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Genetic Subdivision of Stocks of Snapper, *Chrysophrys unicolor*, in Shark Bay, Western Australia

M. S. Johnson,[A] *S. Creagh*[A] *and M. Moran*[B]

[A] Department of Zoology, University of Western Australia, Nedlands, W.A. 6009.
[B] Western Australian Department of Fisheries, Waterman, W.A. 6020.

Abstract

Variation of allozymes in *C. unicolor* from Shark Bay was examined as a test for subdivision of the stocks. Samples from the three major areas of the bay (outer bay, and eastern and western gulfs) were genetically differentiated from each other, showing different allelic frequencies at three of the four polymorphic loci studied. The observed genetic differences support the view that snapper from different areas of Shark Bay represent separate breeding populations.

Introduction

The major fishery for snapper, *Chrysophrys unicolor* (Quoy & Gaimard), in Western Australia is in Shark Bay. Information required for efficient management of that fishery includes a knowledge of whether the fish represent one or several breeding populations. Two factors suggest the possibility of subdivision of snapper stocks within Shark Bay. The first is the relatively sedentary habit of snapper. Although tagging studies in New Zealand and eastern Australia have shown that *Chrysophrys auratus* (with which *C. unicolor* is probably conspecific; see MacDonald 1980) can move large distances, most adults remain in the same area, apparently resulting in the restriction of interbreeding between stocks (Cassie 1956; Paul 1967, 1976; Sanders 1974). Furthermore, estimated salt and water budgets indicate that the rate of exchange of waters between the inner and outer portions of Shark Bay is very low (Smith and Atkinson 1983), reducing the probability of passive dispersal of snapper eggs and larvae between parts of the bay. The second factor that raises the possibility of subdivision of snapper stocks is the environmental heterogeneity of Shark Bay. The outstanding feature of the bay is the steep 'negative' gradient in salinities, an increase from 36 g l^{-1} in the outer bay to 60–70 g l^{-1} in the eastern heads of the bay (Davies 1970; Logan and Cebulski 1970). Snapper are found throughout this gradient and are common at salinities up to at least 50 g l^{-1}. Such an extreme range of salinities could well impose selection against migration between different areas of the bay, enhancing the probability of breeding isolation.

One test of such isolation would be genetic comparisons between fish from different areas. As a source of genetic markers, electrophoresis of enzymes is very useful in the detection of isolated breeding populations (reviews in de Ligny 1969; Shaklee 1983), including separate populations of snapper in New Zealand (Smith *et al.* 1978). A broad geographic study of genetic variation in snapper from Australian waters suggested the presence of at least one separate population in Shark Bay (MacDonald 1980). In this paper, we present the results of electrophoretic comparisons of snapper from different parts of Shark Bay, as a test for further subdivision of snapper stocks in this region.

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Materials and Methods

The study was based on 849 snapper collected between April and October 1984 from Shark Bay and the immediately adjacent ocean. The samples came from five major areas, defined on the basis of geographical proximity and salinity (Fig. 1): Cape Cuvier, immediately to the north of Shark Bay; Koks Island area, at the entrance to the bay; Denham Sound; Freycinet Estuary, at high salinities in the head of the western gulf of the bay; and the Faure Island area, at high salinities in the eastern gulf.

Either whole fish or tissue samples were frozen immediately upon capture, and were subsequently kept at −70°C pending electrophoresis. Length and sex of each fish were recorded, and scales were taken to allow aging.

