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Genetic stock structure of the southern African hakes *Merluccius capensis* and *M. paradoxus*

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ABSTRACT: We estimated the genetic components of geographic variation among stocks of 2 sympatric southern African hakes, *Merluccius capensis* and *M. paradoxus*, using allozyme population markers detected by protein electrophoresis. In *M. capensis* 6 of 33 protein-coding loci were sufficiently polymorphic to test hypotheses of genetic stock structure. Significant but unexplained allele frequency differences were detected between sexes at 5 locations. Significant allele frequency differences between Namibian and South African samples were detected for *Ck-A*, indicating at least some genetic subdivision between these regional stocks. The absolute amount of differentiation, however, was small (average genetic distance only 0.0008). On average over loci, 98.3 % of the total gene diversity was contained within samples, 0.7 % was due to differences between sexes, 0.7 % to differences among locations within regions, and 0.3 % to differences between regions. In *M. paradoxus* significant allele frequency differences were detected for *Mpi* among the South African samples, but the amount of differentiation between samples was very small. There were no significant allele frequency differences between Namibian and South African samples. Most of the gene diversity (98.7 %) was contained on average within samples, 0.3 % was due to differences between sexes, 0.2 % to differences between locations within regions and 0.3 % to differences between regions. A review of morphological variation together with the genetic data presented here suggest that both species of hake are minimally subdivided into 2 regional stocks. The most conservative approach to the management of the regional stocks of hake is to manage the Namibian and South African stocks independently of one another

INTRODUCTION

Two sympatric species of hake, *Merluccius capensis* and *M. paradoxus*, inhabit the coastal waters of southern Africa and support a large bottom trawl fishery. The former species generally inhabits continental shelf waters to a depth of 440 m, whereas the latter species inhabits deeper waters from 140 to 850 m. The geographic distributions of both fishes are closely associated with the cold water of the northward flowing Benguela Upwelling System on the west coast (Botha 1980, Shannon 1985). *M. capensis* is distributed between 12 °S lat. on the west coast of Africa to about 27 °E long. on the south coast, but *M. paradoxus* has a more restricted geographic distribution between 18 °S lat. on the west coast to about 31.5 °E long. on the south coast. Although the cranial morphology (Franca 1954, van Eck 1969, Botha 1971, Bentz 1976) and the genetic profiles (Jones & Mackie 1970, Grant et al. 1988, Becker et al. 1988) of these species are distinct, it is impractical to identify the proportions of each species in partially processed commercial landings.

The 2 species of southern African hakes are harvested by bottom trawl more or less continuously on the west coast from the Agulhas Bank to Walvis Bay depending upon bottom topography. Because of its greater geographic range *Merluccius capensis* is also fished in the northern part of Namibia. These geographic distributions of fishing effort also reflect the more or less continuous distributions of the 2 species (Macpherson et al. 1986, Payne et al. 1986). Concentrations of larvae and juveniles, however, are more patchy. In *M. capensis*, high concentrations of larvae and juveniles are generally found off the Orange River and to the south, but the centers of these concentrations vary from year to year. On the other hand, larvae and juveniles of *M. paradoxus* are found off southern Namibia and off Cape Point in more offshore waters (Macpherson et al. 1986, Payne et al. 1986). The degree to which these concentrations of larvae and juveniles are isolated from one another is not known.

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One important consideration in the commercial exploitation of a fishery resource is the identification of any discrete population or stock units that might exist. These idealized stock units are usually thought of as self-maintaining groups of fish that are temporally or spatially isolated from one another and because of their isolation are generally thought to be genetically distinct to some degree or another (Ricker 1972, Booke 1981). Reproductive isolation between stocks of marine fishes may arise by homing to different spawning areas (e.g. Pacific herring *Clupea pallasi,* Hourston 1982) or by hydrographic features which reduce or prevent migration between areas. For example, Iles & Sinclair (1982) have proposed that stocks of Atlantic herring *Clupea harengus* are structured at the larval stage by oceanographic gyres which create stable larval-retention areas.

