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# Age and growth of school mackerel (*Scomberomorus queenslandicus*) and spotted mackerel (*S. munroi*) in Queensland east-coast waters with implications for stock structure

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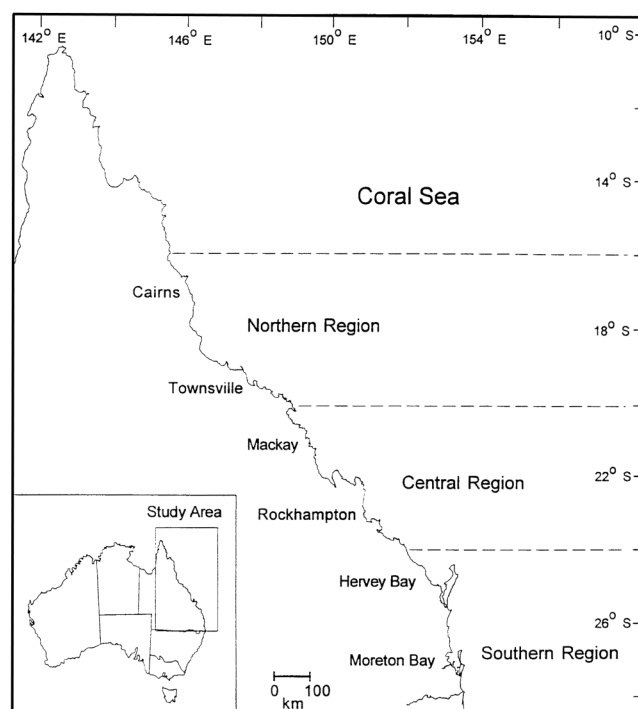
**Abstract.** Age and growth of school mackerel (*Scomberomorus queenslandicus*) and spotted mackerel (*S. munroi*) in east-coast waters, Queensland, Australia (16°S to 28°S), were determined to provide population parameters required for stock assessment and fisheries management. Female school mackerel ( $L_{\infty} = 651$  mm,  $K = 0.59$ ,  $t_0 = -1.41$ ) were estimated to grow to a greater asymptotic length, but at a slower rate, than males ( $L_{\infty} = 628$  mm,  $K = 0.71$ ,  $t_0 = -1.26$ ). Growth patterns of school mackerel differed between geographic regions and suggested the existence of separate stocks throughout the east-coast distribution. In contrast, female spotted mackerel ( $L_{\infty} = 849$  mm,  $K = 0.46$ ,  $t_0 = -1.54$ ) were estimated to reach a greater asymptotic length at a faster rate than males ( $L_{\infty} = 768$  mm,  $K = 0.23$ ,  $t_0 = -4.33$ ). There was no difference in growth between spotted mackerel from different regions, suggesting that there is a single stock along the Queensland east coast. Identification of school and spotted mackerel populations in Queensland east-coast waters will enable the species to be managed on the basis of stock structure across this range.

*Extra keywords:* otolith, fisheries, management

## Introduction

School mackerel (*Scomberomorus queenslandicus*) and spotted mackerel (*S. munroi*) are inshore, schooling species that coexist in coastal waters of northern Australia and southern Papua New Guinea (Collette and Russo 1984). These species together with grey mackerel (*S. semifasciatus*) and narrow-barred Spanish mackerel (*S. commerson*) form important commercial and recreational fisheries throughout Queensland, the Northern Territory, Western Australia, and to a lesser extent northern New South Wales. School and spotted mackerel are enmeshed in set gill-nets or in ring-netting operations in commercial fisheries and form the basis of popular recreational fisheries throughout their range, but particularly from Moreton Bay to Townsville (Fig. 1). In Queensland, where the majority of school and spotted mackerel are captured, the commercial fishery averaged 160 t between 1992 and 1995, while the recreational sector removed at least half of that amount (Cameron and Begg, unpublished).

School mackerel often inhabit turbid coastal waters, embayments and estuaries, in contrast to spotted mackerel which are more common in offshore, open waters (Munro 1943; Collette and Russo 1984). Tag–recapture data suggest that school mackerel typically move only short distances,



**Fig. 1.** Sampling locations of school and spotted mackerel.

whereas spotted mackerel follow a cyclic migratory pattern along the Queensland east coast (Begg *et al.* 1997). Tag-recapture data have led to the hypothesis that several separate stocks of school mackerel exist along the east coast, whereas spotted mackerel are thought to form a single stock (Begg *et al.* 1997). However, examination of biological population characteristics such as ageing patterns and growth rates is also required if stock boundaries are to be defined more accurately.

Data derived from ageing studies are necessary for interpreting population dynamics and impacts of fisheries exploitation. Use of ageing information is related to construction of age-length keys for direct application in assessment models such as virtual population analysis, estimation of growth parameters for inputs in yield-per-recruit models, and comparative studies of growth in different stocks (Pauly 1987). Comparative ageing studies of different stocks can provide indirect evidence of population structure (Ihssen *et al.* 1981). Investigation of recruitment sources and growth patterns in fish from different regions can be used to identify the stock structure of a species (Casselman *et al.* 1981; Sutter *et al.* 1991).

*Scomberomorus* species have been aged almost exclusively by studying otoliths (Beaumariage 1973; Powell 1975; Sturm 1978; Johnson *et al.* 1983; Fable *et al.* 1987; Manooch *et al.* 1987; Collins *et al.* 1989; DeVries *et al.* 1990; Sturm and Salter 1990; McPherson 1992; Schmidt

*et al.* 1993; Govender 1994; DeVries and Grimes 1997; Peters and Schmidt 1997). Whole and sectioned otoliths were also used as the ageing structures for the present study owing to their permanency, continual growth pattern and availability.

In Australia, ageing studies of *Scomberomorus* species have been limited to narrow-barred Spanish mackerel; McPherson (1992) used whole otoliths to examine the age and growth rates of stocks off the east coast and northern Australia. The present study aimed to examine the age structure and growth characteristics of school and spotted mackerel in Queensland east-coast waters. Spatial patterns in growth rates were used to provide insights into stock structure.

