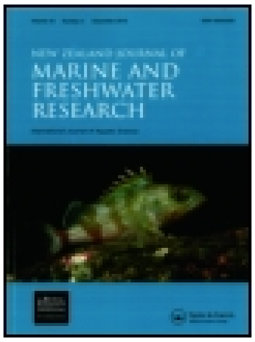

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Age, growth, and sexual maturity of two New Zealand endemic skates, *Dipturus nasutus* and *D. innominatus*

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Age, growth, and sexual maturity of two New Zealand endemic skates, *Dipturus nasutus* and *D. innominatus*

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Abstract Rough and smooth skates (*Dipturus nasutus* (Banks 1841) and *D. innominatus* (Garrick & Paul 1974)) were aged by counting growth bands on X-rays of thick sections of vertebral centra. Band counts were imprecise, but there was no between-reader bias. Age estimates were not validated. The oldest rough skate was 9 years old, but few were more than 6 years old. Females may live longer than males. The combined sexes von Bertalanffy growth curve was $L_t = 91.3\ (1 - e^{-0.16[t + 1.20]})$. Half the males matured by c. 52 cm pelvic length (PL) and 4 years, and females by 59 cm PL and 6 years. The oldest smooth skate in the sample was 24 years, but longevity probably exceeds that. Females appear to live longer than males. The combined sexes von Bertalanffy growth curve was:
$L_t = 150.5\ (1 - e^{-0.095[t + 1.06]})$. Half the males matured by c. 93 cm PL and 8 years, and females by 112 cm PL and 13 years. Smooth skate are late maturing and long-lived relative to other skates, whereas rough skate are early maturing with a moderate life span.

Keywords age; growth; maturity; longevity; weight; skates; *Dipturus nasutus*; *Dipturus innominatus*

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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 c. 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). Smooth skates are much larger than rough skates, with the former reaching at least 158 cm pelvic length and the latter at least 79 cm pelvic length (Francis 1997).

Rough and smooth skates are both fished commercially, with c. 60% of recent landings coming from the east coast of the South Island; most of the rest is taken from the remainder of the South Island (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 markets first developed for them in Europe, and peaked at 2997 t in 1993–94 (Francis 1997, 1998); since then landings have declined to c. 2500 t per year.

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 & Meyers 1998; Dulvy et al. 2000; Dulvy & Reynolds in press 2002). Conversely, some smaller species have expanded their populations (Walker & Heessen 1996). Dulvy & Reynolds (in press 2002) reviewed skate biological parameters and concluded that size, as a proxy for longevity, is a potential