Several methods have been employed to measure the amount of relatedness between stocks. Tagging is one method, which yields direct evidence of migration (e.g. Haugen et al. 1969), but cannot be applied to hakes because few fish survive the transit to the surface (Jones 1974). Other approaches are to define stocks (e.g. salmon) by geographic differences in body morphology or meristic characters or by the analyses of otoliths (Ihssen et al. 1981). But these methods depend upon finding pronounced environmental differences between areas, a situation that does not occur in the range of southern African hakes. None of these techniques, however, yields unequivocal data on the genetic relatedness between stocks. In the present study we have chosen protein electrophoresis to estimate the genetic component of geographic variation in the southern African hakes (Allendorf & Utter 1979). We assume that electrophoretic variants are neutral or nearly neutral to the effects of natural selection and thus largely reflect the historical effects of population size and migration (Lewontin 1974).

There have been few genetic studies of other species of hake in the genus *Merluccius*. One electrophoretic study of the Pacific hake (*M. productus*), however, demonstrated the presence of allele-frequency differences between populations located in Puget Sound, a large marine embayment, and offshore oceanic populations (Utter & Hodgins 1969, 1971, Utter et al. 1970). Another study of the North Atlantic hake (*M. merluccius*), however, failed to detect any genetic differentiation among populations (Mangaly & Jamieson 1978).

The purpose of this study was to investigate the genetic relationship between Namibian and South African stocks of the 2 species of hake. In our experimental design we subdivided our samples for each species into 2 groups that more or less concided with the political boundary between Namibia and South Africa because this subdivision also appeared to reflect regional differences in morphology. There is a large potential for movement between locations at different life-history stages for each of these species. Fish spawn offshore in deep water in spring, and pelagic eggs and larvae drift in currents near the surface in the thermocline. Juveniles begin to lead a demersal existence during their first year (Botha 1973). Although extensive seasonal, longshore migration characterizes other species of hake (Bailey et al. 1982), the amount of migration in the 2 southern African species is uncertain. Botha (1980) argued from annual catch data that there was no strong seasonal patterns of migration in the Cape of Good Hope area. There is, however, some evidence of seasonal migration in Namibian waters (Inada 1981, Anon. 1986).

MATERIALS AND METHODS

Tissue samples or whole fish of *Merluccius capensis* (13 locations) and *M. paradoxus* (10 locations) were collected from coastal waters extending from northern Namibia to the south coast of South Africa (Table 1; Fig. 1). Although the morphologies of these species are superficially very similar, they can be identified by differences in the gill arch tubercles (van Eck 1969). Samples were frozen and held at −25 °C until laboratory analyses.

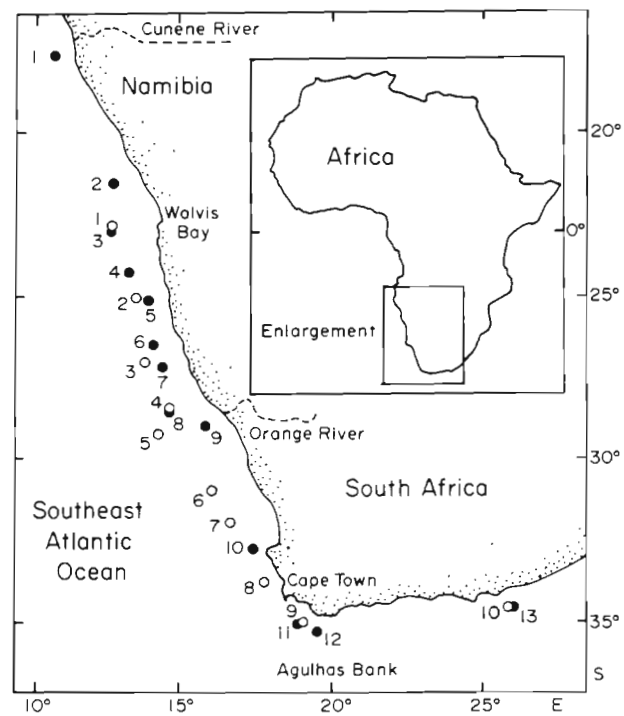

Fig. 1 Sampling locations of *Merluccius capensis* (●) and *M. paradoxus* (○) used in study of genetic variation