## Materials and methods

### Ageing

School and spotted mackerel were collected monthly from commercial net fishers and recreational anglers from June 1992 to January 1995 (Table 1). Specimens were kept on ice, then frozen until needed for laboratory analyses. Samples were obtained from the Queensland east coast, south of 16°S. This coastline was subdivided into northern, central and southern regions for subsequent analyses (Fig. 1). Areas north of the 'northern' region were not sampled owing to the remoteness of these areas, and because of economic and logistic constraints of sampling over this broad geographic region. Samples were obtained from a number of independent collections at each area, usually representing fish caught from several different schools. Fish were measured (length to caudal fork LCF, mm) and weighed (wet weight, g), and their sex was determined by macroscopic examination of the gonads. Sagittal otolith pairs, reached by a horizontal incision that exposed the brain cavity, were removed, washed and dried.

**Table 1.** Sampling of school and spotted mackerel for age determination

Month	School mackerel					Spotted mackerel				
	Region	Line (n)	10-cm net (n)	12.5-cm net (n)	Length range (mm)	Region	Line (n)	10-cm net (n)	12.5-cm (n) net	Length range (mm)
January	Southern	119	2	–	350–695	Southern	5	181	–	490–740
February	Southern	7	4	–	405–635	Southern	11	151	–	544–715
March	Southern	–	20	–	465–580	Southern	1	77	–	540–705
April	Southern	18	2	–	473–619	Southern	1	–	–	780
May	Central	27	–	–	460–660	Central	4	–	–	485–820
June	Southern	8	–	–	516–680	Central	2	–	–	530–675
	Central	81	–	–	311–690					
July	Southern	14	–	–	470–623	Northern	47	–	–	550–785
	Northern	26	–	–	450–570					
	Central	51	–	–	310–685					
August	Southern	7	22	–	380–645	Northern	18	–	272	448–840
	Northern	42	–	56	450–668					
	Central	14	–	–	506–670					
September	Southern	–	49	–	449–625	Northern	–	–	193	552–925
	Central	37	–	–	430–729					
	Southern	–	126	–	455–700					
October	Central	125	–	–	437–720	Central	6	–	–	602–655
	Southern	5	132	–	460–705					
November	Central	7	–	–	560–860	Southern	5	56	–	521–860
	Southern	78	5	–	460–675					
December	Central	4	–	–	610–660	Southern	141	214	–	460–790
	Southern	60	24	–	330–784					

Whole otoliths were examined in vegetable oil on a blackened background and illuminated by reflected light. A dissecting microscope (12.5× magnification) was used to observe the banding pattern in whole individual otoliths. Otoliths were classified into age groups based on the number of opaque nonmarginal bands (following the method of Beaumariage 1973). A band (annulus) was considered complete when a translucent zone was visible outside its distal edge (Fig. 2). Whole otoliths were mounted in resin and a thin section (0.3 mm) was cut through the focus with a diamond-edged circular saw. The section was then mounted on a glass slide for microscopic examination. Up to 20 otoliths from each age class were sectioned transversely. The same two readers independently aged the otoliths to maintain objectivity. Any otoliths whose interpretation varied between the readers were excluded from the analyses.

Otolith radii and marginal increments were measured on the concave posterior surface of the otolith (Fig. 2). Distances from the focus to the otolith edge, and from the distal edge of the last annulus to the otolith edge, were measured by a computer optical imagery system (OPTIMAS). Relationships between fish length and otolith radii were determined to provide insights into otolith growth. In addition, for otoliths to be used as valid ageing structures, otolith mark formation needs to be periodic (Powell 1975), and this was examined by marginal increment analysis.

#### Data analysis

Agreement between readers on the age of whole and sectioned otoliths was calculated by using indices of percent agreement and Beamish and Fournier's (1981) average percent error. Age bias plots modified from

Campana *et al.* (1995) were determined for whole and sectioned otoliths to detect any differences in age between the two structures and between readers. The degree of conformity between ages estimated from the same otoliths that were aged both whole and sectioned were determined to assess which structure would be used for further ageing. Monthly marginal increments were plotted for the first three age classes for school mackerel, and for the initial age class for spotted mackerel. Additional age classes for school and spotted mackerel could not be assessed for analyses of the margins because the final annulus of older fish typically extended to the edge of the otolith. One-way fixed-effects analyses of variance were used to compare the marginal increments between months of capture for each age class to discern any pattern in annulus formation. Tukey's studentized range (HSD) test was used for *a posteriori* comparisons.

Otolith radii were related to fish length by linear regression analysis.  $\text{Log}_e$ -transformed data for otolith radii standardized residuals and linearized power relationships. Fork length (LCF)–total length (TL), and LCF–weight relationships were estimated for individual species and sexes by linear regression analysis.  $\text{Log}_e$ -transformed weight data standardized the residuals. Individual sexes (within species) and species (sexes combined) were compared by analyses of covariance. Data were pooled across regions for all these analyses.

Estimates of growth parameters for the von Bertalanffy growth curve,  $L_t = L_\infty (1 - e^{-K(t - t_0)})$ , were obtained using otolith length-at-age data. von Bertalanffy growth curve parameters ( $L_\infty$ ,  $K$ ,  $t_0$ ) were determined by Marquardt nonlinear iterative least-squares regression analysis (Anon. 1990). Growth parameters were calculated for individual sexes and regions. Growth models were fitted to length-at-age data pooled across gear-types to

