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Age, growth, maturity, and mortality of rough and smooth skates (*Dipturus nasutus* and *D. innominatus*)

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EXECUTIVE SUMMARY

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Rough and smooth skates were aged by counting growth bands on X-rays of thick vertebral sections. Initial band counts by each of two readers showed poor precision (coefficient of variation = 18–20%) but no between-reader bias. During a second joint count, both readers agreed on a final age for most sections (2–3% were unreadable). The age estimates have not been validated.

For rough skates, the greatest estimated age was 9 years for a 70 cm pelvic length female, but few were more than 6 years old. Females may live longer than males. Growth rates were not tested for differences between the sexes because of small sample sizes, but there were no apparent differences. The combined sexes von Bertalanffy growth curve was $L_t = 91.3\ (1 - e^{-0.16[t + 1.20]})$. Males reached 50% maturity at about 52 cm and 4 years, and females at 59 cm and 6 years. The most plausible estimate of *M* was 0.25–0.35.

For smooth skates, the greatest estimated age was 24 years for a 133 cm long female, but because they grow to at least 158 cm, longevity probably exceeds that. Females appear to live longer than males. Growth rates were not tested for differences between the sexes because of small sample sizes, but there were no apparent differences. The combined sexes von Bertalanffy growth curve was $L_t = 150.5\ (1 - e^{-0.095[t + 1.06]})$. Males reached 50% maturity at about 93 cm and 8 years, and females at 112 cm and 13 years. However, the small sample size of mature animals, particularly females, meant that the maturity ogives were poorly defined. The most plausible estimate of *M* was 0.10–0.20.

1. INTRODUCTION

Rough and smooth skates (*Dipturus nasutus* (Banks, 1841) and *D. innominatus* (Garrick and Paul 1974), formerly classified in the genus *Raja*) are endemic to New Zealand. They range throughout mainland New Zealand, the Challenger Plateau, Chatham Rise, Campbell Plateau, and Bounty Plateau, but have not been recorded from the Kermadec Islands (Francis 1997, Anderson et al. 1998). Trawl survey records indicate that both species have similar depth distributions (range about 10–1450 m; mean depth 370 m for rough skate and 412 m for smooth skate), but some of the deeper records of rough skate are thought to be mis-identifications of smooth skate (Francis 1997, Anderson et al. 1998). Both species are most abundant on the continental shelf, and are rare in depths greater than 700 m (Anderson et al. 1998, Beentjes & Stevenson 2000, Stevenson & Hanchet 2000).

Rough and smooth skates are both fished commercially, with about 60% of recent landings coming from the east coast of the South Island (QMA 3); most of the rest is taken from the remainder of the South Island and Subantarctic (QMAs 5–7) (Francis 1997, 1998). Commercial landings statistics do not adequately separate catches of the two species. Landings of both species combined increased rapidly from 1978, when European markets first developed, to peak at 2997 t in 1993–94 (Francis 1997, 1998); since then landings have declined to about 2500 t per year.

Estimates of skate growth rate, age at maturity, longevity, and natural mortality rate are required for stock assessment. Many skate species have been aged using growth bands laid down on their vertebral centra (Ishiyama 1951a, 1951b, Daiber 1960, Richards et al. 1963, Du Buit 1977, Ryland & Ajayi 1984, Waring 1984, Du Buit & Maheux 1986, Abdel-Aziz 1992, Natanson 1993, Zeiner & Wolf 1993, Gelsleichter et al. 1998, Walker 1998, Walmsley-Hart et al. 1999). Ages have been validated for seven species of shallow water skates. Techniques used for visualising the vertebral bands in skates include decalcification, staining (with haematoxylin and eosin, alizarin, copper sulphate, lead acetate, Mallory's solution, cobalt nitrate, ammonium sulphate, safranine, or silver nitrate), clearing (with alcohol, acetone, xylene, or ethylene glycol), and X-radiography. Whole or half centra, and thin or thick sections, have all been tried.

This study, funded by the Ministry of Fisheries under projects INS9802 and MOF1999/04L, had the following objectives.

1. To determine age and growth of both rough and smooth skates in QMA 3
2. To estimate natural mortality rates (*M*) of both rough and smooth skates

We tested a range of potential ageing techniques, and then used the best technique to age samples of rough and smooth skate vertebrae. We also developed growth curves, and estimated natural mortality rates, and length and age at maturity for both species.

2. METHODS

2.1 Age and growth

Vertebrae were collected from skates caught by R. V. *Kaharoa* during trawl surveys of east coast South Island in 1997–2000 (Figure 1, Tables 1 and 2). Smooth skate were caught in relatively low numbers, and we were unable to obtain adequate samples from the surveys. We therefore supplemented our sample with smooth skate vertebrae collected by Ministry of Fisheries scientific observers aboard commercial trawlers. Most of the vertebrae were collected from the central part of QMA 3, but some smooth skate observer samples and one specimen collected on a *Tangaroa* trawl survey came from outside QMA 3 (Figure 1).

For each skate, a block of 3–10 of the largest vertebrae was removed from in front of the pelvic fins and frozen. The largest vertebrae were used for ageing because it was anticipated that they would show the greatest band spacing and therefore resolution. Officer et al. (1996) reported significantly higher band counts in large thoracic vertebrae than in small cervical and precaudal vertebrae for *Mustelus antarcticus* and *Galeorhinus galeus*.

Vertebral samples were labelled with capture location, sex, and pelvic length (PL, measured from the tip of the snout to the posterior margin of the pelvic fins, to the centimetre below actual length). In the laboratory, vertebrae were thawed and trimmed of muscle and connective tissue. Individual centra were then separated and immersed in 42 $g.l^{-1}$ sodium hypochlorite until all of the muscle and connective tissue had been removed (about 1 h). Excessive soaking tended to dissolve the centra and made the articulating surfaces brittle and crumbly. After overnight soaking in freshwater, vertebrae were air-dried for 1 week.

Initial trials using X-radiography of whole centra and thick sections, and examination of thick sections under transmitted and reflected light, showed that X-radiography of thick sections produced the clearest banding patterns. Consequently, thick sections were used for ageing our samples. No stains were tested as adequate results were obtained without staining. Vertebrae from rough skates less than 50 cm PL and smooth skates less than 60 cm PL were small (centrum radius less than 4 mm) and poorly calcified. This made sectioning and X-raying difficult and time consuming, and interpretation of banding patterns difficult. We therefore aged most of the rough skates greater than 50 cm and smooth skates greater than 60 cm, and a small subsample of shorter skates.

