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Preliminary Investigation of Mitochondrial DNA Variation in Jack Mackerel (*Trachurus declivis*, Carangidae) from South-eastern Australian Waters

A. J. Smolenski[A], *J. R. Ovenden and R. W. G. White*

Fish Research Group, Department of Zoology, University of Tasmania, GPO Box 252C, Hobart, Tas. 7001, Australia.
[A] Present address: Department of Genetics and Human Variation, La Trobe University, Bundoora Campus, Vic. 3083, Australia.

Abstract

A preliminary investigation of the genetic structure of jack mackerel (*Trachurus declivis*, Carangidae) in south-eastern Australian waters was conducted by using restriction enzyme analysis of mitochondrial DNA (mtDNA). Seventy-five jack mackerel samples were collected from two localities: off Eden in New South Wales and off south-eastern Tasmania. Fish were sampled twice at each locality. Mitochondrial DNA was extracted from developing ovary tissue and heart tissue. The 75 jack mackerel samples were screened with 11 six-base and four four-base enzymes. The level of genetic diversity in jack mackerel was low. The six-base enzyme analysis found limited evidence of reproductive isolation between New South Wales and Tasmanian samples of jack mackerel. However, an analysis of a subset of 42 jack mackerel with four four-base enzymes found evidence of temporal differences in the mtDNA diversities of two Tasmanian samples of jack mackerel.

Extra keywords: population genetics.

Introduction

The fishery for jack mackerel (*Trachurus declivis*, Carangidae) is the largest single-species fishery in Australia, with a purse-seine fishing venture aimed exclusively at this species (Williams *et al.* 1987). The fish are used as a protein source for fish meal as well as for crayfish bait and, to a lesser extent, in tinned pet food (Williams *et al.* 1987). There are no reliable estimates of the abundance of jack mackerel in south-eastern Australian waters.

Jack mackerel are distributed along the entire southern coast of Australia and occur in all Tasmanian coastal waters (Stevens and Hausfeld 1982; Williams and Pullen 1986). Fish in south-eastern Australian waters mature at approximately 27 cm fork length and grow to a maximum length of 46 cm (Webb and Grant 1979; Williams and Pullen 1986). Stevens and Hausfeld (1982) calculated the theoretical maximum age of jack mackerel to be approximately 15 years.

Spawning occurs from late spring to mid summer in south-eastern Australian waters and tends to peak during January (Jordan 1992). Jack mackerel are thought to spawn along the entire eastern coast of Tasmania, with high egg densities being reported along the edge of the continental shelf (Jordan 1992). In south-eastern Australian waters, they feed primarily on crustaceans, with a particular preference for euphausids (Webb 1976). Young *et al.* (1993) found that the euphausid *Nyctiphanes australis* tended to be the dominant prey item in the stomachs of *T. declivis*, especially during the start of the fishing season in autumn. In a study of the feeding ecology of larval jack mackerel, Young and Davis (1992) found that crustacean microzooplankton and occasionally bivalve veligers were the main prey items.

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An allozyme study of jack mackerel in Australian waters by Richardson (1982) identified eight polymorphic loci that were useful in determining the stock structure of this species. That study identified a distinct subpopulation of jack mackerel in Western Australian waters. However, in the case of the south-eastern Australian fish, clear stock delineation was not evident although seven of the eight polymorphic loci revealed an excess of homozygotes.

The present paper describes the use of restriction enzyme analysis of mitochondrial DNA (mtDNA) as a means of determining the genetic structure of jack mackerel in south-eastern Australian waters. The rapid rate of evolution of the mitochondrial genome (Brown *et al.* 1979) and the clonal inheritance of this molecule through the maternal lineage (Avise 1987) make it a sensitive means of investigating genetic differentiation at the intraspecific level (Ovenden 1990). Restriction enzyme analysis of mtDNA has been useful in resolving the genetic structure of a number of species of marine fish, including orange roughy (*Hoplostethus atlanticus*; Smolenski *et al.* 1993), striped bass (*Morone saxatilis*; Wirgin *et al.* 1988) and cod *Gadus morhua*; Dahle 1991).

The jack mackerel fishery is a relatively recent development, and important data on the biology of this species are only now coming to light (Jordan 1992; Williams and Pullen 1993). It is anticipated that the potentially high resolving power of mtDNA analysis may provide a refined picture of the genetic structure of jack mackerel in south-eastern Australian waters, thereby contributing to an informed management policy.

