

Growth rate, age at maturity, longevity and natural mortality rate of Ray's bream (*Brama* sp.)

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**Final Research Report for
Ministry of Fisheries Research Project TUN2003/01
Objective 2**

National Institute of Water and Atmospheric Research

September 2004

Final Research Report

Report Title: Growth rate, age at maturity, longevity and natural mortality rate of Ray's bream (*Brama* sp.).

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1. Date: 29 September 2004

2. Contractor: National Institute of Water and Atmospheric Research Limited (NIWA).

3. Project Title: Productivity of important non-target species caught in the tuna longline fishery.

4. Project Code: TUN2003/01

5. Project Leader: M.P. Francis

6. Duration of Project:

Start date: October 2003

Completion date: September 2004

EXECUTIVE SUMMARY

This report addresses Objective 2 of Project TUN2003/01, Productivity of important non-target species caught in the tuna longline fishery, “To determine the growth rate, age at maturity, longevity and natural mortality rate of Ray’s bream (*Brama brama*).” There are several very similar species of *Brama*, and it is possible that more than one is taken in the New Zealand fishery. The most common is believed to be southern Ray’s bream, *B. australis*. It is assumed that the otoliths examined in this study came from this species.

Length frequency data were obtained from observer and research trawl survey databases, and otoliths from 30–56 cm fish were selected from these same sources.

Otoliths from 252 fish were thin-sectioned and read under high magnification with transmitted light. They were difficult to interpret, showing a variety of growth patterns not characteristic of standard annual zones seen in other species. Less than half (43–49%) were scored with moderate uncertainty or better, and only 12–19% were scored as good or clear. In general, only otoliths with more than about 12 zones were clear, and most of these came from fish longer than 48 cm. This high uncertainty in the age estimates, and their status as being unvalidated, means the growth curve estimates must be interpreted with some caution, particularly for the younger age classes.

Otoliths were read blind (without knowing fish length) by one reader, and with known length by two readers. Within-reader variability (blind cf. known-length) was high but with no bias. Between-reader variability (length-known) was also high but with no bias. When fish length was known, length-at-age variability was lower and the shapes of the fitted growth curves were more plausible.

Few young fish were aged (and with low reliability). The growth curves imply rapid early growth, to about age 5, at 40–45 cm, and then slow growth to 56 cm. Maximum age was 25.

Length and age at maturity could not be adequately estimated because although gonad maturity stages were available for fish sampled from tuna longline catches and research trawl surveys, these stages do not distinguish between resting mature fish and fish that are maturing for the first time. Most of the fish above 35 cm or about 2 years old were resting or maturing, though it is not known what proportion of the latter were maturing for the first time. It appears that fish longer than about 40 cm and older than about 5 years are mature. It is surprising that although staged samples were available from winter, summer and autumn, ripe fish were virtually absent. New Zealand Ray’s bream may spawn only in more northerly waters than have been sampled so far.

The natural mortality coefficient M was estimated using Hoenig’s (1983) regression method, and with a Chapman-Robson estimator. Neither method provided a good estimate of M with the present data, but the most plausible estimate was in the range 0.10–0.15.

The trawl catch is estimated to be based mainly on 4 to 11 year old fish, and the bycatch in the tuna longline fishery mainly on 5 to 11 year old fish, but the relatively flat growth curve means that length is not a good predictor of age for fish over about 5 years old.

1. INTRODUCTION

Ray's bream are taken on tuna longlines, ranking second numerically in the non-tuna bycatch (after blue shark) but because of their low individual weight their annual landings in this fishery have been only about 10–30 t (Francis et al. 2004, Ayers et al. 2004). They comprise a much larger bycatch of trawlers working outer shelf and continental slope grounds, with recent annual landings of 300–500 t. They have not been studied in New Zealand, and even the species composition of “Ray's bream” in the fishery remains uncertain (Stewart 2001). This study was directed at determining the growth rate, age at maturity, longevity and natural mortality rate of the species most commonly taken in the fishery, currently believed to be southern Ray's bream, *Brama australis*. It was undertaken following the review by Francis & Griggs (2001) which established that although Ray's bream were moderately important in both fisheries, very little information was available on this species.

Ray's bream are not currently in the Quota Management System (QMS).

2. BACKGROUND INFORMATION

2.1 Identity

Ray's breams are pomfrets, in the family Bramidae. The genus *Brama* contains eight species, two of which are present in New Zealand, together with a species of the related genus *Xenobrama* (Stewart 2001). *Brama brama* was first reported in New Zealand (as *Toxotes squamosus*) in 1875. A second very similar species was recognised about 1970 (Mead 1972) but not named (as *B. australis*) until 1991 (Pavlov 1991); the two are difficult to distinguish from external characters. The third species, *Xenobrama microlepis*, was described at about the same time (Yatsu & Nakamura 1989); it is widespread in the South Pacific, extending on to the Chatham Rise, and recognisable from its coloration which includes bronze to golden hues.

The distribution and relative abundance of these three species in New Zealand waters is uncertain (Stewart 2001), although most specimens in the Museum of New Zealand's collection are *Brama australis* and *Xenobrama microlepis* (Stewart 2001). We assume that the otoliths used in this study, archived from fish identified as “Ray's bream”, are predominantly or wholly from *Brama australis*. Of the 252 otoliths used, 200 were photographed, and although they showed considerable variation in shape they could not be categorised into two or more groups which might represent different species. However, otoliths have not been taken from formally identified fish specimens, and it is possible that interspecific differences are small.

Because several species of *Brama* are remarkably similar in outward appearance, we consider it likely that some of the published work on their biology may not have correctly identified the species involved. Most studies (nominally) are on *B. brama* (Atlantic pomfret), which grows to 50 cm, in the Atlantic, Indian, and Pacific oceans; *B. japonica* (Pacific pomfret), to 60+ cm, in the northern and central Pacific ocean; and *B. australis* (southern pomfret), to 53 cm, in the southern Pacific Ocean from New Zealand to Chile.

Brama brama was initially named *Brama raii* after the naturalist Ray. This name was subsequently synonymised, but *B. brama* and similar species are still often called Ray's bream, as well as pomfrets – the more widely used common name for most members of this family.

2.2 Age and growth

Given the uncertainty over specific identification, the close morphological similarity of species, and the rather surprising but unvalidated results obtained from previous ageing work, a brief account of the relatively few studies on the three most important species of *Brama* is given here.

Rodriguez (1980) described the growth rate of *B. brama* off Spain as “fast”; he presented length frequencies extending over 18 months showing size modes which can reasonably be interpreted as an age group increasing from 28 cm in September to 36 cm in May, i.e., the Northern Hemisphere’s autumn to spring. He extrapolated this to much less convincing length modes of larger fish at about 40 and 50 cm and suggested that only three age groups were present. Otoliths were examined (procedure not stated) but gave no assistance in determining age. Pearcey et al. (1993) studied 21–50 cm *B. japonica* in the North Pacific and described two length frequency modes, apparently of 0+ and 1+ to 6+ fish. They used annual zones and assumed daily microincrements in otolith thin sections to describe early growth as fast, and obtained ages of 1 to 6 from whole otoliths. Savinykh & Vlasova (1994) examined whole stained otoliths of 14–54 cm *B. japonica* from the North Pacific and found a maximum age of 9 years, but with 3 and 4 year fish predominating in the catch. Pavlov (1994) examined only 11 whole otoliths of 13–48 cm *B. australis* from the southeast Pacific Ocean, described early growth as rapid, and implied that subsequent growth was also relatively fast in what appeared to be a short-lived species; the estimated lengths at ages one to six were 13–17, 21–26, 26–32, 31–36, 36–48, and 40–47 cm. Bigelow et al. (1995) used length frequencies and otolith thin sections for 35–47 cm *B. japonica* in the North Pacific. Length modes suggested four or five year classes, while otoliths – based on counts of growth rings assumed to be daily – gave ages of only 0 to 3 years. Lobo & Erzini (2001) used readings of whole otoliths for 32–56 cm *B. brama* from Portugal to identify age groups 3 to 12, but did not describe their procedures.

In most of these published accounts the otolith ageing methodology was poorly defined, and the few illustrations presented did not clarify the growth zone interpretations described or inferred. There was no mention, in any of the accounts seen, of whether the otolith growth zones were clear or difficult to interpret.

For species of *Brama*, maximum ages of 4 to 6 years seem implausibly low, but ages of 9 to 12 years seem reasonable for a mesopelagic fish.

2.3 Reproduction and maturity

There is little information on reproduction. Some records of gonad state in the MFish observer database suggest that females mature at about 43 cm (Francis & Griggs 2001). This would indicate that many fish taken by bottom and midwater trawl are immature, and most fish taken on tuna longlines are mature.

There is little information on reproduction and size or age at maturity in *Brama* species elsewhere, the latter point made more difficult by uncertainties in ageing (see Section 2.2). Pavlov (1994), working on *B. australis* in central and eastern South Pacific waters, suspected spawning to be geographically dispersed and to occur over an extended season.

3. METHODS

3.1 Size frequencies

Size frequency data were obtained from the Observer and Research Trawl Survey databases. Because only a general overview was required, and there were suspected identification issues (potentially three species coded as one), no breakdown by region was attempted. Trawl survey data were examined by month and quarter to determine whether this provided additional information on a mode of small fish at 30–35 cm.

3.2 Otoliths and other hard parts

3.2.1 Collection and preparation

Otoliths were taken from archived sets of otolith pairs collected opportunistically over recent years by scientific staff on research trawl surveys and by Fisheries Observers in 2003, identified only as “Ray’s bream, RBM”. Associated data included length, sex, and date. They were selected non-randomly, to cover as wide a size range of fish as possible, with some bias towards larger fish sizes to compensate for the broader range of ages and to obtain a good definition of maximum age.

Initially, 20 otoliths were photographed whole using transmitted light, and then thin sections made. Trial readings of these 20, and then a further 30 sections by two experienced readers revealed that whole otoliths could not be read (though irregular banding was present), and that thin sections were extremely difficult to interpret. Best results were obtained from the largest fish, and it was considered possible that two species were involved. Before sectioning any further otoliths (requiring their destruction) a digital image was captured of the sulcal (medial, or inner) surface of each, to record their morphology should it be discovered that two species were present.

Each otolith had an optimal sectioning line scribed with a fine pencil on to its lateral face while being viewed with polarised transmitted light under a stereomicroscope (Figure 1). This line was essentially transverse through the shortest (dorso-ventral) axis, passing through the nucleus but angled slightly to bisect a growth prism (small “bump” on the edge). Otoliths were then embedded in an epoxy mould in sets of five, with these lines aligned (after tests showed that single-section preparations had no advantage). Thin sections were cut using a dual-bladed diamond saw. After being attached to a microscope slide with a thermoplastic cement, the sliced sections were carefully ground down with petrographic papers to a thickness of 300–400 μm . The progress of the grind was periodically checked under a microscope until a banding pattern considered countable became apparent. Final lap-polishing with 1 μm alumina paste gave a defect-free surface. No cover-slip was used, but prior to reading the surface was brushed with a high-refraction immersion oil.

Two fish obtained during this study were additionally sampled for vertebrae, scales and fin rays (in lieu of spines), in addition to otoliths. The fin rays (dorsal, anal, pectoral) were also thin-sectioned after cleaning in household bleach, drying, embedding in epoxy resin and sectioned/ground as outlined above for otoliths.

3.2.2 Terminology

The main growth markings visible in otolith thin sections, and assumed to be annual, are termed **zones** in this account. They vary in appearance from the standard pattern of alternating dark and light “rings” (although they are not regular or circular), to groupings of finer dark bands (with each group comprising a zone) and with little intervening light material. Because of potential confusion over the

commonly used terms opaque, translucent, and hyaline, we use the purely descriptive terms 'dark' and 'light', referring to the appearance of the zone when viewed with light transmitted through the thin section. When clearest (in the larger fish) the dark zones are usually narrower and may represent a slow-growth (probably winter and/or spawning) period, but we are not certain of this and do not incorporate this assumption in our analysis. We found it easier and more logical to count the dark zones, and believe that if we had, with difficulty, counted the light zones our results would have been essentially the same.

3.2.3 Age determination

Scales and fin ray sections from the two additional fish were examined under a compound microscope at various magnifications. Vertebral surfaces were examined under angled transmitted light.