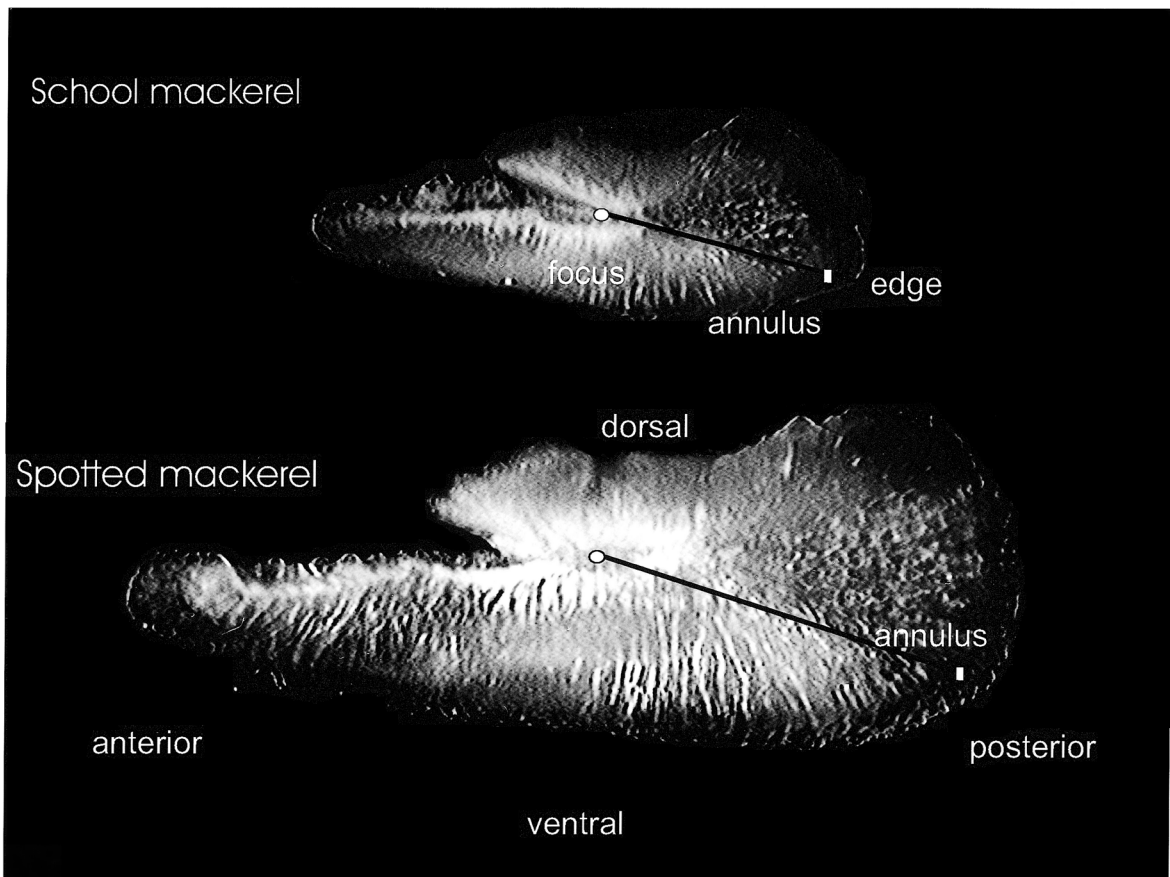


Fig. 2. Features examined in whole otoliths of school and spotted mackerel for age determination.

**Table 2.** TL–LCF (mm), and log<sub>e</sub>-transformed weight (g)–LCF (mm) relationships of school mackerel

Sex	Relationship	Intercept s.e.	Slope s.e.	<i>n</i>	<i>r</i> <sup>2</sup>
Combined	[TL] = 35.362 + 1.055[LCF]	11.302	0.022	115	0.95
Female	Log <sub>e</sub> [weight] = 3.766 + 0.006[LCF]	0.047	0.00009	129	0.97
Male	Log <sub>e</sub> [weight] = 3.781 + 0.006[LCF]	0.047	0.00009	173	0.96
Combined	Log <sub>e</sub> [weight] = 3.775 + 0.006[LCF]	0.033	0.00007	302	0.97

increase sample numbers and age classes examined. Growth curves were compared between sexes (within species) by likelihood ratio tests following Kimura (1980). Mean lengths-at-age were compared between samples collected by the different gear-types, between sexes, and between regions by using one-way fixed-effects analyses of variance or unpaired *t*-tests depending on the number of factors being compared. Tukey's studentized range (HSD) test was used for *a posteriori* comparisons.

## Results

### School mackerel

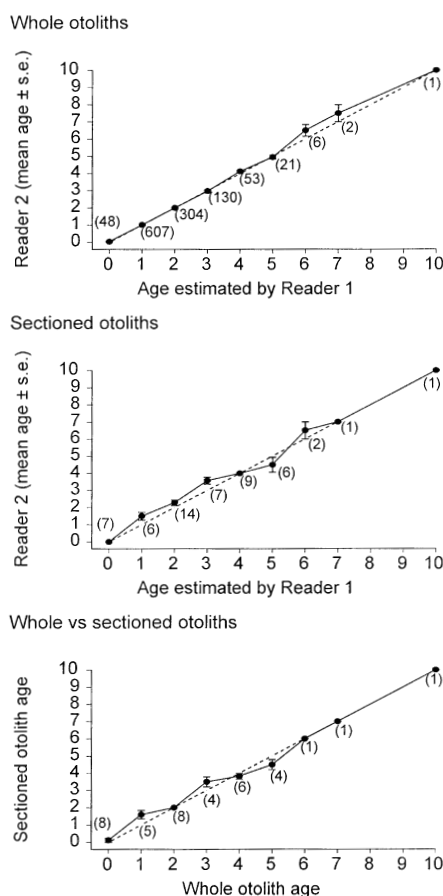
School mackerel had a significant linear relationship between TL and LCF ( $F = 2398.25$ ; d.f. 1, 113;  $P < 0.0001$ ). School mackerel sexes had similar length–weight regression slopes (ANCOVA:  $F = 0.03$ ; d.f. 1, 298; n.s.); however, males had a significantly larger intercept for their length–weight relationship (ANCOVA:  $F = 6.65$ ; d.f. 1, 299;  $P < 0.0104$ ) (Table 2).

Whole otoliths of school mackerel were more precisely aged than sectioned otoliths owing to their greater readability and clarity. In total, 1172 whole otoliths were examined, with 1034 of these having been aged the same by two independent readers (88% agreement; 2.8% average error) (Fig. 3). Likewise, 53 sectioned otoliths were examined, with 38 of these having been aged the same (72% agreement; 5.6% average error). A total of 29 of the 38 otolith sections that were aged the same by the readers had the same age as that for their corresponding whole otolith (76% agreement; 7.0% average error). No systematic age difference was observed between ages estimated for whole and sectioned otoliths (Fig. 3). Whole otoliths, therefore, were used for age and growth assessments.

Significant linear relationships of otolith radius with LCF for school mackerel showed that otolith growth was directly correlated with fish growth (Fig. 4). Marginal increment analysis confirmed that formation of otolith marks is periodic, and thus the use of otoliths as ageing structures was validated. Annuli appeared to be formed on an annual basis in school mackerel of one and two years of age from December to February, when marginal increments were generally at their shortest distance (Fig. 5). Significant monthly variation in mean marginal increments was observed for one-year-old (1-way ANOVA:  $F = 16.57$ , d.f. 11, 595;  $P < 0.0001$ ), two-year-old (1-way ANOVA:  $F = 5.29$ , d.f. 10, 207;  $P < 0.0001$ ) and three-year-old fish (1-way ANOVA:  $F = 4.21$ , d.f. 6, 40;  $P < 0.0023$ ). Marginal

increments were significantly smaller in December, January and February for one-year-old fish (HSD,  $P < 0.05$ ), in January for two-year-old fish (HSD,  $P < 0.05$ ), and in February for three-year-old fish (HSD,  $P < 0.05$ ).