Loci were designated using evolutionary nomenclature inferred from tissue distributions of gene expression (e.g. Markert et al. 1975, Fisher et al. 1980, Frick 1983). Otherwise, loci encoding functionally similar proteins were numbered by the mobilities of their products beginning from the cathodal end of a gel. Alleles for each species were designated by their electrophoretic mobilities relative to the most common allele for that species, which was arbitrarily designated 100. Alleles migrating cathodally from the origin were prefixed with a minus sign. The names of the loci examined, their Enzyme Comission numbers, buffers and tissues giving the best results are presented in Table 2.

RESULTS

Merluccius capensis

Table 3 presents the allele frequency data for 13 polymorphic loci. Six loci, *Ck-A, Gpi-A, Gpi-B, Pgm-A, Pep-B* and *Pep-D,* were sufficiently polymorphic to test hypotheses of population genetic structure. Individuals were sexed in Samples 1, 2, 4, and 6 to 12. Graphical representations of the frequencies of the most-common alleles for polymorphic loci along with 95 % confidence intervals are presented in Fig. 2.

We used the *G*-test for goodness of fit (Sokal & Rohlf 1981) to test for departures from Hardy-Weinberg proportions. Genotypic frequencies of loci having rare genotypes were pooled according to Swofford & Selander (1981). Significant departures from Hardy-Weinberg expectations were detected for *Ck-A* among males of Sample 11 ($G_1 = 5.240$, $p < 0.05$) and among pooled individuals in this sample ($G_1 = 6.07$, $p < 0.05$). Significant departures were detected for *Pep-B* in Sample 1 (females $G_1 = 4.32$, $p < 0.05$; pooled over sexes $G_1 = 4.22$, $p < 0.05$) and in Sample 8 (males $G_1 = 5.94$, $p < 0.05$; pooled over sexes $G_1 = 9.61$, $p < 0.01$). For *Pep-D*, significant departures appeared in Sample 9 (males $G_1 = 5.31$, $p < 0.05$; pooled over sexes $G_1 = 11.04$, $p < 0.01$) and in Sample 10 (males $G_1 = 10.33$,

Table 1. *Merluccius capensis* and *M. paradoxus*. Locations, dates, depths and sizes of samples used for electrophoretic analyses

Sample no.	Location	Date collected	Depth (m)	Sample size		
				Total	Male	Female
Merluccius capensis						
Namibia						
1.	19°42′ S, 11°48′ E	16 Jan 86	195	64	26	38
2.	22°03′ S, 13°31′ E	28 Jan 86	136	100	50	50
3.	23°02′ S, 13°05′ E	14 Jan 84	384	94		
4.	24°29′ S, 13°36′ E	31 Jan 84	350	85	46	39
5.	25°01′ S, 14°06′ E	17 Jan 84	179	101		
6.	26°07′ S, 14°17′ E	18 Jan 84	216	100	46	54
7.	27°02′ S, 14°35′ E	19 Jan 84	298	100	42	58
8.	27°57′ S, 14°58′ E	20 Jan 84	193	91	36	55
South Africa						
9.	28°52′ S, 16°28′ E	24 Jan 84	86	100	28	72
10.	32°55′ S, 17°40′ E	12 Jan 84	301	101	51	50
11.	35°15′ S, 19°25′ E	07 Jan 84	303	100	62	38
12.	35°00′ S, 19°05′ E	26 Nov 84	150	50	24	26
13.	34°20′ S, 25°40′ E	29 Nov 84	205	50		
Merluccius paradoxus						
Namibia						
1.	23°02′ S, 13°05′ E	14 Jan 84	384	89		
2.	25°08′ S, 13°38′ E	29 Jan 84	450	98		
3.	27°03′ S, 14°08′ E	28 Jan 84	420	76		
4.	27°57′ S, 14°58′ E	20 Jan 84	130	100		
South Africa						
5.	29°01′ S, 14°36′ E	22 Jan 84	299	99	58	41
6.	31°30′ S, 16°00′ E	15 Jan 84	478	82	26	56
7.	32°05′ S, 16°40′ E	14 Jan 84	346	94	38	56
8.	33°40′ S, 17°30′ E	28 Jan 84	357	98	41	57
9.	34°40′ S, 18°25′ E	09 Jan 84	305	101		
10.	34°20′ S, 25°40′ E	27 Jan 84	205	46		