Otolith sections were read under a compound microscope at 100× magnification, using transmitted light. Ray's bream otoliths were unfamiliar to the two readers in this study, and initial difficulties were encountered in establishing a zone-counting protocol. Most of the first 20 sections prepared were considered almost unreadable, but three had moderate to clear countable zones. The next set of 30 otoliths provided a similar low proportion of clear otoliths, but from these 50 it was possible to determine the general nature of growth zones.

The first 50 sections were read independently by the two readers and used to determine the feasibility of an agreed age-reading protocol. Agreement was poor, Reader 2 being biased higher by about two zones than Reader 1, and with some large discrepancies in both directions; however, for the oldest (and clearest) otoliths, readings were very similar. A subset of 10 sections was then read in collaboration, with the image projected on a screen so that all features could be seen and discussed. Most sections were considered by both readers to be unclear, but agreed readings were obtained, usually closer to the initial lower reading of Reader 1. After an interval of one week these 50 sections were then re-read independently. This time there was no bias, but still some considerable differences, both between readers, and between the agreed age (when the section was viewed and discussed) and the age subsequently read.

The full set of 252 sections was then read. Reader 1 considered that blind reading (without knowledge of fish length) was too difficult and unproductive, and used fish length as an aid. (The size of each otolith section was a partial cue for both readers, but the otoliths were small and there was little apparent difference in size between those from small (30–40 cm) and medium (40–45 cm) sized fish, but a distinct difference in size and shape from the largest (46–56 cm) fish.) Reader 2 did a blind reading, and then after an interval of a few days re-read the full set also using fish length as an aid.

The readability of each otolith section was scored on a 5-point scale: 1, clear; 2, good; 3, adequate but moderate uncertainty; 4, unclear and considerable uncertainty; 5, essentially unreadable but an estimate can be made.

The two age readings of each otolith by Reader 2 were used to assess the effect of knowing the length of fish on the age estimate. The readings by Reader 1 and 2 when both knew the length of the fish at the time of ageing were used to assess between-reader bias. Bias was determined from age-bias plots, and precision from plots of the coefficient of variation of age estimates against age (Campana et al. 1995). These methods have been shown to be better at detecting reader bias, and estimating precision in the presence of bias, than other frequently used techniques (Campana et al. 1995). An index of average percentage error (APE) and mean coefficient of variation CV across all age classes were calculated to enable comparison among sets of age determinations (Campana et al. 1995):

$$APE_j = 100 \times \frac{1}{R} \sum_{i=1}^R \frac{|x_{ij} - x_j|}{x_j}$$

$$CV_j = 100 \times \frac{\sqrt{\sum_{i=1}^R \frac{(x_{ij} - x_j)^2}{R-1}}}{x_j}$$

where x_{ij} is the i th age determination of the j th fish, x_j is the mean age of the j th fish, and R is the number of times each fish is aged. When APE_j and CV_j are averaged across many fish, they become an index of average percent error and the mean coefficient of variation respectively. The CV index is numerically 1.414 times greater than the APE index.

3.2.4 Growth rate estimation

Nothing is known about the timing of spawning of Ray's bream in New Zealand. In the North Atlantic, *Brama brama* spawns over a protracted period between spring and autumn (Mead 1972). In the North Pacific, *B. japonica* also spawns over a lengthy period (Shimazaki 1989; Pearcey et al. 1993; Savinykh 1994). Similarly, nothing is known about the timing of otolith zone deposition. We therefore did not assign a theoretical birthday for ageing New Zealand Ray's bream, and we did not correct ages for the time of year during which specimens were caught. However, most fish (80%) used in this study were caught during a two-month period, 21 April – 19 June 2003.

Growth curves were fitted to the length-at-age data using the von Bertalanffy growth model:

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

where L_t is the expected length at age t years, L_∞ is the asymptotic maximum length, K is the von Bertalanffy growth constant, and t_0 is the theoretical age at zero length. Growth curves were fitted separately to the length-at-age data for each sex using non-linear regression techniques based on the Marquardt-Levenberg least squares algorithm in the graphical and statistical package SAS.

Growth curves were compared between the two sexes using likelihood ratio tests. Cerrato (1990) used Monte Carlo simulations to investigate the performance of a variety of methods (likelihood ratio test, t-test, univariate chi-squared test, and Hotelling's T^2 test) for comparing von Bertalanffy growth curves. He concluded "The likelihood ratio test is the most accurate of the procedures considered in this study and whenever possible it should be the approach of choice". Likelihood ratio tests are usually based on Kimura's (1980) maximum likelihood method of minimising the sum of least squared residuals. However, Kimura's method depends on an assumption that the residuals from the fitted von Bertalanffy curves are additive, normally distributed and have constant variance. Instead, we used a distribution-free randomisation technique, which is not constrained by the distribution pattern of the residuals. A problem occurs if the two data sets being compared have different age frequencies; e.g. one data set may have mainly old fish and the other mainly young fish. The randomisation process might result in inappropriate allocation of fish to each data set. This was overcome by selecting randomly **within age classes** (A. Dunn, NIWA, pers. comm.).

3.3 Maturity

MFish observers aboard tuna longliners recorded gonad development stages for 179 males and 180 females collected between 21 April and 29 June 2003. Nearly all these fish came from the west coast of the South Island. The gonad staging scheme used by observers is shown in Appendix 1. Unfortunately this staging scheme does not distinguish between immature and mature fish: in the non-

spawning season, the gonads of mature fish that have previously spawned and are reproductively ‘resting’ look very similar to the gonads of immature fish that are maturing for the first time. ‘Immature’ and ‘resting’ fish are combined in the observer staging scheme. Since the results indicate that Ray’s bream were not spawning in April–June (see below), separation of immature and resting fish would only have been possible if the observers had been experienced in staging Ray’s bream, but none was. Thus the combining of immature and resting stages is not likely to have affected the outcome.

Gonad development stages have also been recorded for Ray’s bream during research trawl surveys. The MFish *trawl* database has 182 gonad stage records, most of which came from Chatham Rise surveys during December–January ($N = 106$, tan0101, tan0201, tan0301) and west coast South Island trawl surveys during August–September ($N = 50$, tan9911, tan0007). These surveys used a seven-point gonad staging scheme which is similar to the observer staging scheme, except that ‘immature’ and ‘resting’ fish are separated, and ‘spent’ fish are divided into ‘partially spent’ and ‘spent’ categories.

Because none of the gonad staging detected spawning fish (see section 4.4.3), it is difficult to use the data to distinguish between immature and mature Ray’s bream. However, inferences are made below about the maturity composition of the samples from the relative proportions of the different gonad stages in the samples. For this purpose, we collapsed the seven research survey gonad stages into the same five stages used by observers.

3.4 Natural mortality

The maximum age of fish in the samples provides a measure of longevity, albeit a biased one. Actual longevity is likely to be greater than that recorded in a relatively small sample, particularly if the population has been fished. An estimate of the natural mortality coefficient, M , was obtained using a technique based on an observed empirical relationship between M and longevity (Hoenig 1983). 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 estimated the total mortality rate (Z) from the aged sample of the population using the Chapman-Robson estimator (Chapman & Robson 1960):

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

where \bar{a} is the mean age above the recruitment age and n is the sample size. Dunn et al. (1999) showed that this estimator performed better than other catch curve methods in most situations. However, in this study, our sample size was small and unlikely to be a random sample from the population.

4. RESULTS

4.1 Size frequencies

Ray's bream captured by bottom or near-bottom trawl during research surveys range from 25 cm to 57 cm, with a mode of small fish at 30–34 cm, and the main mode of large fish at 38–46 cm (Figure 2). Fish taken as bycatch on tuna longlines are on average larger, and they cover a bigger size range (20–85 cm). The mode of small fish is not apparent, and the main mode is at 43–52 cm. Males and females (not shown separately) had similar size distributions. Longlines thus appear to take the larger fish in the population (or that part of it accessible to fishing), and method-specific selectivity probably accounts for the difference in size frequencies of the trawl and longline samples.

The trawl survey data were subdivided by quarter to determine whether there was any information on growth of the 30–34 cm fish, but there was no shift in modal size.

The tuna longline bycatch size distribution has a long tail extending to 85 cm (a 135 cm record was excluded as a probable error). It is not known whether these represent only *Brama* spp., or whether they might include larger but superficially similar bramid fishes, in particular the big-scale pomfret *Taractichthys longipinnis* which is known to reach these sizes and could be mis-identified or mis-coded. When these data are subdivided by year (Figure 3), most years show the main size distribution extending to 55 cm, with very few larger fish. In 1997, there are many more fish in the size range 50–62 cm, but relatively few of the largest (65–85 cm) fish (not shown). From 1999 to 2003 there is a slight decrease in modal size and relatively more smaller fish. It is not known whether the annual variability reflects a change in the fish population or differences in fishing patterns by the tuna fleet.

The most complete and comparable sequence of trawl catches were made during Chatham Rise research surveys from 1995 to 2004 (Figure 4), comprising 65% of the total measured trawl catch. Size frequency modes vary considerably, and several interpretations – not mutually exclusive – are possible:

1. The size frequencies are random, reflecting only the relatively uniform size distribution of fish in schools or in an area.
2. The modes represent strong year classes, and some movement between years represents growth.
3. There are different species present on the Chatham Rise, with different modal sizes.

Most (80%) of the otoliths used in this study were collected from tuna longline fish captured in 2003; they therefore came from slightly smaller than average fish (see Figure 3), but were selected non-randomly from the whole sample to include as many large fish as possible.

4.2 Scales, fin rays, and vertebrae

Scales were small and narrow, and had no structural pattern that could be interpreted as growth zones.

Ray's bream have no fin spines, only soft rays. Their thin sections did have apparent growth checks, but counts were difficult and subjective, and seemed dependent on the thickness of the section. Reader 1 obtained counts of 6–7 for fish 1 with a final otolith-count of 6, and 8–12 for fish 2 with a final count of 12. Reader 2 obtained fin ray counts of 8–9 (otolith-counts 8, 12), and 9–11 (otolith-counts 10, 13) for fish 1 and 2 respectively.

Vertebral centra had poorly defined growth checks. Reader 1 obtained counts of 6–8 and 9–10 for fish 1 and 2, and Reader 2 made counts of 9 and 12, respectively.

Although there was some general similarity between the different counts they were considered unreliable and of little or no value in cross-checking the otolith counts.

4.3 Otoliths

4.3.1 Whole otoliths

Whole otoliths viewed and photographed in both transmitted and reflected light showed only an irregular pattern of banding (see Figure 1) that could not be interpreted as growth zones.

4.3.2 Otolith shape

There was considerable variation in otolith shape (see Figure 1) that was only partially dependent on fish size. Observed differences include width (otolith and rostrum), curvature of the dorsal and ventral edges, slope or angle of the posterior end, angle of the antirostrum, and extent of the sulcal groove. The latter variability is not obvious in the figure, but the groove can terminate before reaching the posterior edge or extend through it and create an indentation. Some variability seemed almost at the level that would discriminate species, but there appeared to be a continuous gradation in all characters. It was not possible to subdivide the otoliths into more than one “type”, which may indicate that this study was based on only one species, but the otolith images for 200 of the 252 otoliths have been archived in case it is necessary to re-examine them to distinguish species, or at least determine which species was involved in this study.

4.3.3 Otolith thin sections

Recognition of growth zones

Most otolith sections can only be categorised as “unclear”. Only otoliths from the largest fish, 45 cm and above, were given readability scores of 1 or 2 (good to clear). These fish had typical growth zones, with light and dark zones of equal size, or light (assumed to be fast-growth) zones wider than dark zones. Otolith sections from the smaller fish had a more compressed and almost continuous sequence of fine bands across most parts of the section, with few typical zones. Several features were used to identify and count growth zones (Figures 5, 6). In the following account “a”, “b”, etc., refer to the labels on these two figures.

