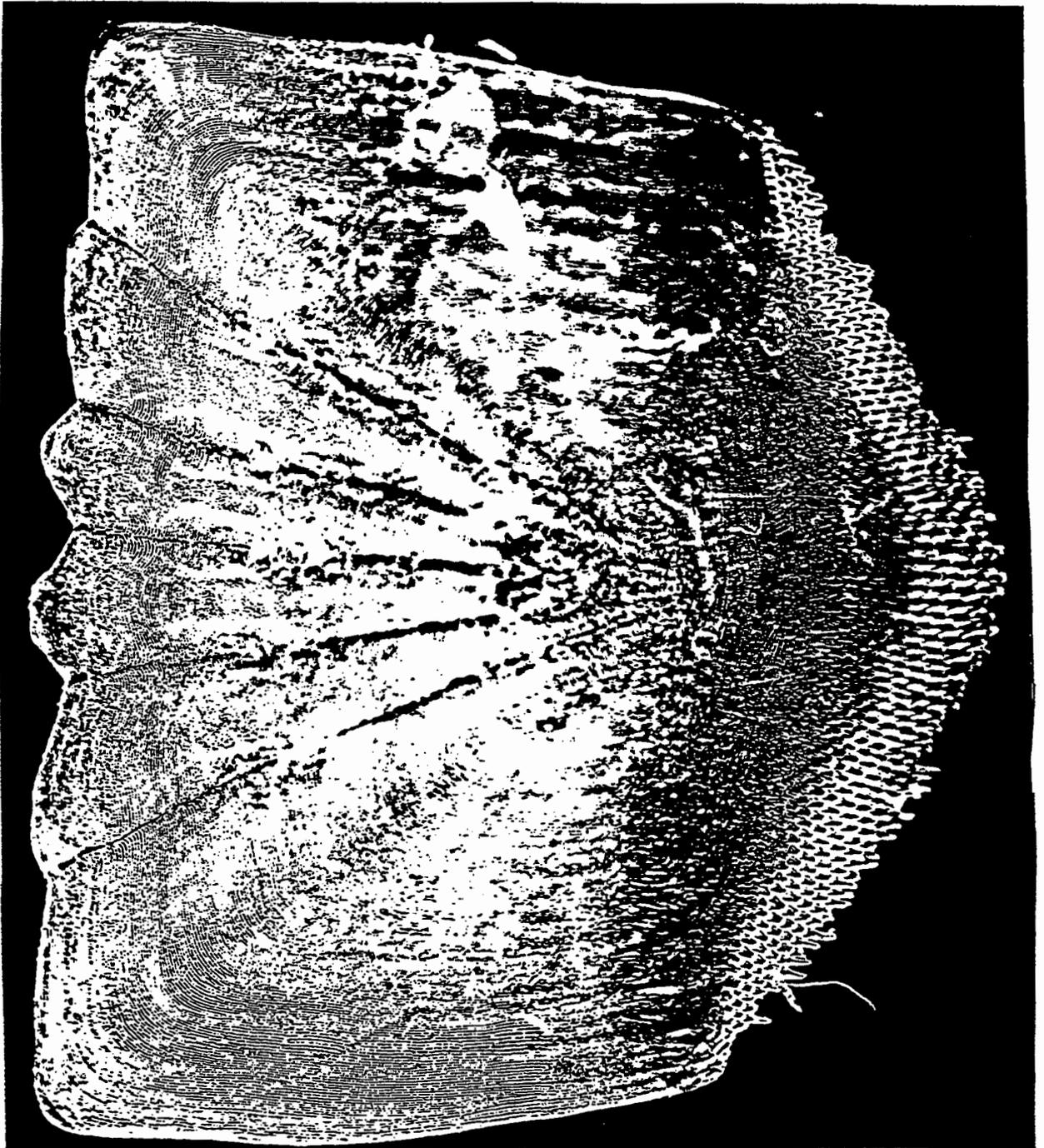


Figure 3: Diagrammatic representation of a rubyfish otolith section with 18 dark zones. A, entire section, as seen in transmitted light. Zones on the long dorsal and ventral axes can usually be seen but are always split into narrow bands. B, the zones are clearest adjacent to each edge of the sulcus (arrowed); the first few zones are usually clearest near the dorsal edge of the sulcus, on the inner collicular crest. C, an interpretation of the sequence of dark zones in the sulcal region (zone ranges are approximate): #1 is multi-banded and often reduces to a narrow zone; #2-5 are multi-banded; #6-8 are multi-banded with the inner and outer (bordering) bands of each zone more prominent; #9-12 are variable but often also have two prominent bands with faint inner bands; #13+ usually have two or more bands when viewed under high magnification, spaced closely with a greater distance to the next set of bands (= zone). D, at the sulcal margin a single band within a zone may be divided. E, adjacent to the sulcal region two (sometimes more) of the narrow outer zones may merge into one. F, in some otoliths from larger and older fish (see Figure 2) there may be a region, particularly near the edge, where the narrow zones are relatively darker at intervals of 4-6 zones. Interpretation by L.J.P.



**Figure 4:** Scale from a 36 cm female rubyfish, showing circuli which run parallel to the scale's anterior and lateral margins, and numerous relatively obscure annuli. These are usually clearest on the antero-lateral axes, but the count of annuli along one axis often differs from that along the other.