Female school mackerel that were successfully aged ranged in size from 310 to 784 mm LCF. Males were between 312 and 695 mm LCF. The oldest female aged was seven years and the eldest male was ten years. Of those school mackerel aged, 45 were young-of-year fish; (84%) of these young-of-year fish were sampled in central Queensland waters using hook and line during June and July. Differences in lengths-at-age were found between line- and net-caught



**Fig. 3.** Age-bias plots between ages estimated by two independent readers and between whole and sectioned otoliths of school mackerel.

samples (Table 3). Samples that were caught by net tended to be larger than line-caught fish for any given age.

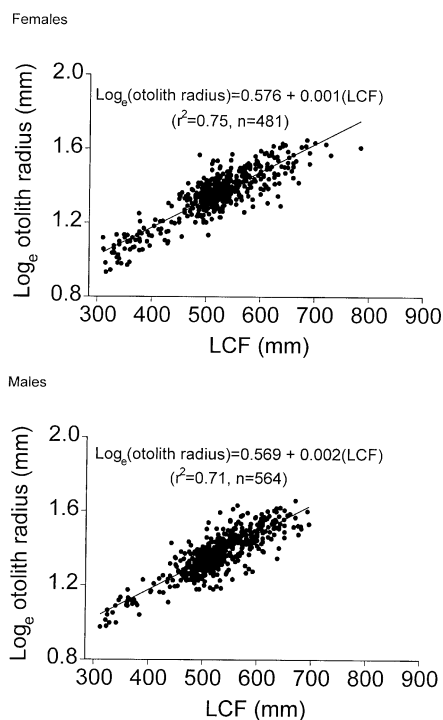
Kimura's (1980) applied likelihood ratio test indicated that female and male school mackerel have similar von Bertalanffy growth curves (ages 0 to 5:  $\chi^2 = 7.028$ ; d.f. 3; n.s.) (Fig. 6 and Table 4). Separate analyses by gear-type and region provided further support for these growth patterns because generally no differences in lengths-at-age were detected between each sex (Table 5). Similar growth patterns for school mackerel collected from the three regions were observed for each sex, with a progressive decline in growth coefficients ( $K$ ) in samples from northern to southern waters (Fig. 6 and Table 4). In contrast, greater asymptotic lengths ( $L_\infty$ ) were predicted for school mackerel sampled from southern than from northern waters (Table 4). Differences in growth between school mackerel from the different regions were confirmed by additional comparisons of length-at-age data among gear-types (Table 6). Significant differences among regions in lengths-at-age were detected for each sex.

#### Spotted mackerel

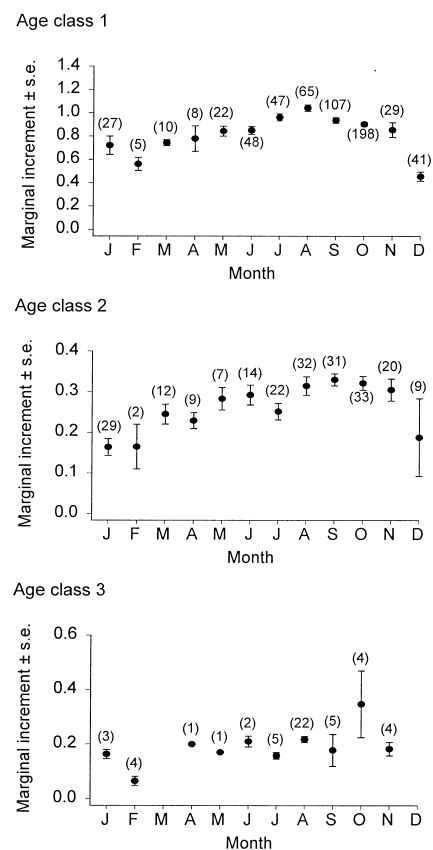
Spotted mackerel had a significant linear relationship between TL and LCF ( $F = 3393.21$ ; d.f. 1, 120;  $P < 0.0001$ ) (Table 7). Spotted and school mackerel had similar LCF-TL regression slopes (ANCOVA:  $F = 0.57$ ; d.f. 1, 233; n.s.). However, the intercept for spotted mackerel was greater than

for school mackerel (ANCOVA:  $F = 104.50$ ; d.f. 1, 234;  $P < 0.0001$ ). Similar length-weight regression slopes (ANCOVA:  $F = 1.53$ ; d.f. 1, 500; n.s.) and intercepts (ANCOVA:  $F = 2.94$ ; d.f. 1, 501; n.s.) were estimated for spotted mackerel sexes (Table 7). Length-weight data pooled for the sexes demonstrated that spotted mackerel have a significantly lesser slope in their length-weight relationship than school mackerel (ANCOVA:  $F = 146.02$ ; d.f. 1, 802;  $P < 0.0001$ ).

In total, 1385 whole otoliths of spotted mackerel were examined with 1279 of these aged the same by the two readers (92% agreement; 1.5% average error) (Fig. 7). Of those whole otoliths examined, 62 were sectioned, with 42 of these sectioned otoliths aged the same (68% agreement; 7.8% average error). A total of 37 of the 42 otolith sections that were aged the same by the readers had the same age as that for their corresponding whole otolith (88% agreement; 1.3% average error). As is the case with school mackerel, no consistent age difference was observed between ages estimated for whole and sectioned otoliths of spotted mackerel, confirming the use of whole otoliths for age and growth assessments (Fig. 7).



**Fig. 4.**  $\text{Log}_e$ -transformed otolith radius-LCF (mm) relationships of school mackerel (regions combined).



**Fig. 5.** Monthly mean marginal increments (mm)  $\pm$  s.e. of school mackerel age classes 1 to 3 (sexes and regions combined).