There was a relatively large central core, always very dark (a), but containing one or more light zones or bands (b). These could easily be interpreted as annual growth zones, as their spacing often continued logically into the sequence of zones outside the core, but they were considered to represent checks within the first season’s growth. The size of this dark core did not seem to be influenced by section thickness, but the checks within it were more easily seen (and more confusing) in very thin sections. Determining the position of the first zone was problematic, particularly in young fish; it was sometimes assumed to be marked by an indentation in the section’s edge (c), but more often it was taken to be the edge of the dark core where it extended into the ridges either side of the sulcus (d). Its position on the long axes of the section (dorsal and ventral of the otolith) was difficult to locate, and usually determined by following a dark zone out from the sulcal region. It often extended a considerable distance along these long axes in small otoliths. In large otoliths, giving counts of 12 or more, there were typical alternating dark and light zones (e), but the relative width of light and dark zones varied considerably, and the latter usually comprised several fine bands. Growth zones were often clearest in the sulcal region (f), but were sometimes ambiguously doubled or paired (g). Most dark growth zones comprised sets of closely-spaced fine bands, with only slightly wider spaces between them (h), although the orientation of each set of bands was usually slightly different.

Recognising these as zones was, of necessity, subjective. Where these sets of bands met the edge of the sulcus they sometimes appeared to subdivide into two, with the outer bands becoming darker than the central bands (i). However, where these sets of bands met the outer edge of the section (medial otolith surface) they often became compressed into a darker area (j), which improved their recognition. The most recently formed growth zones, most clearly seen at the tips of the otolith sections (k) and at the end of the sulcal ridge projections, were often much narrower and more poorly defined than preceding zones; they comprised fewer fine bands, but were considered to represent complete rather than partial zones.

Large otoliths provided the clearest counts, and the otolith section with the highest count, 24 or 25 (good agreement between readings) is illustrated in Figure 7. Counts along the three labelled axes gave similar results, but the narrow outermost zones are difficult to see in the illustration.

Clarity of growth zones

Although the directly comparable zone counts by the two readers were made with knowledge of fish length, this was not considered to have influenced the readability score of 1–5 assigned to each section. The scores are subjective, of course, but there was close similarity in the assessments of readability made by the readers (Table 1).

Good readability was only obtained with zone counts of seven or higher. Most otoliths, particularly those with zone counts of eight or less, were assessed as unclear. Reader 1 assessed relatively more otoliths as essentially unreadable than did Reader 2, but the difference between categories four and five is highly subjective. Both readers recorded an estimated zone count from otoliths in category five, but with little confidence.

Otolith edge interpretation

The overall difficulty in distinguishing growth zones in these otoliths extended to the impossibility of determining their marginal state. The outermost growth zones were often poorly defined (see “k” in Figures 5 and 6) and at different distances from the margin on different parts of the otolith. In addition, in the younger otoliths, where the more widely spaced zones might enable one to define the marginal state, the distinction between dark and light zones was unclear (see “h” in Figure 5). In the older otoliths, dark and light zones were more distinct but they were narrowly spaced near the margin, which in combination with a shadowed edge lighting artefact, made it impossible to determine which zone was at the edge.

4.4 Otolith growth zone counts

4.4.1 Reading precision and accuracy

When both readers knew fish length, there was complete agreement in 17% of the sample, 57% agreement to within one zone, and 81% agreement to within two zones.

A comparison of the otolith zone counts made by Reader 2 when fish length was known and unknown revealed a large amount of variability: APE was 14.1% and CV was 19.9% (Figure 8A). In a review of fish ageing studies, Campana et al. (2001) found that many ageing studies are carried out with an APE less than 5.5% and a CV less than 7.6%. Our results are not directly comparable with these, because the comparison in Figure 8 is between two different ageing protocols as well as between two readings by the same reader. However, it is clear that the readings have very low precision. Much of this imprecision is due to the low readability of the otoliths. When only otoliths having readability scores 1–3 are considered, the precision improved (APE 10.3%, CV 14.6%) but was still poor (Figure 8B). Despite the poor ageing precision, there was little evidence of bias between the two readings, except for the first two age classes (1+ and 2+) (Figure 8); i.e., although age was difficult to

estimate, in general the estimates did not depend on whether the reader knew the fish length. However, knowing the length of **small** fish did affect the age estimates.

A between-reader comparison of otolith zone counts made with knowledge of fish length also produced low precision, and there was little improvement when otoliths having readability scores 4–5 were omitted (Figure 9). There was no significant bias between readers except for the first four age classes (Figure 9A), which Reader 1 aged slightly higher than Reader 2. This effect declined substantially when only otoliths with readability scores 1–3 were considered (Figure 9B). The CV for the between-reader comparison was high (40–80%) for fish less than five years old, but declined steadily to about 20% in fish older than 10 years (Figure 10).

4.4.2 Growth

The relationships between length and estimated age for the three otolith readings are shown in Figure 11. When fish length was unknown (Figure 11B), the data showed high variability, and poor conformity with the shape normally seen in fish growth curves. When fish length was known (Figure 11A, C), variability was lower and the shapes of the relationships were more plausible. Von Bertalanffy growth curves were fitted separately by sex and reader to the readings made when length was known. Restricting the data sets to otoliths with readability 1–3 had little effect on the fitted growth curves (Figure 12A, B). We therefore report parameter estimates for the full data sets (readability 1–5) in Table 2.

For both readers and sexes, t_0 was strongly negative, and the Y intercepts were highly positive (about 20 cm for Reader 1 and 30 cm for Reader 2 (Figure 11)). There are several possible reasons for this:

1. Our otolith zone counts underestimate true age (especially for young fish);
2. Fishing gears (trawl and hooks) selectively capture only the larger fish from each of the youngest age groups, biasing mean lengths upwards;
3. Fish grow very fast during the first year of life, and the lack of data for fish shorter than 30 cm means that the left-hand ends of the growth curves are poorly defined;
4. Failure to convert otolith zone counts to chronological ages using the time difference between spawning and capture resulted in underestimation of ages (any bias would be less than one year).

The growth curves generated for both readers indicate that males grow slightly longer than females (Figures 11, 12). The difference between the sexes was significant for Reader 1 ($p = 0.016$) and almost significant for Reader 2 ($p = 0.056$).

A comparison of the growth curves between the two readers showed that they were very similar over most of the age and length range, but diverged for fish aged less than five years (Figure 12C). The difference was apparent for both sexes, and is a result of Reader 1 ageing young fish slightly older than Reader 2 (Reader 1 had no 1+ fish whereas Reader 2 had several; Figure 11). The growth curves of Reader 1 seem more plausible because of their smaller intercepts on the Y-axis; thus we recommend that the growth parameters for Reader 1 shown in Table 2 be used to model growth in this species. The parameter correlation matrix for Reader 1 is shown in Table 3.

4.4.3 Maturity

The size range of Ray's bream caught by the tuna longline fishery was well represented in the gonad stage data collected by observers (compare Figures 2 and 13). Most fish were staged as immature/resting, or maturing, with a higher proportion of the former present for males than for females (Figure 13). A subsample of the fish measured and staged by observers was also aged by us. For males, immature/resting and maturing fish were spread throughout the age range of 4–25 years

(Figure 14). For females, immature/resting fish were most common at ages 3–6; older fish were mainly maturing. Since most fish sampled were at the upper end of the size range for Ray's bream, we suggest that most of these fish were mature, though reproductively inactive. However, some of the smaller, 3–6 year-old fish may have been immature.

Ray's bream caught during trawl surveys and staged for gonad development were mostly in the length range 35–50 cm (Figure 15), which represents fish in the larger length mode (see Figure 2). All fish from the Chatham Rise in December–January were immature/resting or maturing, with a higher proportion of the latter for females than for males (Figure 15). Inspection of the original gonad stages recorded on a seven-point scale showed that all the immature/resting fish were in fact resting rather than immature. Maturing females as small as 36 cm were present.

Fifty fish sampled from the west coast South Island in August–September trawl surveys were also mainly immature/resting or maturing. Only three fish were recorded as ripe.

In the absence of fish in or near spawning condition, it is not possible to make definitive statements about length or age at maturity. Most fish above 35 cm or about 2 years old were resting or maturing, though it is not known what proportion of the latter were maturing for the first time. It appears that fish longer than about 40 cm and older than about 5 years are mature, but the length and age at which half of the fish reach maturity may be lower than these values.

4.4.4 Natural mortality

Using a longevity estimate of 25 years, Hoenig's (1983) regression method produced an M estimate of 0.17. However, considering the relatively small sample size and the possible effect of fishing on the stock, true longevity may be greater than 25 years, and M may have been over-estimated.

Ray's bream recruit to the trawl fishery at a fork length of 25–30 cm (see Figure 2), corresponding to an age of 2–3 years. Using an age at recruitment of 2–5 years, the Chapman-Robson estimator produced estimates of Z of 0.11–0.12. If these are valid estimates of Z , then M would be less than or equal to 0.12. However, the aged sample used to estimate Z was small and not representative of the catch or the population (otoliths were selected from relatively more large fish).

A plausible estimate of M for Ray's bream, taking into account both the above results, is 0.10–0.15.

4.4.5 Age structure of the commercial catch

Because our growth curve is not well defined at the lower end, it is only possible to estimate that the trawl catch will be based mainly on 4 to 11 year old fish (assuming that commercial trawlers catch fish of a similar size range to research trawlers), and the bycatch in the tuna longline fishery will be based mainly on 5 to 11 year old fish. However, the relatively flat growth curve means that length composition is not a good predictor of age composition for fish over about 5 years old.

5. DISCUSSION

Hard parts, general

Although only a brief examination could be made of scales and hard skeletal parts during this study, it appeared unlikely that they would add to the information contained in otoliths. The latter, however, were very unclear for the youngest fish in the sample examined, and there is some difficulty in determining the position of the first annual zone at or near the edge of the very dark central core.

Further investigation of another hard structure with markings representing early growth might clarify this.

Otolith readability

Both readers found most otolith thin sections from this species difficult to interpret, and gave low readability scores to a high proportion (51 to 57%) of the sample of 252 fish. Despite low reading precision, there was no detectable bias between readers except for the youngest age classes for which only a few, very ambiguous otoliths were available. Despite this, both readers remain cautious; they consider that although they could recognise and count the same patterns within the otoliths, these were often not typical growth zones, and the counts can only be considered to be unvalidated ages.

The between-reader comparison was based on known-length readings. The unknown-length readings by Reader 2 were not completely blind, in that some indication of fish size was available from the size and shape of the otolith section; this was more obvious for the largest fish in the sample, which had conspicuously broad otolith sections, than for the small (but not smallest) fish. These blind readings were judged too unreliable, in this first ageing study of the New Zealand species of *Brama*, to provide data for a sensible growth curve. The known-length readings are considered the best estimates of age at this time. Future work will need to take into better account the issue of low otolith readability when establishing an ageing protocol. We cannot define a protocol at this time.

Early growth extrapolated from the growth curve

The lower end of the growth curve is poorly defined. The von Bertalanffy curve derived from Reader 1’s counts appears more plausible, but it still intersects the x-axis at a negative value. In part, this results from the growth curve being based on counts (estimated whole ages) rather than ages adjusted for additional growth after the time of formation of the last counted ring. Each fish could be up to one year older than the recorded count. Estimates of the growth rate of young fish can be made using two “extreme” scenarios. If the zone counts of Reader 1 are increased by one year, then fish grow to about 30 cm in three years, giving a mean growth rate of 10 cm per year. If the zone counts of Reader 2 are not corrected for capture date, then fish reach about 30 cm in one year, giving a mean growth rate of 30 cm per year. Both scenarios indicate rapid initial growth, which is consistent with general statements in most of the published accounts of the growth of *Brama* species. However, most of these accounts are based on poorly-described otolith interpretations, although Rodriguez (1980) does present extensive length frequency data which clearly show rapid modal growth of *B. brama* from 33 cm to 41 cm in 12 months, which he somewhat ambiguously interprets as growth in the second year.

General comparison with previous age and growth studies

The growth curves derived in this study are not greatly dissimilar to that of Lobo & Erzini (2001) for *Brama brama*, though their lengths at age are lower at ages less than about seven, and their data extend only to 12 years. Other studies on *Brama* spp. (e.g., Pavlov (1994) on *B. australis*) suggest much faster growth and lower maximum ages, but it is difficult to assess the reliability of these studies from the information presented. Although “lengths at age” are not listed or plotted in a comparable way between these two studies and the present one, approximate values from the three studies (sexes combined) are given below.