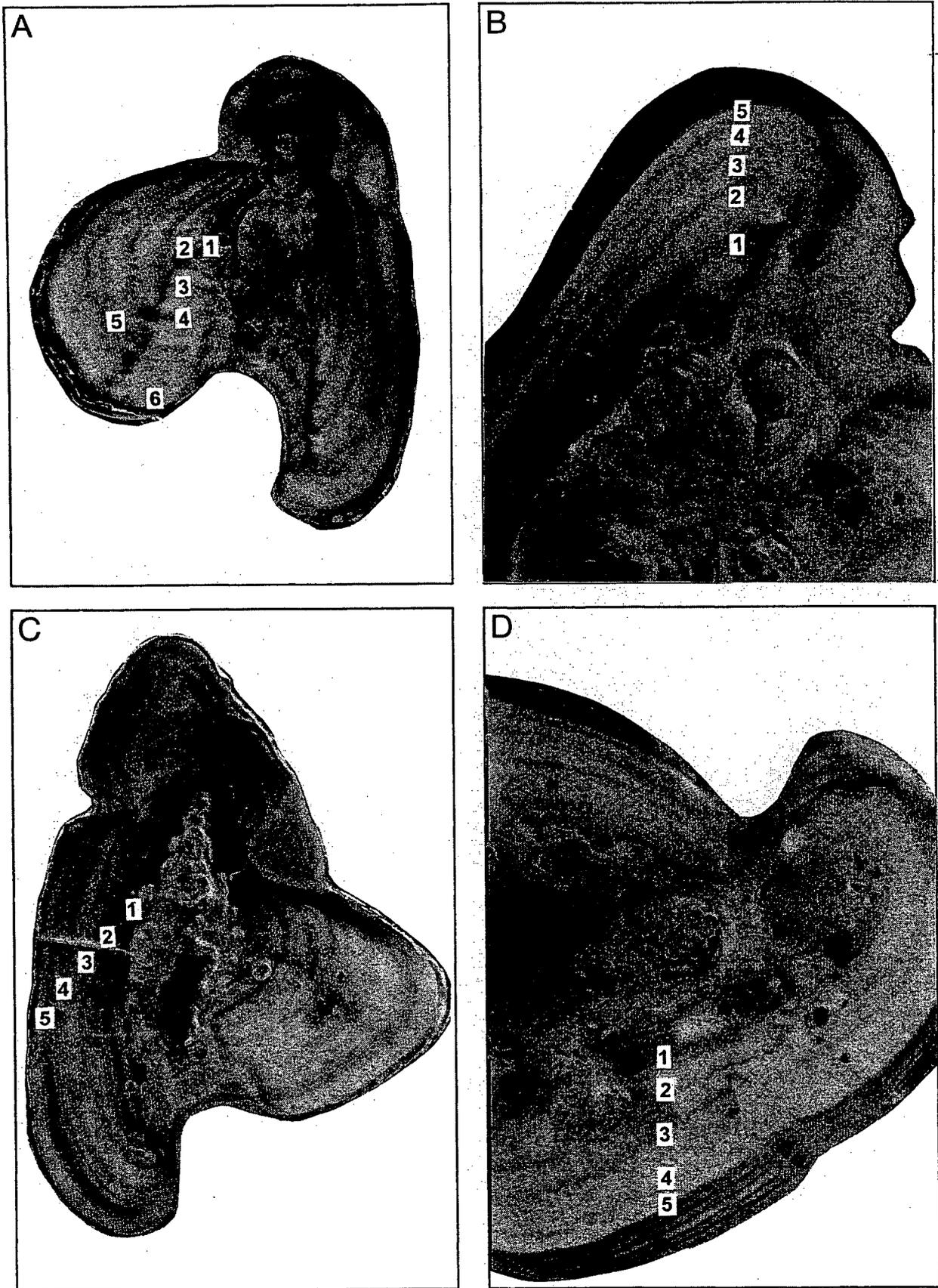


Figure 5: Spine sections from rubyfish, showing 5 or 6 inner broad growth zones and rings (as numbered), followed by a sequence of very narrow rings visible only at certain places on the margin. (A) dorsal spine, 36 cm F; (B) dorsal spine, 40 cm F; (C) anal spine, 33 cm M; (D) anal spine, 40 cm F.