Materials and Methods

Trachurus declivis was collected from two sites along the south-eastern Australian coast: off Eden in New South Wales (NSW) and off Eaglehawk Neck in Tasmania. The NSW samples were collected from two localities by the Department of Primary Industry and Energy, Bureau of Rural Resources, in November 1988; initially, fish were caught within a 10-km radius of 36°20′S,150°14′E and referred to as NSW Sample 1 (NSW1). The following day, fish were collected within a 20-km radius of 36°56′S, 150°18′E (NSW2), using mid-water trawls (between 100 and 120 m depth). The samples from Eaglehawk Neck (43°1·5′S,147°55′E) were collected with a beach seine in January 1989 and April 1990.

For mtDNA analysis, 29 fish were chosen arbitrarily from the two NSW samples (NSW1, $n=14$; NSW2, $n=15$) and 46 fish were chosen from the Tasmanian 1989 ($n=30$) and 1990 ($n=16$) samples. The length of the NSW fish was $33\cdot7\pm1\cdot6$ cm (mean ± s.d., $n=29$) and the weight was $449\cdot0\pm57\cdot7$ g (mean ± s.d., $n=29$). The length of the fish from the Tasmanian 1989 sample was $33\cdot2\pm1\cdot7$ cm (mean ± s.d., $n=30$). The length and weight data for the Tasmanian 1990 sample are unavailable.

Mitochondrial DNA was extracted from developing ovary and heart tissue by using a phenol/chloroform extraction method described by Chapman and Powers (1984).

The jack mackerel genomes were screened with 11 six-base enzymes. A subset of 42 individuals was screened with four four-base enzymes. The conditions for the six-base and four-base enzyme assays have been described previously (Smolenski *et al.* 1993).

The restriction sites recognized by analysis with six-base restriction enzymes were mapped upon the jack mackerel mitochondrial genome by using the single- and double-digest technique described previously (Smolenski *et al.* 1993). The fragment sizes were converted to number of base pairs mapped clockwise from the *Bgl*II site (Fig. 1). The mapping of the jack mackerel genome was aided by the use of a computer package written for this purpose (Ovenden *et al.* 1992).

The observed and expected six-base and four-base haplotype frequencies were compared by using a χ^2 test. A Monte Carlo method (Roff and Bentzen 1989) was used to test the significance of the χ^2 values, which were compared with the values obtained from 1000 randomizations of each data set.

The G statistic (G_{st}) was used to estimate the amount of interpopulational genetic subdivision of jack mackerel samples and is equal to the amount of variation in the whole data set that is due to the division of the population into a series of interbreeding populations (Takahata and Palumbi 1985). Restriction-site presence or absence data in binary form were used to test the six-base enzyme data, whereas restriction fragment data were used for the four-base enzyme analysis. The significance of using site versus fragment data is discussed in Smolenski *et al.* (1993). A bootstrap method (Palumbi and Wilson 1990) was used to evaluate the significance of the G_{st} analysis.

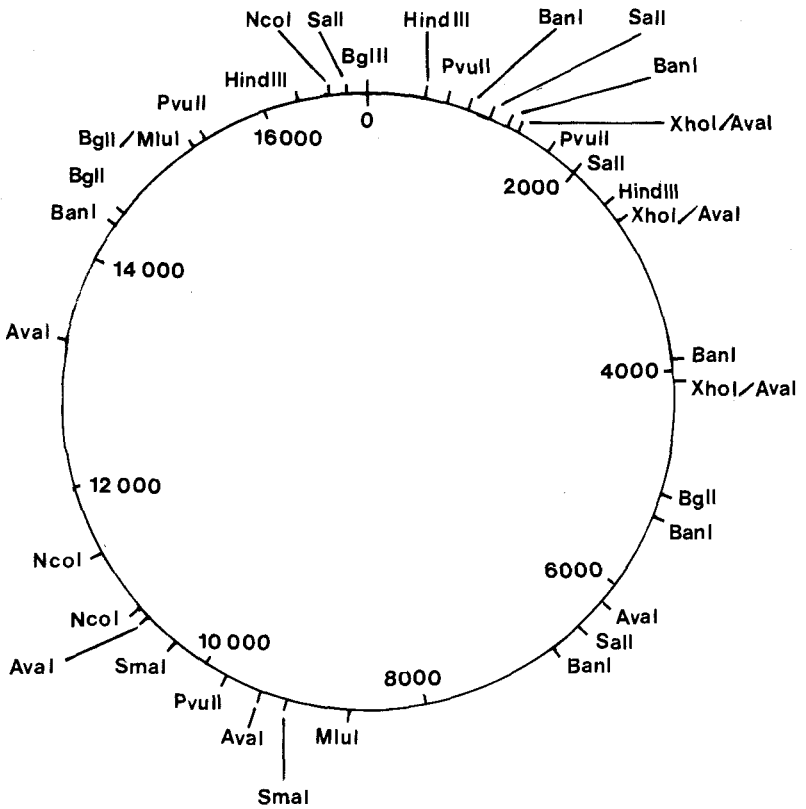

Fig. 1. Map of the jack mackerel mitochondrial genome (common haplotype AAAAAAAAAAA). Restriction sites are mapped clockwise from the *Bgl*II site. A size scale for the restriction sites (in base pairs) is shown around the inside of the map.