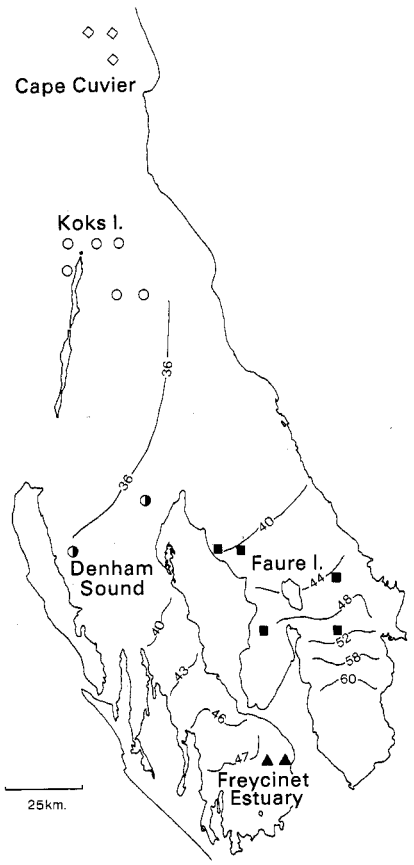

Fig. 1. Map of Shark Bay, Western Australia, showing sites from which samples of *C. unicolor* were collected, and average surface salinities (g l^{-1}; after Logan and Cebulski 1970; Smith and Atkinson 1983). The different symbols indicate subsamples within each of the five main areas.

Enzymes were extracted by grinding one volume of tissue in two volumes of 10% (w/v) sucrose containing 0·1% (v/v) mercaptoethanol and 0·1% (v/v) bromphenol blue. Electrophoresis was carried out in horizontal starch gels (Electrostarch, Lot 392). Initially, extracts of eye, muscle and liver from a sample of 45 fish from the Faure Island area were examined for 20 enzymes: adenosine deaminase, alcohol dehydrogenase, creatine kinase, carboxylesterase, guanine deaminase, glutamate dehydrogenase, glucose-6-phosphate dehydrogenase, glucose-6-phosphate isomerase, glycerol-3-phosphate dehydrogenase, isocitrate dehydrogenase ($NADP^+$), L-lactate dehydrogenase, malate dehydrogenase, malate dehydrogenase ($NADP^+$), mannose-6-phosphate isomerase, 'nothing' dehydrogenase, phosphogluconate dehydrogenase, phosphoglucomutase, L-iditol dehydrogenase, superoxide dismutase and xanthine dehydrogenase. Four of these enzymes were chosen for analysis from liver extracts in all samples: carboxylesterase (EST; EC 3.1.1.1); isocitrate dehydrogenase ($NADP^+$) (IDH; EC 1.1.1.42); mannose-6-phosphate isomerase (MPI; EC 5.3.1.8); glucose-6-phosphate isomerase (GPI; EC 5.3.1.9). Other than these four, the only enzymes that were variable were alcohol dehydrogenase and adenosine deaminase, which

showed too little activity for consistent scoring, and phosphoglucomutase, for which the variant alleles were too rare to allow comparisons of frequencies between areas. The results of our preliminary survey of electrophoretic variation in snapper from the Faure Island area are similar to those of MacDonald (1980) for specimens from a wide range of Australian sites.

MPI and GPI were examined in the Tris–EDTA–borate buffer, and IDH in the Tris–maleate buffer of Selander *et al.* (1971). Alleles at each of these loci were labelled alphabetically, in order of decreasing electrophoretic mobility of their corresponding allozymes. It was necessary to examine EST in both the Tris–maleate and the lithium hydroxide buffers (Selander *et al.* 1971), as not all of the 11 alleles detected could be distinguished with either buffer system alone. The groups of alleles detected using each buffer were, in order of decreasing mobilities of their allozymes:

Lithium hydroxide: a, b, $c+d$, e, f, $g+h$, $i+j$, k
Tris–maleate: a, b, c, e, $d+f+g+i$, h, j, k

Such increased sensitivity gained by using more than one buffer system is by no means unique (e.g. Singh *et al.* 1976).