Hyper-mineralised vertebral bands (Officer et al. 1997) were counted by two readers from digital images obtained from X-rayed sections. Both readers carried out an initial training exercise by counting bands on a subsample of the sections while knowing the size and sex of the skate. The two readers then counted bands on all sections without knowing the size and sex. All sections for which the two initial readings disagreed were re-examined by both readers, who discussed their interpretations and then assigned an agreed age to the specimen. Initial band counts were assessed for between-reader ageing bias and precision using age-bias plots, and plots of the coefficient of variation (c.v.) against age, as recommended by Campana et al. (1995).

Nothing is known about the timing of band deposition or the seasonality of hatching from the egg case in rough and smooth skates (though hyper-mineralised bands are laid down during winter in *Mustelus antarcticus* (Officer et al. 1997)). We therefore did not assign a theoretical birthday for skate ageing. The potential for misclassification of ages was minimised by the collection of most vertebral samples during a relatively short season (December–January). The vertebrae of the smallest skates of both species had one band, which is consistent with the deposition of a "birth band" soon after birth or hatching, as in many sharks and at least one skate (Abdel-Aziz 1992). Therefore, the (unvalidated) age assigned to each skate was the agreed band count minus one for the birth band.

Growth curves were 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_∞ is the asymptotic maximum length, K is the von Bertalanffy growth constant, and t_0 is the theoretical age at zero length. Sample sizes were too small to warrant tests for differences in growth rate between the two sexes.

2.2 Maturity

Maturity status was determined for a subsample of the aged skate using a three-stage maturity scale (Francis & Ó Maolagâin 2000).

Immature. Males – claspers do not extend beyond posterior edge of pelvic fins. Females – ovarian eggs small and white (no vitellogenesis).

Maturing. Males – claspers extend beyond posterior edge of pelvic fins, but are soft and uncalcified. Females – ovarian eggs medium with some vitellogenesis producing a light yellow colour.

Mature. Males – claspers extend beyond posterior edge of pelvic fins, are heavily calcified, and the terminal cartilages can be splayed open. Females – ovarian eggs large with active vitellogenesis producing an orange colour.

Larger samples of skates collected from both east and west coast South Island trawl surveys between 1996 and 2000 were used to estimate length at maturity using the same maturity scale.

Maturity ogives were fitted to the length and age at maturity data separately by sex using probit analysis (Pearson & Hartley 1962). This analysis assumes that the length or age at which a randomly selected fish reaches maturity is normally distributed. Two parameters, the mean and standard deviation of the normal distribution, were fitted. Each maturity ogive is the cumulative distribution function for the associated normal distribution. The probit function was fitted by maximum likelihood. Mean lengths at maturity, and their associated confidence limits, were corrected for downward rounding of length measurements by adding 0.5 cm.

2.3 Natural mortality

Estimates of the natural mortality coefficient, M, were obtained using two 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).

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 aged 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 $p = 0.01$ is the proportion (1%) of the population that reaches age A (or older).

Pauly (1980) examined the relationship between reported values of M, the von Bertalanffy growth parameters (K and L_∞), 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.

3. RESULTS

3.1 Rough skate

Vertebral sections were the typical elasmobranch "bow-tie" shape (Figure 2A). Growth bands were visible across the entire X-rayed section, though band clarity varied between the two halves, and the two sides within each half. Frequently, bands could be counted only on part of the section. Bands were generally clearer for smooth skate than for rough skate.

After discussing their initial vertebral band counts, final ages were agreed by the two readers for 134 of the 137 aged skates; the remaining 3 specimens (2.2%) were discarded as unreadable. For the 133 vertebrae that were aged independently by both readers, the counts were the same for 72 vertebrae (54%) and within one band for 110 vertebrae (83%). The remaining vertebrae had differences of 2–3 bands (Figure 3A). There was no systematic bias between readers, but only ages 4–6 had adequate sample sizes to assess this (Figure 3B; note that the error bars are one standard error around the mean, so mean counts falling within two error bars of the expected 1:1 relationship are not significantly different). Ageing precision was poor (mean c.v. = 18.0%) for ages 4–6.

The greatest estimated age was 9 years for a 70 cm female, but few skates were more than 6 years old (Figure 4). There was no apparent difference in length-at-age between males and females in age classes 4–6; the differences between the mean lengths (female minus male) were 0.6 cm (age 4), 2.5 cm (age 5), and –0.5 cm (age 6). A growth curve fitted to the data for both sexes combined had the parameter estimates (with standard errors) L_∞ = 91.3 cm (± 7.5), K = 0.16 (± 0.03) and t_0 = –1.20 years (± 0.30).

Male rough skates reached 50% maturity at 51.7 cm (95% confidence limits 51.1–52.4 cm) and 4.3 years (3.9–4.6 years) (Figure 5). Females matured at 59.1 cm (58.4–59.7 cm) and 5.7 years (5.3–6.3 years). The confidence bands did not overlap between the sexes, indicating that there were significant differences in length and age at maturity: males matured at a smaller size and younger age than females.

Hoenig's regression and rule-of-thumb methods produced similar estimates of M (Table 3). If the regression method is regarded as more reliable than the rule-of-thumb approximation, M is estimated to be 0.47 for a maximum age of 9 years. However, considering the small sample size and the heavily fished nature of the rough skate population along east coast South Island, true longevity is probably greater than 9 years. Our largest aged skate was 70 cm PL, compared with a known maximum length of at least 79 cm PL (Francis 1997). For longevities of 12 and 15 years, M would be 0.35 and 0.28 respectively (Table 3).

Using the von Bertalanffy growth parameters and a mean Timaru water temperature of about 14 °C (Greig et al. 1988), Pauly's method produced an M estimate of 0.25 (Table 4). For temperatures between 12 and 16 °C, M would be in the range 0.23–0.27.

3.2 Smooth skate

The appearance of the growth bands in X-rayed sections was similar to that for rough skates (Figure 2B). Of 101 smooth skate vertebrae that were X-rayed, one was considered unreadable and for two others the readers could not agree on a final age (3.0%). Of the remaining 98 skates, one had no length or sex data, and another was measured but not sexed. Initial counts by both readers of 100 vertebrae were the same for 39 vertebrae (39%) and within one band for 70 vertebrae (70%). The remaining vertebrae had differences of up to 6 bands (Figure 6A). There was no systematic bias between readers, but sample sizes were small (Figure 6B). Ageing precision was poor (mean c.v. = 19.8%) for ages with sample sizes of greater than 5 (ages 7–12).

