Abstract.—The concentrations of 11 elements in individual whole sagittal otoliths from school mackerel (*Scomberomorus queenslandicus*) and spotted mackerel (*Scomberomorus munroi*) collected in east coast waters of Queensland, Australia (16°S to 28°S) were determined by using inductively coupled plasma atomic emission spectroscopy (ICP-AES). Spatial and ontogenetic variation in otolith elemental composition was examined to make inferences about the stock structure of these species. Stepwise canonical discriminant analyses of the concentrations of barium, potassium, magnesium, manganese, sodium, phosphorus, sulphur, and strontium were used to differentiate groups of fish. These analyses identified an optimum grouping of at least two stocks of school mackerel and a single stock of spotted mackerel in the study region, although our results showed that the most informative comparisons were made among fish of the same year class. The age of fish in collected samples produced strongly significant effects on mean elemental composition of otoliths. These patterns offered independent support for hypotheses about stock structure from previous tagging, catch monitoring, ageing, and reproductive studies. Discrimination between school and spotted mackerel stocks will enable the species to be managed on the basis of stock structure throughout their east coast distribution.

Stock discrimination of school mackerel, *Scomberomorus queenslandicus*, and spotted mackerel, *Scomberomorus munroi*, in coastal waters of eastern Australia by analysis of minor and trace elements in whole otoliths

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Manuscript accepted 25 February 1998.
Fish. Bull. 96:653–666 (1998).

Spanish mackerels of the genus *Scomberomorus* have restricted ranges and are found in coastal waters of eastern Australia within the confines of the 20°C isotherm (Munro, 1943). Throughout their range they form the basis of important commercial, recreational, and artisanal fisheries, which are characterized by mixed gear types, seasonal availability at widespread points of capture, and movement or migration through various coastal jurisdictions (Trent et al., 1987; Johnson et al., 1994). These traits make it necessary, but difficult, to identify the stock structure of *Scomberomorus* species for effective fisheries management.

Tag-recapture information, catch and effort data, reproductive studies, larval surveys, and protein electrophoresis have recently been used to determine the stock structure of king mackerel (*Scomberomorus cavalla*) in the Gulf of Mexico and Atlantic Ocean (Sutter et al., 1991; Johnson et al., 1994). In northern Australia, stock structure of the large narrow-barred Spanish mackerel (*Scomberomorus commerson*) has been inferred from protein electrophoresis (Shaklee et al., 1990), whereas hypothetical stock structures have been developed for the "lesser" mackerels—school mackerel (*Scomberomorus queenslandicus*) and spotted mackerel (*Scom-*

beromorus munroi)—from tagging, catch data, and ageing and reproductive patterns (Begg et al., 1997; Begg and Sellin, 1998; Begg, in press).

School and spotted mackerel co-occur in coastal waters of northern Australia and southern Papua New Guinea (Collette and Russo, 1984). Within Australian waters they are a major part of set gillnet and ring-net commercial fisheries and support popular recreational fisheries, especially in the region from Moreton Bay to Townsville (Fig. 1). Between 1992 and 1995 the Queensland commercial catch averaged 160 metric tons, and the recreational landings were estimated to be at least half as large as their commercial counterparts (Cameron and Begg[1]). Tag-recapture data indicate that school mackerel move small distances, in contrast to spotted mackerel that migrate annually along the Australian east coast (Begg et al., 1997). Both species reach 100 cm in fork length (LCF, tip of snout to fork of tail) and 8 kg in weight (Collette and Russo, 1984), and first maturity occurs within 2 years of age, between 35 and 50 cm LCF (Begg, in press). Along the Queensland east coast, school mackerel spawn between October and January, whereas spotted mackerel spawn from August to October in northern Queensland waters (Begg, in press). A number of separate school mackerel stocks are thought to exist along the Queensland east coast, whereas spotted mackerel may form a single stock (Begg et al., 1997; Begg and Sellin, 1998; Begg, in press).

[1] Cameron, D. S., and G. A. Begg. 1998. Fisheries biology and interaction in the northern Australian small mackerel fishery. Fisheries Research and Development Corporation 92/144. Unpublished manuscript.

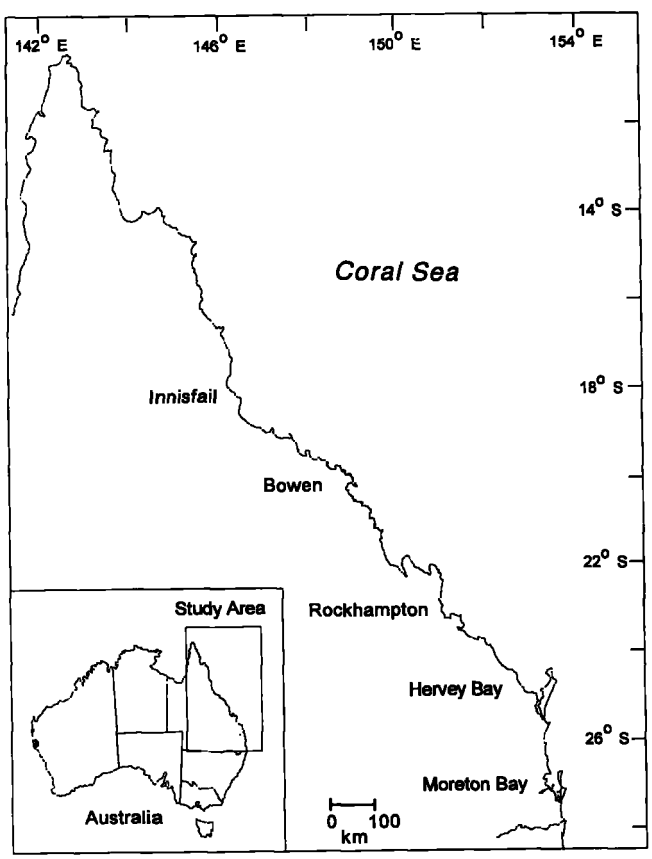

Figure 1
Sampling locations for school and spotted mackerel.

The lack of a direct and widely applicable technique to trace larval dispersal has encouraged development of a wide range of methods to deduce stock structure (Thresher et al., 1994) including analysis of the elemental composition of otoliths (Mulligan et al., 1987; Campana et al., 1994; Thresher et al., 1994; Edmonds et al., 1995; Proctor et al., 1995; Kalish et al., 1996). Inference about stock structure from these studies presumes that geographically distinct stocks possess a characteristic elemental composition that reflects the chemical constituents of the environment in which the fish reside.