Goodness-of-fit χ^2 tests were used to compare observed genotypic frequencies within samples to those expected under Hardy–Weinberg equilibrium. To avoid statistical difficulties associated with small expected values for some genotypic classes at these multiallelic loci, the tests were made using pooled homozygous and pooled heterozygous classes, and a χ^2 with one degree of freedom. Departures of observed heterozygosity (H_o) from expected (H_e) were expressed as

$$D = (H_o - H_e)/H_e .$$

To compare allelic frequencies between samples, we used contingency χ^2 tests. Within each of the five main areas, we had two or more subsamples (Fig. 1). Comparisons of allelic frequencies between subsamples within areas showed few significant differences, no more than expected by chance in a large number of independent χ^2 tests. Also, no differences were found between males and females, so the allelic frequencies are presented only for the pooled samples for each area. This pooling provided reasonable sample sizes for comparisons between areas. The ages of fish in our samples ranged from 1 to 14 years. This wide range generally rendered sample sizes of individual cohorts too small for useful comparisons. The exceptions were reasonably large samples of 1+-year-old fish from Koks Island and Freycinet Estuary, and these were treated separately in the analyses. For convenience, the fish that were 2 years or older are referred to as 'adults'.

Variation among areas was quantified in two ways. First, the standardised variance in allelic frequencies, F_{ST} (Wright 1978), was calculated for each of the four loci, as the average F_{ST} of the alleles at that locus, weighted by their frequencies. Second, Nei's (1978) unbiased genetic distance was calculated for each pair of areas. Since only the four polymorphic loci were used, the values of genetic distances obtained cannot be compared with other published values, but they do quantify the relative amounts of genetic divergence among the samples. The values of genetic distances were summarised by UPGMA clustering (Sneath and Sokal 1973).

Results

For samples from each of the five major areas, there were no significant departures of observed heterozygosity from expectations under random mating, but there was a trend towards deficits of heterozygotes. Averaging D over all areas (weighting by sample size), the mean deficit of heterozygotes was significantly different from zero for EST in both 1+ year olds and adults, and non-significant deficits occurred in all but one other comparison (Table 1). The trend towards heterozygote deficits is more obvious in the 1+ year olds, which had an average deficit of 13% for the four loci. This was significantly larger than the average deficit of 6% for the adults (t-test; Table 1).

Allelic frequencies in fish from the five areas are presented in Table 2. Since the focus of this study was possible isolation of stocks in the inner gulfs of Shark Bay, we first compared allelic frequencies in samples from the outer bay (including Cape Cuvier and Koks Island). These two samples showed no significant differences in allelic frequencies at any of the four loci and were consequently pooled for comparisons with samples from the inner bay. The relatively small and geographically intermediate sample from Denham Sound was genetically homogeneous with the ocean fish. Comparisons among samples from the ocean, Freycinet

and Faure areas, on the other hand, showed significant differences in allelic frequencies at each of the four loci. For simplicity, the ocean samples from Cape Cuvier and Koks Island were pooled for analysis of these differences (Table 3).

Table 1. Departures of observed from expected heterozygosity, averaged among samples of *C. unicolor* from Shark Bay

Fish that were 2 years or older are referred to as adults. *N*, number in sample. *D*, departure of observed from expected heterozygosity. $*P < 0{\cdot}05$; $**P < 0{\cdot}01$

Locus	1+ year olds			Adults		
	N	*D*	χ^2	*N*	*D*	χ^2
Est	252	−0·143	4·53*	588	−0·133	8·09**
Idh	250	−0·044	0·57	591	−0·055	2·22
Mpi	251	−0·153	1·28	591	−0·074	0·43
Gpi	247	−0·165	1·04	572	+0·035	0·09
Average		−0·126			−0·057	
s.e.		0·028			0·035	

In adults from the Freycinet and Faure areas, the EST^f allele was at higher frequency than in the ocean sample. This was the only difference common to the two inner portions of the bay. The clearest contrast between samples of adults was for Idh^g, which had its lowest frequency in the Faure area, and highest in Freycinet Estuary. The fish from Freycinet had significantly lower frequencies of Mpi^c than those from the ocean, and the Faure fish had higher frequencies of Gpi^c than found in either Freycinet or the ocean. The most striking difference was the occurrence of the Idh^a and Idh^b alleles at a combined frequency of almost 0·10 in the Faure area, and less than 0·01 outside that area. In summary, comparisons between ocean, Freycinet and Faure samples revealed significant differences in allelic frequencies at three of the four loci between each pair of areas, and at all four loci overall. The sample of fish from Denham Sound was smaller and genetically indistinguishable from the ocean group, but was significantly different from Freycinet for *Gpi* and from Faure for *Est* and *Idh*.