The greatest estimated age was 24 years for a 133 cm female, but few skates were more than 15 years old (Figure 7). There was no apparent difference in length-at-age between males and females up to age 11, but there was some indication of a divergence beyond that. A growth curve fitted to the data for both sexes combined had the parameter estimates (with standard errors) L_∞ = 150.5 cm (± 6.3), K = 0.095 (± 0.009), and t_0 = –1.06 years (± 0.3).

Male smooth skates reached 50% maturity at 93.3 cm (95% confidence limits 91.3–95.1 cm) and 8.2 years (7.3–9.0 years) (Figure 8). Females matured at 112.2 cm (105.9–119.1 cm) and 13.0 years (11.1–14.8 years). However, the female maturity ogives were poorly defined because of small sample sizes of larger fish. Our aged samples contained only 21 mature males and 6 mature females. The confidence bands did not overlap between the sexes, indicating that males matured at a smaller size and younger age than females.

Hoenig's regression and rule-of-thumb methods produced similar estimates of M (see Table 3). The regression method produced an M estimate of 0.17 for a maximum age of 24 years. However, considering the small sample size, and the heavily fished nature of the smooth skate population along east coast South Island, true longevity is probably greater than 24 years. Our largest aged skate was 138 cm PL, compared with a known maximum length of at least 158 cm PL (Francis 1997). For longevities of 30 and 40 years, M would be 0.14 and 0.10 respectively (see Table 3).

Using the von Bertalanffy growth parameters and a mean Timaru water temperature of about 14 °C (Greig et al. 1988), Pauly's method produced an M estimate of 0.17 (Table 4). For temperatures between 12 and 16 °C, M would be in the range 0.16–0.18.

4. DISCUSSION

Growth bands were relatively clear and unambiguous in the inner and outer regions of the vertebrae of rough and smooth skates, but were less clear (often split) in the intermediate region. The latter bands caused some difficulties in ageing skates, as evidenced by the poor agreement between readers and high c.v.s for their initial counts. However, when the two readers discussed their initial readings, they reached agreement in assigning ages to nearly all of the vertebrae. Nevertheless, errors of 1–3 years are likely in some of our ages. We believe that ageing errors would decline, and precision would increase, with increased reader experience (neither reader had previous experience in ageing skates, though one reader had previously aged sharks using vertebrae). The magnitude of any errors is unlikely to unduly affect the fitted growth curves, or estimates of longevity and age at maturity. A new method of ageing skates from growth bands in their caudal thorns has been developed (Gallagher & Nolan 1999), and may prove to be suitable for rough and smooth skates.

Our age estimates are unvalidated, and the timing of band formation is unknown. However, annual band formation has been validated in seven other shallow water skate species using marginal increment analysis and oxytetracycline injection (Holden & Vince 1973, Ryland & Ajayi 1984, Abdel-Aziz 1992, Natanson 1993, Zeiner & Wolf 1993), and corroborated in four species using growth rate estimates from length-frequency analysis and tagging experiments (Abdel-Aziz 1992, Walker 1998). In another study, modal length-frequency analysis produced results that were inconsistent with those from vertebral ageing for the first three age classes, possibly because of incorrect assignment of the birth date and therefore definition of the age classes, or sampling that was biased towards the larger juveniles (Ryland & Ajayi 1984, Brander & Palmer 1985). These results give us some confidence that the bands we counted in rough and smooth skate vertebrae are deposited annually.

Although no statistical tests were conducted, there was no evidence of different growth rates for males and females of either species. However, sample sizes were small, particularly among the older age classes. For both species, the oldest individuals were females, suggesting that they have greater longevity than males.

Our oldest rough and smooth skates were 9 and 24 years respectively, but both species grow considerably larger than our largest aged specimens. This suggests that longevity in both species may substantially exceed the greatest ages found in the present study. The greatest age previously reported for a skate is 23 years in *Raja batis* (Du Buit 1977). *Raja pullopunctata* has been reported to reach 18 years (Walmsley-Hart et al. 1999), but no other species appears to live longer than 15 years (Ishiyama 1951a, 1951b, Richards et al. 1963, Ryland & Ajayi 1984, Waring 1984, Abdel-Aziz 1992, Zeiner & Wolf 1993, Walker 1998, Walmsley-Hart et al. 1999). Smooth skate therefore live much longer than most other skates, whereas rough skate longevity is comparable with that of many other species. Females of many skate species live slightly longer than males, as we found for rough and smooth skates.

Male and female rough skates mature at about 52 and 59 cm, and 4 and 6 years respectively. Male and female smooth skates mature at about 93 and 112 cm, and 8 and 13 years respectively. Thus females mature at greater sizes and ages than males in both species, and smooth skates mature at substantially greater sizes and ages than rough skates. In other skates, females typically mature at lengths and ages similar to or greater than males (Richards et al. 1963, Nottage & Perkins 1983, Ryland & Ajayi 1984, Abdel-Aziz 1992, Zeiner & Wolf 1993, Walker 1998, Walmsley-Hart et al. 1999).

The methods used to estimate M in this study are crude. Both Hoenig's and Pauly's methods are based on regressions that have large amounts of unexplained variability. This might be the source of the different results obtained from the two methods in various studies. For rough skate, Hoenig's method produced higher estimates of M than did Pauly's method, whereas for smooth skates both methods produced similar results. For butterfish (*Odax pullus*) and rubyfish (*Plagiogeneion rubiginosus*) Hoenig's method produced lower estimates of M than did Pauly's method (Paul et al. 2000a, 2000b). While we have no objective reason for preferring either method, we believe the most plausible estimates of M are 0.25–0.35 for rough skate and 0.10–0.20 for smooth skate.

Several species of large North Atlantic skates have undergone dramatic population declines over large parts of their former range, to the point of near extinction, as a result of overfishing (Brander 1981, Casey & Myers 1998, Dulvy & Reynolds in press 2001). Other smaller species have expanded their populations (Walker & Heessen 1996). Dulvy and Reynolds (in press 2001) reviewed skate biological parameters and concluded that size, as a proxy for longevity, is a potential indicator of vulnerability of skates to extinction. They suggested that New Zealand's smooth skate may be highly vulnerable to extinction because of its large size and lack of a depth refuge from trawling. Our results show that smooth skate are late maturing and long-lived, relative to other skates, whereas rough skate are early maturing with a moderate life span. Both species probably have low fecundity (they lay large yolky eggs in leathery egg cases on the seabed). However, a review of trawl survey estimates of the relative abundance of skates around South Island revealed no evidence of declining biomass for either species between 1992 and 1999 (Francis 1997, M. Francis unpubl. data). For the east coast of South Island (QMA 3), the trawl surveys covered much of the spatial and depth range of the two species, and most c.v.s were reasonable (20–25%), so major declines in abundance should have been detectable. This suggests that there is no immediate risk of extinction for either species. However, fishing mortality of both species has undoubtedly increased in the last decade, because a higher proportion of the catch has been landed; formerly, many skates would have been returned to the sea alive, as they are hardy and can survive capture by trawls (M. Francis, pers. obs.). Because of their biological characteristics, increased catches, and the lessons of population crashes of large skates in the North Atlantic, it is important that smooth skate abundance is closely monitored in future.