The elemental composition of otoliths has been measured by analysis of dissolved whole otoliths and by scanning otolith cores or sections with a variety of different electron beam and laser probes (Gunn et al., 1992; Campana et al., 1994). Solution-based or "bulk" chemical analyses of otoliths have the benefits of greater replication in sample sizes through reduced time and cost for preparation, calibration, and measurement (Campana and Gagné, 1995; Campana et al., 1995). However, bulk analysis of whole otoliths incorporate an integrated chemical signal that represents the entire ontogenetic history and home range of individual fish in a nonlinear form that is governed by the growth of the otolith matrix in terms of both rate of deposition and volumetric considerations. Consequently, the mean composition of an otolith in a bulk analysis could be disproportionately dominated by the deposition of material prior to capture, preventing fine-scale resolution of individual affinities with spawning grounds and larval habitats (Campana et al., 1995).

The present study was conducted to determine the utility of elemental analysis of whole otoliths in studying the prevailing hypotheses of a multistock complex for school mackerel and a single stock for spotted mackerel in coastal waters of eastern Australia. Analyses were specifically structured to account for and distinguish the influence of fish age on elemental composition of otoliths. Interpretation of stock structure in this study relates to Ihssen et al.'s (1981) definition of a stock as "a group of randomly mating, reproductively isolated individuals of a single species with temporal or spatial integrity."

Materials and methods

Otolith chemistry

School and spotted mackerel were collected monthly from commercial and recreational fisheries along the Queensland east coast, south of 16°S, between June 1992 and February 1995 (Fig. 1). School mackerel were sampled from three geographic areas and spotted mackerel from four (Table 1). Samples were obtained from independent collections at each area, usually representing fish caught from several different schools. Specimens were kept on ice, then frozen until length to caudal fork (LCF, mm) was measured, sex was determined, and both sagittae were removed, washed, dried, and weighed. Fish were aged from whole and sectioned sagittae according to Begg and Sellin (1998).

Precautions were taken to prevent confounding of results based on sexual maturity, size, and age. All samples were sexually mature, between the lengths of 492 mm and 790 mm LCF (Table 1). Fish of the same age (2-year-old school mackerel; 3-year-old spotted mackerel) were selected to minimize age-related variation amongst samples. Additional samples of 1-year-old school mackerel from Rockhampton and 1-year-old spotted mackerel from Moreton Bay and Hervey Bay were examined in relation to the older samples from the same areas to investigate the effects of age on the concentrations of elements in sagittae.

Whole otoliths used in the analysis were cleaned of oil and organic residuals in an ultrasonic bath, rinsed in distilled water, and oven-dried at 60°C for 15 hours. Otoliths were dissolved in 0.5 mL of a Lefort aqua regia solution (75% nitric and 25% hydrochloric acid) and placed in an AIM500 block digester at 90°C for 30 minutes. After cooling, the solutions were made up to 10 mL with distilled water and analyzed with a Varian Liberty 220 inductively coupled plasma atomic emission spectrometer (ICP-AES). Eleven elements (Ba, Ca, Fe, K, Li, Mg, Mn, Na, P, S, and Sr) were analyzed from each otolith, and the concentrations were standardized for individual otolith weights.

Minimum detection limits for the elements were determined by averaging a series of acid blank solutions for both species that were regularly interspersed throughout the samples. The minimum detectable solution concentration for each element (mg/L) was converted to the minimum detectable otolith concentration (mg/Kg) by using the solution volume and the smallest whole otolith weight actually analyzed. This procedure ensured that the most conservative (largest) minimum detection limits were used in the analyses. Three standard solutions were included regularly among the samples to calibrate measurements. The standards covered the entire weight range of otolith material used in the analyses. Only those elements measured in concentrations above the minimum detection limits of the ICP-AES were used in the statistical analyses.

Data analysis

The chemical composition of school and spotted mackerel whole otoliths sampled from the different areas was analyzed to identify the optimum groupings of fish in order to make inferences about stock structure. All data were examined for normality and homogeneity of variances, and concentrations of Mg and Na in school mackerel otoliths, and K, Mg, Na, and P in otoliths of spotted mackerel, were $\log_e$-transformed to enable statistical analysis. Analysis of covariance (ANCOVA) was used to determine the effect of area of collection (the main effect) on the concentration of each element, while controlling for effects due to fish length (the covariate). Elemental concentrations for which area-by-length interactions were significant were not included in further analy-

Table 1

Data from school and spotted mackerel samples used in otolith trace element analyses.

School mackerel					Spotted mackerel				
Date	Area	*n*	Length range (mm)	Age (yr)	Date	Area	*n*	Length range (mm)	Age (yr)
Nov 1993	Moreton Bay	19	512–614	2	Feb 1994	Moreton Bay	30	555–685	1
Jun 1993	Rockhampton	25	492–574	1	Feb 1994	Hervey Bay	28	544–715	1
Jun 1993	Rockhampton	19	552–640	2	Dec 1993	Hervey Bay	29	552–790	3
Aug 1993	Bowen	22	545–632	2	Aug 1993	Bowen	32	605–670	3
					Jul 1993	Innisfail	28	585–665	3

ses. Elements for which concentrations were significantly correlated with length were corrected for statistical analysis as

$$AC = C - rL,$$

where AC = the corrected concentration, adjusted for fish length;
C = the concentration of a given element (mg/Kg) for a fish of fork length L (mm); and
r = the regression coefficient or the "common slope" for the covariate length (Edmonds et al., 1989).

ANCOVA and other subsequent analyses were also performed with otolith weight as the covariate, but they showed lower power in discriminating among groupings of fish. This lower discriminatory power was probably a result of the greater measurement errors in obtaining otolith weights in relation to measurement of fish length. Therefore, concentrations of elements corrected for length only were used in the final discriminant analyses.

Multivariate analysis of variance (MANOVA) was used to compare the mean corrected elemental concentrations of samples from the different areas. One-way fixed effects and unbalanced analyses of variance (ANOVA) were then used to compare concentrations of individual elements in samples from different areas to explain differences detected by the MANOVAs. Significance levels were corrected for multiple testing with the Bonferroni adjustment factor. Tukey's studentized range (HSD) tests were used for *a posteriori* comparisons of the different areas for each significant element.

Principal component analysis (PCA) of the corrected concentrations of elements was used to investigate grouping patterns by area and fish age. ANOVA was performed on the first (PC I) and second (PC II) principal components to test differences among proposed groups. Forward stepwise canonical discriminant analyses were used to detect differences in the length-corrected chemical composition of otoliths for school and spotted mackerel from the different areas. The significant ($P<0.05$) canonical variates (CV) provided by each analysis represented the optimal combination of areas and elements that provided the best overall discrimination between the samples. The pooled-within-groups correlations of significant length-corrected elemental concentrations with each canonical variate approximated the contribution of the respective element to the discrimination between areas. Wilks's lambda denoted the statistical significance of the discriminatory power of the overall model, ranging from 1.0 to 0.0 (perfect discrimination). ANOVA and HSD were used on the significant discriminant functions to test pairwise comparisons among groups detected by the discriminant analysis. Jack-knifed cross-validation procedures were used to give an unbiased estimate of classification success (SYSTAT, 1997).