Table 2. Enzymatic proteins (Enzyme Commission numbers), locus abbreviations, tissues with strongest expression, and electrophoretic buffers used in study of southern African hakes. Tissues: M, skeletal muscle; H, heart muscle; L, liver; E, eye fluids. Buffer components: (1) Gel: 0.03M Tris, 0.005M citric acid, 0.0006M lithium hydroxide, 0.003M boric acid (pH 8.5); electrode: 0.06M lithium hydroxide, 0.3M boric acid (pH 8.1). (2) Gel: 1:4 dilution of electrode buffer; electrode: 0.18M Tris, 0.1M boric acid, 0.004M NaEDTA. (3) Gel: 1:14 dilution of electrode solution; electrode: 0.15M Tris, 0.05M citric acid (pH 6.9). (4) Buffer 2 but with addition of 50 mg NAD to the gel and 75 mg NAD to the cathodal electrode compartment

Protein	Locus	Tissue (s)	Buffer
Creatine kinase (2.7.3.2)	*Ck–A*	M	1
	Ck–B	E, M	1
Glucosephosphate isomerase (5.3.1.9)	*Gpi–A*	M	1
	Gpi–B	M	1
Glyceraldehyde phosphate dehydrogenase (1.2.1.12)	*Gap–1*	M	4
	Gap–2	E	4
Glycerol-3-phosphate dehydrogenase (1.1.1.8)	*Gpd–1*	M	3
	Gpd–2	M	3
	Gpd–3	M	3
Guanine deaminase (3.5.4.3)	*Gda*	H, L	2
Isocitrate dehydrogenase (1.1.1.42)	*Idh–A*	M, H	3
Lactate dehydrogenase (1.1.1.27)	*Ldh–A*	M	1
	Ldh–B	M	1
	Ldh–C	L	1
Malate dehydrogenase (1.1.1.37)	*Mdh–A*	M	3
	Mdh–B	M	3
Malic enzyme (1.1.1.40)	*Me*	L, M	3
Mannosephosphate isomerase (5.3.1.8)	*Mpi*	H, M	2
Nucleoside phosphorylase (2.4.21)	*Np*	E	2
Peptidase (3.4.11)	*Pep–A*[1, 2]	M, H	2
	Pep–B[3]	M	2
	Pep–C[1]	M	2
	Pep–D[4]	M	2
	Pep–X[5]	M	2
Phosphoglucomutase (2.7.5.1)	*Pgm–A*	M	1
	Pgm–B	M, L	1
Phosphogluconate dehydrogenase (1.1.1.44)	*Pgd*	M	3
Protein (non-specific)	*Pt–1*	M	1
	Pt–2	M	1
	Pt–3	M	1
	Pt–4	M	1
	Pt–5	M	1
Superoxide dismutase (1.15.1.1)	*Sod–1*	H, L	1
Sorbitol dehydrogenase (1.1.1.14)	*Sdh*	L	1

[1] Substrate: leucyl-tyrosine
[2] Not resolved for routine scoring
[3] Substrate: leucyl-glycyl-glycine
[4] Substrate: phenylananine-proline
[5] Substrate: appeared using leu-tyr and leu-gly-gly

$p < 0.01$; pooled over sexes $G_1 = 9.01$, $p < 0.01$). A significant departure was also detected for *Pgm-A* in Sample 5 ($G_1 = 6.38$, $p < 0.05$).