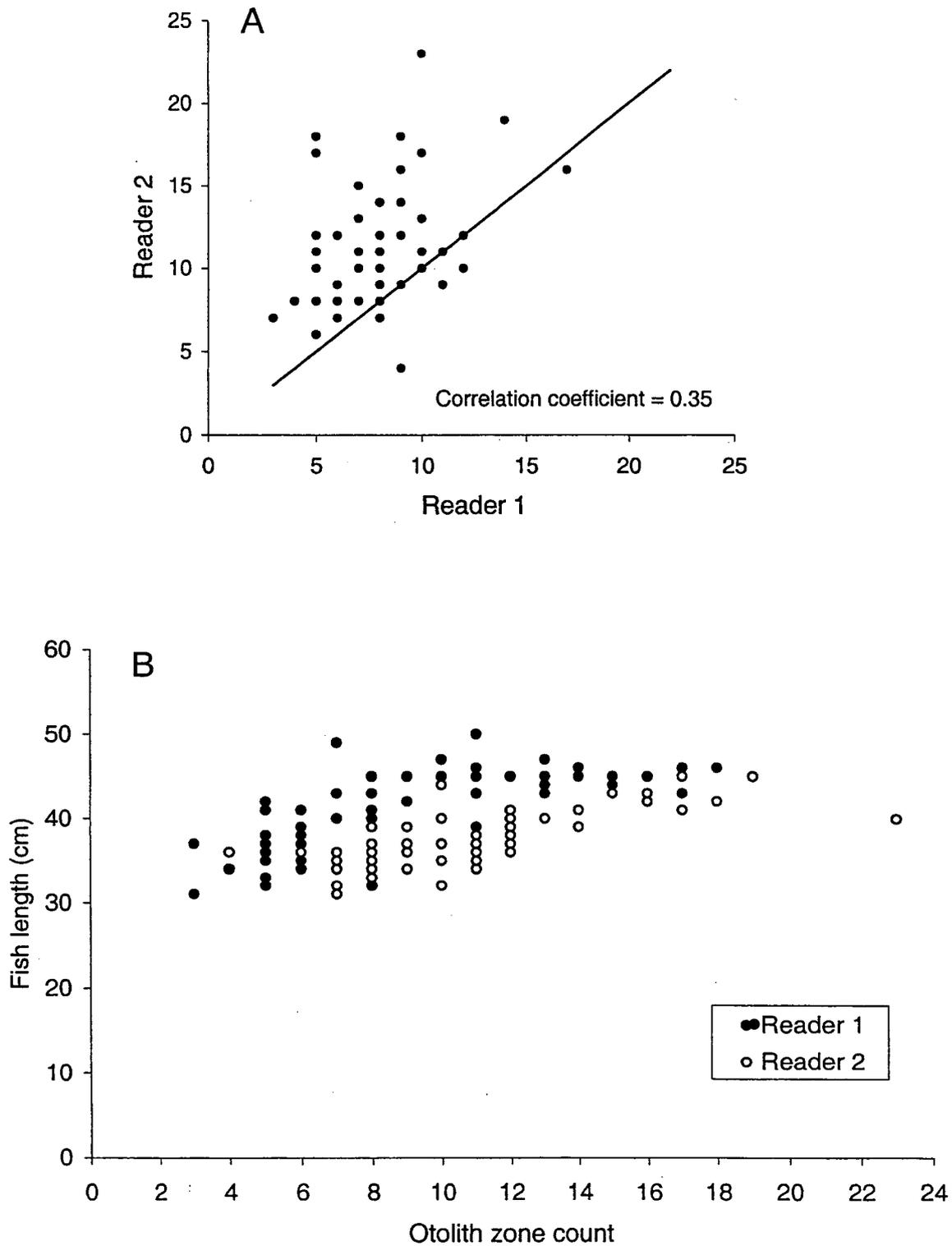


Figure 6: Between-reader comparison of rubyfish age estimates (otolith zone counts) from an initial sample of 90 fish. These zones are subjective groupings of the narrow bands in the outer region of the otolith into hypothetical "growth zones", based on the presence and spacing of some relatively darker bands (see Figure 2). (A) reader 1 versus reader 2; note, some points are over-plotted. Diagonal line at unity. (B) fish lengths plotted against these age estimates, by reader.