Results

School mackerel

We measured the concentration of 11 trace and minor elements in whole otoliths of school mackerel (Fig. 2). Iron and lithium were highly variable, often at concentrations below the detection limits of the spectrometer, and were excluded from data analyses. Calcium was also excluded because its high concentration (31.4–44.7%) would mask contribution of trace elements in the data analyses. The remaining elements (Ba, K, Mg, Mn, Na, P, S, and Sr) were present in measurable quantities, suitable for statistical analyses. ANCOVA indicated that none of these eight elements were correlated with fish length for school mackerel. However, there was a significant interaction in the concentration of Ba with area of collection and fish length (ANCOVA, $F=2.75$, df=3, 76, $P<0.05$); therefore the Ba data were not used in the discriminatory analyses. This interaction was caused by an inverse relationship between Ba concentration and fish length for school mackerel from Bowen, whereas samples from the other areas all showed positive correlations between Ba concentration and fish length.

School mackerel from each age class in each area were found to have significantly different mean elemental composition of otoliths (MANOVA, Pillai's trace=1.013, $F=5.54$, df=21, 228, $P<0.0001$). Mean concentrations of individual elements, except for S and Sr, varied significantly among school mackerel from the different areas and between different age classes (Fig. 2). Sodium, P, and Mg concentrations differed the most among the study areas, and there were significant differences in concentrations of Na and P between fish from Bowen and those from Rockhampton and Moreton Bay. There were also significantly higher concentrations of K in otoliths of Bowen fish, compared with those from Rockhampton (HSD, $P<0.05$). No significant differences in elemental composition of otoliths were detected between 2-year-old school mackerel from Rockhampton and Moreton Bay. In contrast, significant differences were found for Mg, Mn, Na, and P concentrations between 1- and 2-year-old fish from Rockhampton, suggest-

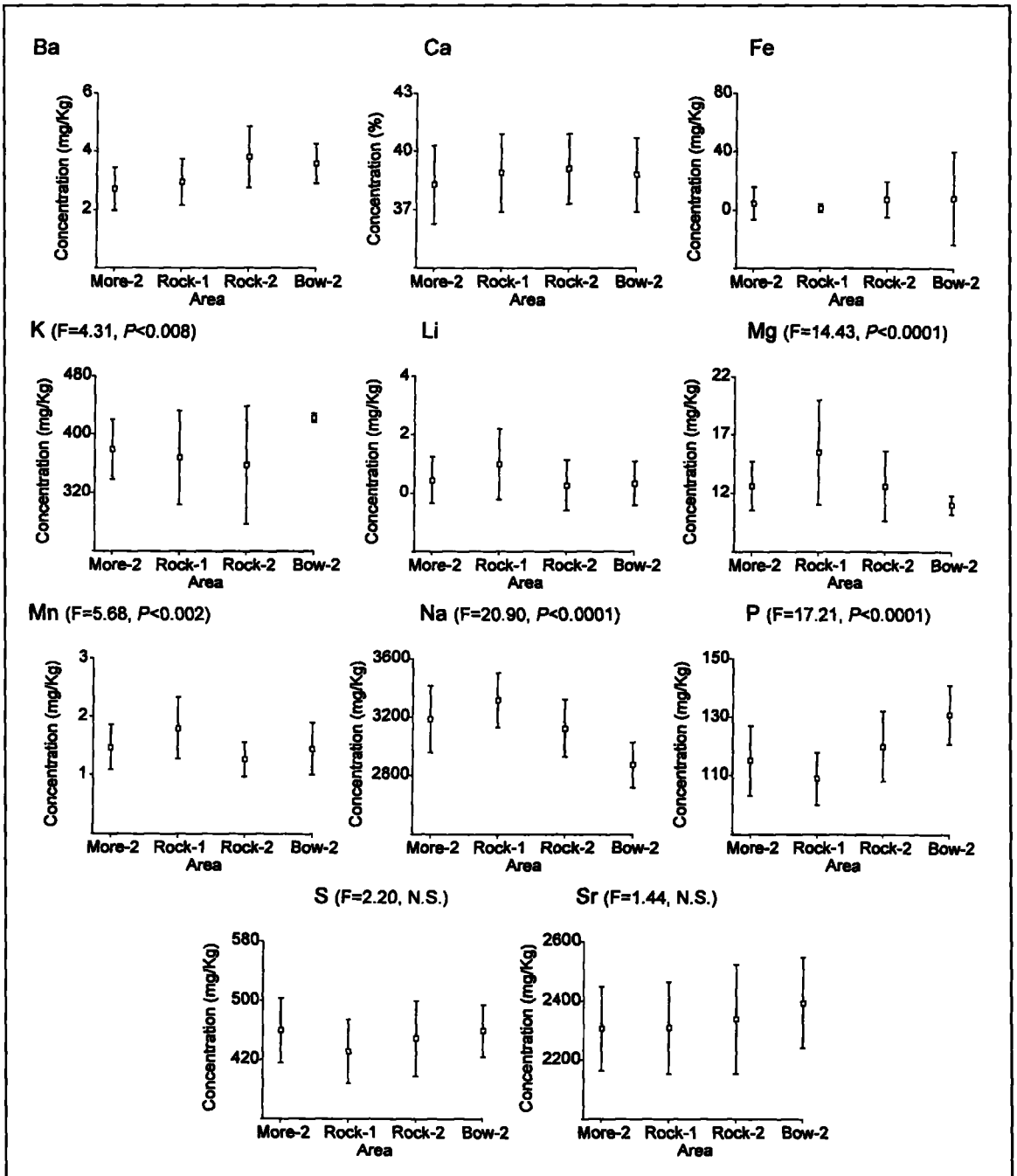

Figure 2

Mean elemental concentrations (± standard deviation) of school mackerel otoliths sampled from the different areas and *F*-values determined from ANOVA showing significant elements among samples (df=3, 80; N.S.=nonsignificant result). Minimum elemental detection limits of the inductively coupled plasma atomic emission spectroscopy (ICP-AES) (all units are in mg/Kg, except Ca which is measured as a %): Ba = 0.78; Ca = 544; Fe = 23.9; K = 353; Li = 15.0; Mg =10.9; Mn = 1.10; Na = 1250; P = 54.1; S =191; Sr = 3.24.

ing a strong effect of age at collection in measurement of the elemental composition of otoliths in this area (HSD, $P<0.05$). Sodium showed the most significant differences in these univariate analyses (Fig. 2) and was selected as the common variable for scatterplots in Figure 3. Scatterplots of the relationships between Na and the other significant elemental concentrations revealed similar spatial patterns