	Length (cm) for age groups:											
	1	2	3	4	5	6	7	8	9	10	11	12
Lobo & Erzini			33	36	39	41	44	46	48	50	52	54
Pavlov	15	24	29	33	42	44						
This study	32	36	40	43	45	46	47	48	48	49	49	50

Note: Lengths for age groups 1–4 from the present study are considered inaccurate (too high) because of small sample size, gear selectivity, and difficulties in otolith interpretation.

Maturity

Length and age at maturity could not be adequately estimated because maturity data for ripening and running ripe fish were not available. If fish in spawning condition had been sampled, the gonad development stages recorded by observers and on research surveys would have been interpretable as maturity indicators. It is surprising that although staged samples were available from winter (west coast South Island trawl survey), summer (Chatham Rise) and autumn (west coast South Island longline fishery), ripe fish were virtually absent. This differs from literature reports that *Brama brama* from the North Atlantic spawn over a protracted period between spring and autumn (Mead 1972), and North Pacific *brama japonica* also have a lengthy spawning period (Shimazaki 1989, Pearcey et al. 1993, Savinykh 1994). Those species appear to prefer subtropical waters over 19.5 °C for spawning, so perhaps New Zealand Ray's bream spawn in waters further north than those sampled so far. Clearly, identification of the location and timing of spawning are important areas of further research and are a pre-requisite for obtaining good estimates of length and age at maturity.

Fisheries Implications

The results indicate that Rays bream are initially fast-growing and probably mature early, consequently most of the commercial catch is of adult fish. With a maximum age of 25 years, there are potentially many age classes in the recruited population, although our sample showed most of the exploited fish were aged 4 to 11. Length frequency data from the Chatham Rise suggest there may be some variability in year class strength, which – with year-to-year differences in the movement of Ray's bream on to fishing grounds – will result in variability in commercial catch rates and size composition. The overall productivity of the Ray's bream (one or more species) most commonly taken in New Zealand waters remains uncertain. The features of rapid early growth, early maturity, the stock comprising a moderate number of year classes, and a probably wide distribution in offshore waters (see map in Bagley et al. 2000), indicate good productivity. However, estimates of *M* determined from maximum age are low, suggesting relatively low productivity.

Remaining uncertainties

Ageing problems Our difficulty in recognising a growth zone pattern in the otoliths that could be assumed as annual was not caused by the usual problem of distinguishing between “checks” and “true zones”, but by the variety of otolith markings – from distinct dark and light zones to sets of fine dark lines – that appeared to represent an annual growth cycle. The sets of fine lines that predominated in the otoliths of younger fish are similar to those we have observed in the otoliths of other fish species which inhabit moderately deep water, and there is an obvious need to determine what they represent. Is the lack of clarity related to migratory behaviour – the fish moving with water masses rather than remaining within water with a strong seasonal temperature signal? But if so, why should the oldest otoliths be relatively clear? The large central zone, which we have interpreted as representing only 0+ growth despite the presence of quite clear banding within it, is also a puzzle. Does it really signify very fast early growth, perhaps as a consequence of juveniles inhabiting productive near-surface waters?

Species identification Two very similar species of *Brama* occur off New Zealand, plus the similar-sized *Xenobrama*. We believe that our sample of otoliths came mainly or wholly from one species, probably *B. australis*, but better identification guides are required so that future otolith collections taken at sea can be correctly attributed to species. The proportion of each species in the commercial catch (by tuna vessels and trawlers) needs to be determined. The three species may have sufficiently similar biological parameters to be managed as one “stock”, or there may be important differences that are masked by combining the data. We found no obvious visible evidence for more than one age/length relationship, i.e., the growth curve was estimated with no large outliers. However, it is possible that the oldest and clearest otoliths came from a second species, i.e., different species of

Brama (and *Xenobrama*) have different maximum ages. We could not detect any consistent difference in otolith morphology between the smallest and largest fish in our sample.

The maximum age we obtained is dependent on the age composition of fish in the otolith sample available to us. The largest fish in the sample, at 56 cm, approximates the upper limit of the main size mode of fish measured as “Ray’s bream”, with a much smaller number of fish extending to 85 cm. If these are the same species, and given the relatively flat growth curve estimated, the maximum age will almost certainly be much greater than the 24 or 25 years we obtained. *Brama* spp. are known or suspected to migrate for spawning, and because relatively few New Zealand fish have been recorded as ripe it is possible that the largest mature individuals are seldom caught by the fisheries we sampled. Alternatively, the 60 to 85 cm fish recorded as “Ray’s bream” might be the larger bramid *Taractichthys longipinnis*. The true identity of fish larger than 65 cm needs investigation.

6. ACKNOWLEDGMENTS

We thank the fisheries observers and the scientific staff who measured Ray’s bream and collected otoliths during sea trips. We acknowledge the assistance of Lynda Griggs in collating and providing the observers’ data and otoliths. Andrew Stewart of the Museum of New Zealand provided useful information on the probable identity of our Ray’s bream sample. We are grateful to Nick Davies, NIWA, for his constructive review of our manuscript. This project was funded by the Ministry of Fisheries under project code TUN2003/01.

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Table 1: Relationship between fish “age” (zone count) and readability score for the 252 otolith sections, when fish lengths were known but otoliths read randomly by size.

Zone count ²	Reader 1 Readability score ¹					Reader 2 Readability score ¹				
	1	2	3	4	5	1	2	3	4	5
1								3	3	
2				7				1	5	
3			2	3	1				4	
4			4	15	3			4	13	
5			22	33	4			6	26	
6			17	27	6			9	28	2
7		1	3	8	1		1	16	30	1
8		3	4	7	4		1	7	17	
9	2	3	9	3			1	11	5	
10		4	5	1			1	9	7	
11	1	4	4	1		1	5	5	2	
12	1		3			1	2	2		
13	2	8		2			2	4		
14		6		1		1	2	2		
15	1	3	1			2	4		1	
15+	2	7	1			2	3			
Totals	9	39	75	108	21	7	22	79	141	3

Notes:

1. Readability scores: 1, clear; 2, good; 3, adequate but moderate uncertainty; 4, unclear and considerable uncertainty; 5, essentially unreadable but a guesstimate can be made.

2. Zone count, not age. Unvalidated ages, based on these counts would be up to one year greater, although it was not possible to assess the marginal status of the otoliths, or establish a realistic birth-date from reproductive information.

Table 2. Ray’s bream growth curve parameters by reader and sex. All curves were from readings in which fish length was known. One 64 cm male outlier was omitted from the fitted curves. SE, standard error; R₁, Reader 1; R₂, Reader 2. We recommend that the growth parameters for Reader 1 be used to model growth in this species.

Otolith reading	Sex	Sample size	$L_{\infty} \pm SE$ (cm)	$K \pm SE$	$t_0 \pm SE$ (years)
R ₁	Male	119	52.29 ± 0.59	0.226 ± 0.022	-2.44 ± 0.53
R ₁	Female	130	49.60 ± 0.46	0.282 ± 0.024	-1.80 ± 0.39
R ₂	Male	119	54.10 ± 1.76	0.135 ± 0.027	-6.38 ± 1.50
R ₂	Female	130	49.19 ± 0.94	0.222 ± 0.035	-4.03 ± 0.86

Table 3. Correlation matrices for the Von Bertalanffy growth parameters for Reader 1 (see Table 2).

	L_{∞}	K	t_0
Males			
L_{∞}	1.0000	-0.8246	-0.6498
K	-0.8246	1.0000	0.9529
t_0	-0.6498	0.9529	1.0000
Females			
L_{∞}	1.0000	-0.8405	-0.6683
K	-0.8405	1.0000	0.9515
t_0	-0.6683	0.9515	1.0000

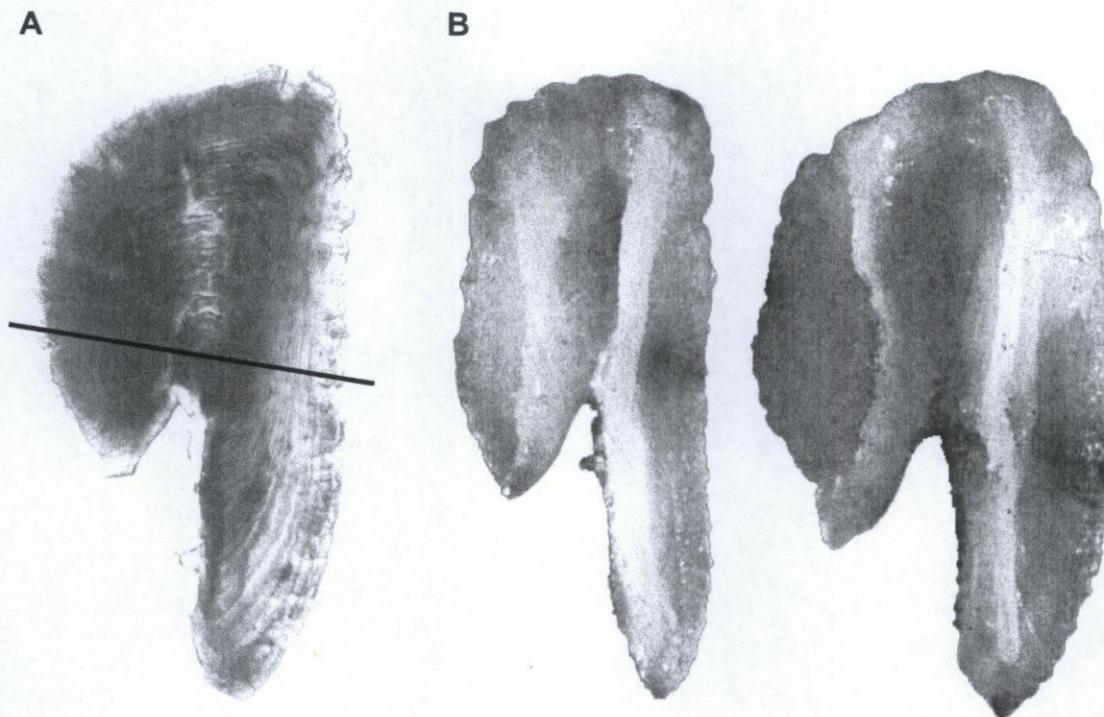


Figure 1: Ray's bream otoliths, illustrated here anterior (rostral) end downwards. A, distal (lateral) surface of an otolith viewed by transmitted light, 46 cm female. A generalised pattern of dark and light zones is apparent, but they cannot be resolved into the 8 or 9 zones counted by both readers in a thin cross section. This was among the clearest of the subsample of 24 otoliths viewed whole. The line marks the orientation of the transverse thin section. B, medial (inner) surface of two otoliths viewed in reflected light, illustrating differences in robustness and shape; shown here at the same scale. Left, 52 cm male; right, 53 cm male.

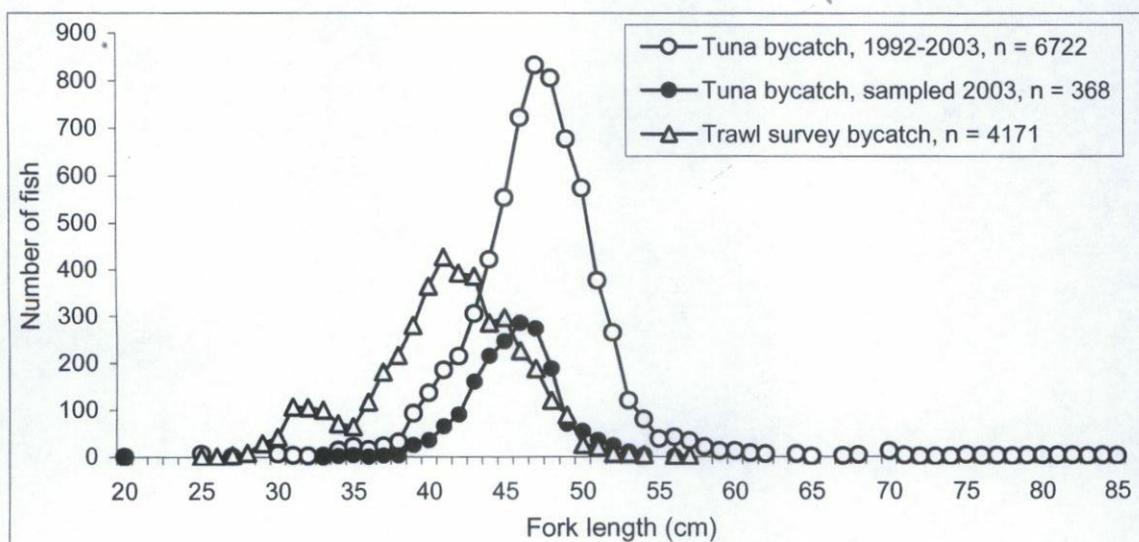


Figure 2: Size frequency of Ray's bream taken in New Zealand by the trawl fishery (research survey data) and the tuna longline fishery (observer data). The trawl catch data are from all available years (1995–2003). The tuna bycatch data for all available years (1992–2003), and for 2003, the year for which otoliths were available.