The number of base substitutions per base pair (∂) between pairs of individual fish and between pairs of composite six-base enzyme haplotypes was calculated by using the maximum-likelihood method of Nei and Tajima (1983). The calculation of ∂ from the presence or absence of four-base restriction fragment data is described by Nei and Li (1979). The standard deviation of ∂ was calculated according to Nei and Tajima (1983) (Smolenski *et al.* 1993).

The method for calculating the mean net ∂ between populations and the group variance of ∂ is described by Nei and Jin (1989). Student's *t*-test was used to determine whether the net diversity estimates were significantly different from zero (Smolenski *et al.* 1993). However, because the pairwise comparison of net diversity estimates between localities is not statistically independent, a sequential Bonforroni test (Rice 1989) was carried out on significant net nucleotide diversity estimates. The level of significance, α (where $\alpha = 0{\cdot}05$), was adjusted by using this method to obtain a corrected significance level, α'.

Results

Six-base Enzyme Survey

An estimate of the size of the mitochondrial genome in jack mackerel was obtained by averaging the sum of all the fragments for each haplotype, resulting in a value of $16\,432 \pm 460$ base pairs (mean $\pm$ s.d.).

The restriction enzyme survey of 75 jack mackerel genomes with 11 six-base enzymes identified 48 restriction sites. Of the 11 restriction endonucleases used to survey the mitochondrial genome of jack mackerel, four enzymes (*Nco*I, *Pvu*II, *Sal*I and *Sma*I) identified no restriction site variation. The remaining restriction endonucleases identified between one and five different morphs each. Of the 75 genomes surveyed, *Ban*I produced five variant morphs and *Ava*I identified three different morphs. Five enzymes (*Bgl*I, *Bgl*II, *Hin*dIII, *Mlu*I and *Xho*I) identified one rare morph each: *Bgl*II, *Hin*dIII, *Mlu*I and *Xho*I each produced one rare morph that had gained one restriction site in comparison with the common morph, whereas the rare morph identified by the enzyme *Bgl*I differed from the common morph by one restriction site loss. The three rare morphs (B, C and D) identified by *Ava*I had each gained one restriction site in comparison with the common morph. The enzyme *Ban*I identified three rare morphs (B, E and F) that differed from the common morph by one restriction site gain, whereas the rare morphs C and D had both lost a restriction site in comparison with the common morph (Fig. 2).

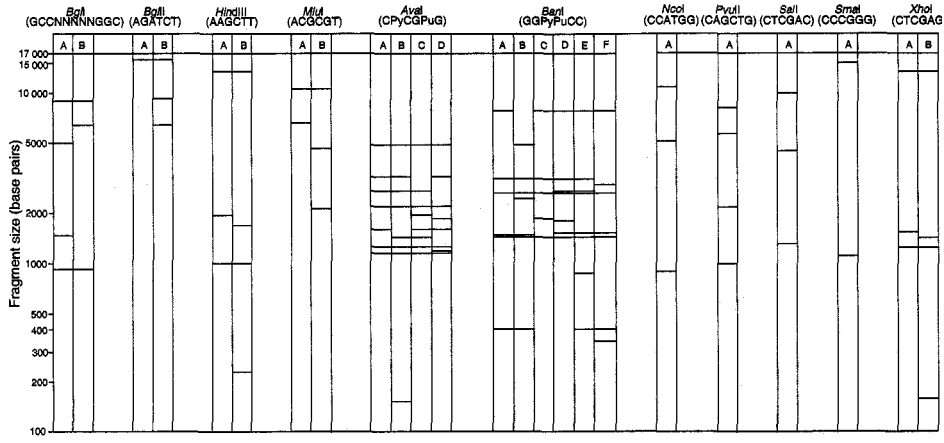

Fig. 2. Fragment patterns for jack mackerel mitochondrial haplotypes identified by 11 six-base restriction enzymes. Recognition sequences of the restriction enzymes are in parentheses.

The six-base restriction enzyme survey identified 12 mitochondrial haplotypes. The most common haplotype (AAAAAAAAAAA) was recorded in 22 of 29 individuals collected in NSW waters and in 36 of 46 fish collected in Tasmanian waters. The fish from NSW waters were characterized by seven unique haplotypes, each represented by one individual. Among the fish from Tasmanian waters, 10 individuals possessed five rare haplotypes. The rare haplotype AEAAAAAAAAA was found in six individuals exclusively from Tasmanian waters (Table 1). Apart from the common haplotype (AAAAAAAAAAA), only one rare haplotype (AAABAAAAAAA) was recorded from both NSW and Tasmanian waters (Table 1).