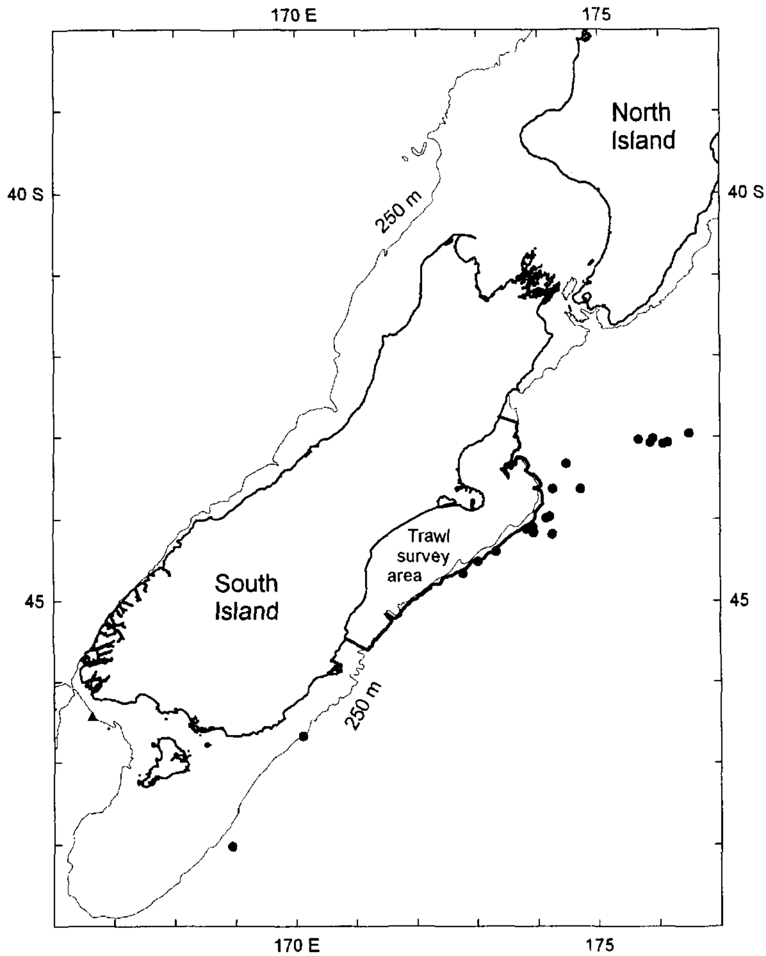

Fig. 1 Map of southern New Zealand showing the east coast of the South Island *Kaharoa* trawl survey area from which most skate (*Dipturus* spp.) samples were collected. Also shown are the locations of additional smooth skate samples collected by observers (dots) and a *Tangaroa* trawl survey (triangle).

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. It is therefore important to monitor the status of New Zealand's skate stocks, and to determine whether current catches are having a negative impact on the stocks.

Estimates of skate growth rate, age at maturity, and longevity are required for stock assessment. Elsewhere, many skate species have been aged using growth bands laid down on their vertebral centra (Ishiyama 1951a,b; 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). 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. Ageing techniques have been validated for seven species of skates using injections of oxytetracycline or marginal increment analysis (Holden & Vince 1973; Ryland & Ajayi 1984; Abdel-Aziz 1992; Natanson 1993; Zeiner & Wolf 1993).

In this study, we tested a range of potential ageing techniques, and then used the best technique to estimate the ages of samples of rough and smooth skate vertebrae. We also developed growth curves and estimated the length and age at maturity for both species.

METHODS

Age and growth

Vertebrae were collected from rough and smooth skates caught by the research trawler *Kaharoa* during trawl surveys off the east coast of the South Island between 1997 and 2000 (Fig. 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 smooth skate sample with vertebrae collected by Ministry of Fisheries scientific observers aboard commercial trawlers.

For each skate, a block of 3–10 of the largest thoracic vertebrae was removed from the posterior end of the body cavity, 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 provide best resolution. Officer et al. (1986) 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 bleach (42 g litre^{-1} sodium hypochlorite) until all of the muscle and connective tissue had been removed (c. 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 were conducted using: (1) X-radiography of whole centra and thick (300–500 μm) sagittal sections that were cut with a double-bladed diamond saw; and (2) examination of thick sagittal sections under transmitted and reflected light. X-rays were taken with a Phillips 45 kV X-ray machine at 5 mA using Kodak Industrex grade "R" film. A series of test exposures was taken of the entire set of samples, and the exposure producing the best contrast and clarity was used for examination.

X-radiography of thick sections produced the clearest banding patterns. Consequently, thick sections were used for ageing our samples. Usually, only one vertebra was sectioned per skate, but occasionally two or three were sectioned. No stains were tested. Vertebrae from rough skates <50 cm

Table 1 Rough skate (*Dipturus nasutus*) sample collection details and numbers of vertebrae aged by sex. (kah, *Kaharoa* trawl survey.)

Trip	Dates	Sampled			Aged		
		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 (*Dipturus innominatus*) 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.)

Trip	Dates	Sampled			Aged		
		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