We used a hierarchical analysis of allele frequencies with the *G*-test for independence (Sokal & Rohlf 1981) to test for heterogeneity between sexes in each sample at the lowest level of population organization, among locations within regions, and between regions (northern or Namibia and southern or South Africa) at the highest nested level. The sums of the *G* values and their associated degrees of freedom over loci give summary statistics for each comparison. At the lowest level of population structure, significant allele frequency differences between sexes appeared in Sample 2 (*Pep-B*, $G_1 = 5.74$, $p < 0.05$), Sample 7 *Ck-A*, $G_1 = 7.61$, $p < 0.01$), Sample 9 (*Ck-A*, $G_1 = 5.47$, $p < 0.05$) and Sample 10 (*Gpi-B*, $G_1 = 5.37$, $p < 0.05$; *Pgm-A*, $G_1 = 5.50$, $p < 0.05$).

There was no significant allele-frequency heterogeneity among Samples 10 to 13 from the southern region. On the other hand, we detected significant heterogeneity among Samples 1 to 9 from the northern region for *Gpi-A* ($G_{16} = 28.49$, $p < 0.05$). At the highest nested level, there was a highly significant degree of

Table 3. *Merluccius capensis*. Allelic frequencies. The following loci were fixed for the 100 allele: *Ck–B, Gap–1, Gpd–A, Gpd–B, Gpd–C, Ldh–C, Mdh–B, Mpi, Np, Pep–X* (leu-tyr), *Pgd, Pt–1, Pt–2, Pt–3, Pt–4, Pt–5, Sdh, Sod*