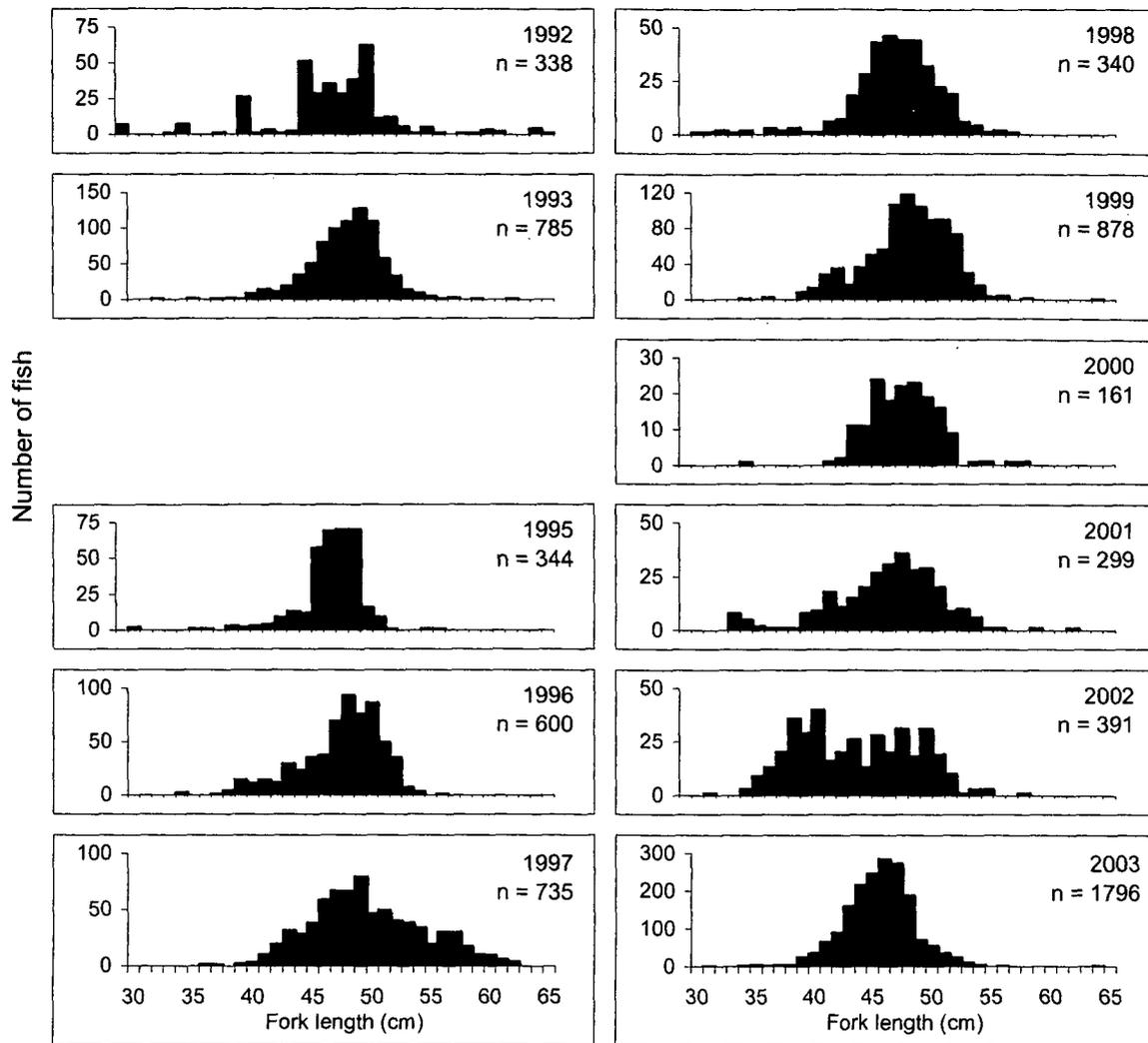


Figure 3: Size frequency of Ray's bream taken in New Zealand by the tuna longline fishery (observer data), by year. Note: no fish were measured in 1994.

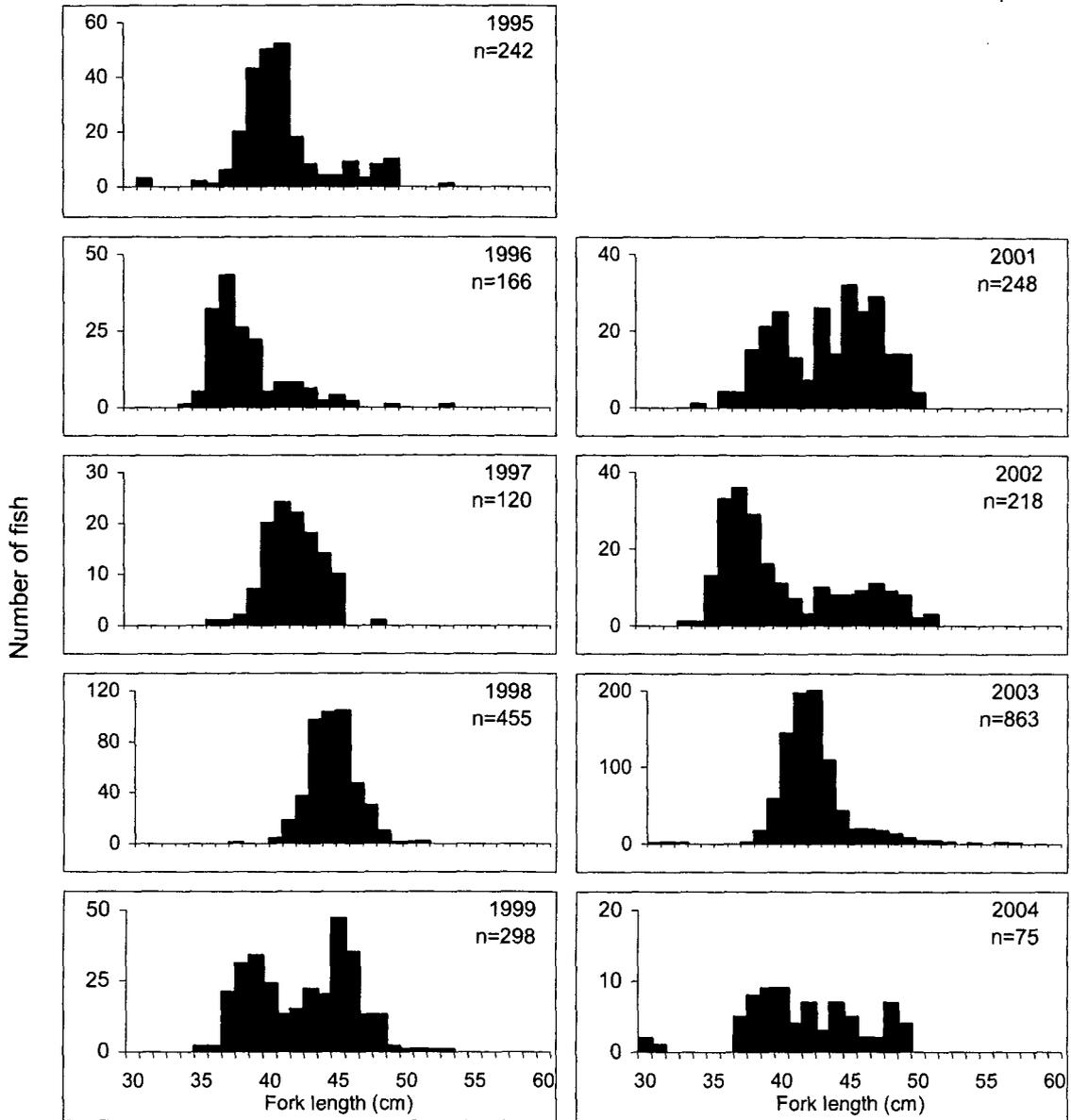


Figure 4: Size frequency of Ray's bream taken on Chatham Rise January research trawl surveys, by year. Note: no fish were measured in 2000 (n = 34).

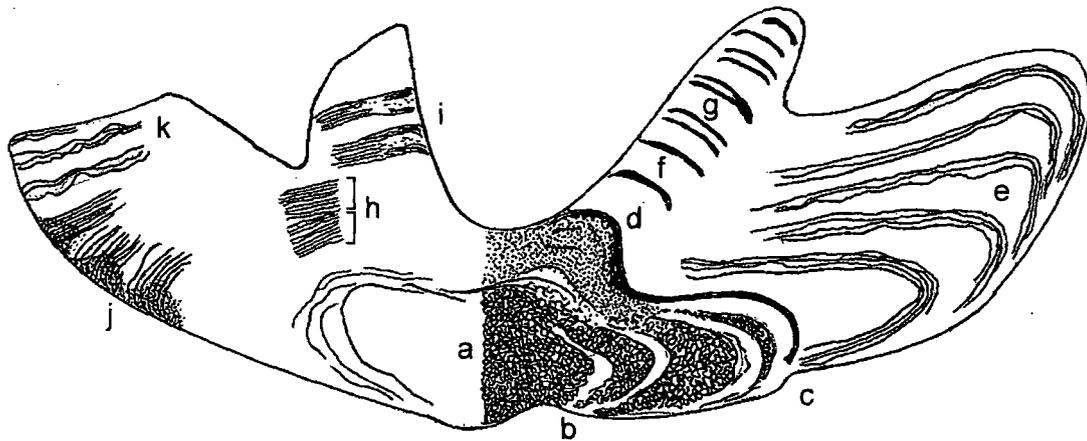


Figure 5: Diagram of a Ray's bream otolith thin cross-section, as viewed by transmitted light, illustrating the features used to identify and count growth zones (only some of these features would be visible in each otolith).

a, large dark central core region.

b, light banding within the core region, often alternating with dark banding in a pattern similar to that usually interpreted as annual zones.

c, the outer limit of the dark core was sometimes associated with a marginal indentation.

d, in the sulcal region the dark core was often considerably expanded.

e, in clear otolith sections, relatively narrow dark zones (comprising several fine lines) alternated with broader light zones.

f, narrow dark zones were often present in the sulcal region, but

g, were sometimes split or paired.

h, in most otoliths, growth zones comprised sets of fine lines, were closely spaced, and recognised by (i) slightly greater spacing between each set, (ii) slightly different orientation of each set, and (iii) colour variation between sets; two sets (zones) are illustrated.

i, in the sulcal region, sets of lines (= zones) were sometimes split into darker pairs but were counted as a single unit.

j, at the section's margin, sets of lines (= zones) were sometimes associated with dark areas.

k, the outermost growth zones in most otoliths were sometimes narrow, irregular, and poorly defined; grouping of the fine lines into zones here was problematic.