**Table 3. Gear-type comparisons of school mackerel mean length-at-age data ( $\pm$  s.e.)**  
n.s., non significant

Age class	Sex	Region	<i>n</i>	Line		<i>n</i>	Net		Gear comparison		
				Mean LCF	s.e.		Mean LCF	s.e.	<i>t</i>	d.f.	<i>P</i>
1	Female	Northern	14	475	6	1	541	–	–	–	–
		Central	91	515	3	–	–	–	–	–	–
		Southern	62	433	9	105	515	3	10.53	165	0.0001
	Male	Northern	9	483	7	1	607	–	–	–	–
		Central	98	519	3	–	–	–	–	–	–
		Southern	51	487	7	158	503	2	2.78	207	0.0060
2	Female	Northern	12	508	7	10	589	6	8.44	20	0.0001
		Central	30	584	6	–	–	–	–	–	–
		Southern	29	541	9	35	562	7	1.92	62	n.s.
	Male	Northern	4	530	12	12	586	8	3.67	14	0.0025
		Central	25	582	6	–	–	–	–	–	–
		Southern	58	542	4	35	557	7	1.93	91	n.s.
3	Female	Northern	8	528	9	6	613	6	7.49	12	0.0001
		Central	6	605	32	–	–	–	–	–	–
		Southern	8	584	10	8	624	7	3.34	14	0.0049
	Male	Northern	3	554	12	9	605	6	4.31	10	0.0015
		Central	7	602	15	–	–	–	–	–	–
		Southern	20	580	8	10	602	9	1.69	28	n.s.

Otolith growth was correlated with fish growth, and periodic mark formation in spotted mackerel otoliths validated their use as ageing structures. There were significant linear relationships between otolith radius and LCF (Fig. 8). Monthly differences in the marginal increments of one-year-old spotted mackerel otoliths were determined (1-way ANOVA:  $F = 35.38$ ; d.f. 6, 392;  $P < 0.0001$ ), with marginal increments being significantly lower from August to December (HSD,  $P < 0.05$ ) when annuli were formed, although the data were sparse between April and July (Fig. 9). Additional age classes could not be assessed for marginal analyses because the final annulus of older fish typically extended to the edge of the otolith.

Female spotted mackerel ranged from 485 to 860 mm LCF. Males were between 448 and 751 mm LCF. Females were aged to five years and males to seven years. Only one

spotted mackerel, captured in the central region in May, was young-of-year. As was the case for school mackerel, differences in lengths-at-age were detected between spotted mackerel captured by the different gear-types (Table 8). Net-caught samples were generally larger than those captured by hook and line for a given age.

Spotted mackerel were predicted to reach larger asymptotic lengths but have lower growth coefficients than school mackerel (Table 9). Distinct sex-specific growth curves were observed for spotted mackerel ( $\chi^2 = 1069.3$ ; d.f. 3;  $P < 0.0001$ ), with females typically having greater asymptotic lengths and growth coefficients than males (Fig. 10 and Table 9). Separate analyses by gear-type and region provided additional support to these sex-specific growth curves, with females being significantly larger than males for any given age (Table 10). Within each sex, spotted

**Table 4. von Bertalanffy growth parameters ( $\pm$  95% confidence intervals) calculated from length-at-age data of school mackerel**

Sex	Region	<i>n</i>	$L_{\infty}$ (95% c.i.)	<i>K</i> (95% c.i.)	$t_0$ (95% c.i.)
Female	Northern	58	573 (541, 605)	1.226 (–0.009, 2.460)	–0.478 (–1.837, 0.881)
	Central	154	656 (633, 680)	0.771 (0.647, 0.896)	–0.969 (–1.122, –0.816)
	Southern	262	885 (554, 1216)	0.171 (–0.007, 0.349)	–3.656 (–5.940, –1.372)
	Combined	474	651 (623, 678)	0.585 (0.454, 0.716)	–1.411 (–1.749, –1.074)
Male	Northern	47	616 (587, 644)	0.954 (0.322, 1.586)	–0.716 (–1.776, 0.344)
	Central	155	636 (616, 656)	0.878 (0.740, 1.016)	–0.913 (–1.059, –0.767)
	Southern	356	708 (641, 775)	0.287 (0.161, 0.414)	–3.220 (–4.371, –2.069)
	Combined	558	628 (614, 641)	0.709 (0.610, 0.808)	–1.262 (–1.472, –1.053)

**Table 5.** Sex comparisons by gear type and region of school mackerel mean length-at-age data ( $\pm$  s.e.)  
n.s., non significant

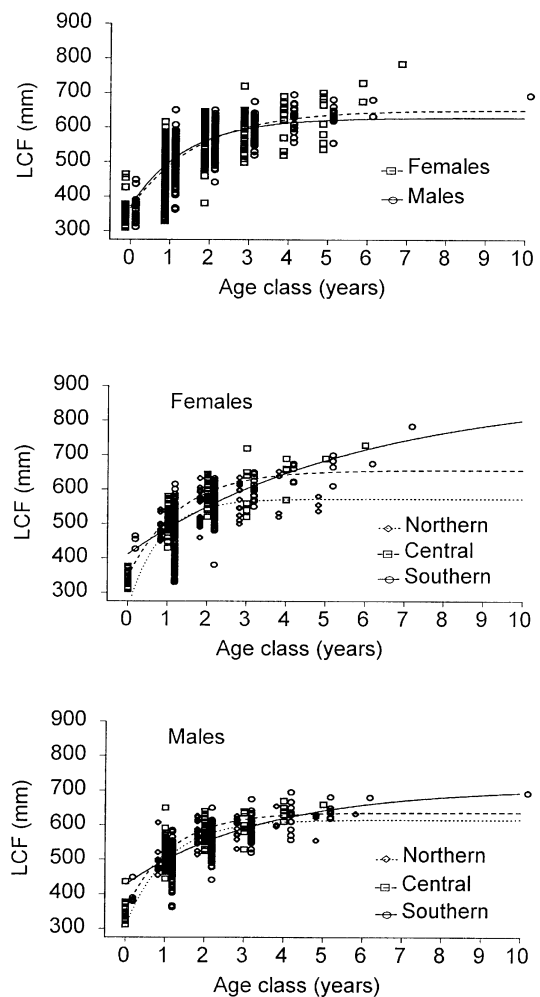
Age class	Gear	Region	Sex comparison		
			<i>t</i>	d.f.	<i>P</i>
0	Line	Northern	–	–	–
		Central	–0.81	36	n.s.
		Southern	–	–	–
	Net	Northern	–	–	–
		Central	–	–	–
		Southern	2.25	5	n.s.
1	Line	Northern	–0.81	21	n.s.
		Central	–0.97	187	n.s.
		Southern	–4.56	111	0.0001
	Net	Northern	–	–	–
		Central	–	–	–
		Southern	3.43	261	0.0007
2	Line	Northern	–1.54	14	n.s.
		Central	0.23	53	n.s.
		Southern	–0.14	85	n.s.
	Net	Northern	0.31	20	n.s.
		Central	–	–	–
		Southern	0.51	68	n.s.
3	Line	Northern	–1.62	9	n.s.
		Central	0.09	11	n.s.
		Southern	0.25	26	n.s.
	Net	Northern	0.99	13	n.s.
		Central	–	–	–
		Southern	1.81	16	n.s.
4	Line	Northern	–	–	–
		Central	0.11	9	n.s.
		Southern	1.03	13	n.s.
	Net	Northern	–0.38	3	n.s.
		Central	–	–	–
		Southern	–	–	–
5	Line	Northern	–	–	–
		Central	–	–	–
		Southern	0.57	7	n.s.
	Net	Northern	–	–	–
		Central	–	–	–
		Southern	–	–	–