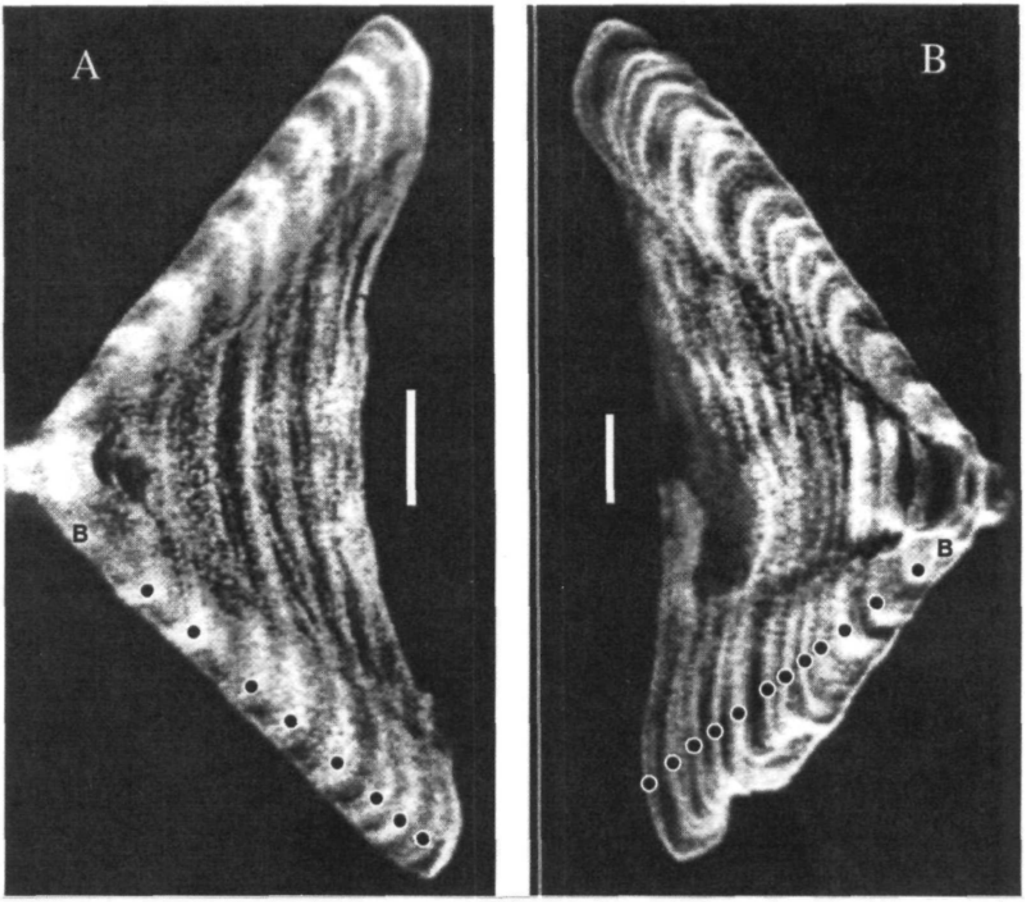

Fig. 2 Digitally enhanced X-radiographs of one-half of thick sections through the vertebral centra of: **A**, a 67 cm pelvic length mature female rough skate (*Dipturus nasutus*); and **B**, a 96 cm pelvic length maturing female smooth skate (*Dipturus innominatus*). The agreed ages (excluding the birth 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.)

and smooth skates <60 cm were small and poorly calcified. This made sectioning and X-radiography difficult and time consuming, and interpretation of banding patterns difficult. We therefore aged most of the rough skates >50 cm and smooth skates >60 cm, and a small subsample of shorter skates.

Two readers counted the white, hyper-mineralised vertebral bands (Officer et al. 1997), in un-enhanced digital images obtained from X-rayed sections (Fig. 2). These bands were generally clearest along the four "arms" of the corpus calcareum. Readers examined the entire section, including the intermedialia, when making their band count. Both readers carried out an initial training exercise by counting bands on a subsample of the sections with full knowledge of the size and sex of the skates. The two readers then counted bands on all sections without this knowledge. 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. Band counts were assessed for between-reader ageing bias and precision using age-bias plots, and plots of the coefficient of variation (CV) 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:

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

where L_t is the expected length at age t years, L_∞ is the asymptotic mean 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.

Maturity

Maturity status was determined for a subsample of the aged skate using a 3-stage maturity scale (Francis & Ó Maolagáin 2000): Immature—males, claspers do not extend beyond the posterior edge of pelvic fins; females, ovarian eggs small and white (no vitellogenesis). Maturing—males, claspers extend beyond the 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 the posterior edge of pelvic fins, are heavily calcified, and the terminal cartilages can be splayed open; females, ovarian eggs are large with active vitellogenesis producing an orange colour.

Larger samples of skates collected from trawl surveys off both the east and west coasts of the South Island between 1996 and 2000 were used to estimate length at maturity using the same maturity scale. Length-weight relationships were also derived from these larger samples, and they were tested for differences between the two sexes using homogeneity of slopes tests on log-transformed data.

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.