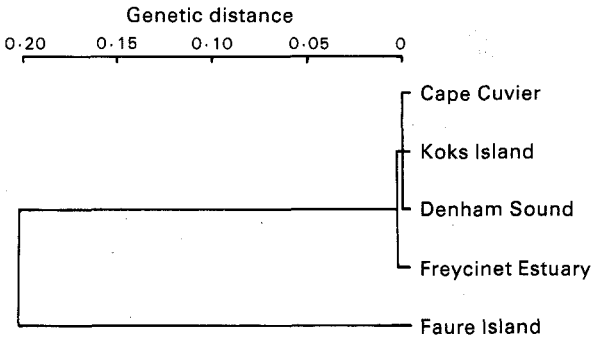

Fig. 2. Phenogram of genetic distances among samples of *C. unicolor*.

A clear summary of the pattern to this variation is provided by the phenogram of genetic distances (Fig. 2), which shows the sample from Faure to be the most different. Although this heterogeneity of allelic frequencies among areas is statistically significant, the differences were not large. Among samples from the ocean area, Freycinet Estuary, and the Faure area, the average F_{ST} ($\pm$s.e.) for the four loci was $0{\cdot}016 \pm 0{\cdot}004$. For perspective, the same calculations were made among the three cohorts (ages 1, 6 and 7) represented by 60 or more

Table 2. Allelic frequencies and comparison of observed with expected heterozygosity (*D*) in samples of *C. unicolor*

\+ Allelic frequency < 0·005. – Allele not detected. Sample sizes are given in parentheses

Locus and allele	Adults					1+ year olds	
	Cape Cuvier (90)	Koks Island (230)	Denham Sound (47)	Freycinet Estuary (130)	Faure Island (98)	Koks Island (61)	Freycinet Estuary (191)
Est							
a	0·01	0·01	–	–	0·01	0·01	–
b	0·02	0·01	0·01	+	0·01	0·03	0·02
c	0·05	0·05	0·06	0·05	0·04	0·10	0·06
d	0·01	0·03	0·02	0·03	0·04	0·01	0·02
e	0·08	0·06	0·08	0·04	0·02	0·04	0·08
f	0·74	0·70	0·67	0·80	0·79	0·72	0·73
g	0·01	0·02	–	0·03	0·01	0·07	0·03
h	0·02	0·07	0·06	0·02	0·04	0·02	0·02
i	0·01	0·01	0·02	0·01	0·01	–	0·02
j	0·04	0·03	0·04	0·02	0·02	0·01	0·02
k	0·01	0·02	0·02	0·01	0·02	–	0·01
D	−0·16	−0·09	−0·08	−0·17	−0·19	−0·26	−0·11
Idh							
a	–	+	0·01	–	0·07	–	–
b	–	0·01	–	–	0·03	–	–
c	0·22	0·24	0·24	0·15	0·18	0·18	0·23
d	0·01	–	0·01	–	0·02	–	–
e	0·65	0·60	0·62	0·60	0·61	0·62	0·62
f	–	+	–	–	–	–	–
g	0·12	0·15	0·12	0·25	0·10	0·20	0·14
D	−0·12	−0·01	−0·22	+0·01	−0·12	+0·06	−0·08
Mpi							
a	0·02	0·01	0·03	0·02	0·05	0·04	0·04
b	0·02	0·02	–	0·05	0·02	0·02	0·06
c	0·96	0·95	0·96	0·90	0·93	0·03	0·90
d	0·01	0·01	0·01	0·04	0·01	–	0·01
D	+0·01	−0·04	+0·05	−0·28	−0·02	+0·05	−0·22
Gpi							
a	0·02	+	–	0·03	0·01	–	–
b	0·05	0·04	0·02	0·05	0·01	0·05	0·05
c	0·93	0·93	0·98	0·91	0·99	0·94	0·92
d	0·01	+	–	0·01	–	0·01	0·02
D	+0·42	−0·04	−0·01	−0·03	−0·03	−0·06	−0·24