mackerel appeared to have similar growth characteristics regardless of the region in which they were caught (Fig. 10 and Table 9), and this was supported by length-at-age data in the analysis by gear-type (Table 11).

## Discussion

### Ageing

*Scomberomorus* species have traditionally been aged by using whole otoliths because they are easier to prepare than sectioned otoliths (Manooch *et al.* 1987), and because whole



**Fig. 6.** von Bertalanffy growth curves fitted to length-at-age data for each sex in school mackerel ( $R^2 = 0.99$  for each von Bertalanffy model).

otoliths in mackerel are laterally compressed and have reduced transverse growth. Greater problems in clarity and hence in reliability were encountered in the interpretation of school and spotted mackerel otolith sections than with whole otoliths. Higher indices of average percent error and lower percent agreement between readers for ages estimated from sectioned otoliths than for those from whole otoliths reflected the lower confidence of the readers in using sectioned otoliths for ageing purposes. Likewise, Collins *et al.* (1989) found poor ageing agreement between whole and sectioned otoliths (47%) for king mackerel (*Scomberomorus cavalla*) from the Atlantic coast of the USA. Discrepancies in the distribution of ages estimated from the same whole and sectioned otoliths may be attributable to differences in opacity and appearance of otoliths from fish of different provenance. Otoliths of the same species of fish from different areas can have different annulus patterns, reflecting different growth rates of separate stocks (Williams and



**Table 6. Regional comparisons of school mackerel mean length-at-age data ( $\pm$  standard error) (n.s. - non significant)**

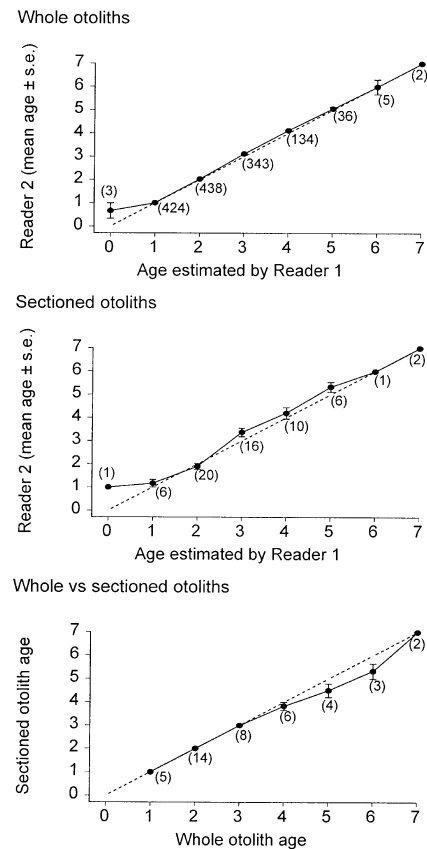
Age class	Gear	Sex	Region comparison			Regional differences (HSD; $P < 0.05$ )
			$F$ or ( $t$ )	d.f.	$P$	
1	Line	Female	53.47	2, 164	0.0001	North/Central/South
		Male	14.18	2, 155	0.0001	
	Net	Female	–	–	–	–
		Male	–	–	–	–
2	Line	Female	18.38	2, 68	0.0001	North/Central/South
		Male	13.65	2, 84	0.0001	
	Net	Female	–1.94	43	0.0500	North/South
		Male	–2.23	45	0.0310	North/South
3	Line	Female	5.53	2, 19	0.0128	North/Central
		Male	2.10	2, 27	n.s.	
	Net	Female	1.23	12	n.s.	–
		Male	–0.22	17	n.s.	–
4	Line	Female	4.90	2, 7	0.0467	North/Central
		Male	1.32	2, 15	n.s.	
	Net	Female	–	–	–	–
		Male	–	–	–	–

Bedford 1974), or differences in the manner in which material is deposited, that in turn may affect the clarity and readability of the structure.

Although only a small number of otoliths were sectioned and aged in this study, the lack of any apparent systematic bias in ages between whole and sectioned otoliths confirmed the use of whole otoliths as the preferred ageing structure for school and spotted mackerel. Generally, other *Scomberomorus* ageing studies have found little difference in ages estimated from whole or sectioned otoliths, supporting the use of the former structure as the preferred ageing configuration. Johnson *et al.* (1983) had a 97% agreement between age estimates from whole and sectioned otoliths for king mackerel from the south-eastern USA, with similar results observed by Manooch *et al.* (1987) for king mackerel, and by Fable *et al.* (1987) and Schmidt *et al.* (1993) for Spanish mackerel (*Scomberomorus maculatus*).

**Table 7. TL–LCF (mm), and  $\log_e$ -transformed weight (g)–LCF (mm) relationships of spotted mackerel**

Sex	Relationship	Intercept s.e.	Slope s.e.	$n$	$r^2$
Combined	[TL] = 61.953 + 1.034[LCF]	10.500	0.018	122	0.97
Females	$\log_e$ [weight] = 4.469 + 0.005[LCF]	0.066	0.0001	223	0.90
Males	$\log_e$ [weight] = 4.316 + 0.005[LCF]	0.129	0.005	281	0.66
Combined	$\log_e$ [weight] = 4.453 + 0.005[LCF]	0.063	0.0001	504	0.81

**Fig. 7.** Age-bias plots between ages estimated by two independent readers and between whole and sectioned otoliths of spotted mackerel.