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Table 1: Rough skate sample collection details and numbers of vertebrae aged by sex. KAH, *Kaharoa* trawl survey.

				Sampled			Aged
Voyage	Dates	Females	Males	Total	Females	Males	Total
KAH9704	Dec 1997–Jan 1998	49	41	90	19	19	38
KAH9809	Dec 1998–Jan 1999	97	76	173	51	39	90
KAH9917	Dec 1999–Jan 2000	5	1	6	5	1	6
Total		151	118	269	75	59	134

Table 2: Smooth skate sample collection details and numbers of vertebrae aged by sex. Some totals include unsexed skates. KAH, *Kaharoa* trawl survey; TAN, *Tangaroa* trawl survey; obs, scientific observer trip.

				Sampled			Aged
Trip	Dates	Females	Males	Total	Females	Males	Total
KAH9704	Dec 1997–Jan 1998	24	19	43	13	8	22
KAH9809	Dec 1998–Jan 1999	33	36	69	10	20	30
KAH9917	Dec 1999–Jan 2000	7	13	20	6	12	18
TAN9805	Apr 1998	0	1	1	0	1	1
obs1173	Dec 1998–Jan 1999	12	3	15	12	3	15
obs1200	Feb–Mar 1999	14	5	25	9	2	12
Total		90	77	173	50	46	98

Table 3: Rough and smooth skate mortality rate estimates for three longevities using Hoenig's regression method and a rule-of-thumb approximation to it.

	Estimation method	
Species and longevity	Hoenig's (1983) regression	Hoenig's rule-of-thumb
Rough skate		
9 years	0.47	0.51
12 years	0.35	0.38
15 years	0.28	0.31
Smooth skate		
24 years	0.17	0.19
30 years	0.14	0.15
40 years	0.10	0.12

Table 4: Rough and smooth skate mortality rate estimates for three temperatures using Pauly's (1980) regression.

	Temperature (°C)		
Species	12	14	16
Rough skate	0.23	0.25	0.27
Smooth skate	0.16	0.17	0.18

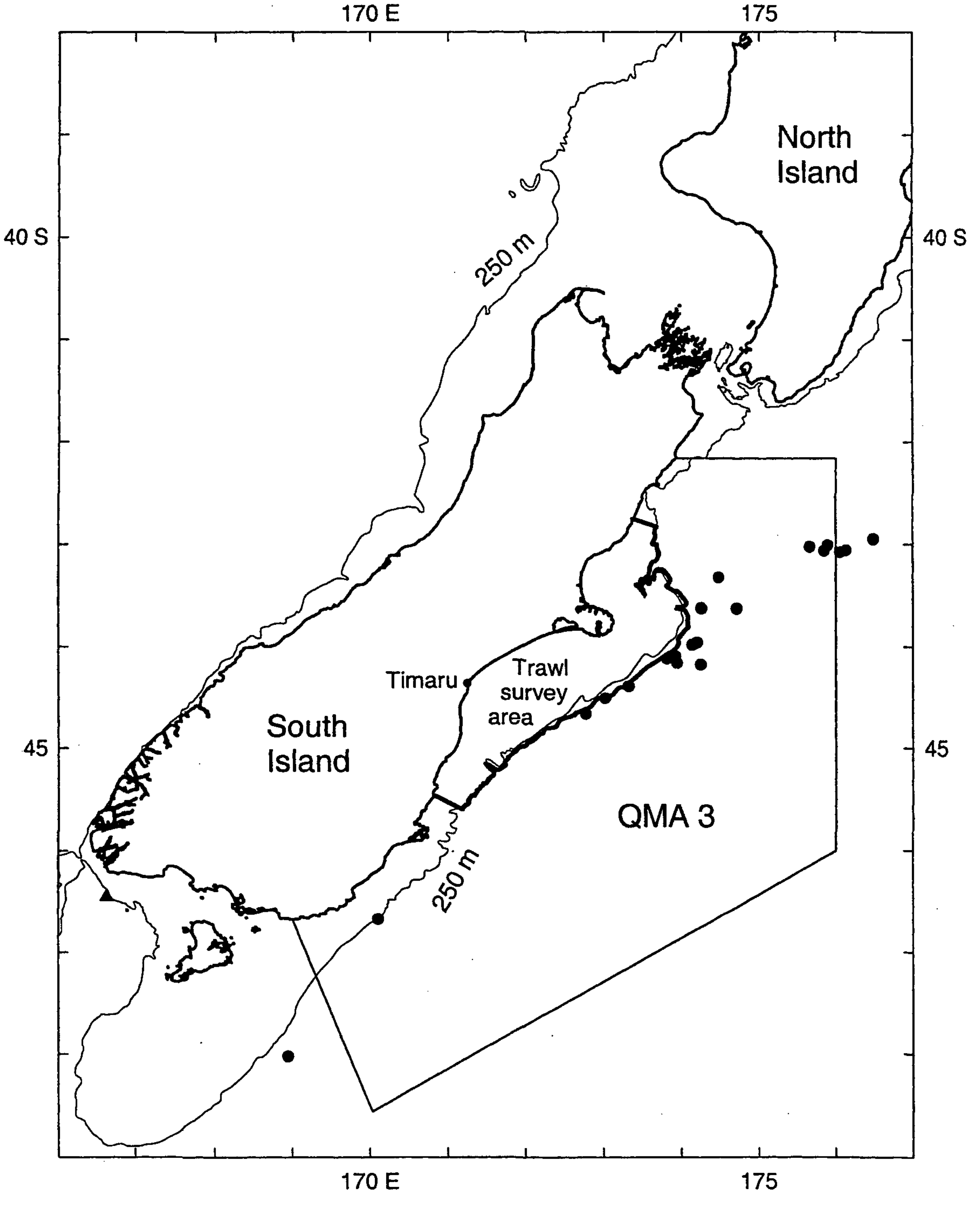

Figure 1: Map of New Zealand showing the east coast South Island trawl survey area from which most skate samples were collected. Also shown are the locations of additional smooth skate samples collected by observers (dots) and a *Tangaroa* trawl survey (triangle).