The amount of mtDNA restriction site variation that was due to population subdivision (G_{st}) calculated from the presence or absence of restriction sites was 37%. This estimate lies within the range of G_{st} estimates calculated from 1000 randomizations (bootstrapped G_{st}) of the original data set (29% to 39%) and may not, therefore, indicate population subdivision.

The χ^2 test was used to test the null hypothesis that there is no geographical partitioning of jack mackerel six-base enzyme haplotypes. The resulting χ^2 value, tested for significance by the Monte Carlo method (Roff and Bentzen 1989), produced a non-significant result ($P \leqslant 0{\cdot}053 \pm 0{\cdot}014$).

Table 1. Geographical distribution and number of jack mackerel haplotypes identified by six-base enzyme analysis

NSW1, New South Wales Sample 1; NSW2, New South Wales Sample 2; T.89, Tasmanian 1989 sample; T.90, Tasmanian 1990 sample. The order of the 11 enzymes in the composite haplotypes is *Ava*I, *Ban*I, *Bgl*I, *Bgl*II, *Hin*dIII, *Mlu*I, *Nco*I, *Pvu*II, *Sal*I, *Sma*I and *Xho*I

Haplotype	NSW1	NSW2	T.89	T.90	Total
AAAAAAAAAAA	8	14	22	14	58
AAABAAAAAAA	1	0	1	0	2
ACAAAAAAAAA	0	1	0	0	1
AEAAAAAAAAA	0	0	5	1	6
AEAABAAAAAA	1	0	0	0	1
AFAAAAAAAAA	1	0	0	0	1
BABAAAAAAAB	1	0	0	0	1
ABAAAAAAAAA	1	0	0	0	1
ADAAAAAAAAA	1	0	0	0	1
CAAAAAAAAAA	0	0	1	0	1
DAAAAAAAAAA	0	0	1	0	1
AAAAABAAAAA	0	0	0	1	1
Total	14	15	30	16	75

The mtDNA diversity, or mean number of base substitutions per nucleotide, for all jack mackerel individuals analysed with six-base enzymes in this study was $0{\cdot}1363 \pm 0{\cdot}0723\%$ ($n = 75$). Intrapopulational diversity estimates are summarized in Table 2.

Table 2. Mean intrapopulational mtDNA diversity estimates (%) and standard errors (%) for four jack mackerel populations analysed with six-base and four-base enzymes

Analysis and population	Diversity	s.e.	*n*
Six-base analysis			
New South Wales (Sample 1) 1988	0·2962	0·1236	14
New South Wales (Sample 2) 1988	0·0314	0·0334	15
Eastern Tasmania 1989	0·1654	0·1031	30
Eastern Tasmania 1990	0·0286	0·0305	16
Four-base analysis			
New South Wales (Sample 1) 1988	0·3652	0·1298	8
New South Wales (Sample 2) 1988	0·3077	0·1137	10
Eastern Tasmania 1989	0·6263	0·1279	16
Eastern Tasmania 1990	0·5235	0·1432	8

Four-base Enzyme Survey

Four restriction enzymes recognizing sequences of four bases were used to survey a subset of 42 individuals selected from the 75 genomes surveyed with six-base enzymes (NSW Sample 1, $n = 8$; NSW Sample 2, $n = 10$; Tasmanian 1989 Sample, $n = 16$; Tasmanian 1990 sample, $n = 8$). The four four-base enzymes produced 160 restriction fragments for the four enzymes. The enzymes *Dde*I and *Taq*I identified 13 and 12 different restriction morphs, respectively. The enzyme *Mbo*I identified 19 unique restriction morphs, and *Msp*I was the most variable enzyme, identifying 28 unique restriction morphs.

The four-base analysis of 42 jack mackerel genomes identified 36 unique composite mitochondrial haplotypes (Table 3). There was no common haplotype, and only three four-base haplotypes (AAAA, ABAA and ABCA) occurred more than once (Table 3).