Locus	Allele	Sample number												
		1	2	3	4	5	6	7	8	9	10	11	12	13
Ck–A	150	–	–	–	–	–	–	0.010	–	–	–	–	–	–
	100	0.812	0.850	0.799	0.847	0.837	0.862	0.790	0.800	0.806	0.696	0.750	0.740	0.710
	96	–	–	–	–	0.005	0.040	–	–	–	–	–	–	–
	85	0.188	0.150	0.196	0.153	0.158	0.138	0.160	0.200	0.194	0.304	0.250	0.260	0.290
	70	–	–	0.006	–	–	–	–	–	–	–	–	–	–
	2N	128	200	184	170	196	196	200	170	196	194	200	100	100
Gda	100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.995	1.000	1.000	1.000
	90	–	–	–	–	–	–	–	–	–	0.005	–	–	–
	2N	128	200	188	170	202	200	200	182	200	202	200	100	100
Gpi–A	250	–	–	0.005	–	–	0.005	–	0.005	–	–	–	–	0.010
	100	0.242	0.145	0.258	0.159	0.248	0.160	0.190	0.132	0.170	0.198	0.237	0.160	0.150
	–80	–	–	–	0.006	–	–	–	–	–	–	–	–	–
	–100	0.671	0.805	0.688	0.771	0.708	0.760	0.770	0.791	0.740	0.767	0.707	0.800	0.810
	–200	0.047	0.050	0.048	0.065	0.040	0.075	0.040	0.071	0.075	0.035	0.056	0.040	0.020
	2N	128	200	186	170	202	200	200	182	200	202	198	100	100
Gpi–B	110	–	–	–	–	0.010	–	–	–	–	–	–	–	–
	100	0.984	0.950	0.952	0.929	0.931	0.985	0.955	0.945	0.945	0.965	0.965	0.950	0.990
	90	–	0.005	–	–	–	–	–	–	–	–	–	–	–
	83	0.016	0.030	0.027	0.047	0.050	0.010	0.045	0.038	0.030	0.015	0.010	0.020	–
	75	–	–	–	–	–	0.005	–	–	–	–	–	–	–
	70	–	0.021	0.022	0.010	–	–	–	0.016	0.025	0.020	0.025	0.030	0.010
	60	–	0.005	–	–	–	–	–	–	–	–	–	–	–
	2N	128	200	186	170	202	200	200	182	200	202	200	100	100
Idh–A	10	1.000	1.000	1.000	0.987	0.994	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	85	–	–	–	0.013	0.006	–	–	–	–	–	–	–	–
	2N	128	200	188	170	202	200	200	182	200	202	200	100	100
Ldh–A	100	1.000	0.995	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	–200	–	0.005	–	–	–	–	–	–	–	–	–	–	–
	2N	128	200	188	170	202	200	200	182	200	202	200	100	100
Ldh–B	100	1.000	1.000	1.000	1.000	1.000	0.990	0.995	1.000	1.000	0.985	0.995	0.990	0.980
	70	–	–	–	–	–	0.010	0.005	–	–	0.015	0.005	0.010	0.020
	2N	128	200	188	170	202	200	200	182	200	202	200	100	100
Mdh–A	180	–	–	–	0.006	–	–	–	–	–	–	–	–	–
	100	1.000	1.000	0.989	0.988	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	50	–	–	–	0.006	–	–	–	–	–	–	–	–	–
	2N	128	200	188	170	202	200	200	182	200	202	200	100	100
Me	105	1.000	1.000	0.987	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.980	0.990
	100	–	–	0.013	–	–	–	–	–	–	–	–	0.020	0.010
	2N	128	200	188	170	202	200	200	182	200	202	200	100	100
Pep–D	103	–	–	0.006	0.013	–	–	0.010	–	–	0.020	0.036	0.030	0.020
	100	0.508	0.566	0.529	0.677	0.602	0.551	0.526	0.630	0.540	0.611	0.521	0.540	0.610
	94	0.062	0.030	0.092	0.038	0.051	0.081	0.088	0.032	0.070	0.040	0.089	0.010	–
	90	–	–	–	–	–	–	0.021	–	0.005	–	–	–	–
	85	0.422	0.394	0.374	0.272	0.347	0.369	0.356	0.312	0.380	0.323	0.354	0.410	0.360
	80	0.008	0.010	–	–	–	–	–	0.026	0.005	0.005	–	0.010	0.010
	2N	128	198	174	158	196	198	194	154	200	198	192	100	100
Pep–B	105	0.421	0.320	0.394	0.442	0.326	0.420	0.449	0.377	0.296	0.406	0.365	0.306	0.306
	100	0.563	0.660	0.606	0.569	0.613	0.570	0.546	0.565	0.679	0.589	0.609	0.612	0.592
	95	0.016	0.020	–	0.009	0.062	0.010	0.005	0.058	0.015	0.005	0.026	0.082	0.102
	90	–	–	–	–	–	–	–	–	0.010	–	–	–	–
	2N	126	200	170	116	194	200	196	154	196	180	192	98	98
Pgm–A	125	0.008	–	0.016	–	–	0.005	–	0.023	–	0.005	–	–	–
	115	0.055	0.050	0.027	0.065	0.025	0.051	0.070	0.068	0.060	0.074	0.060	0.030	0.060
	110	0.008	0.010	–	–	0.010	–	–	–	0.005	–	–	0.040	–
	100	0.883	0.980	0.903	0.894	0.950	0.899	0.875	0.864	0.885	0.891	0.885	0.900	0.880
	80	0.008	–	–	0.012	0.005	–	–	–	0.005	–	–	0.040	–
	75	0.031	0.030	0.016	0.012	0.010	0.035	0.025	0.028	0.030	0.020	0.045	0.030	0.030
	60	0.008	0.020	0.320	0.006	–	0.005	0.015	–	0.015	0.005	–	–	0.010
	55	–	–	0.005	0.012	–	0.005	0.015	0.017	–	0.005	0.010	–	0.010
	2N	128	200	186	170	202	198	200	176	200	202	200	100	100
Pgm–B	103	0.008	–	–	0.029	–	–	–	–	–	–	–	0.020	–
	100	0.961	0.985	0.995	0.953	1.000	1.000	1.000	0.989	1.000	0.995	1.000	0.980	0.970
	95	0.016	0.015	0.005	0.012	–	–	–	0.011	–	0.005	–	–	–
	90	0.0008	–	–	0.006	–	–	–	–	–	–	–	–	–
	2N	128	200	188	170	202	200	200	182	200	202	200	100	100