Table 3. Summary of heterogeneity χ^2 tests of allelic frequencies among samples of adult *C. unicolor*

Fish that were 2 years or older are referred to as adults. *$P < 0·05$; **$P < 0·01$; ***$P < 0·001$; n.s., $P > 0·05$. – No test possible

Comparison	*Est*					*Idh*				*Mpi*			*Gpi*	
	c	*d*	*e*	*f*	*h*	*a,b*	*c*	*e*	*g*	*a*	*b*	*c*	*b*	*c*
Ocean × Denham	n.s.	–	n.s.	n.s.	n.s.	–	n.s.	n.s.	n.s.	–	–	n.s.	–	n.s.
Ocean × Freycinet	n.s.	n.s.	n.s.	**	*	–	**	n.s.	***	n.s.	*	***	n.s.	n.s.
Denham × Freycinet	–	n.s.	n.s.	n.s.	–	–	n.s.	n.s.	n.s.	–	–	n.s.	–	*
Ocean × Faure	n.s.	n.s.	–	*	n.s.	***	n.s.	n.s.	n.s.	–	–	n.s.	–	**
Freycinet × Faure	n.s.	n.s.	*	n.s.	–	***	n.s.	n.s.	***	n.s.	–	n.s.	–	*
Denham × Faure	–	–	*	–	–	**	n.s.	n.s.	n.s.	–	–	n.s.	–	–

individuals from the Koks Island area. The average F_{ST} among cohorts in this area was 0·009 ± 0·002, nearly 60% as large as the variance among areas.

Only for the 1+-year-old fish from Freycinet and Koks Island were samples sufficiently large to allow comparisons between areas for fish of a single age class. Contrary to the findings for the adults, the 1+ year olds showed no significant differences in allelic frequencies in the two areas (Table 4). For two of the three loci showing differences between the areas for the adults, it is the adults from Freycinet that stand out: Idh^g occurred at a frequency of 0·25 in the older fish in Freycinet, but only 0·13 in the older ocean fish and 0·16 in the combined sample of 1+ year olds; similarly, Est^f was at 0·80 in older Freycinet fish, but only 0·72 in ocean fish, and 0·73 in the 1+ year olds. The results for the third locus, *Mpi*, appear to be different, as allelic frequencies were similar between age groups within each area. However, the lack of significant differences between areas for the 1+-year-old fish makes the results ambiguous, and indicates that sample sizes were inadequate.

Table 4. Summary of heterogeneity χ^2 tests of allelic frequencies in different age groups of *C. unicolor*

Fish that were 2 years or older are referred to as adults. $*P < 0·05$; $**P < 0·01$; $***P < 0·001$; n.s., $P > 0·05$. – No test

Comparison	*Est*					*Idh*			*Mpi*			*Gpi*	
	c	*d*	*e*	*f*	*h*	*c*	*e*	*g*	*a*	*b*	*c*	*b*	*c*
Between age groups													
Ocean	*	–	n.s.	n.s.	–	n.s.	n.s.	–	–	–	n.s.	n.s.	n.s.
Freycinet	n.s.	n.s.	*	*	n.s.	*	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.
Between ocean and Freycinet													
1 year olds	n.s.	–	n.s.	n.s.	–	n.s.	n.s.	n.s.	–	–	n.s.	n.s.	n.s.
Adults	n.s.	n.s.	n.s.	**	*	**	n.s.	***	n.s.	*	***	n.s.	n.s.