Table 3. Geographical distribution and number of jack mackerel four-base haplotypes

NSW1, New South Wales Sample 1; NSW2, New South Wales Sample 2; T.89, Tasmanian 1989 sample; T.90, Tasmanian 1990 sample. The order of the four enzymes in the composite haplotypes is *Dde*I, *Mbo*I, *Msp*I and *Taq*I

Haplotype	NSW1	NSW2	T.89	T.90	Total
AAAA	1	0	1	0	2
AAB'B	1	0	0	0	1
AAQA	0	0	1	0	1
AASB	0	0	1	0	1
AAUC	1	0	0	0	1
ABAA	1	2	2	0	5
ABCA	0	2	0	0	2
ABDA	0	1	0	0	1
ABLA	0	0	1	0	1
ACXA	0	1	0	0	1
ACZA	0	1	0	0	1
ADHE	0	0	1	0	1
ADIB	0	0	1	0	1
AERA	0	0	1	0	1
AHGA	0	0	1	0	1
APBA	0	0	1	0	1
BAA'B	1	0	0	0	1
BAAA	0	1	0	0	1
BAAB	1	0	0	0	1
BACB	1	0	0	0	1
CABJ	0	0	0	1	1
CBAI	0	0	0	1	1
CFAA	0	0	0	1	1
CGBG	0	0	0	1	1
CMEA	0	0	0	1	1
DABA	0	1	0	0	1
DKKA	0	0	1	0	1
EIMH	0	0	0	1	1
FJJD	0	0	1	0	1
GCYK	0	0	0	1	1
HBFL	0	0	0	1	1
IEAC	0	0	1	0	1
JNOF	0	0	1	0	1
KOPA	0	0	1	0	1
LQEA	1	0	0	0	1
MRVA	0	1	0	0	1
Total	8	10	16	8	42

The bootstrapped G_{st} estimate for the four jack mackerel samples was 24%. The G_{st} values calculated from 1000 randomizations of the data set ranged from 16% to 22%. This result suggests population subdivision because the true G_{st} value (24%) was greater than the randomly generated G_{st} values.

The χ^2 tests comparing all localities were carried out for enzyme-specific morphs that occurred more than once. Enzyme-specific morphs that occurred only once were omitted in order to avoid inflated significance values. The null hypothesis being tested was that there was no geographical separation of the jack mackerel four-base morphs. Each χ^2 result was tested for significance by the Monte Carlo method (Roff and Bentzen 1989). Three enzymes

(*Dde*I, *Mbo*I and *Taq*I) yielded a significant result ($P \leqslant 0{\cdot}001$, $P \leqslant 0{\cdot}035 \pm 0{\cdot}011$ and $P \leqslant 0{\cdot}043 \pm 0{\cdot}0029$, respectively). The enzyme *Msp*I produced the only non-sigificant result ($P \leqslant 0{\cdot}056 \pm 0{\cdot}014$; Table 4).

Table 4. Geographical distribution and number of jack mackerel *Dde*I, *Mbo*I, *Msp*I and *Taq*I morphs that occurred more than once

Enzyme	Locality	Morph				
		A	B	C	D	E
*Dde*I	New South Wales Sample 1	4	3	0		
	New South Wales Sample 2	7	2	0		
	Eastern Tasmania 1989	14	0	0		
	Eastern Tasmania 1990	0	0	5		
*Mbo*I	New South Wales Sample 1	6	0	0	0	0
	New South Wales Sample 2	3	5	2	0	0
	Eastern Tasmania 1989	4	3	0	2	2
	Eastern Tasmania 1990	0	2	0	0	0
*Msp*I	New South Wales Sample 1	3	0	0		
	New South Wales Sample 2	4	0	2		
	Eastern Tasmania 1989	4	0	0		
	Eastern Tasmania 1990	2	2	0		
*Taq*I	New South Wales Sample 1	3	4			
	New South Wales Sample 2	10	0			
	Eastern Tasmania 1989	11	3			
	Eastern Tasmania 1990	2	0			

Table 5. Mean interpopulational mtDNA diversity estimates (%) and standard errors (%) for four jack mackerel populations analysed with four-base enzymes
Underlined numbers represent possibly significant values

Population comparison	Diversity	s.e.
NSW Sample 1 1988 *v.* NSW Sample 2 1988	0·0296	0·0182
NSW Sample 1 1988 *v.* eastern Tasmania 1989	0·0193	0·0149
NSW Sample 1 1988 *v.* eastern Tasmania 1990	0·1147	0·0224
NSW Sample 2 1988 *v.* eastern Tasmania 1989	0·0058	0·0222
NSW Sample 2 1988 *v.* eastern Tasmania 1990	0·0861	0·0315
Eastern Tasmania 1989 *v.* eastern Tasmania 1990	0·0770	0·0087