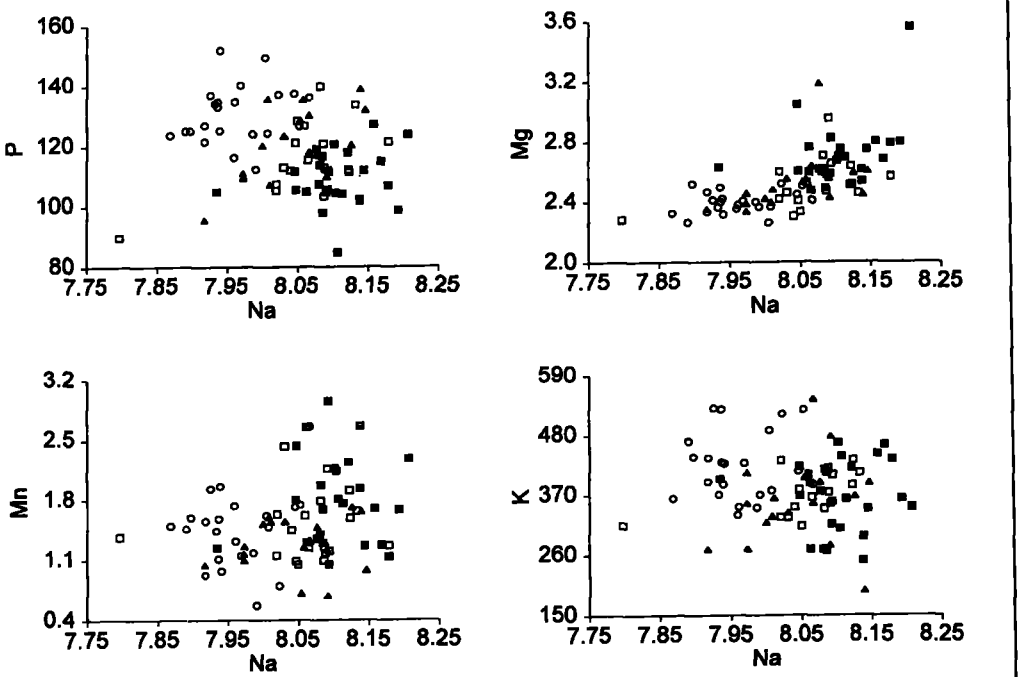

Figure 3

Scatterplots of significant elemental ratios showing grouping patterns of area and age school mackerel samples. Open circle = Bowen 2-year-old fish; open square = Moreton Bay 2-year-old fish; solid square = Rockhampton 1-year-old fish; and solid triangle = Rockhampton 2-year-old fish. Mg and Na are $\log_e$-transformed concentrations.

in the otolith chemical composition among samples from the different areas (Fig. 3). The ratio of Na to P concentrations provided the best discrimination among areas, with Bowen samples distinguishable from Rockhampton and Moreton Bay, and samples from Rockhampton and Moreton Bay once again overlapping in their elemental composition (Fig. 3).

Principal component analysis provided further support for the strength of these proposed grouping patterns (Fig. 4). Bowen samples were distinguished from those from the other areas mainly on the first principal component (PC I) where most of the variation was explained by differences in P concentration, whereas Na and Mg contributed most to the variation in the second principal component (PC II). These two components described almost 57% of the total variation in the data. Rockhampton and Moreton Bay samples showed a similar distribution of PC scores, in contrast to samples from Rockhampton that showed some degree of separation between 1- and 2-year-old fish. ANOVA supported these patterns with significant differences detected for both the PC I (F=24.89, df=3, 80, P<0.0001) and PC II scores (F=6.30, df=3, 80, P<0.0007) among the samples. Bowen samples had significantly higher PC I scores

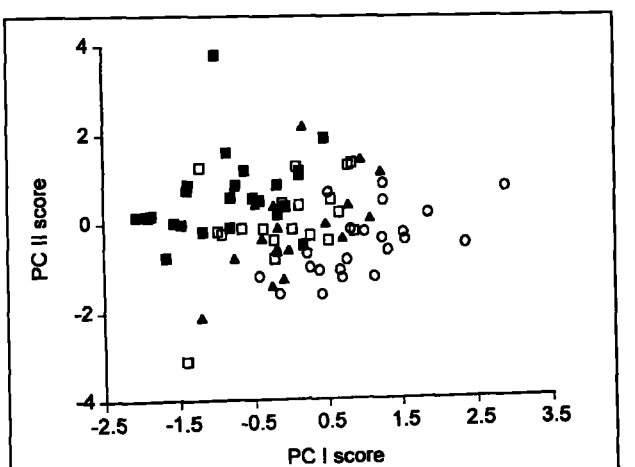

Figure 4

Principal component (PC) analysis of school mackerel otolith elemental concentrations indicating grouping patterns. Open circle = Bowen 2-year-old fish; open square = Moreton Bay 2-year-old fish; solid square = Rockhampton 1-year-old fish; and solid triangle = Rockhampton 2-year-old fish.

than those from Rockhampton and Moreton Bay, and no differences were found between 2-year-old fish

from Rockhampton and Moreton Bay. The samples of 1-year-old fish from Rockhampton had PC I scores that were significantly different from all the 2-year-old samples, and PC II scores that also were significantly different from the other samples, but not from Moreton Bay (HSD, $P<0.05$).

Analyses indicated that school mackerel samples are best separated into three groups: 1) Bowen 2-year-old fish; 2) Moreton Bay and Rockhampton 2-year-old fish; and 3) Rockhampton 1-year-old fish (Wilks's lambda=0.195) (Fig. 5). Similar discriminant patterns were observed when the "significant" elements (K, Mg, Mn, Na, P; Wilks's lambda=0.214) were used in isolation. Significant differences in the discriminant scores were found between these groups for both the first canonical variate (CV I) (ANOVA, $F=74.10$, df=3, 80, $P<0.0001$) and the second (CV II) (ANOVA, $F=6.61$, df=3, 80, $P<0.0001$). Like the results of the PCA analyses, Bowen samples had significantly different CV I scores than those from Rockhampton and Moreton Bay; no differences were found between Rockhampton and Moreton Bay 2-year-old fish; and Rockhampton 1-year-old samples had CV I scores significantly different from all the other groups. The Rockhampton 1-year-old samples also had CV II scores that were significantly different from the other groups, with the exception of fish from Bowen (HSD, $P<0.05$).

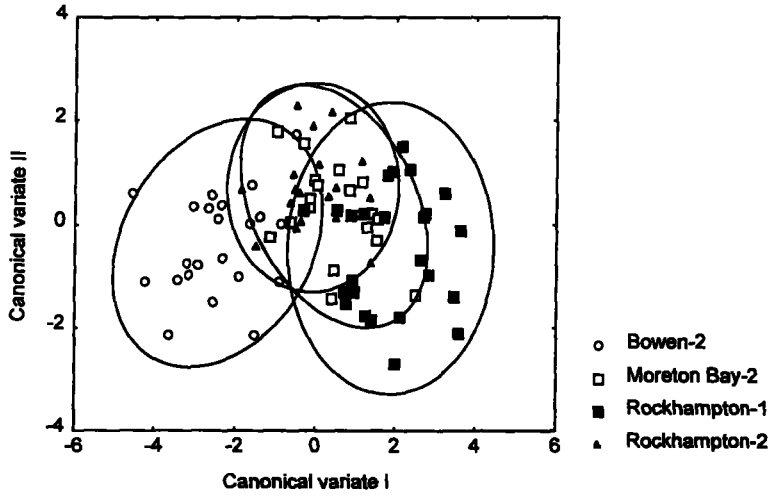

Figure 5

Discrimination between school mackerel samples based on the concentrations of 7 trace elements (± 95% confidence ellipses around the sample mean for each area).