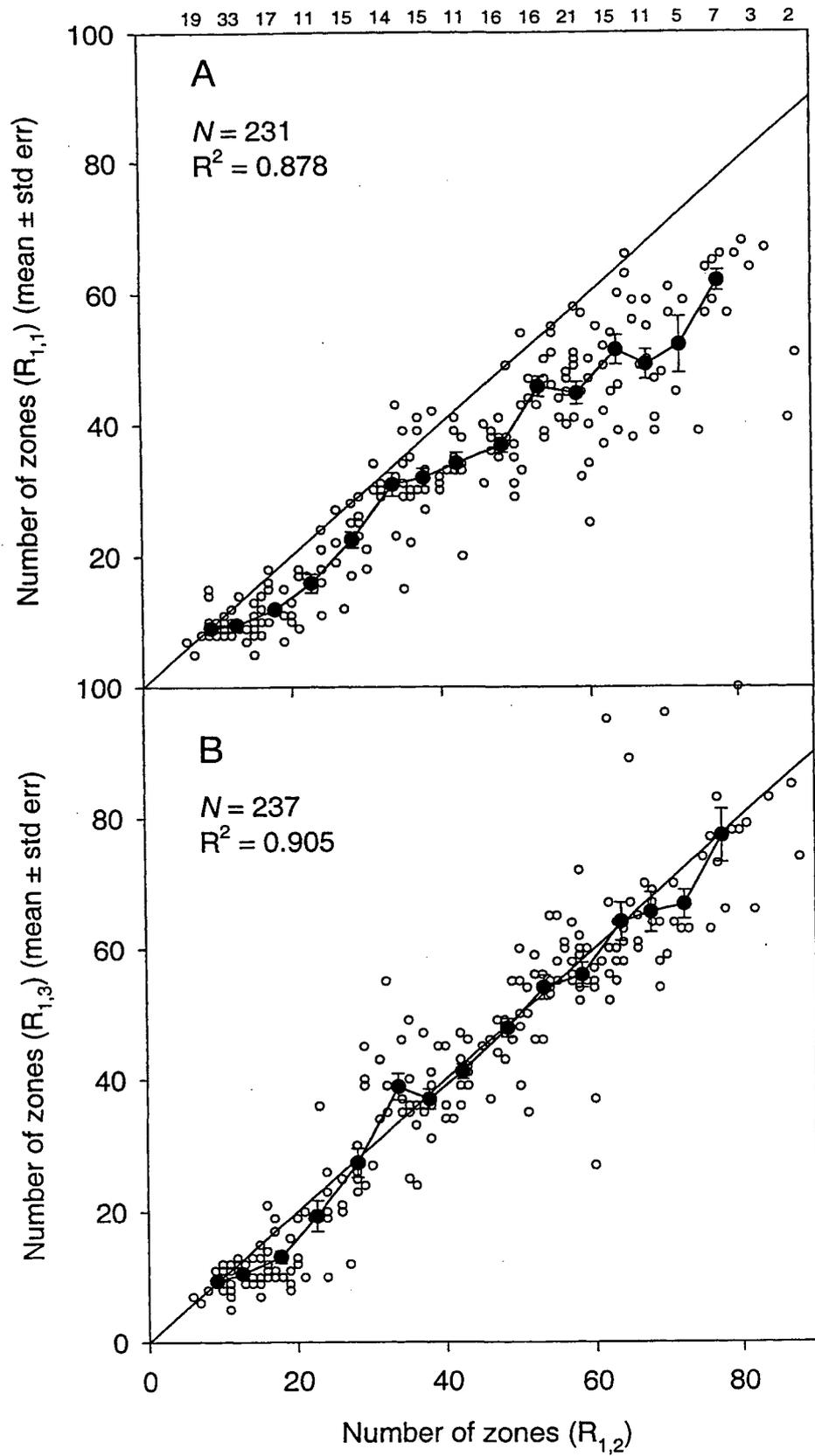


Figure 7: Comparison of actual (open circles) and mean (dots) rubyfish age estimates by reader 1: (A) reading 1 versus reading 2 (R<sub>1,1</sub> and R<sub>1,2</sub>), and (B) reading 3 versus reading 2 (R<sub>1,3</sub> and R<sub>1,2</sub>). Diagonal lines indicate equality of age estimates. The mean plots are for data grouped into 5-year intervals and having sample sizes greater than 3 (sample sizes are shown along the top axis). N, total sample size.