#### Age validation

Marginal increment analysis, the only method used, appeared to validate otolith marks as indicators of annual growth up to two years of age in school mackerel and one year in spotted mackerel. Beyond those ages the proximity of later annuli to the edge reduced the effectiveness of marginal increments. Marginal increments were typically at a minimum from December to February for school mackerel, and from August to December for spotted mackerel, when annulus formation was presumed to occur.

Synchronization of annulus formation with gonad maturation and spawning has been observed in king mackerel throughout Trinidad waters (Sturm and Salter

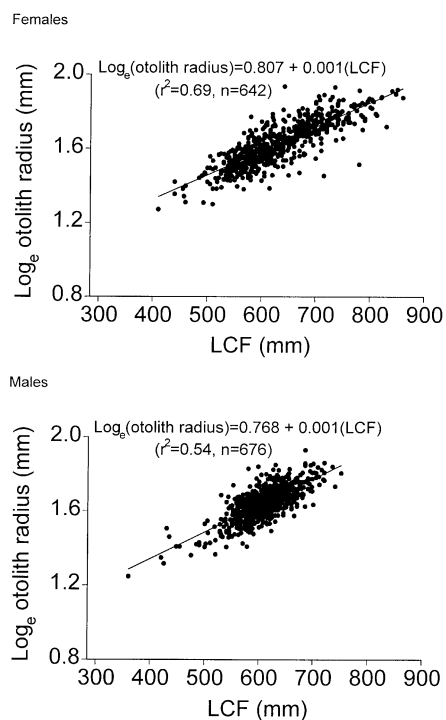
1990) and in narrow-barred Spanish mackerel along the Australian east coast (McPherson 1992). Similarly, annulus formation may be correlated with spawning behaviour in school and spotted mackerel because it coincided with the peak spawning months of October to January for school

mackerel and August to October for spotted mackerel (Begg 1998). It has also been hypothesized that annulus formation is related to seasonal changes in growth rate (Williams and Bedford 1974). Thus, annuli may form when growth slows as a result of the transfer of energy reserves from growth to reproductive processes.

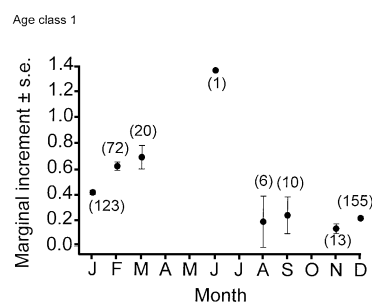
Tag-recapture methods in association with oxytetracycline injections were also attempted as a means of age validation, but were unsuccessful owing to the low recapture rates for both species (Begg *et al.* 1997). Recaptured fish that were injected were usually caught within 40 days of release, which was too soon to observe any substantial growth.

### Growth

School and spotted mackerel grew quickly for the first three years of life, after which growth tended to slow. Similar patterns have been observed for king mackerel (Johnson *et al.* 1983; Manooch *et al.* 1987), narrow-barred



**Fig. 8.**  $\text{Log}_{10}$ -transformed otolith radius–LCF (mm) relationships of spotted mackerel (regions combined).



**Fig. 9.** Monthly mean marginal increments (mm)  $\pm$  s.e. of spotted mackerel age class 1 (sexes and regions combined).

**Table 8.** Gear-type comparisons of spotted mackerel mean length-at-age data ( $\pm$  s.e.)

n.s., non significant

Age class	Sex	Region	n	Line	s.e.	n	Net	s.e.	Gear comparison		
				Mean LCF			Mean LCF		t	d.f.	P
1	Female	Northern	3	539	10	3	696	6	–	–	–
		Southern	91	573	4	275	588	2	3.36	364	0.0009
	Male	Northern	2	451	3	–	–	–	–	–	–
		Southern	5	515	7	39	543	4	2.22	42	0.0318
2	Female	Northern	5	681	8	78	690	4	0.61	81	n.s.
		Southern	25	691	9	62	670	5	–2.19	85	0.0312
	Male	Northern	8	574	6	32	592	6	1.55	38	n.s.
		Southern	23	574	4	168	585	2	2.63	189	0.0092
3	Female	Northern	1	750	–	32	751	10	–	–	–
		Southern	7	725	35	7	718	13	–0.19	12	n.s.
	Male	Northern	34	612	5	142	623	2	2.41	174	0.0171
		Southern	6	624	4	74	617	3	–0.72	78	n.s.
4	Female	Northern	2	760	26	6	769	41	–	–	–
		Southern	1	860	–	1	820	–	–	–	–
	Male	Northern	8	656	10	82	655	3	–0.13	88	n.s.
		Southern	3	674	27	13	641	6	–1.88	14	n.s.

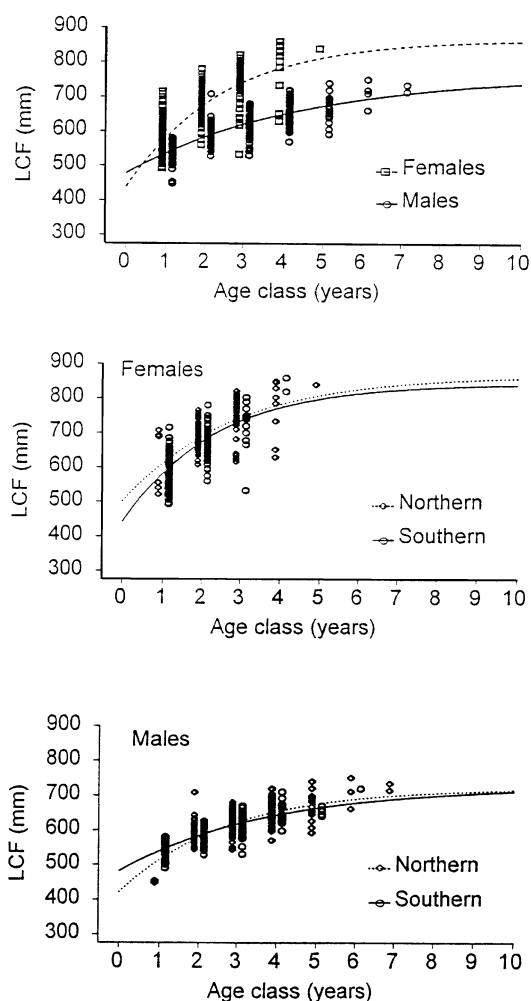
**Table 9.** von Bertalanffy growth parameters ( $\pm 95\%$  confidence intervals) calculated from length-at-age data of spotted mackerel