Variation in Na, P, and Mg concentrations were primarily responsible for the separations apparent among the samples (89%) according to the first canonical variate (Table 2). Bowen fish tended to have lower Na and Mg and higher P concentrations than Moreton Bay and Rockhampton samples (Fig. 2). Approximately 62% of the school mackerel samples were classified into their correct groupings, indicating an overlap in otolith composition of Rockhampton and Moreton Bay samples (Table 3). Overall classification success increased to 77% when these areas were pooled, and individual classification rates improved for Bowen 2-yr-old fish (86%), Moreton Bay and Rockhampton 2-year-old fish (70%), and Rockhampton 1-year-old fish (80%), providing further support for the notion of three distinct groups in elemental composition of otoliths.

Table 2

Discrimination between samples of school mackerel determined by the pooled within-group correlations of elemental concentrations with the significant ($P<0.05$) canonical variates I and II, and the cumulative proportion of the explained variance accounted for by each function for seven elements (Wilks's lambda=0.195).

	Canonical variate	
Element	I	II
Na	0.53	0.07
P	–0.48	0.02
Mn	0.17	–0.72
K	–0.20	–0.40
Mg	0.42	–0.38
S	–0.13	0.24
Sr	–0.13	–0.11
Cumulative proportion	0.89	0.97

Spotted mackerel

The same suite of 11 elements that were used for school mackerel were measured and analyzed for spotted mackerel (Fig. 6). Iron, Li, and Ca were excluded from statistical analyses for the same reasons as they were for school mackerel. Concentrations of Na (ANCOVA, $F=14.02$, df=1, 141, $P<0.0003$; $r=-0.0004597$) and Sr (ANCOVA, $F=6.03$, df=1, 141, $P<0.02$; $r=-0.9227$) in spotted mackerel otoliths were highly correlated with fish length; therefore the data were corrected for length with the respective regression coefficient for the length covariate. Manganese was not used in statistical analyses because a significant interaction in concentrations existed be-

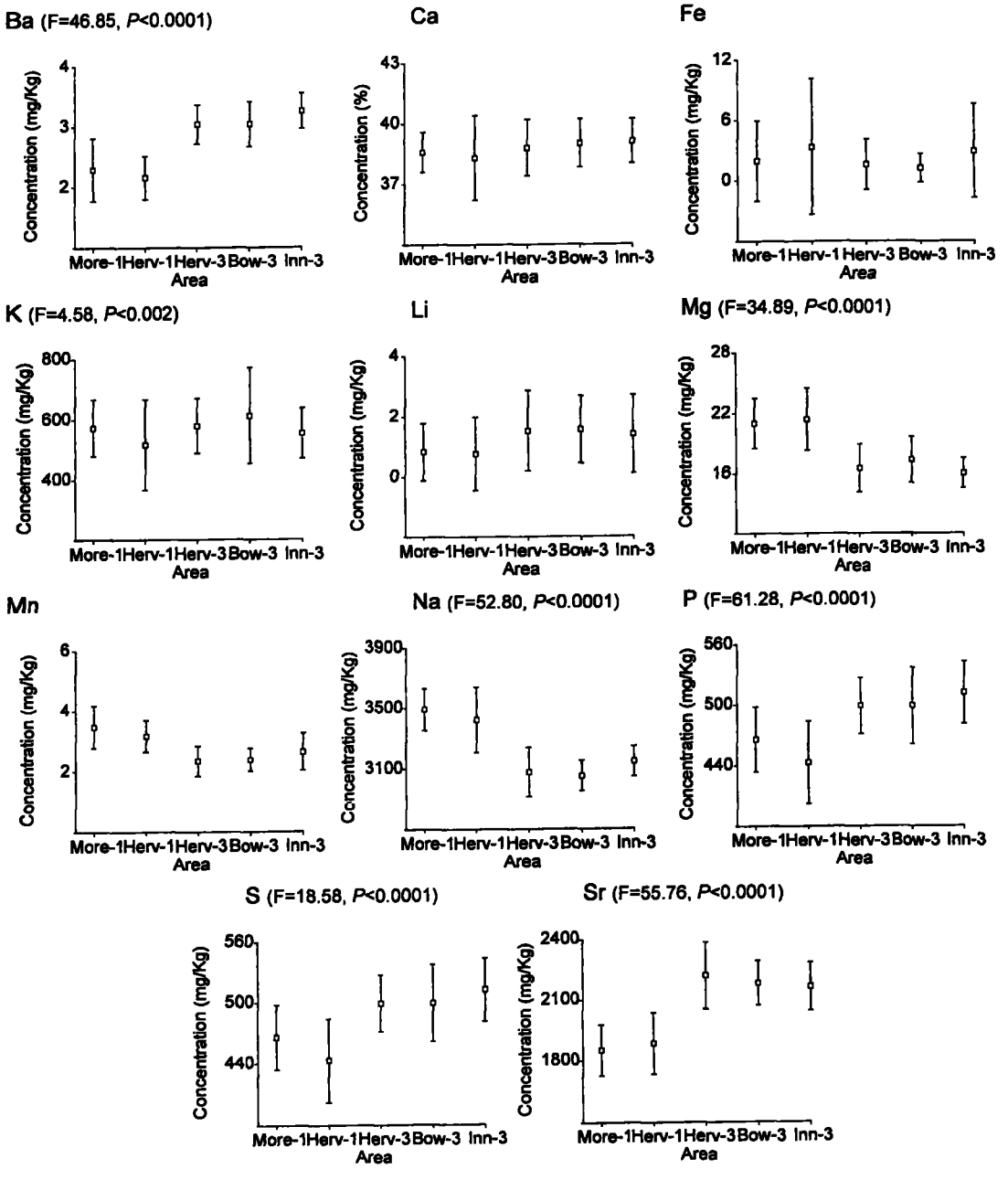

Figure 6

Mean elemental concentrations (± standard deviation) of spotted mackerel otoliths sampled from the different areas and *F*-values determined from ANOVA showing significant elements among samples (df=4, 140). Minimum elemental detection limits of the ICP-AES (all units are in mg/Kg, except Ca which is measured as a %): Ba = 0.78; Ca = 544; Fe = 23.9; K = 353; Li = 15.0; Mg = 10.9; Mn = 1.10; Na = 1250; P = 54.1; S = 191; Sr = 3.24.

tween area of collection and fish length (ANCOVA, F=3.87, df=4, 137, P<0.005). Manganese concentration increased linearly with fish length for Hervey Bay 1-year-old fish, in contrast with the other samples that all showed negative correlations.