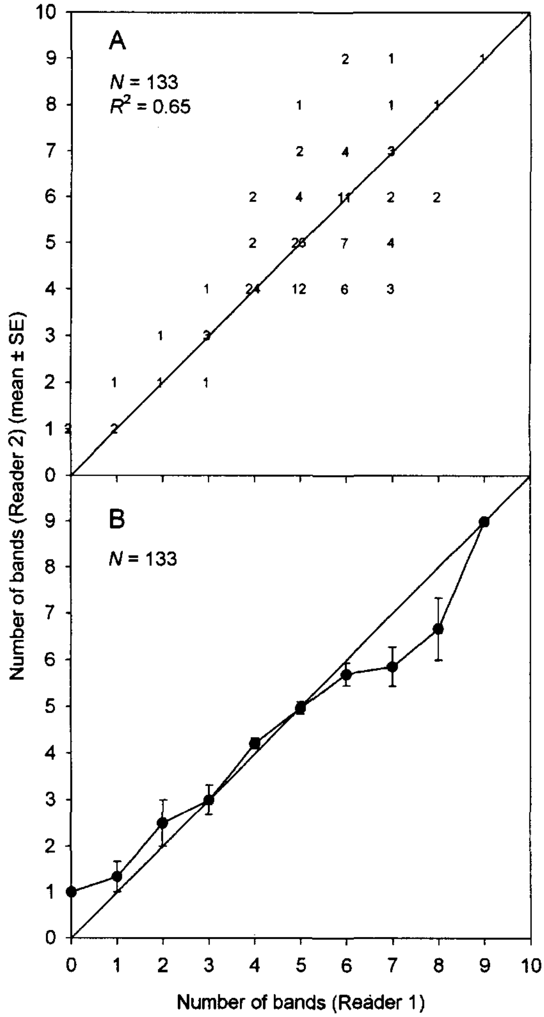

Fig. 3 Between-reader comparison of vertebral band counts for rough skate (*Dipturus nasutus*): **A**, actual counts (numbers represent number of skates); and **B**, mean count of Reader 2 (±1 standard error (SE)) relative to the counts of Reader 1. Diagonal lines indicate the expected relationship.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

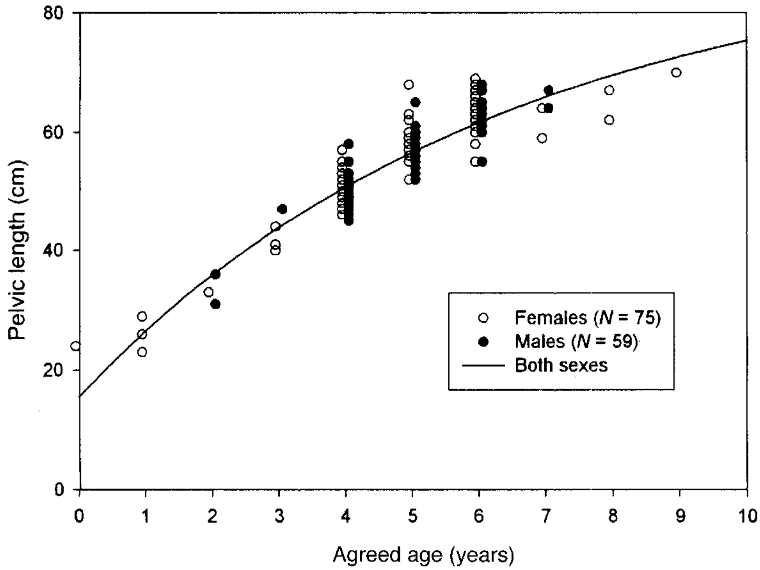

Fig. 4 Rough skate (*Dipturus nasutus*) length-at-age with fitted von Bertalanffy growth curve. Male and female data points were offset slightly from the axis ticks for clarity. (N = sample size.)

RESULTS

Rough skate

Growth bands were visible across the entire vertebra in X-rayed sections (Fig. 2A), though band clarity varied between the two halves, and the two sides within each half. Frequently, bands could not be counted on one or more of the arms of the corpus calcareum. Growth bands were relatively clear and unambiguous in the inner and outer regions of the vertebrae, but were less clear (often split) in the intermediate region.