Sex	Region	<i>n</i>	$L_{\infty}$ (95% c.i.)	<i>K</i> (95% c.i.)	$t_0$ (95% c.i.)
Female	Northern	131	869 (697, 1041)	0.362 (-0.046, 0.771)	-2.371 (-5.217, 0.476)
	Southern	469	923 (681, 1165)	0.308 (0.032, 0.583)	-2.258 (-3.729, -0.787)
	Combined	600	849 (784, 915)	0.459 (0.291, 0.627)	-1.539 (-2.114, -0.964)
Male	Northern	333	723 (680, 766)	0.368 (0.201, 0.535)	-2.370 (-3.805, -0.935)
	Southern	340	727 (665, 789)	0.269 (0.140, 0.398)	-4.041 (-5.660, -2.422)
	Combined	673	768 (710, 826)	0.225 (0.141, 0.310)	-4.329 (-5.656, -3.003)

Spanish mackerel (McPherson 1992; Govender 1994), and Spanish mackerel (Powell 1975; Fable *et al.* 1987). *Scomberomorus* development patterns are consistent with generalized large-prey fast-growth strategies which ensure rapid growth through the early life stages that are vulnerable to predation (Jenkins *et al.* 1984). As is characteristic of *Scomberomorus* species (Beaumariage 1973; Powell 1975;

Sturm 1978; Johnson *et al.* 1983; Fable *et al.* 1987; McPherson 1992; Schmidt *et al.* 1993; DeVries and Grimes 1997), school and spotted mackerel have differential growth patterns between the sexes, with females tending to grow to a larger size ( $L_{\infty}$ ) than males.

School mackerel grew to their asymptotic size at a faster rate than spotted mackerel, but did not grow as large. Reasons for higher growth rates in species when effects of exogenous factors are excluded include lower metabolic rates and increased rates of food consumption (Cui and Liu 1990). The more extensive migration suggested by tag-recapture data for spotted mackerel (Begg *et al.* 1997) may use energy reserves that in school mackerel can be devoted to body conditioning. Alternatively, faster growth of school mackerel may be related to greater food availability within the localized regions that the species inhabits. De Vries *et al.* (1990) suggested that greater food availability was responsible for the higher growth rates observed in king mackerel compared with those in Spanish mackerel. Further research is needed to evaluate the contribution of metabolic processes and food availability to the observed growth rates of school and spotted mackerel.

**Fig. 10.** von Bertalanffy growth curves fitted to length-at-age data for each sex in spotted mackerel ( $R^2 = 0.99$  for each von Bertalanffy model).**Table 10.** Sex comparisons by gear type and region of spotted mackerel mean length-at-age data ( $\pm$  s.e.)

Age class	Gear	Region	Sex comparison		
			<i>t</i>	d.f.	<i>P</i>
0	Line	Northern	6.80	3	0.0065
		Southern	3.56	94	0.0006
	Net	Northern	—	—	—
		Southern	7.79	312	0.0001
2	Line	Northern	11.11	11	0.0001
		Southern	11.25	46	0.0001
	Net	Northern	14.70	108	0.0001
		Southern	22.48	228	0.0001
3	Line	Northern	—	—	—
		Southern	2.68	11	0.0214
	Net	Northern	20.28	172	0.0001
		Southern	10.46	79	0.0001
4	Line	Northern	4.31	8	0.0026
		Southern	—	—	—
	Net	Northern	7.19	86	0.0001
		Southern	—	—	—

**Table 11. Regional comparisons of spotted mackerel mean length-at-age data ( $\pm$  s.e.)**  
n.s., non significant

Age class	Gear	Sex	Region comparison			Regional difference (HSD; $P < 0.05$ )
			<i>t</i>	d.f.	<i>P</i>	
2	Line	Female	0.47	28	n.s.	–
		Male	0.01	29	n.s.	–
	Net	Female	–3.36	138	0.0010	North / South
		Male	–1.16	198	n.s.	–
3	Line	Female	–	–	–	–
		Male	1.04	38	n.s.	–
	Net	Female	–1.47	37	n.s.	–
		Male	–1.84	214	n.s.	–
4	Line	Female	–	–	–	–
		Male	0.76	9	n.s.	–
	Net	Female	–	–	–	–
		Male	–1.58	93	n.s.	–
5	Line	Female	–	–	–	–
		Male	–	–	–	–
	Net	Female	–	–	–	–
		Male	–1.14	25	n.s.	–

#### Implications for stock structure

Differences in growth patterns for school mackerel indicated stock separation along the Queensland east coast. Although these growth curves may have been confounded by selectivity of different gear-types, length-at-age differences for each sex sampled within individual fishing gears confirmed the apparent growth differences between school mackerel from the different regions. Variation in growth patterns from northern to southern waters supported the existence of a population cline. Similar stock differentiation has been found in other *Scomberomorus* species. McPherson (1992) detected differences in lengths-at-age for narrow-barred Spanish mackerel from Australian east-coast and Torres Strait waters, suggesting stock separation between fish from these regions, a conclusion compatible with that of Shaklee *et al.* (1990), who used electrophoretic techniques. Likewise, differences in growth rates of Spanish mackerel (Fable *et al.* 1987) and king mackerel (Sutter *et al.* 1991; DeVries and Grimes 1997) from different geographic areas provided evidence of stock separation in the Gulf of Mexico and Atlantic Ocean for each of these species. In contrast, similar growth patterns of spotted mackerel sampled from different coastal regions indicated that there may be one stock throughout Queensland east-coast waters.

Tag–recapture data for school and spotted mackerel provided additional support for the suggested stock structures along the Queensland east coast (Begg *et al.* 1997). Restricted movements of school mackerel indicated

the existence of a number of stocks, whereas movements of spotted mackerel were characteristic of fish of a single stock undertaking a seasonal migration. Identification of school and spotted mackerel populations in Queensland east-coast waters will enable the species to be managed on the basis of stock structure across this range. Management of spotted mackerel should involve fisheries representatives throughout Queensland. In contrast, management actions for school mackerel could proceed at a regional level owing to the suggested multi-stock structure of the species (Begg *et al.* 1997).

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