Spotted mackerel samples from each area and for each age were found to have significant differences in mean elemental composition of the otoliths (MANOVA, Pillai's trace=1.316, F=9.59, df=28, 548, P<0.0001). Little variation was evident in mean ele-

Table 3

Jack-knifed cross-validation classification matrix of the frequency of assigned cases in each area (and age) used to differentiate school mackerel samples.

		Classification of individual school mackerel by area			
Area	Correct (%)	Bowen (2)	Rock (2)	Rock (1)	Moreton (2)
Bowen (2)	82	18	3	0	1
Rock (2)	50	2	9	1	6
Rock (1)	64	0	3	16	6
Moreton (2)	47	1	4	5	9
Total	62	21	19	22	22

ment concentrations among spotted mackerel of the same age among all areas, whereas most elements varied significantly between samples of different ages (Fig. 6). The samples of 3-year-old fish from Innisfail and Hervey Bay had concentrations of P that were significantly lower than those in otoliths from Bowen fish. Samples from Innisfail also had concentrations of K that were significantly lower than those from Bowen fish (HSD, $P<0.05$). No other significant difference in elemental concentrations were detected between spotted mackerel of the same age. In contrast, significant differences were found for Ba, Mg, Na, P, S, and Sr between 1- and 3-year-old fish (HSD, $P<0.05$), independent of the area from where the samples were taken, once again emphasizing the strong effect of fish age in determining the results of elemental analyses of otolith composition. Scatterplots of the elements showing significant differences, with P as the most significant and common variable, also showed differences between fish of different ages (Fig. 7). In contrast, samples of fish of the same age showed no evidence of differences in otolith composition among areas.

Principal component analysis also showed a strong separation among spotted mackerel of different ages, but no separation of groups by area of collection (Fig. 8). One-year-old and 3-year-old samples were separated on the first principal component that explained almost 50% of the total variation in the data, largely on differences in concentration of P, Sr, Ba, Na, and S. The second principal component explained another 18% of the total variation on the basis of differences in K concentration among the samples. ANOVA showed significant differences among the PC I scores ($F=318.32$, df=4, 140, $P<0.0001$), further confirming pooling of spatial samples of the same age. Bowen, Innisfail, and Hervey Bay samples of 3-year-old fish were all significantly different from Moreton Bay and Hervey Bay 1-year-old fish, whereas no differences were found among samples of the same age (HSD, $P<0.05$).

Spotted mackerel samples were best discriminated into two main groups on the basis of statistically significant differences in elemental composition of the otoliths: 1) 1-year-old fish; and 2) 3-year-old fish (Wilks's lambda 0.045) (Fig. 9). ANOVA on the CV I scores detected significant differences between the different aged samples, providing further support for these patterns ($F=472.09$, df=4, 140, $P<0.0001$). The samples of 3-year-old fish from Bowen, Innisfail, and Hervey Bay all showed significant differences from the 1-year-old fish from Moreton Bay and Hervey Bay, whereas no differences were found among samples of the same age (HSD, $P<0.05$).

Phosphorus, Sr, Na, Ba, and Mg were the main elements that caused the grouping patterns in the first discriminant function that accounted for 97% of the total variation (Table 4). One-year-old spotted mackerel tended to have higher Mg and Na concentrations and lower Ba, P, and Sr concentrations than 3-year-old fish (Fig. 6). The separation patterns observed in the individual discriminations resulted in only 57% of the spotted mackerel samples being correctly classified into their respective groups owing to the strong grouping effect of the samples into their specific age classes, rather than by area (Table 5). Pooling of the results for fish of the same age resulted in a classification success of 100% for each age class, independent of the area from where the samples were collected.

Table 4

Discrimination between samples of spotted mackerel determined by the pooled within-groups correlations of length-corrected elemental concentrations with the significant ($P<0.05$) canonical variates I, II, and III, and the cumulative proportion of the variance accounted for by each function, for the seven significant elements (Wilks' s lambda=0.045).

	Canonical variate		
Element	I	II	III
Ba	−0.31	−0.45	0.06
K	−0.06	0.27	0.64
Mg	0.26	0.40	0.23
Na (length corrected)	0.33	−0.30	0.26
P	−0.35	0.39	0.50
S	−0.19	−0.38	0.30
Sr (length corrected)	−0.34	0.13	−0.34
Cumulative proportion	0.97	0.99	1.00