The mtDNA diversity for all the jack mackerel individuals analysed with four-base enzymes was $0{\cdot}5153 \pm 0{\cdot}1035\%$ ($n = 42$). The intrapopulational mtDNA diversity estimates are summarized in Table 2. The net mtDNA diversity estimates between jack mackerel genomes from pairs of localities ranged from 0·1147% to 0·0058% (Table 5). Student's *t*-test was used to test whether the net diversity estimates were significantly different from zero. In three of these comparisons, the magnitude of the standard error was considerably smaller than the magnitude of the estimate (NSW Sample 1 versus eastern Tasmania 1990, $0{\cdot}1147 \pm 0{\cdot}0224\%$, $P < 0{\cdot}001$, $\alpha' = 0{\cdot}01$; NSW Sample 2 versus eastern Tasmania 1990, $0{\cdot}0861 \pm 0{\cdot}0315\%$, $P < 0{\cdot}01$, $\alpha' = 0{\cdot}0125$; eastern Tasmania 1989 versus eastern Tasmania 1990, $0{\cdot}0770 \pm 0{\cdot}0087\%$, $P < 0{\cdot}001$, $\alpha' = 0{\cdot}008$; Table 5), indicating possible genetic separation between the eastern Tasmanian 1990 sample and the remaining three samples. When both Tasmanian samples of jack mackerel were combined and compared with the combined NSW samples, the resulting net divergence estimate was not significant (diversity $= 0{\cdot}0142 \pm 0{\cdot}0165\%$).

Discussion

The six-base analysis of jack mackerel mtDNA found limited evidence of geographical structuring of mitochondrial haplotypes on the basis of the occurrence of a rare haplotype (AEAAAAAAAAA; Table 1) exclusively in Tasmanian waters. However, this preliminary evidence for stock separation among the jack mackerel samples is not supported by statistical and sequence diversity analysis. The use of enzymes recognizing sequences of four bases found no clear separation of mtDNA haplotypes between the Tasmanian and NSW samples. However, the four-base analysis did provide evidence of genetically distinct schools of jack mackerel occurring off eastern Tasmania in different years (Table 5). Nucleotide sampling errors (or the choice of restriction enzymes) and possibly small sample sizes may explain why the six-base enzyme analysis partitioned heterogeneity in the data in a different way from the four-base analysis. The choice of restriction enzymes may explain the difference in the magnitude of the mtDNA diversity estimates obtained with six-base and four-base enzyme analyses (Table 2) (Smolenski *et al.* 1993).

Care should be taken when making comparisons between six-base and four-base data because the former are based on site data and the latter on fragment data. Six-base enzymes have been useful in determining the genetic structure of a number of species of marine fish (Wirgin *et al.* 1988; Dahle 1991). However, in some cases, six-base enzyme analysis may lack the resolving power to detect much of the genetic variability present within a sample. It has been suggested that if the nucleotide diversity of a sample is less than 0·2%, four-base enzymes are more informative than six-base enzymes (Ovenden 1990). An analysis of mtDNA variation in the deep-sea teleost *Hoplostethus atlanticus*, using four-base enzymes, revealed evidence of reproductive isolation, whereas previous six-base enzyme analysis failed to identify any geographical structuring of mtDNA haplotypes (Smolenski *et al.* 1993).

The presence of genetically distinct schools of jack mackerel occurring off eastern Tasmania lends support to the findings of Richardson's (1982) allozyme study. Richardson found two distinct subpopulations of jack mackerel in Western Australia and New Zealand; the population structure of jack mackerel in south-eastern Australian waters was less clearly defined. Five enzymes (carboxylesterase, isocitrate dehydrogenase, aconitate hydratase, L-iditol dehydrogenase and adenosine deaminase) all revealed an excess of homozygotes in fish collected from south-eastern waters. This excess of homozygotes was presumed to be the result of a Wahlund effect (i.e. the presence of two or more overlapping but genetically distinct groups in a population).

The underlying assumption from Richardson's results is that jack mackerel maintain a relatively strong school fidelity for most of their lives, with only very limited gene flow occurring between schools. However, in a study of the schooling behaviour of jack mackerel, Williams and Pullen (1993) suggest that jack mackerel targeted by fishers primarily form feeding schools especially in the presence of large concentrations of the euphausid *Nyctiphanes australis*. This suggests that, in the absence of zooplankton prey species, the jack mackerel may disperse rather than remain as discrete schools. In the 1989–90 fishing season, there was a marked decline in the abundance of *N. australis*, thought to be the result of a La Niña event (Pullen *et al.* 1989). Consequently, the jack mackerel did not school in coastal waters and instead were caught in deeper water adjacent to the fishing grounds.

Sharp (1978) suggested the possibility of sibship within schools of tuna (*Thunnus* spp.) on the basis of the results of an allozyme study. In the present study, the differences in the intrapopulational diversity estimates between the jack mackerel samples from NSW waters and those from Tasmanian waters suggest that there may be fidelity within schools (Table 2). Further genetic analysis would be required to test for sibship within schools of jack mackerel. Owing to the possible mixing of larvae by ocean currents following spawning, it seems unlikely, however, that jack mackerel would form sibling cohorts. The possibility that groups of the serranid reef fish *Anthias squamipinnis* were settling as sibling cohorts

was tested by Avise and Shapiro (1986), using allozyme electrophoresis. They found no evidence of sibship; instead, juvenile cohorts of *A. squamipinnis* were found to be composed of offspring from several matings.