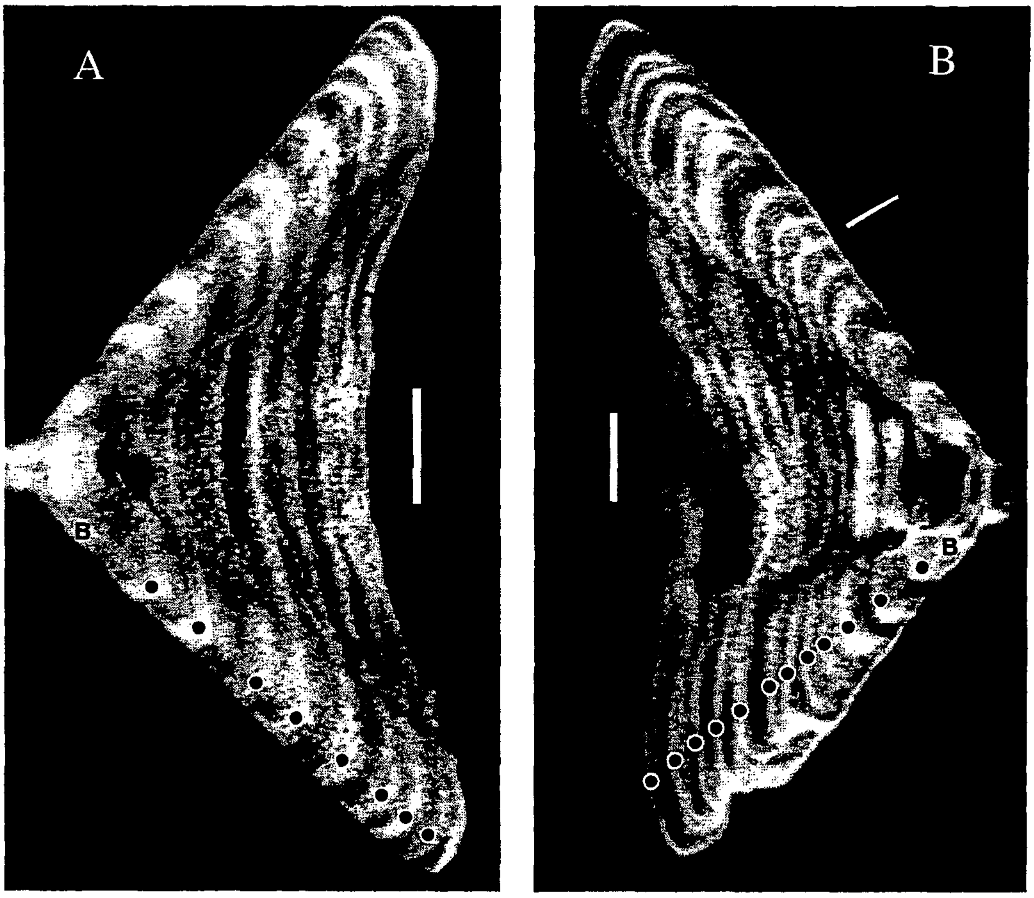

Figure 2: Digitally enhanced X-radiographs of one-half of thick sections through the vertebral centra of (A) a 67 cm pelvic length mature female rough skate; and (B) a 96 cm pelvic length maturing female smooth skate. The agreed ages (excluding the birth band, B) were 8 and 12 years respectively. Bands counted by the two readers are marked with black dots. In (A), an additional band at the margin of the corpus calcareum was not formed across the intermedialia, and was not counted by the readers. Scale bars = 1 mm.

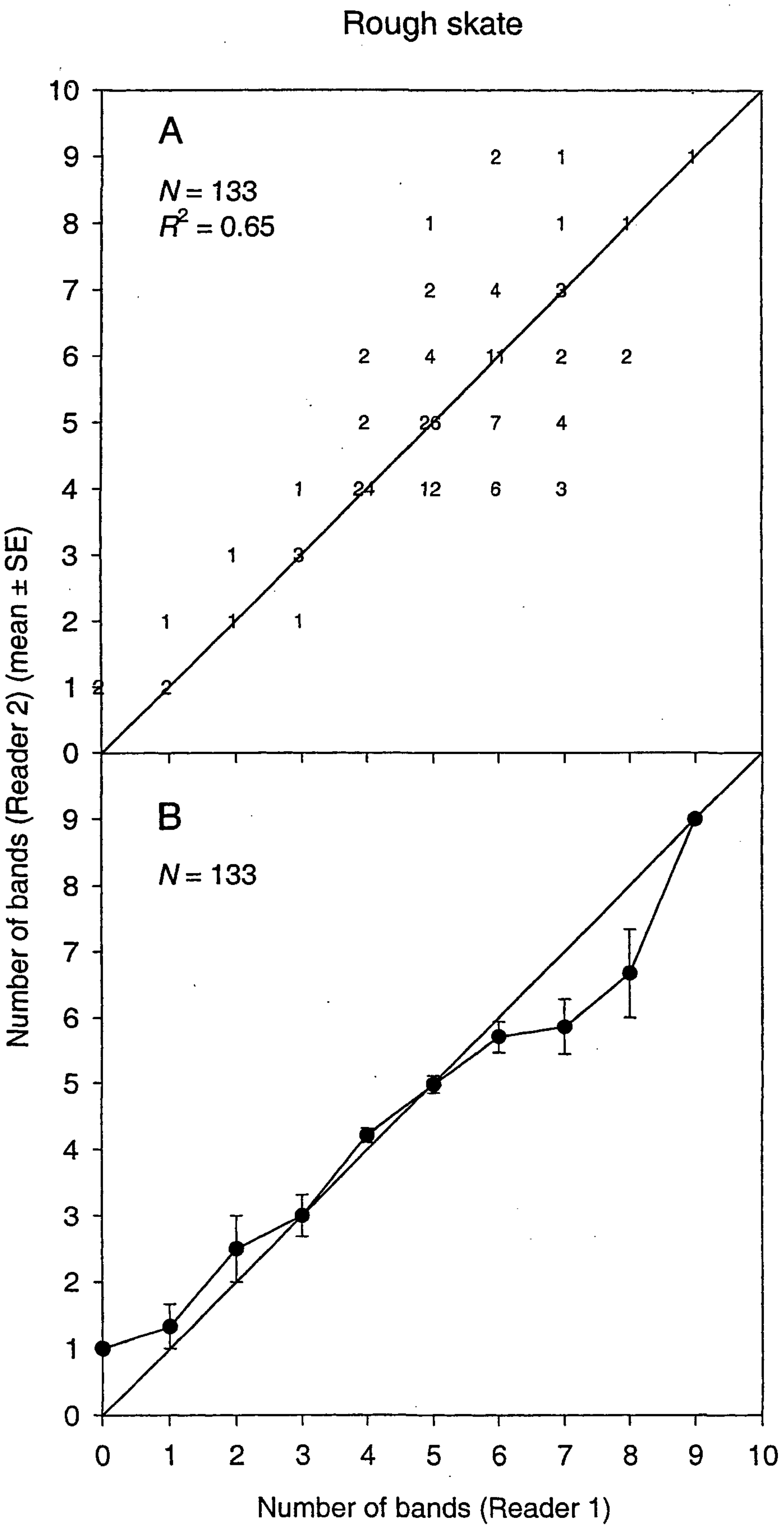

Figure 3: Between-reader comparison of vertebral band counts for rough skate: (A) Actual counts (numbers represent number of skates). (B) Mean count of Reader 2 (±1 standard error (SE)) relative to the counts of Reader 1. Diagonal lines indicate the expected relationship. *N*, total sample size.