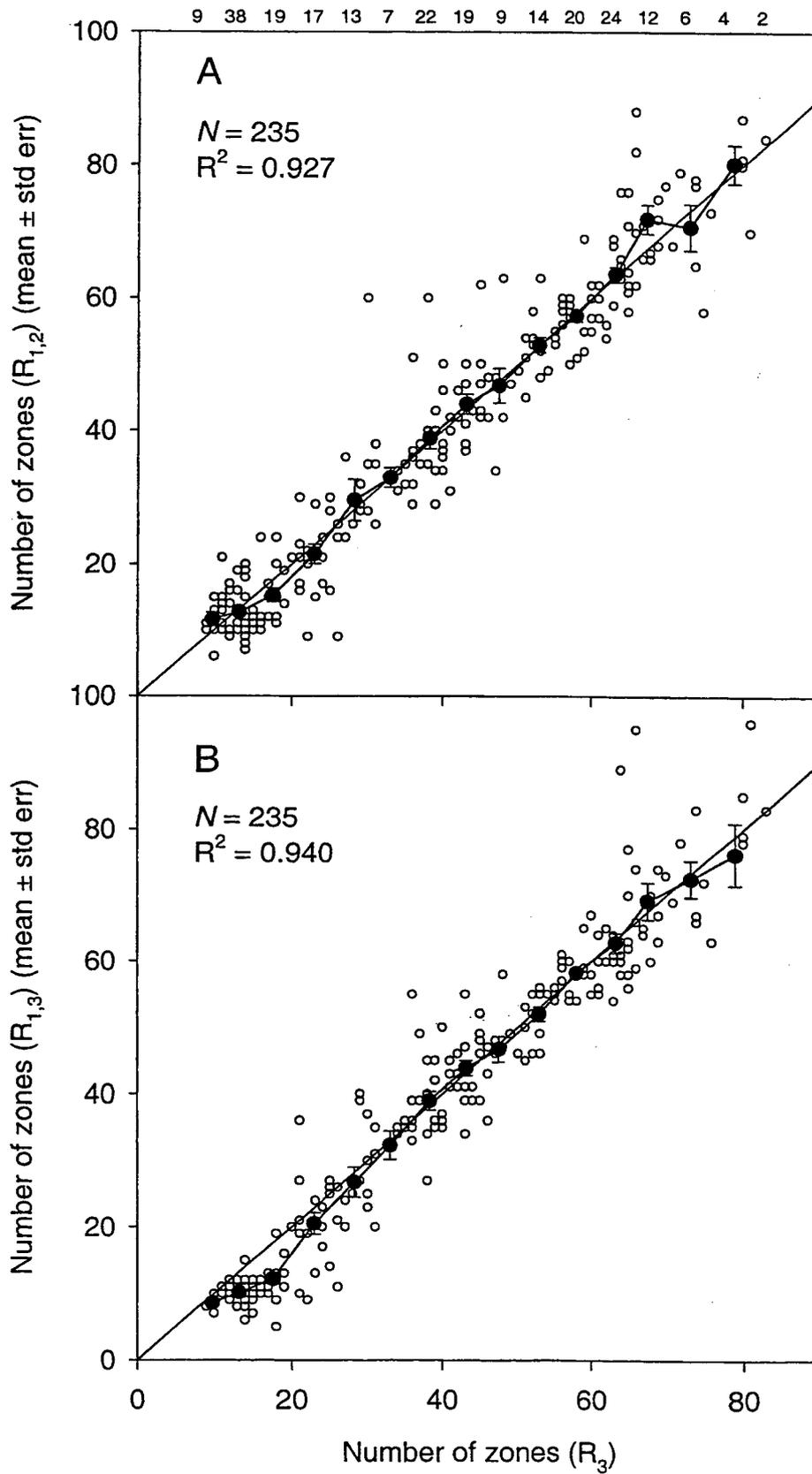


Figure 8: Comparison of actual (open circles) and mean (dots) rubyfish age estimates for readers 1 and 3: (A)  $R_{1,2}$  and  $R_3$ , and (B)  $R_{1,3}$  and  $R_3$ . Diagonal lines indicate equality of age estimates. The mean plots are for data grouped into 5-year intervals and having sample sizes greater than 3 (sample sizes are shown along the top axis).  $N$ , total sample size.