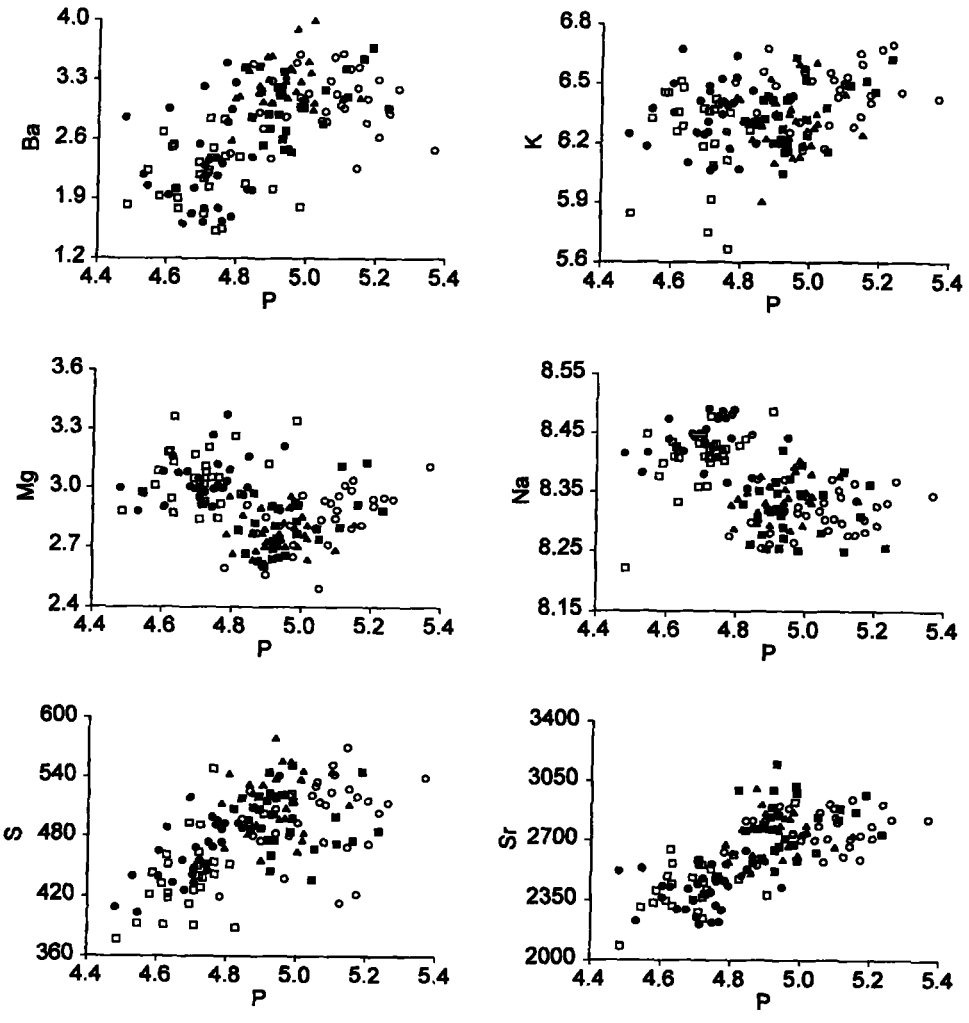

Figure 7

Scatterplots of significant elemental ratios showing grouping patterns of area and age spotted mackerel samples. Open circle = Bowen 3-year-old fish; open square = Hervey Bay 1-year-old fish; solid square = Hervey Bay 3-year-old fish; solid triangle = Innisfail 3-year-old fish; and solid circle = Moreton Bay 1-year-old fish. K, Mg, Na, and P are $\log_e$ transformed concentrations.

Table 5

Jack-knifed cross-validation classification matrix of the frequency of assigned cases in each area (and age) used to differentiate spotted mackerel samples.

		Classification of individual spotted mackerel by area				
Area	Correct (%)	Bowen (3)	Hervey (1)	Hervey (3)	Innisfail (3)	Moreton (1)
Bowen (3)	58	18	0	9	4	0
Hervey (1)	63	0	17	0	0	10
Hervey (3)	34	9	0	10	10	0
Innisfail (3)	68	2	0	7	19	0
Moreton (1)	63	0	11	0	0	19
Total	57	29	28	26	33	29

Discussion

Limitations of elemental analysis of whole otoliths

We found evidence of two separate groups of school mackerel and one group of spotted mackerel in the study region based on the variation in the mean elemental composition of individual fish otoliths of the same age. Such variation has been commonly presumed to reflect prolonged separation of the populations and ultimately stock divergence (Edmonds et al., 1991). However, it is not possible to infer from such studies alone what environmental, dietary, or genetic factors cause spatial patterns. Consequently, a number of wholly different but equally plausible hypotheses could be considered in determining the cause of the patterns observed in the elemental compositions of the otoliths of the two mackerel species, depending on what factors are considered important in determining otolith chemistry.

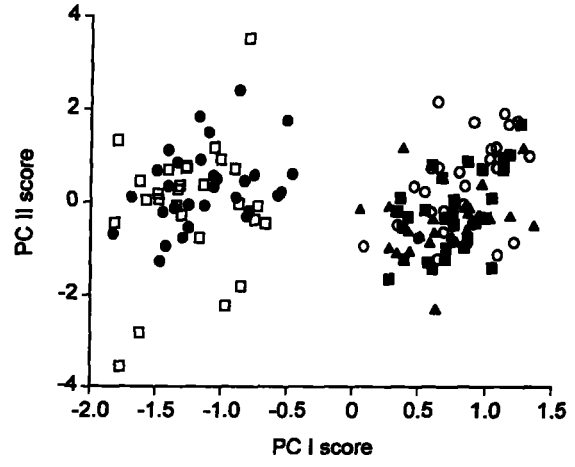

Figure 8

Principal component (PC) analysis of spotted mackerel otolith elemental concentrations indicating grouping patterns. Open circle = Bowen 3-year-old fish; open square = Hervey Bay 1-year-old fish; solid square = Hervey Bay 3-year-old fish; solid triangle = Innisfail 3-year- old fish; and solid circle = Moreton Bay 1-year-old fish.

An obvious explanation is that mean otolith composition differs spatially for school mackerel because their environment (or diet) varies among locations along the east coast, whereas there are no such differences for spotted mackerel because their environment (or diet) is more uniform throughout their range. For example, Proctor et al. (1995) concluded that an inability to discriminate among southern bluefin tuna (*Thunnus maccoyii*) samples with trace-element analysis was due partly to the uniformity of the pelagic environment. Water chemistry and food sources along the east coast of Queensland might be expected to vary among coastal bays, between inshore and offshore waters and between deep and shallow parts of the water column, especially given the strong influence of freshwater input in the wet-dry tropics (Thorrold and McKinnon, 1995). Indeed, the clupeid and engraulid species that form major parts of the diet of both school and spotted mackerel are generally found only in the southern half of the study area (Begg and Hopper, 1997).

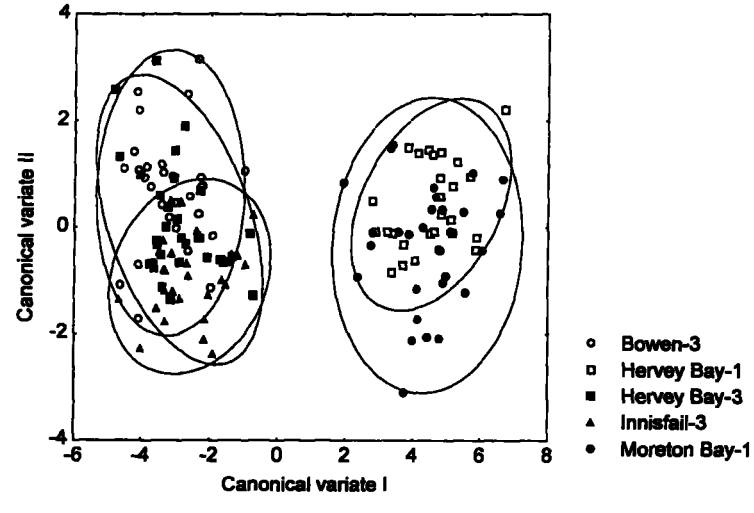

Figure 9

Discrimination between spotted mackerel samples based on the concentrations of the seven (length corrected) trace elements (±95% confidence ellipses around the sample mean for each area).

At present there is no fishery-independent information on the cross-shelf distribution and habitat of school and spotted mackerel and only a coarse understanding of the feeding patterns of both species. School mackerel are thought to inhabit mainly inshore waters, whereas spotted mackerel are thought to be more common offshore (Munro, 1943; Collette and Russo, 1984), although they do move to inshore waters to feed when undertaking seasonal migrations along the coastline (Begg and Hopper, 1997; Begg et al., 1997). School and spotted mackerel are often caught together in the same mixed schools during winter in the shallow northern bays

of the Queensland east coast and in summer in the southern bays, but the location and habitats of juveniles is not well known, particularly for spotted mackerel.