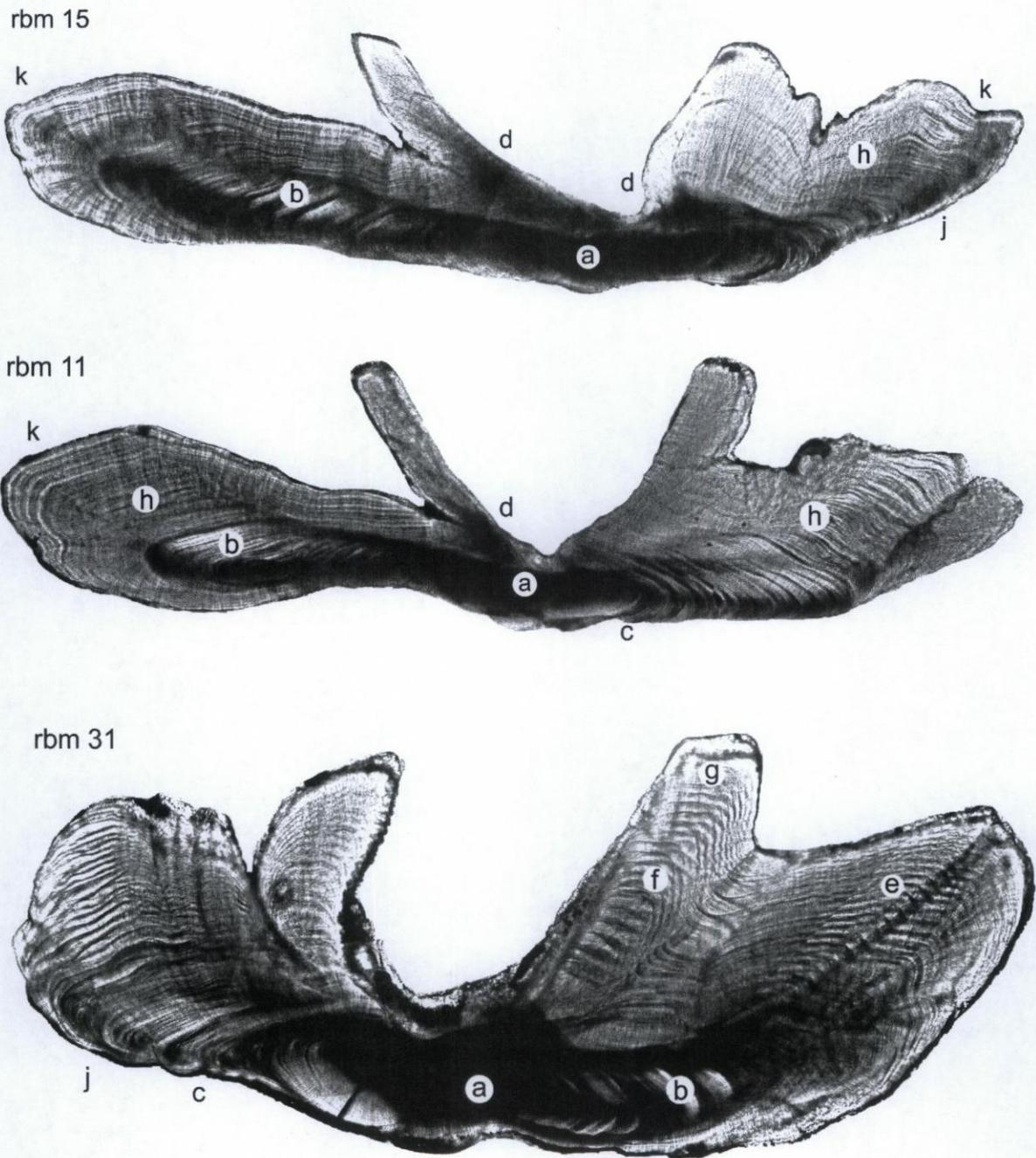


Figure 6: Otolith thin cross-sections, as viewed by transmitted light, demonstrating the increasing clarity of growth zones with increasing fish size. Top, 41 cm male, aged as 6. Centre, 45 cm male, aged as either 9 or 11. Bottom, 54 cm male, aged as either 24 or 25. Labels "a" to "k" refer to the features shown diagrammatically in Figure 5.

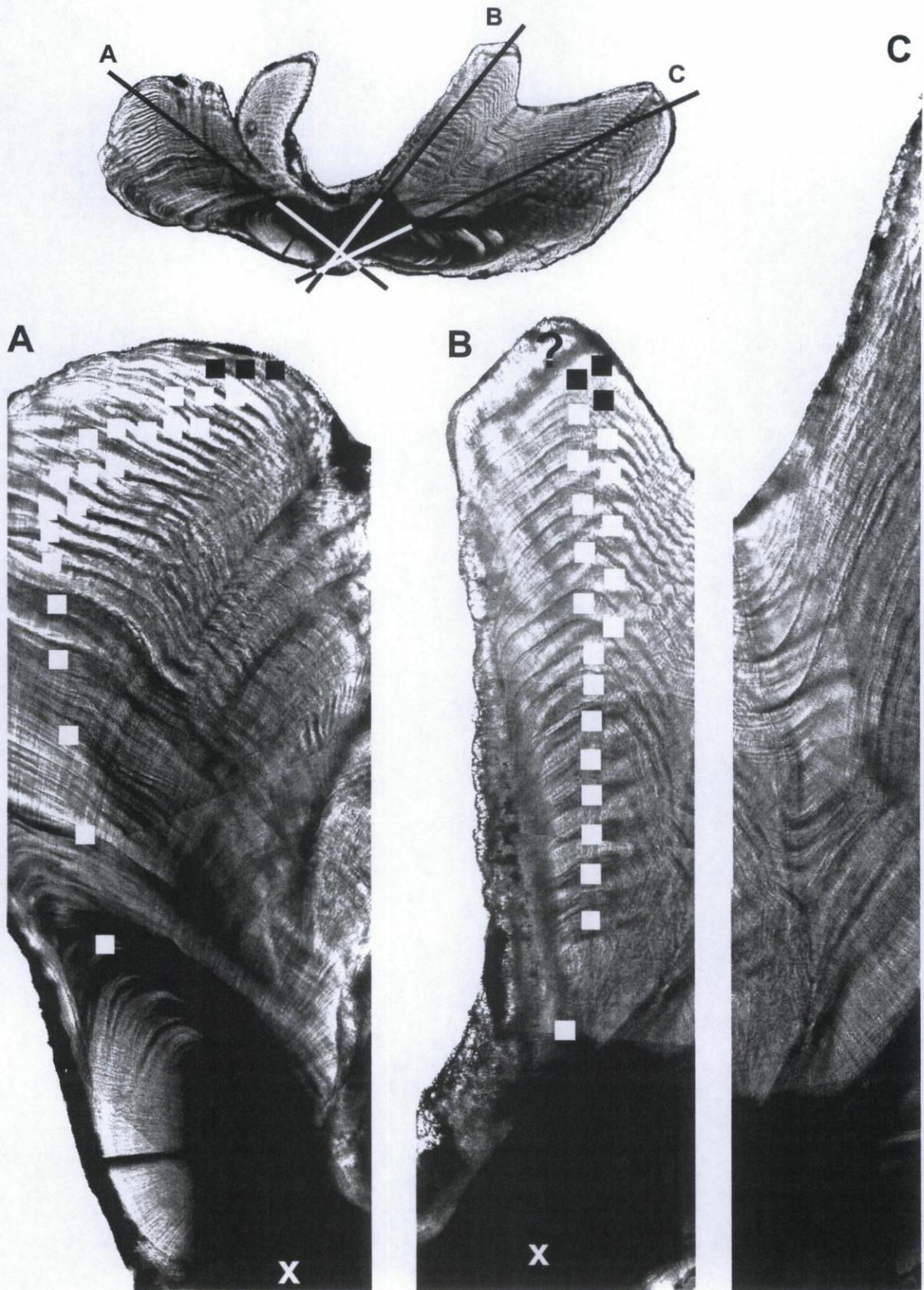


Figure 7: Enlargements of the three areas of an otolith from a large Ray's bream (rbm 31, thin section) illustrating the growth zones (marked as white or black squares) counted along three axes. The centre (focus) of the otolith is marked "x". The fish was a 54 cm male, aged as either 24 or 25 years. The outermost few growth zones are difficult to distinguish at this magnification.

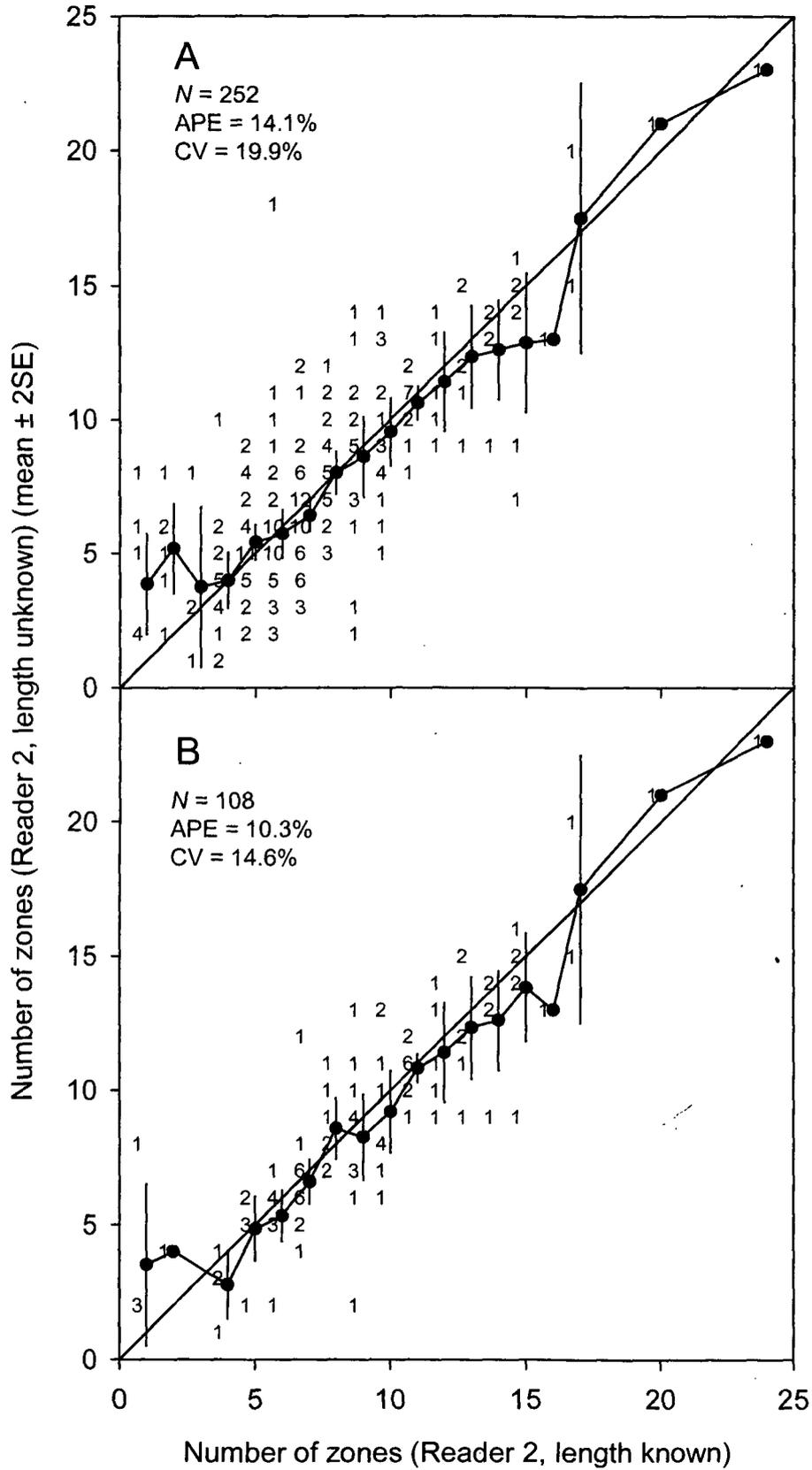


Figure 8: Within-reader comparison of otolith zone counts for Ray's bream. Mean count of Reader 2 (\pm 2 standard errors) when fish length was unknown relative to the counts when fish length was known. (A) All otoliths (readability 1–5). (B) Subset of clearer otoliths (readability 1–3). Diagonal lines indicate the expected relationship. Numbers represent number of fish (offset by -0.25 zones for clarity). *N*, total sample size; APE, average percentage error; CV, coefficient of variation.