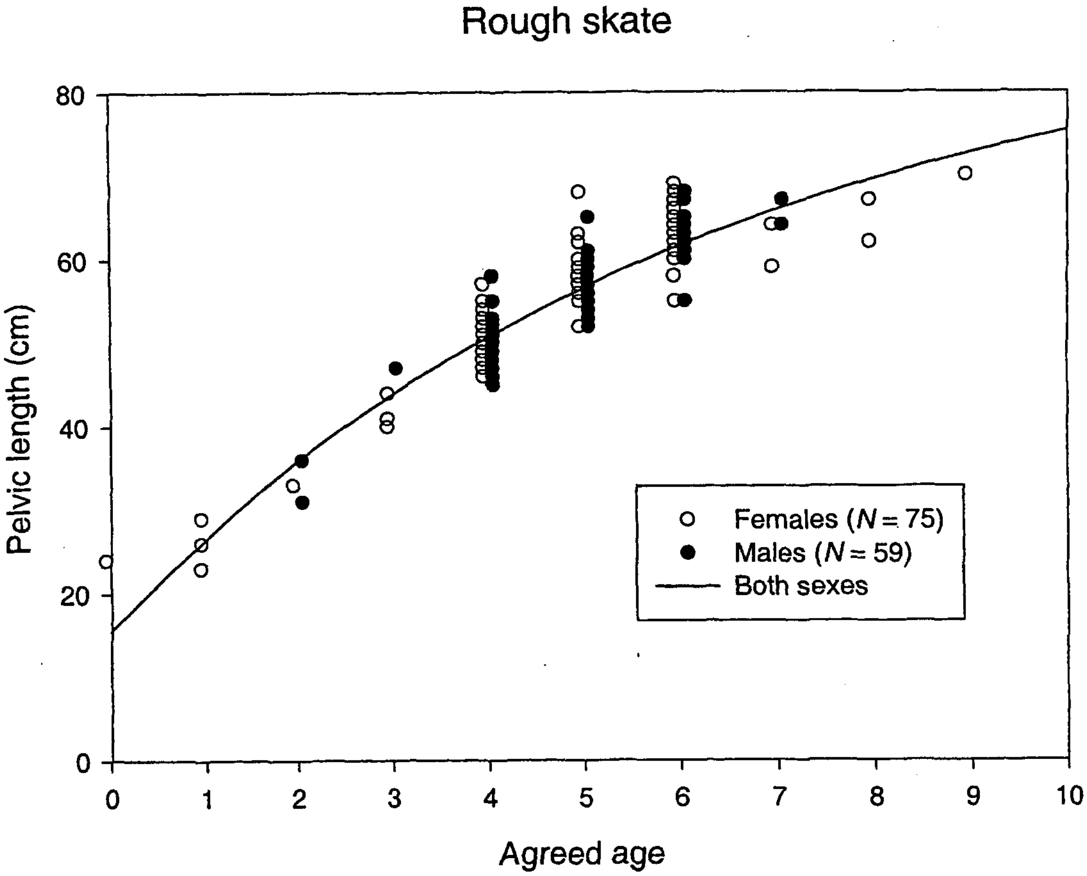

Figure 4: Rough skate length-at-age with fitted von Bertalanffy growth curve. Male and female data points were offset slightly from the axis ticks for clarity. *N*, sample size.