Complementary biological information from other stock identification methods is therefore essential to help interpret results from whole otolith analyses, but some hypotheses regarding stock structure cannot be tested in the absence of knowledge about the factors governing otolith composition. The resolution of the technique is limited further by volumetric considerations and the nature of otolith growth. Even if there were very large consistent differences in composition among individuals at the otolith core during larval and postlarval life, these would be virtually undetectable with bulk analysis, whereas relatively small differences accumulated during later life before capture would have a disproportionately large effect on mean composition. To overcome these problems—which may be accentuated for pelagic species with complex ontogenetic movements (Proctor et al., 1995)—bulk analysis of whole otoliths from juveniles, or excision and analysis of the core regions of otoliths from adult fish (Dove et al., 1996), may provide other, solution-based alternatives to sectioning and electron- or laser-probe techniques.

There may also be temporal variation in stock discrimination patterns, particularly for pelagic species living in coastal areas influenced by boundary currents; Edmonds et al. (1995) demonstrated that variation in composition of pilchard (*Sardinops sagax*) otoliths among years was significantly greater than the variation among sites. Stock discrimination patterns of pilchards were not persistent from one sampling era to the next within a decade. Further bias may be introduced by uneven representation of all life history stages within collections (Edmonds et al., 1995).

Age-related variation

Spatial variation in the concentration of trace elements of school and spotted mackerel was strongly influenced by the age of fish in the samples at time of collection. Differential otolith elemental patterns were found between 1- and 2-year-old school mackerel, and 1- and 3-year-old spotted mackerel throughout the study region. Numerous studies, including this one, support Kalish's (1989) hypothesis that incorporation of trace elements into otoliths is related to growth (Grady et al., 1989; Thresher et al., 1994; Edmonds et al., 1995; Fowler et al., 1995). Consequently, spatial variation in elemental composition of otoliths can be difficult to interpret because of biases related to the size and age of fish in the samples from separate areas.

School and spotted mackerel of different ages from the same area have significantly different patterns in the elemental composition of their otoliths. One-year-old school and spotted mackerel tended to have lower concentrations of P, S, and Sr, while having higher levels of Mg, Mn, and Na in their otoliths compared with older fish. Grady et al. (1989) found similar results for king mackerel where heavy metal concentrations were generally higher in otoliths of younger fish. Differences in the concentrations of trace elements accumulated in the otoliths of fish of different ages from the same stock are not unexpected, particularly if irreversible deposition of elements in otoliths is assumed. Distinct chemical patterns in otoliths of fish of different ages may reflect exposure to similar environments, but for different accumulation periods, or alternatively, may reflect life history differences, such as younger fish inhabiting distinct nursery grounds that are separate from adult habitats.

Not all factors affecting deposition of elements in otoliths are strictly environmental or ontogenetic, nor do they necessarily act in a simplistic manner that reflects ambient environmental chemistry (Kalish, 1989; Campana et al., 1994). Chemical deposition can be regulated by many interacting factors, including water temperature, salinity, age, physiology, growth rates, and activity levels of individual fish (Kalish, 1989, 1990, 1991; Radtke and Shafer, 1992; Rieman et al., 1994; Fowler et al., 1995).

Stock structure and management

Although further research is required to determine the mechanisms responsible for elemental deposition in otoliths of *Scomberomorus* species, particularly the interaction between environmental and genomic controls, the validity of using stock and site-specific elemental "fingerprints" does not rest upon the mechanism underlying otolith formation (Campana and Gagné, 1995). Optimal groupings of mean elemental composition of school mackerel otoliths strongly supported the hypothesis of at least two stocks in the study region—a hypothesis that has been developed with complementary stock identification techniques. Localized movements of tagged school mackerel have shown that there is little exchange between adult fish from different areas throughout Queensland east coast waters; most recaptures occur within the same area of release (Begg et al., 1997). Studies of the timing and location of spawning have also shown that school mackerel spawn concurrently at a number of localities along the east coast (Begg, in press). The species also exhibits differences in growth patterns and genetic variation throughout its distribution on

the east coast (Begg and Sellin, 1998; Begg et al., in press).

The limited movements of school mackerel indicated by tag-recapture data may also explain the overlap observed in the otolith composition of 2-year-old fish collected in Moreton Bay and Rockhampton. Small numbers of tagged school mackerel released in both these locations were recaptured in Hervey Bay between August and January, where they appear to be mixing on a common feeding ground (Begg et al., 1997; Begg and Hopper, 1997).

In contrast, spotted mackerel of the same year class sampled in Queensland east coast waters had similar patterns of elemental composition in their otoliths regardless of the region in which they were collected. This finding strongly supports the hypothesis of a single intermixing stock in the region of sampling derived from previous tagging, genetic, and reproductive studies, and seasonal changes in the location of commercial harvesting. These sources of information suggest an annual large-scale movement of spotted mackerel along the Queensland east coast to southern feeding grounds in summer and a return migration in winter to northern spawning grounds (Begg and Hopper, 1997; Begg et al., 1997; Begg, in press). In addition, similar growth rates and homogeneous genetic conditions of spotted mackerel throughout the study region support the hypothesis of a single east coast stock (Begg and Sellin, 1998; Begg et al., in press).

The longshore East Australian Current possibly provides cues for the migratory cycle of spotted mackerel and may facilitate larval dispersal from the spawning grounds and ultimately stock homogeneity throughout Queensland east coast waters. Proctor et al. (1995) proposed a similar stock structure for southern bluefin tuna on the basis of chemical composition of otoliths from juveniles collected along the major migration route of the species.

Identification of a species' stock structure is an important requirement for effective fisheries management (Rounsefell, 1975). The inability to define stock boundaries could unknowingly prejudice otherwise well-designed management protection efforts (Kutkuhn, 1981). Management of spotted mackerel in Queensland would be best addressed at the state level, because fishing effort in areas remote from one another may have an interaction on a single stock. In contrast, more localized (regional-level) management actions could proceed for school mackerel within Queensland—especially if the stock boundaries can be refined by further tests of the temporal persistence of the patterns described in this study.

The use of otolith trace element analysis holds great potential for stock discrimination in fisheries for other *Scomberomorus* species that share common characteristics of migration through multiple jurisdictions and fishery types. However, the use of bulk analysis of whole otoliths allows us to infer only that there has been prolonged separation of fish at some stage in their life history. Without "life history scans" across otoliths, with techniques such as electron-probe microanalysis (Gunn et al., 1992), we cannot explore the possibility that mean elemental composition is dominated by high concentrations specific to any particular life history stage. There is also need for careful selection of samples among year classes and time periods. Replication of sampling at intervals separated by several years and representation of all ontogenetic stages need to be incorporated in analyses to test for the consistency of spatial patterns in order to provide a more accurate environmental "fingerprint" for discrimination of mackerel stocks.

Acknowledgments

We would like to thank the commercial and recreational fishermen for cooperation and assistance in collection of samples; Steven Campana and four anonymous reviewers for critical comments and suggestions; Steve Cadrin for statistical advice; and Ian Brown and Hamish McCallum for reviews of this work. This study formed part of the Queensland Department of Primary Industries Fisheries Research and Development Corporation grant FRDC 92/144.

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