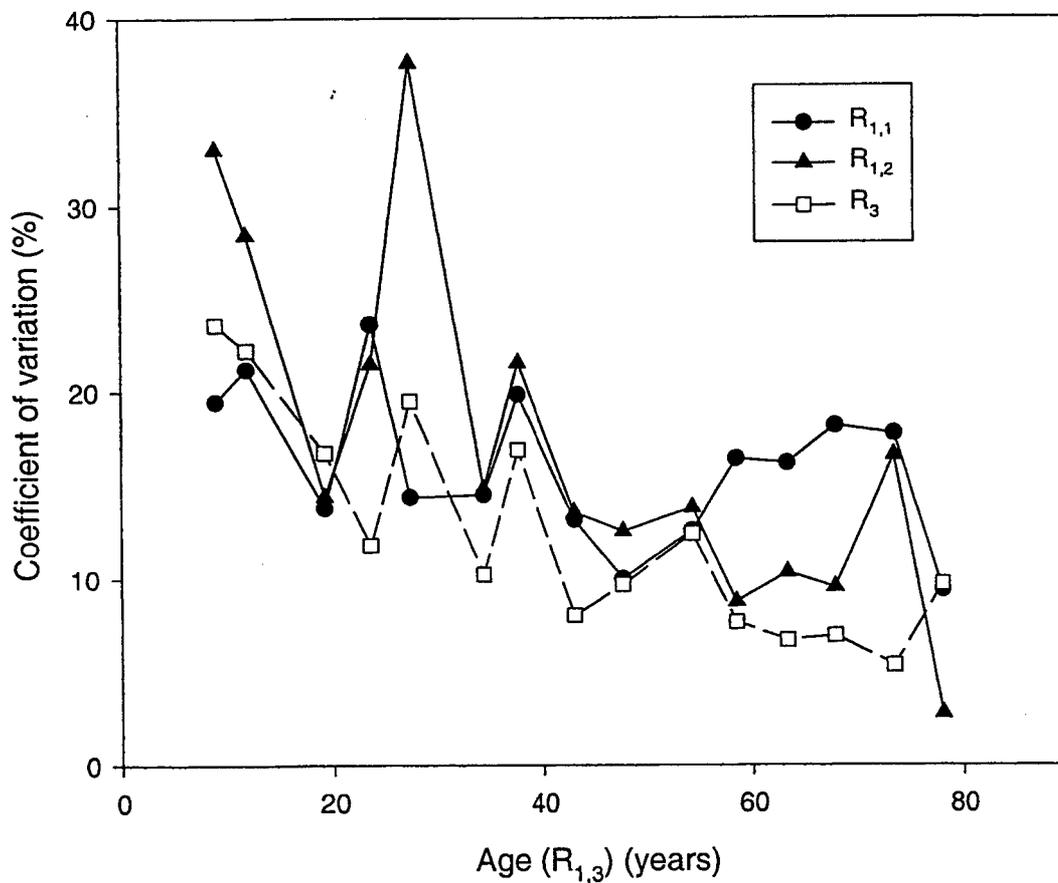
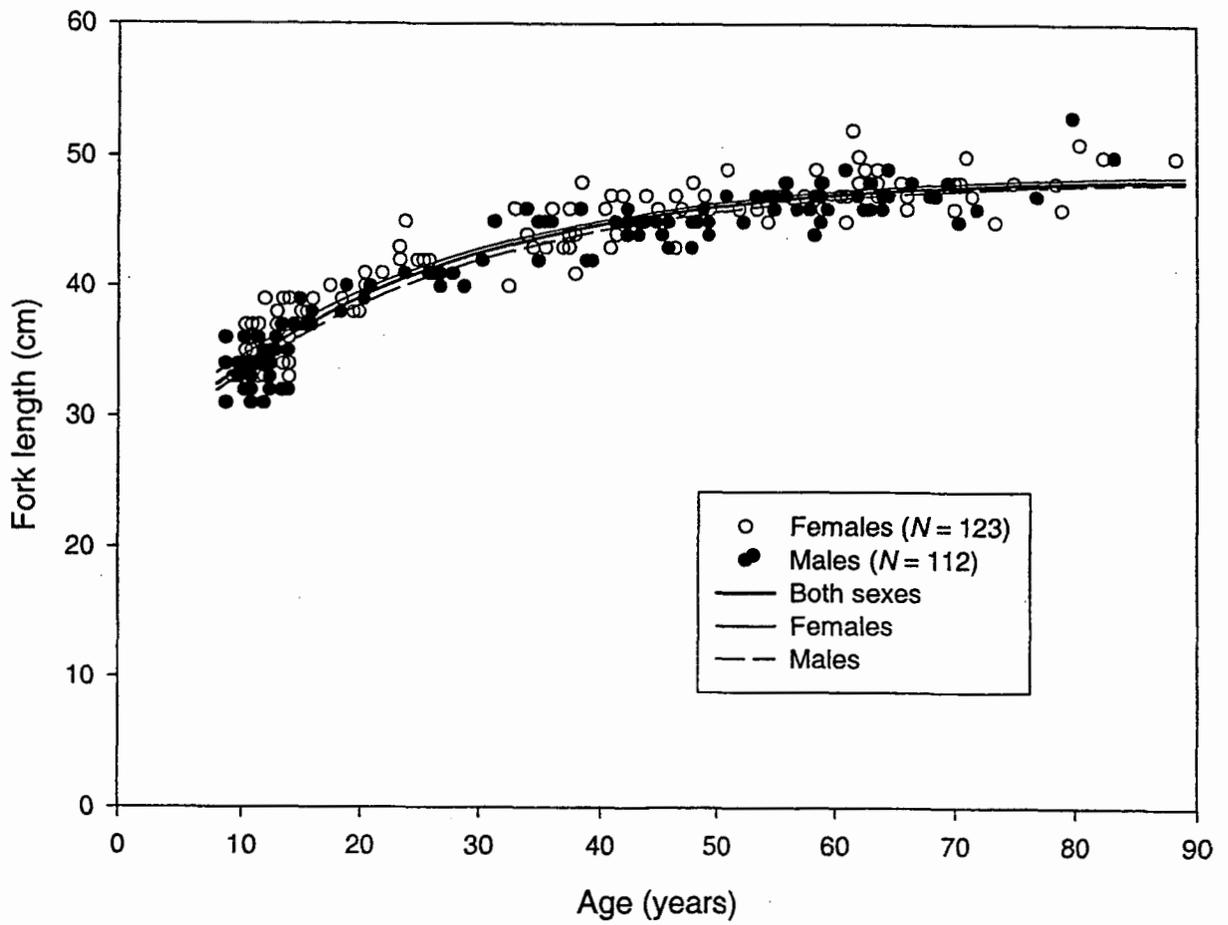


Figure 9: Precision of rubyfish age estimates of reader 3 ( $R_3$ ) and reader 1 ( $R_{1,1}$  and  $R_{1,2}$ ), plotted against the ages determined for the same fish by reader 1 ( $R_{1,3}$ ). The data points are the coefficients of variation of the mean values (grouped in 5-year intervals).



**Figure 10: Relationship between rubyfish length and age (mean of  $R_{1,3}$  and  $R_3$ ) with fitted von Bertalanffy growth curves. Data points for males and females are slightly offset from the axis ticks for clarity.**