Discussion

The rationale of the genetic approach to the detection of distinct breeding populations is that isolation enhances genetic divergence, whether the cause of the divergence is natural selection or genetic drift. Conversely, substantial interbreeding between individuals from different areas would eliminate genetic differences between areas. Thus, the heterogeneity of allelic frequencies among snapper from different areas in Shark Bay implies subdivision of the breeding population. This conclusion is consistent with indications from tagging studies on snapper elsewhere (Cassie 1956; Paul 1967, 1976; Sanders 1974). In Shark Bay, of more than 500 tag recoveries after 1–3 years at liberty, no tagged fish has been found to move from the ocean areas to the inner gulfs, or vice versa; nor has there been any movement between the two gulfs (M. Moran, unpublished data).

An advantage of the genetic approach is that it integrates effects of mixing over the entire life cycle, including untaggable eggs and larvae. This does not necessarily mean, however, that genetic differences between snapper from different areas indicate distinct breeding populations. It is possible for selection within a single generation to produce differences between areas or between cohorts within an area. Several examples are known of genetic differentiation despite considerable mixing of larvae (e.g. Williams *et al.* 1973; Johnson and Black 1984*a*). Indeed, genetic differences among cohorts of snapper from New Zealand are thought to reflect temperatures at the time of production of each cohort (Smith 1979). Since the variance of allelic frequencies among areas of Shark Bay is not much larger than that found among cohorts from Koks Island, it is essential to examine the data carefully for evidence of genetic differences that reflect breeding isolation rather than fluctuations in selective regimes.

The clearest evidence for breeding isolation in Shark Bay is for the fish from the Faure Island area, which also showed the largest amount of genetic divergence. The most striking

peculiarity of snapper from this area is the presence of the Idh^a and Idh^b alleles at a combined frequency of about 0·10. These alleles occurred at a frequency of only 0·01 in Denham Sound and Koks Island, and were not found at all from Cape Cuvier or Freycinet Estuary. Furthermore, in a study of snapper from throughout its Australian range, MacDonald (1980) found Idh^a or Idh^b only in his sample from Shark Bay (from near Koks Island). The conclusion must be that the carriers of these alleles in the Faure Island area were produced in that same area. Since approximately 20% of the snapper from Faure carry these alleles, either as homozygotes or as heterozygotes, at the very least that proportion of the population is resident. The actual degree of isolation is probably much higher. A very small amount of dispersal from the Faure area would account for the presence of Idh^a and Idh^b at low frequencies in the Koks Island and Denham Sound areas.

The evidence for isolation of a population of snapper in Freycinet Estuary is not as straightforward, because differences between this area, Denham Sound and the ocean are relatively small and do not involve unique alleles. Indeed, taken at face value, the comparisons involving 1+-year-old fish provide evidence of gene flow between Freycinet Estuary and the Koks Island area. An explanation apparently consistent with these comparisons is that (1) the stocks in Freycinet receive their recruits from the ocean fish, and (2) in the resident juveniles and adults, frequencies of Est^f and Idh^g change under selection in Freycinet.

Although accounting for the observations, this model requires very strong selection to produce the required changes in allelic frequencies. To illustrate this, we have used a simple model of directional selection, with additive fitness:

Genotype	AA	AB	BB
Fitness	1	$1-0{\cdot}5s$	$1-s$

where s is the selection coefficient. For such selection, the change in allelic frequency in one generation is

$$\Delta q = -0{\cdot}5sq(1-q)/(1-sq),$$

where q is the frequency before selection of the allele that is selected against (Falconer 1967). Taking q as the allelic frequency in the 1+-year-old fish and Δq as the difference in allelic frequency between that cohort and the adults in Freycinet, the selection coefficient can be calculated as

$$s = \Delta q/\{q[\Delta q - 0{\cdot}5(1-q)]\}.$$

For Est^f and Idh^g, s is calculated to be 0·59 and 0·63, respectively, which are very large selection coefficients. The cost of such strong selection can be calculated as

$$L = sq(1-q) + sq^2,$$

where L, the genetic load, is the proportion of the cohort that must die selectively in order to bring about the required change in allelic frequencies. The loads calculated for Est^f and Idh^g are 16 and 53%, respectively. If selection is assumed to act independently on the two loci, the combined load is 61%. Although approximations only, these calculations show that the genetic differences are too large to be reasonably accounted for by varying selection pressures on different cohorts. The implication is that the population in Freycinet Estuary is at least partially isolated, allowing genetic changes to accrue over many generations. Without independent evidence on selection, however, the genetic data cannot provide an estimate of the degree of that isolation.

If it is correct that a distinct breeding population exists in Freycinet Estuary, it means that the sample of 1+-year-old snapper from Freycinet is not representative of that population. Since that sample came from a single trawl, this is possible. The implication is that more than one breeding population may contribute to the stock of juvenile snapper in Freycinet Estuary; one possibility, among others, is that the area is nursery ground for snapper from the outer bay. In order to unravel the complexity of the snapper stock in Freycinet Estuary,

it will be necessary to monitor reproduction and allelic frequencies over a period of at least 12 months.

Two other aspects of the data raise questions for further research. First, the observed deficits of heterozygotes, and the fact that the deficit is larger for younger fish, are typical of many marine animals (e.g. Tracey *et al.* 1975; Johnson and Black 1984*b*; Singh and Green 1984), and a general explanation has not been found. The obvious explanation would be a Wahlund effect, through the mixing of individuals from genetically different groups. Geographical mixing has often been shown to be inadequate as a source of deficits of heterozygotes (e.g. Tracey *et al.* 1975; Johnson and Black 1984*b*), and the same applies to snapper in Shark Bay. For the simple case of two alleles at a locus, the maximal deficit of heterozygotes arising from mixture among areas is F_{ST}, which for snapper in Shark Bay would be less than 2%, compared with the observed deficit of 13% in the 1+-year-old fish. Other possible explanations for these deficits include the presence of rare null alleles, heterogeneity of breeding populations on a finer scale (Tracey *et al.* 1975; Johnson and Black 1984*b*), or opposing effects of natural selection in different phases of the life cycle (Singh and Green 1984). The smaller deficit of heterozygotes in the older fish than in the 1+ year olds is circumstantial evidence for some effect of selection on Shark Bay snapper.

The second aspect of the data warranting further consideration is the role of selection in producing the observed genetic differentiation. The eastern and western gulfs of the bay show similar gradients of both salinity and temperature (Logan and Cebulski 1970). Thus, parallel genetic profiles in the Faure and Freycinet areas could reflect selection associated with these gradients. In only one case, however, did we find such parallelism: the higher frequency of Est^f in samples from both Faure and Freycinet, compared with ocean samples. Support for the interpretation that this consistency results from selection comes from a comparison of our data with those for snapper in New Zealand. Smith (1979) found the frequency of Est^f (his *Est-4*^{2}; see MacDonald 1980) to vary with temperature, so that cohorts produced in cooler years had higher frequencies of Est^f than did those produced in warmer years. In Shark Bay, surface temperatures in winter, the period of reproduction, are lower in the heads of both the western and eastern gulfs compared with the outer bay: a gradient of 6°C was measured in July 1982. Thus, the higher frequency of Est^f in Freycinet and the Faure area is associated with cooler temperatures during the reproductive season, and parallel the temporal pattern observed in New Zealand. Although direct confirmation of a role of selection is beyond the scope of this study, the data show that further work on mechanisms of genetic change in snapper in Shark Bay would be worthwhile.

Acknowledgments

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