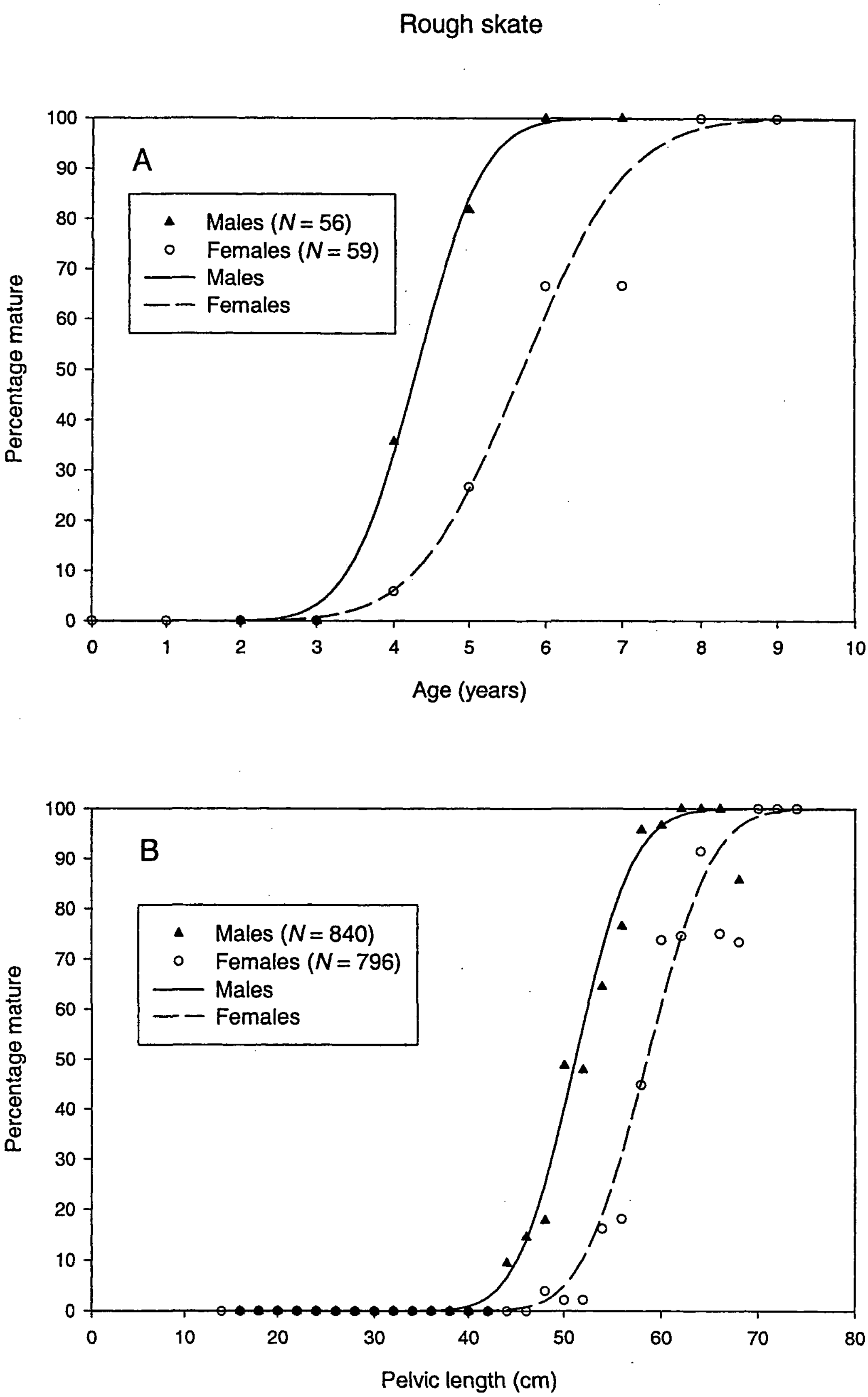

Figure 5: Percentage maturity by (A) age for east coast South Island rough skate, and (B) length for South Island rough skate. Curves were fitted by probit analysis. *N*, sample size.

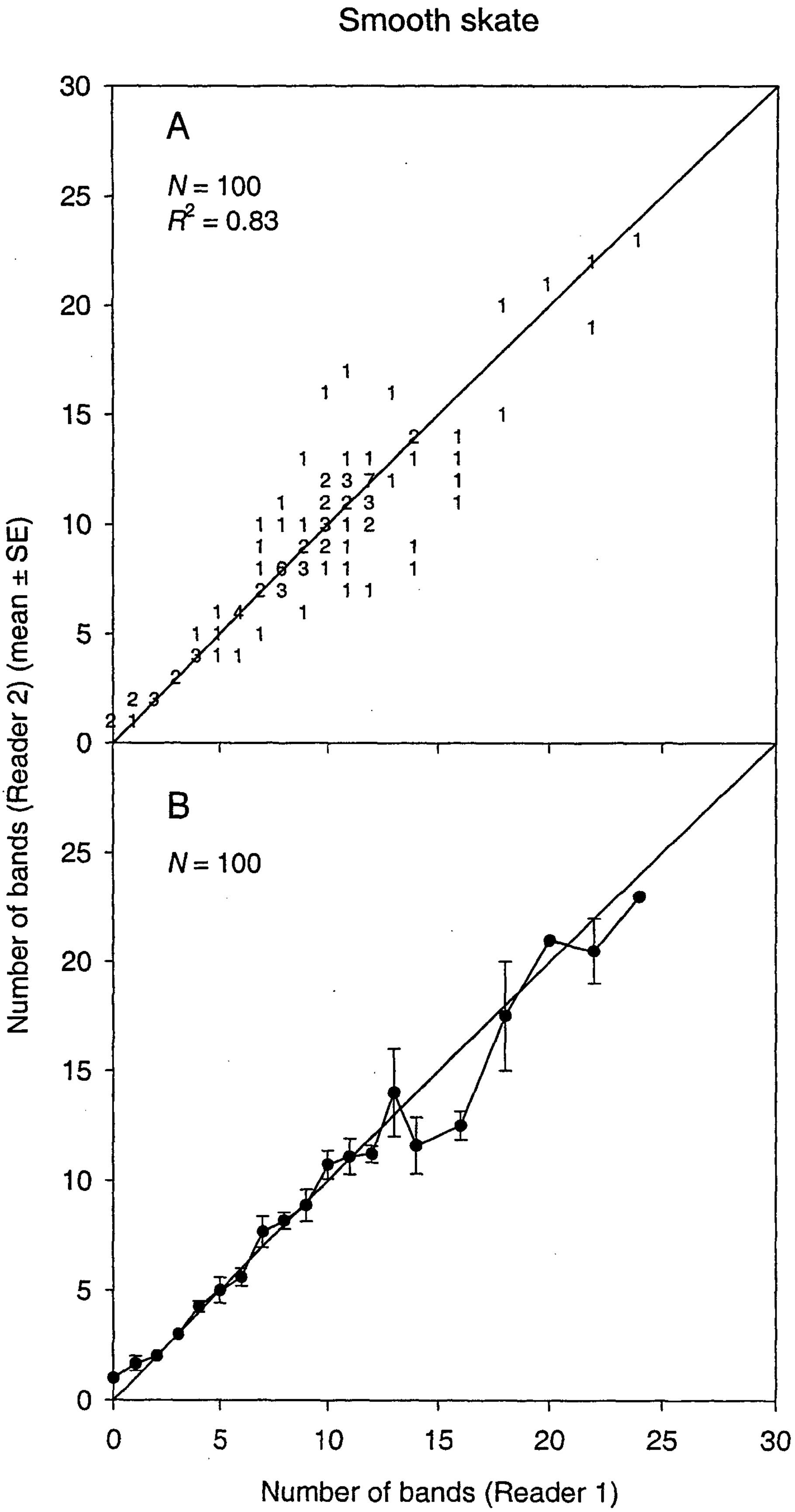

Figure 6: Between-reader comparison of vertebral band counts for smooth skate: (A) Actual counts (numbers represent number of skate). (B) Mean count of Reader 2 (± 1 standard error) relative to the counts of Reader 1. Diagonal lines indicate the expected relationship. *N*, total sample size.