A morphometric analysis of jack mackerel from Australian waters also found evidence of stock separation between fish from the Great Australian Bight and NSW waters (Lindholm and Maxwell 1988). However, no separation was detected between fish from NSW and Tasmanian waters.

Jack mackerel are known to spawn along the entire eastern coast of Tasmania, with spawning activity being concentrated at the edge of the continental shelf (Jordan 1992). The larvae then move toward inshore areas. Jordan (1992) suggests that interannual variation in the local hydrography off eastern Tasmania may affect the onshore movement of jack mackerel eggs and larvae, resulting in higher mortality rates. Fish, such as jack mackerel, that inhabit pelagic waters have the benefit of the greater productivity of surface waters but are also subject to greater predation pressure (Mead *et al.* 1964). In a study of the causes of mortality in North American jack mackerel (*Trachurus symmetricus*), Hewitt *et al.* (1985) found that the principle cause of mortality in yolk-sac larvae was predation. However, starvation was the major cause of mortality in feeding larvae once they had absorbed their yolk sacs. There are no data on the predators of jack mackerel eggs and larvae in Australian waters. It is possible that the loss of large numbers of larval jack mackerel to a combination of poor or no advection to inshore areas and predation may adversely affect subsequent recruitment, resulting in the possible extinction of some mtDNA lineages. Such losses would have the effect of reducing the effective population size of the spawning aggregations, thereby contributing to a lower overall mtDNA diversity. However, the physical and biological factors that determine the pattern of recruitment in jack mackerel remain unclear.

The ability of modern purse-seine vessels to remove almost entire schools during a single netting operation may also have a serious long-term effect on the mtDNA diversity of jack mackerel. In an allozyme study of orange roughy (*Hoplostethus atlanticus*), Smith *et al.* (1991) argued that fishing pressure was directly responsible for a loss of heterogeneity in that species.

The present study has presented some evidence to support Richardson's (1982) view that there may be a number of genetically distinct schools of jack mackerel occurring along the south-eastern coast of Australia. However, an expanded mtDNA study involving further nucleotide and population sampling will be required to determine the population structure of jack mackerel in south-eastern Australian waters.

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References

Avise, J. C. (1987). Identification and interpretation of mitochondrial DNA stocks in marine species. In 'Proceedings of Stock Identification Workshop'. (Eds H. E. Kumpf, R. N. Vaught, C. B. Grimes, A. G. Johnson and E. L. Nakamura.) pp. 105–36. (US National Oceanic and Atmospheric Administration: Panama City Beach, Florida.)

Avise, J. C., and Shapiro, D. Y. (1986). Evaluating kinship of newly settled juveniles within social groups of the coral reef fish *Anthias squamipinnis*. *Evolution* **40**, 1051–9.

Brown, W. M., George, M., and Wilson, A. C. (1979). Rapid evolution of animal mitochondrial DNA. *Proceedings of the National Academy of Sciences of the United States of America* **76**, 1967–71.

Chapman, R. W., and Powers, D. A. (1984). A method for the rapid isolation of mitochondrial DNA from fishes. University of Maryland Sea Grant Program Technical Report No. UM-SGTS 84-05. 11 pp.

Dahle, G. (1991). Cod, *Gadus morhua* L., populations identified by mitochondrial DNA. *Journal of Fish Biology* **38**, 295–303.

Hewitt, R. P., Theilacker, G. H., and Lo, N. C. H. (1985). Causes of mortality in young jack mackerel. *Marine Ecology Progress Series* **26**, 1–10.

Jordan, A. J. (1992). Interannual variability in the oceanography of the east coast of Tasmania and its effects on jack mackerel (*Trachurus declivis*) larvae. In 'Larval Biology'. Australian Society for Fish Biology Workshop, Hobart 1991. (Ed. D. A. Hancock.) Bureau of Rural Resources Proceedings No. 15, pp. 116–21. (Australian Government Publishing Service: Canberra.)

Lindholm, R., and Maxwell, J. G. H. (1988). Stock separation of jack mackerel *Trachurus declivis* (Jenyns, 1841) and yellowtail *T. novaezealandiae* (Richardson, 1843) in southern Australian waters, using principal component analysis. CSIRO Marine Laboratories Report No. 189.

Mead, G. W., Bertelsen, E., and Cohen, D. M. (1964). Reproduction among deep-sea fishes. *Deep-sea Research* **11**, 569–96.

Nei, M., and Jin, L. (1989). Variance of the average numbers of nucleotide substitutions within and between populations. *Molecular Biology and Evolution* **6**, 290–300.