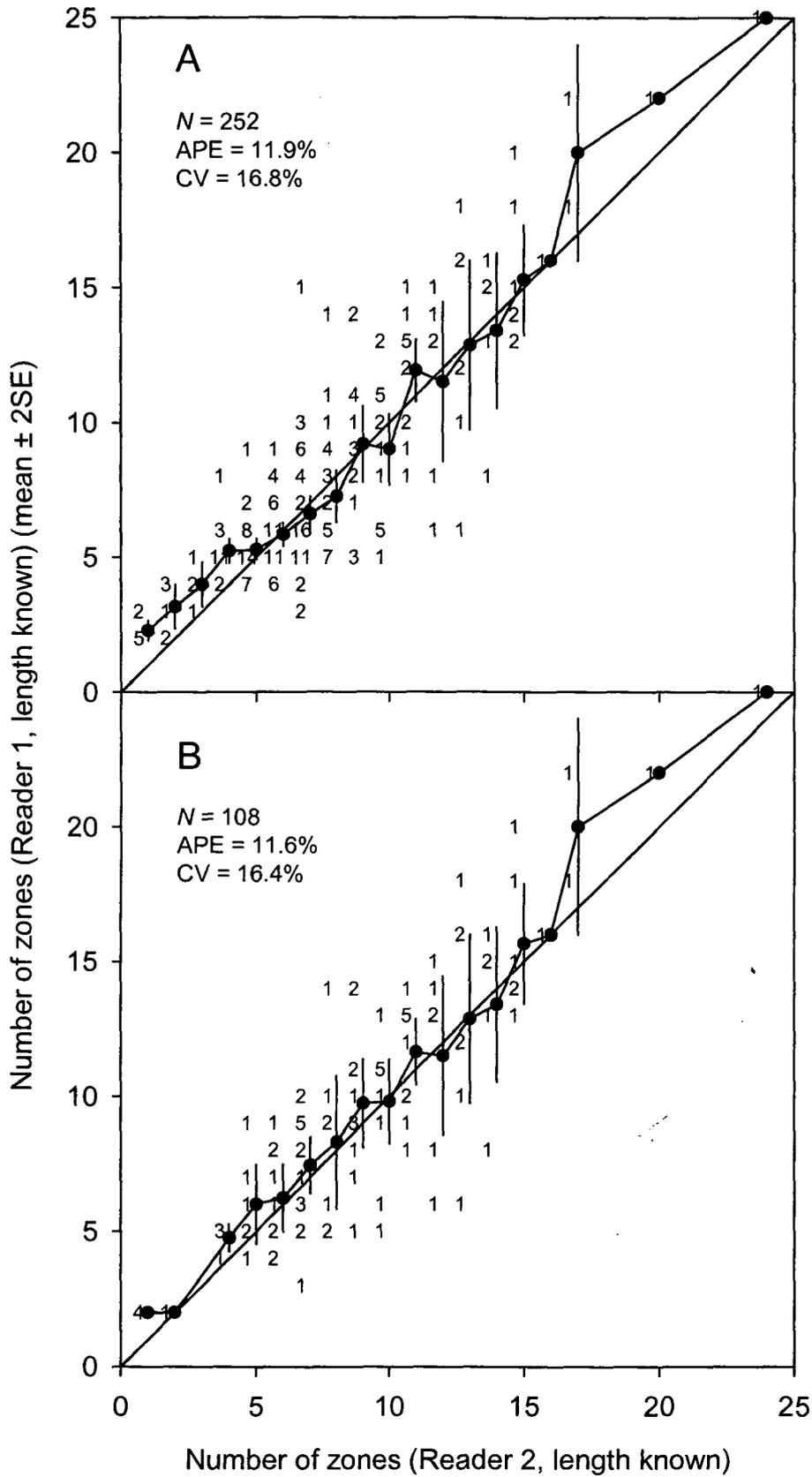


Figure 9: Between-reader comparison of otolith zone counts for Ray's bream when fish length was known. Mean count of Reader 1 (\pm 2 standard errors) relative to the count of Reader 2. (A) All otoliths (readability 1–5). (B) Subset of clearer otoliths (readability 1–3). Diagonal lines indicate the expected relationship. Numbers represent number of fish (offset by -0.25 zones for clarity). N , total sample size; APE, average percentage error; CV, coefficient of variation.

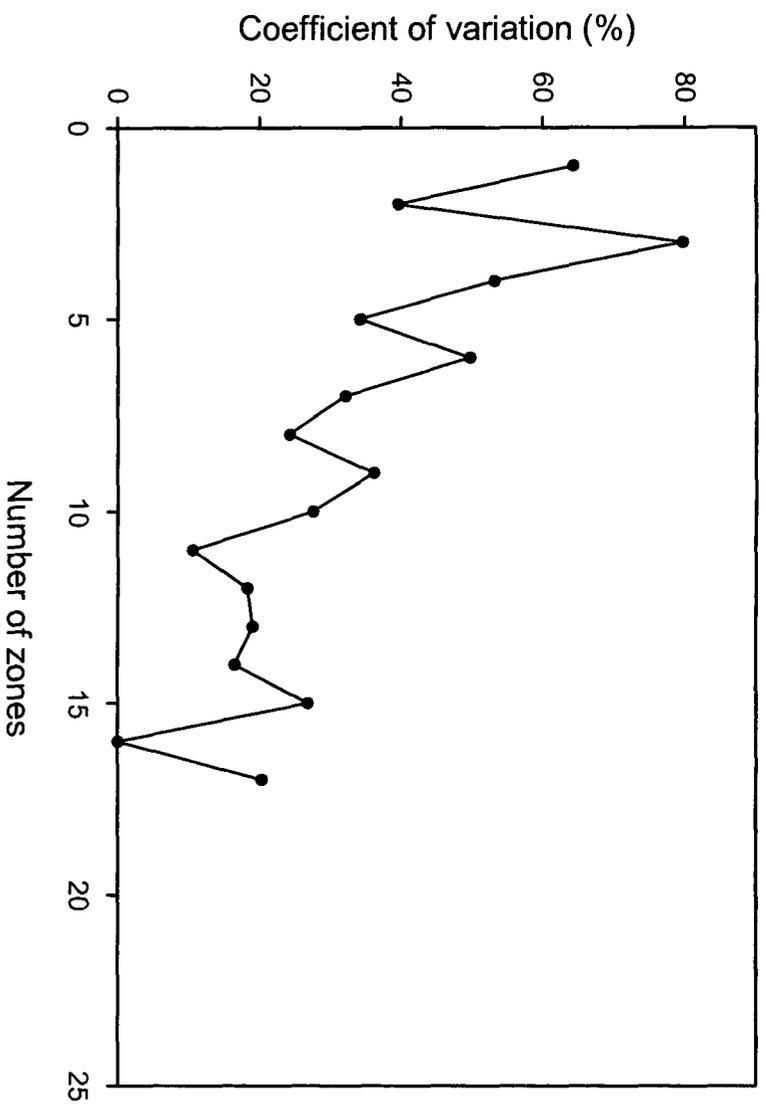


Figure 10. Mean coefficient of variation by age class for the between-reader otolith comparison.

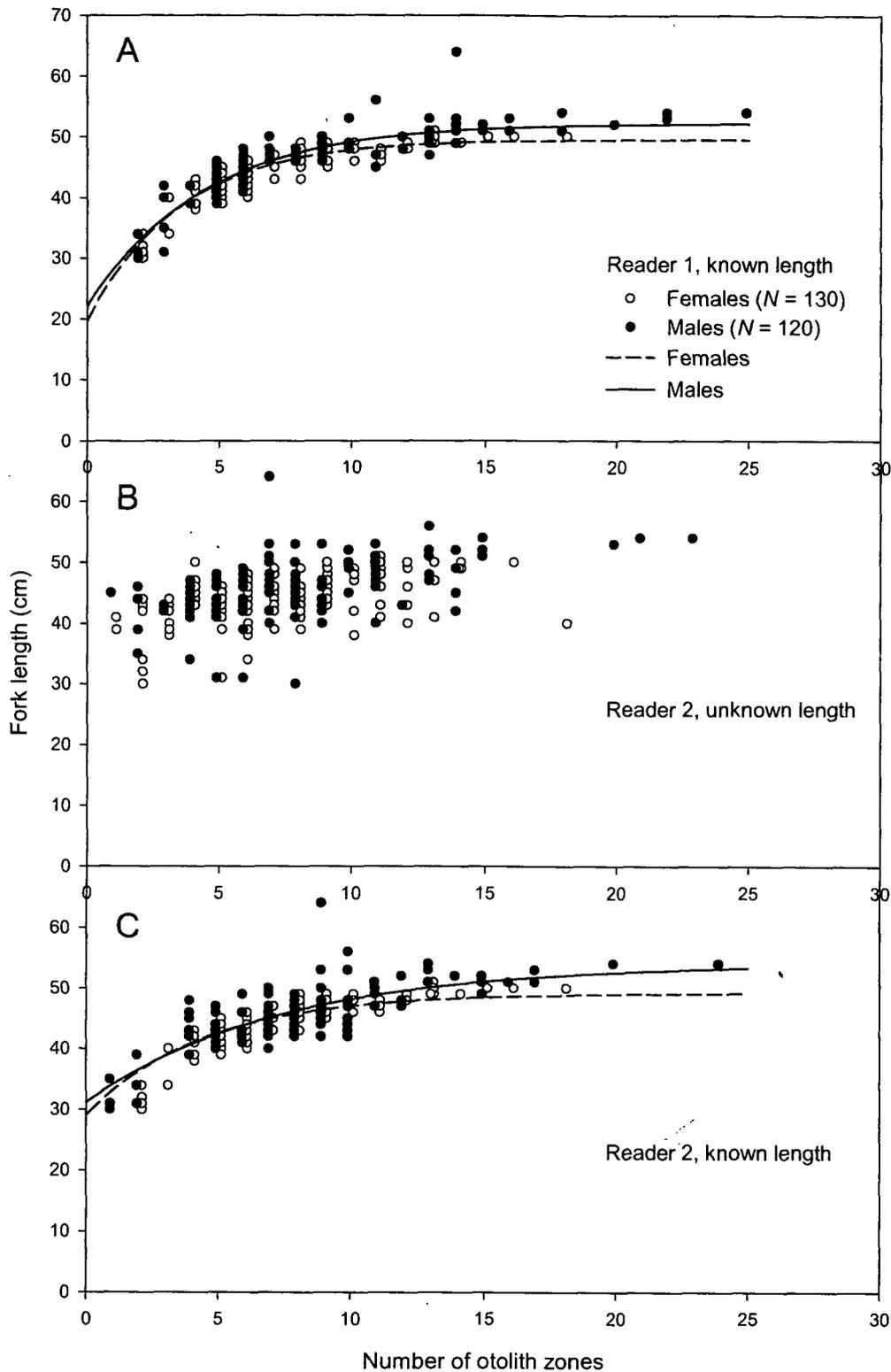


Figure 11: Ray's bream length-at-age relationships for two readers based on otolith zone counts made with and without information on fish length. Male and female data points are offset slightly from the axis ticks for clarity. One length outlier (64 cm male) was omitted from the fitted curves. N , sample size.