After discussing their initial vertebral band counts, final ages were agreed by the two readers for 134 of the 137 "aged" specimens; the remaining three 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 (Fig. 3A). There was no systematic bias between readers (Fig. 3B), but only ages 4–6 had adequate sample sizes to assess this. Ageing precision was poor (mean CV = 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 (Fig. 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 (the length at which half the skates were mature) at 51.7 cm (95% confidence limits 51.1–52.4 cm) and 4.3 years (3.9–4.6 years) (Fig. 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.

At lengths greater than c. 40 cm, female rough skates were heavier than males of the same length. The slopes of log-weight versus log-length regressions were significantly different for the two sexes ($P < 0.0001$):

Males: Log_{10} Weight = –4.452 + 2.860 Log_{10} Pelvic length (N = 1049)

Females: Log_{10} Weight = –4.613 + 2.969 Log_{10} Pelvic length (N = 977)

where length is measured in centimetres and weight in kilograms.

Smooth skate

The appearance of the growth bands in X-rayed sections was similar to that for rough skates (Fig. 2B), but bands were generally clearer for smooth

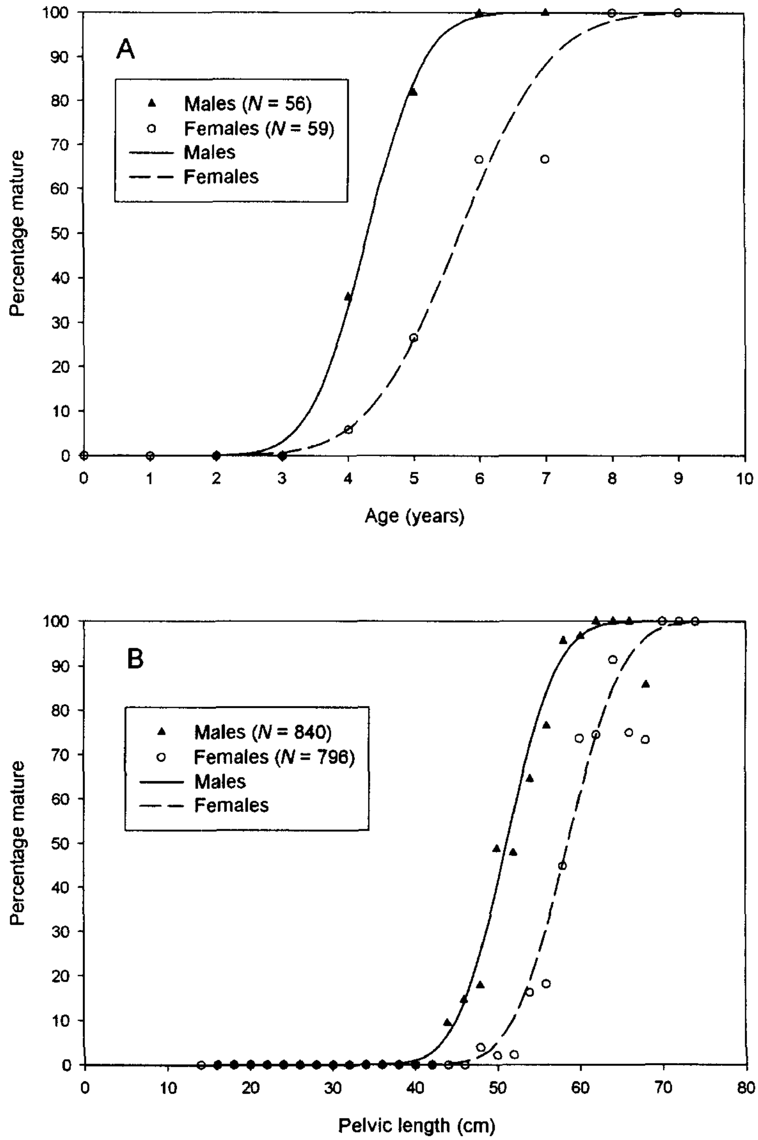

Fig. 5 Percentage maturity by: **A**, age for east coast South Island, New Zealand, rough skate (*Dipturus nasutus*); and **B**, length for South Island rough skate. Curves were fitted by probit analysis. (N = sample size.)

skate. 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 six bands (Fig. 6A). There was no systematic bias between readers, but sample sizes were small (Fig. 6B). Ageing precision was poor (mean CV = 19.8%) for ages with sample sizes 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 (Fig. 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 (±0.30).