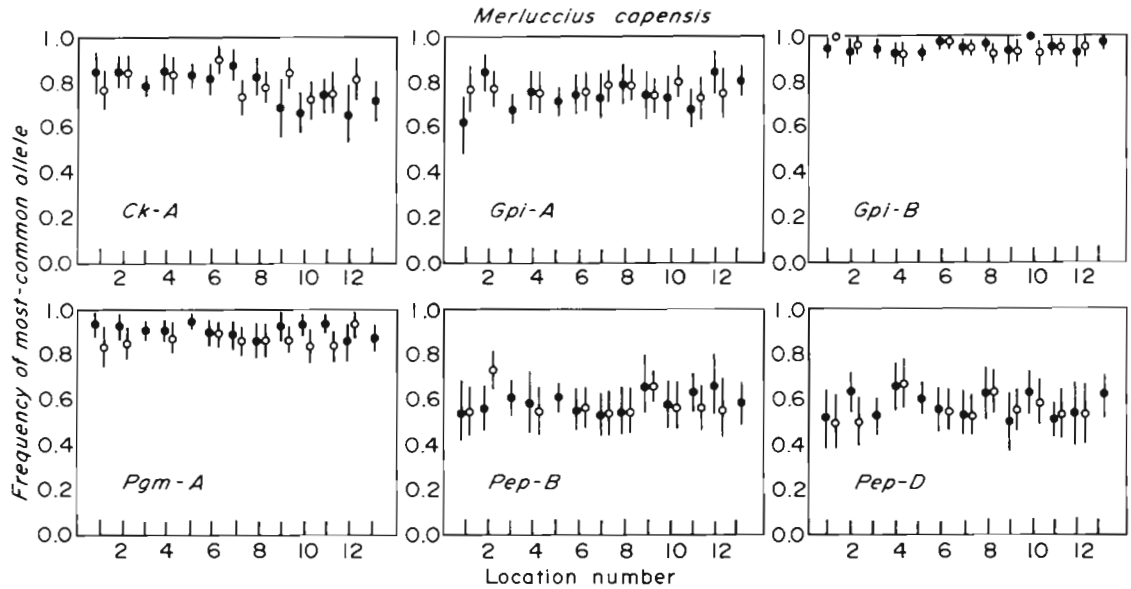

Fig. 2. *Merluccius capensis*. Frequencies of most common alleles in samples. (•) Frequencies of males; (o) frequencies of females. Vertical bars represent 4 binomial standard errors and approximate a 96 % confidence interval. Location numbers as in Table 1 and Fig. 1

heterogeneity between Namibian and South African samples for *Ck-A* ($G_2 = 22.32$, $p < 0.001$). The frequencies of the *Ck-A*^{100} allele pooled over locations for these 2 regions were 0.823 and 0.724, respectively. Although none of the other enzymes showed significance for this comparison, the *G*-statistic summed over all loci was also highly significant ($G_7 = 30.92$, $p < 0.01$).

This heirarchical analysis of allele frequency heterogeneity is not entirely appropriate because significantly different allele frequencies at lower nested levels should not be pooled for comparisons at higher levels. To circumvent this problem we computed an approximate *F* ratio by dividing the summed *G* statistics by their degrees of freedom, and comparing the heterogeneity at one nested level with that at the next lower level (Smouse & Kojima 1972). These results show that the degree of allele-frequency heterogeneity between samples within each of the regions was not greater than the heterogeneity between sexes (Namibia, $F_{56,56} = 1.73$, ns; South Africa $F_{21,21} = 0.54$, ns). There was, however, a significant degree of heterogeneity between Nambian and South African stocks relative to the degree of heterogeneity among samples within each of these stocks ($F_{7,77} = 3.186$, $p < 0.01$).