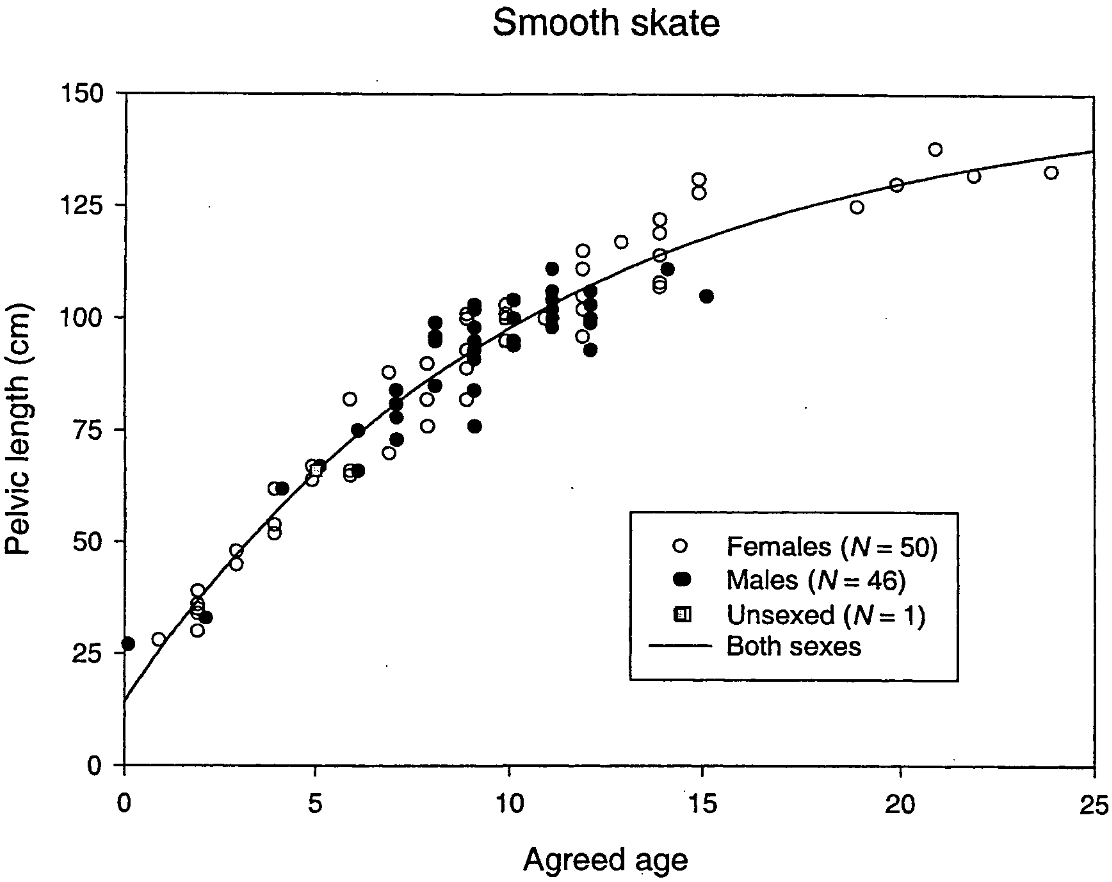

Figure 7: Smooth skate length-at-age with fitted von Bertalanffy growth curve. Male and female data points were offset slightly from the axis ticks for clarity. *N*, sample size.

Smooth skate

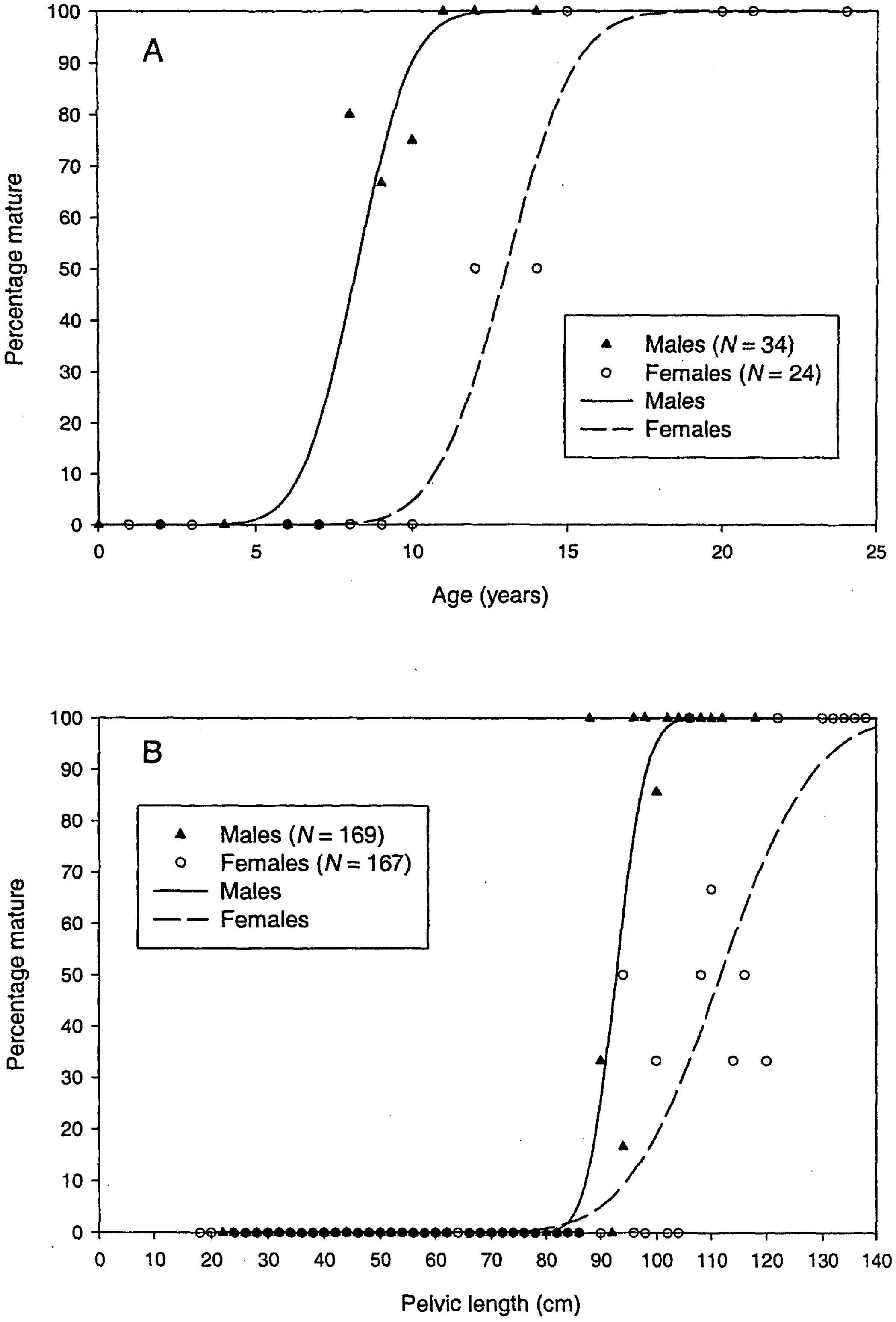

Figure 8: Percentage maturity by (A) age for east coast South Island smooth skate, and (B) length for South Island smooth skate. Curves were fitted by probit analysis. *N*, sample size.