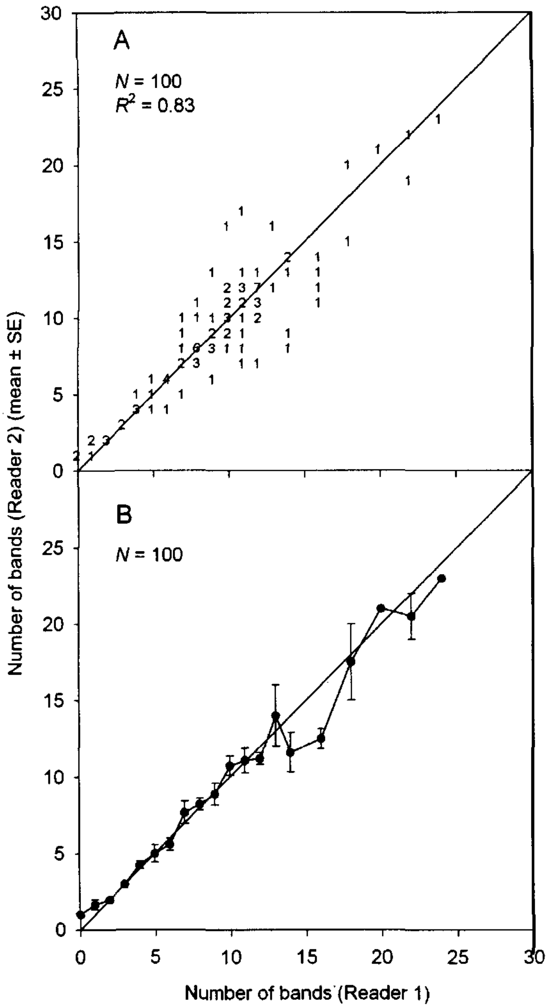

Fig. 6 Between-reader comparison of vertebral band counts for smooth skate (*Dipturus innominatus*): **A**, actual counts (numbers represent number of skate); and **B**, mean count of Reader 2 (±1 standard error (SE)) relative to the counts of Reader 1. Diagonal lines indicate the expected relationship. (N = total sample size.)

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) (Fig. 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.

At lengths greater than c. 80 cm, female smooth skates were heavier than males of the same length. The slopes of log-weight versus log-length regressions were significantly different for the two sexes (P = 0.013).

Males: Log_{10} Weight = –4.578 + 2.929 Log_{10} Pelvic length (N = 310)

Females: Log_{10} Weight = –4.659 + 2.978 Log_{10} Pelvic length (N = 313)

where length is measured in centimetres and weight in kilograms.

DISCUSSION

Growth bands were relatively clear and unambiguous in the inner and outer regions of the vertebrae of both 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 CVs for their band counts. However, when the two readers discussed their 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 (Gallagher & Nolan 1999) 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 a further 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 &

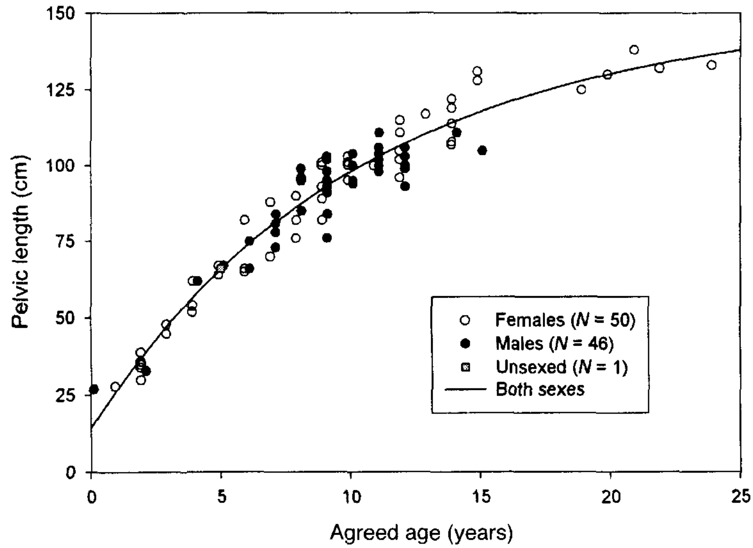

Fig. 7 Smooth skate (*Dipturus innominatus*) length-at-age with fitted von Bertalanffy growth curve. Male and female data points were offset slightly from the axis ticks for clarity. (N = sample size.)