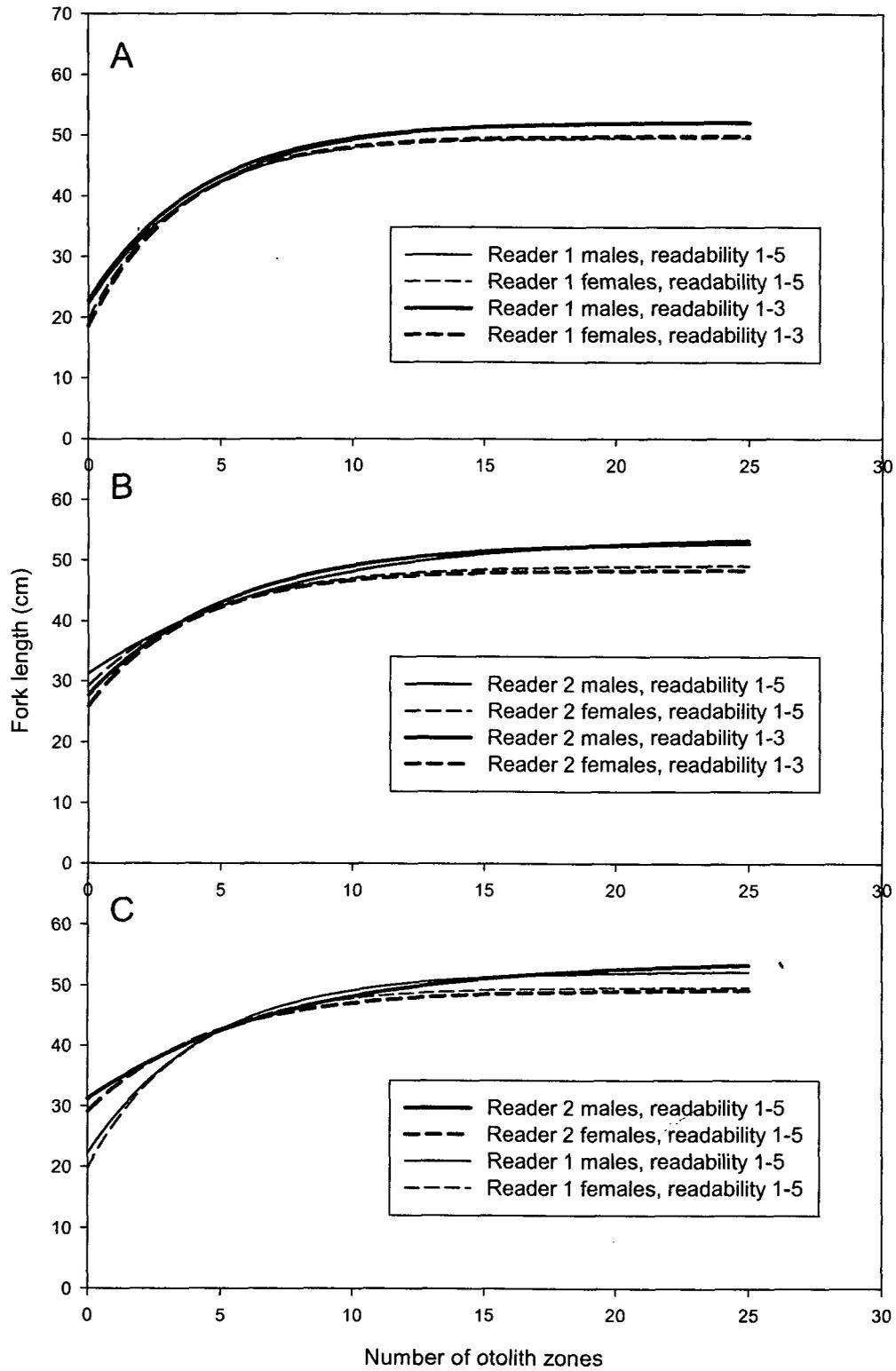


Figure 12: Ray's bream length-at-age relationships for two readers based on otolith zone counts made with information on fish length.

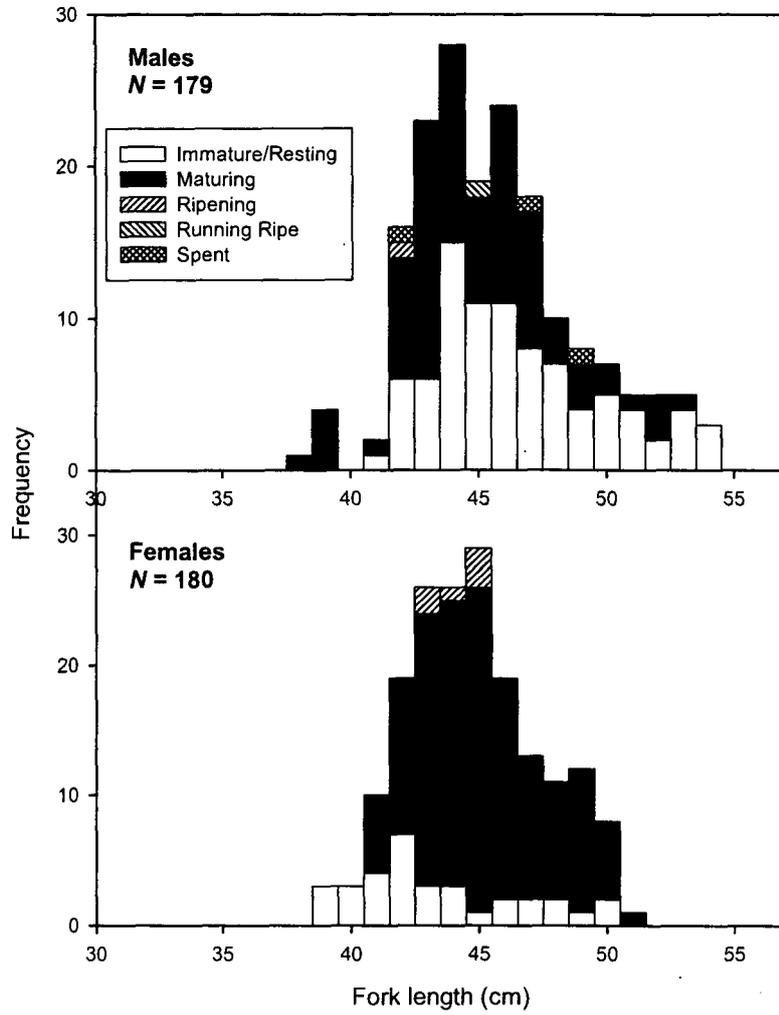


Figure 13. Relationship between gonad development stage and fork length for male and female Ray's bream sampled from tuna longline vessels in April–June 2003. Gonad staging scheme is shown in Appendix 1. *N*, sample size.

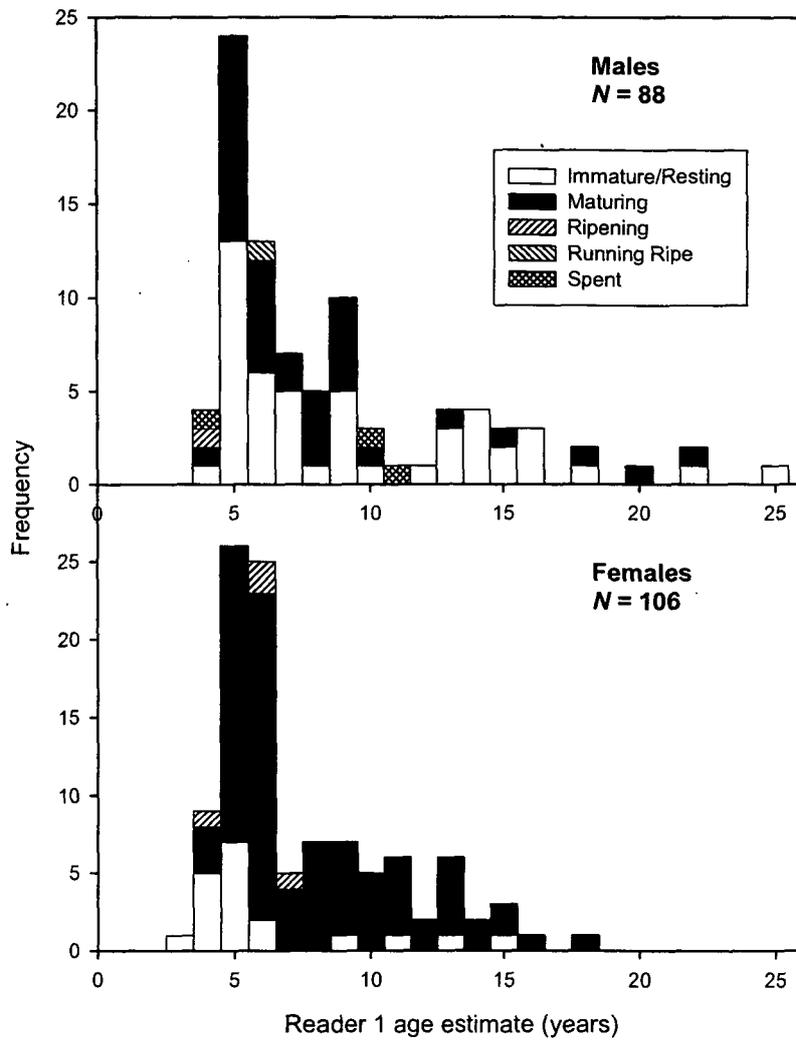


Figure 14. Relationship between gonad development stage and estimated age for male and female Ray's bream sampled from tuna longline vessels in April-June 2003. Gonad staging scheme is shown in Appendix 1. N, sample size.

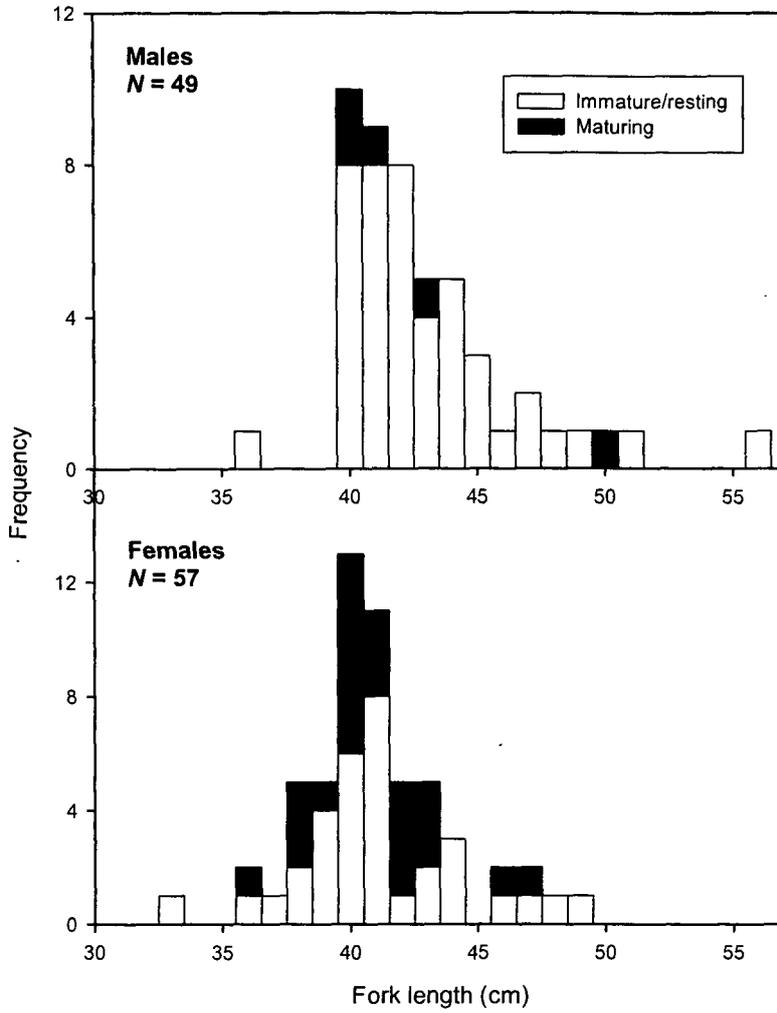


Figure 15. Relationship between gonad development stage and fork length for male and female Ray's bream sampled from Chatham Rise research trawl surveys in December–January 2000–01 to 2002–03. Gonad staging scheme is shown in Appendix 1. N, sample size.

Appendix 1. Gonad staging scheme used for Ray's bream by observers on tuna longline vessels

Stage	Description	Males	Females
1	Immature/resting	Testis small, thin (ribbon-like), translucent, colourless	Ovary translucent or pink, small with no eggs visible; can occur in both small and large fish
2	Maturing	Testis becoming swollen, translucent creamy white (though blood vessels may give it an overall pinkish appearance), narrow and angular, milt not expressible from ducts when cut	Eggs visible, opaque/coloured, but not hyaline (clear); ovaries can get quite large and solid in this stage; colour will vary between species, but maturing ovaries are generally creamy white to orange; if held up to the light or cut, a small ovary thought initially to be Stage 1 may show some developing eggs: it is then to be classed as Stage 2
3	Ripening	Testis large, pink-white, milt expressible when cut and squeezed	Ovary large and firm; clear eggs are present (more than just one or two); the ovary can appear quite mottled with clear eggs interspersed with the opaque maturing eggs
4	Running ripe	Testis large, white or bloodshot, milt flows freely with slight external pressure	Ovary large, thin-walled and fragile; large clear eggs flow out freely, or are obvious in large numbers when the ovary is cut
5	Spent	Testis appears shrivelled, thin, hardened, and bloodshot. Milt may still flow from collecting duct when cut and squeezed	Ovary flaccid and bloody, size much reduced from Stage 4; some residual large clear or opaque eggs may still be present