Nei, M., and Li, W. H. (1979). Mathematical model for studying genetic variation in terms of restriction endonucleases. *Proceedings of the National Academy of Sciences of the United States of America* **76**, 5269–73.

Nei, M., and Tajima, F. (1983). Maximum likelihood estimation of the number of nucleotide substitutions from restriction sites data. *Genetics* **105**, 207–17.

Ovenden, J. R. (1990). Mitochondrial DNA and marine stock assessment: a review. *Australian Journal of Marine and Freshwater Research* **41**, 835–53.

Ovenden, J. R., Bywater, R., and White, R. W. G. (1992). A program for the estimation of restriction endonuclease site position from restriction fragment size and number—an aid for mtDNA analysis. *Journal of Heredity* **83**, 240–1.

Palumbi, S. R., and Wilson, A. C. (1990). Mitochondrial DNA diversity in the sea urchins *Strongylocentrotus purpuratus* and *S. droebachiensis*. *Evolution* **44**, 403–15.

Pullen, G., Jenkins, G., and Williams, H. (1989). Where are they? *Fishing Today* **2**(1), 31.

Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution* **43**, 223–5.

Richardson, B. J. (1982). Geographical distribution of electrophoretically detected protein variation in Australian commercial fishes. I. Jack mackerel, *Trachurus declivis* Jenyns. *Australian Journal of Marine and Freshwater Research* **33**, 917–26.

Roff, D. A., and Bentzen, P. (1989). The statistical analysis of mitochondrial DNA polymorphism: χ^2 and the problem of small samples. *Molecular Biology and Evolution* **6**, 539–45.

Sharp, G. D. (1978). Behavioural and physiological properties of tunas and their effects on vulnerability to fishing gear. In 'The Physiological Ecology of Tunas'. (Eds G. D. Sharp and A. E. Dizon.) pp. 397–449. (Academic Press: New York.)

Smith, P. J., Francis, R. I. C. C., and McVeagh, M. (1991). Loss of genetic diversity due to fishing pressure. *Fisheries Research (Amsterdam)* **10**, 309–16.

Smolenski, A. J., Ovenden, J. R., and White, R. W. G. (1993). Evidence of stock separation in Southern Hemisphere orange roughy (*Hoplostethus atlanticus*, Trachichthyidae) from restriction enzyme analysis of mitochondrial DNA. *Marine Biology (Berlin)* **116**, 219–30.

Stevens, J. D., and Hausfeld, H. F. (1982). Age determination and mortality estimates on an unexploited population of jack mackerel *Trachurus declivis* (Jenyns, 1841) from south east Australia. CSIRO Marine Laboratories Report No. 148.

Takahata, N., and Palumbi, S. R. (1985). Extranuclear differentiation and gene flow in the finite island model. *Genetics* **109**, 441–57.

Webb, B. F. (1976). Aspects of the biology of jack mackerel *Trachurus declivis* (Jenyns) from south-east Australian waters. *Tasmanian Fisheries Research* **10**, 1–14.

Webb, B. F., and Grant, C. J. (1979). Age and growth of jack mackerel *Trachurus declivis* (Jenyns) from south-eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **30**, 1–9.

Williams, H., and Pullen, G. (1986). A synopsis of biological data on the jack mackerel *Trachurus declivis* Jenyns. Tasmania Department of Sea Fisheries Marine Laboratories Technical Report No. 10.

Williams, H., and Pullen, G. (1993). Schooling behaviour of jack mackerel, *Trachurus declivis* (Jenyns), observed in the Tasmanian purse seine fishery. *Australian Journal of Marine and Freshwater Research* **44**, 577–87.

Williams, H., Pullen, G., Kucerans, G., and Waterworth, C. (1987). The jack mackerel purse seine fishery in Tasmania 1986–87. Tasmania Department of Sea Fisheries Marine Laboratories Technical Report No. 19.

Wirgin, I. I., Proenca, R., and Grossfield, J. (1988). Mitochondrial DNA diversity among populations of striped bass in the south eastern United States. *Canadian Journal of Zoology* **67**, 891–907.

Young, J. W., and Davis, T. L. O. (1992). Feeding ecology and interannual variations in diet of larval jack mackerel, *Trachurus declivis* (Pisces: Carangidae), from coastal waters of eastern Tasmania. *Marine Biology (Berlin)* **113**, 11–20.

Young, J. W., Jordan, A. R., Bobbi, C., Johannes, R. E., Haskard, K., and Pullen, G. (1993). Seasonal and interannual variability in krill (*Nyctiphanes australis*) stocks and their relationship to the fishery for jack mackerel (*Trachurus declivis*) off eastern Tasmania, Australia. *Marine Biology (Berlin)* **116**, 9–18.

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