Palmer 1985). Overall, 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 live longer than males.

Our oldest rough and smooth skates were 9 (for a 70 cm female) and 24 years (133 cm female) respectively, but both species grow considerably larger than our largest aged specimens: rough skates reach at least 79 cm and smooth skates at least 158 cm (Francis 1997). 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,b; Richards et al. 1963; Ryland & Ajayi 1984; Waring 1984; Abdel-Aziz 1992; Zeiner & Wolf 1993; Walker 1998; Walmsley-Hart et al. 1999). Smooth skates 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 c. 52 and 59 cm, and 4 and 6 years respectively. Male and female smooth skates mature at c. 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; Skjaeraasen & Bergstad 2000).

The near-extinction of several species of large North Atlantic skates led Dulvy & Reynolds (in press 2002) to suggest that size is a potential indicator of vulnerability of skates to extinction. They also 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 the 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 the South Island, the trawl surveys covered much of the spatial and depth range of the two species, and most CVs 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

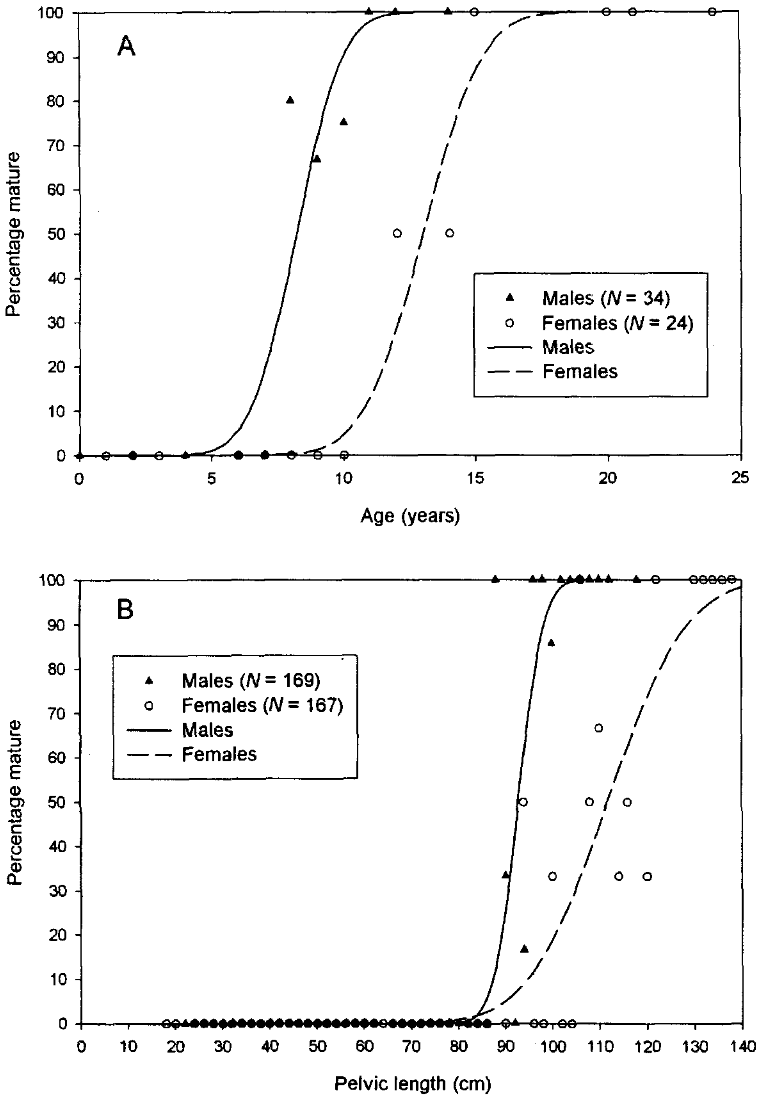

Fig. 8 Percentage maturity by: **A**, age for east coast South Island, New Zealand, smooth skate (*Dipturus innominatus*); and **B**, length for South Island smooth skate. Curves were fitted by probit analysis. (N = sample size.)

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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