We used the gene diversity analysis of Nei (1973) with the computing algorithm of Chakraborty et al. (1982) to estimate the relative amounts of gene differentiation between samples at 3 levels of subdivision. Total gene diversity (H_T) was partitioned into its components where $G_{SP} = (H_P - H_S)/H_T$ was the diversity due to differences between sexes (*S*) within populations (*P*), $G_{PR} = (H_R - H_P)/H_T$ was the relative diversity due to differences between populations within regions (*R*), and $G_{RT} = (H_T = (H_T - H_R)/H_T$ was the relative diversity due to differences between regions. The residual gene diversity was the proportion due to within-sample variation. These statistics were averaged over loci to yield a summary statistic for each level of population subdivision. Since the sexes of individuals were not identified in all samples, we used an incomplete experimental design at the lowest level of our analysis in which gene diversity was averaged only over those samples for which data were available. This did not affect the rest of the analysis, because the allele-frequency data were pooled for the the computation of gene diversities at the next hierarchical level of population division.

Average sample heterozygosities ranged from 0.054 to 0.070 and averaged 0.063 over all samples. The gene diversity analysis indicated that this within-sample variability represented 98.3 % of the total variability on average over loci. Allele-frequency differences between sexes represented 0.6 %, differences between samples within regions represented 0.7 %, and differences between regions represented 0.3 % of the total genetic variability. The average genetic distance (Nei 1972) between samples from the 13 locations was 0.0006 and a UPGMA cluster analysis (Sneath & Sokal 1973) revealed no meaningful geographic relationships among the samples.

Merluccius paradoxus

Allele frequencies of 15 polymorphic loci are presented in Table 4. Six loci, *Idh-B, Me, Mpi, Pep-D,*

Table 4. *Merluccius paradoxus*. Allelic mobilities were measured using the most common allele in *M. capensis* for each locus. The following loci were fixed for the 100 allele in all populations: *Ck–B, Gap–2, Gda, Gpd–A, Gpd–B, Ldh–C, Mdh–A, Pep–X* (leu-tyr), *Pt–1, Pt–2, Pt–3, Pt–4, Sdh*. Other loci were fixed for the following alleles: *Ck–A* (65), *Np* (110), *Pt–5* (97)

Locus	Allele	Sample number									
		1	2	3	4	5	6	7	8	9	10
Gap–1	100	–	–	–	–	–	0.006	–	0.005	–	–
	200	1.0	1.0	1.0	1.0	1.0	0.994	1.0	0.995	1.0	1.0
Gpd–C	100	0.008	–	–	0.006	–	–	–	–	–	–
	90	0.992	1.0	1.0	0.994	1.0	1.0	1.0	1.0	1.0	1.0
Gpi–A	800	–	–	–	0.015	–	–	–	–	–	–
	700	–	–	–	–	–	–	–	–	0.005	–
	400	0.017	0.020	0.020	0.020	0.020	0.018	0.032	0.005	0.025	0.022
	350	–	–	–	0.030	0.010	–	0.005	–	–	–
	50	0.983	0.974	0.966	0.945	0.955	0.976	0.957	0.995	0.970	0.946
	–100	–	0.005	0.007	0.005	–	–	0.005	0.005	–	0.033
	–350	–	–	–	–	–	0.006	–	–	–	–
	–700	–	–	0.007	–	–	–	–	–	–	–
	2N	178	196	148	200	198	164	188	196	200	92
Gpi–B	90	0.006	–	–	–	–	–	0.005	0.010	0.005	0.033
	83	0.989	1.000	0.993	0.995	1.000	1.000	0.989	0.985	0.995	0.967
	60	0.006	–	0.007	0.005	–	–	–	0.005	0.005	–
	2N	178	196	148	200	198	164	188	196	200	92
Idh–A	100	0.207	0.144	0.152	0.175	0.199	0.116	0.172	0.155	0.121	0.207
	80	0.741	0.856	0.826	0.760	0.786	0.872	0.817	0.845	0.869	0.772
	40	0.052	–	0.022	0.065	0.015	0.012	0.011	–	0.010	0.022
	2N	174	194	138	200	196	164	186	194	198	92
Ldh–A	1000	0.006	0.005	0.020	0.010	0.025	0.018	0.016	0.010	0.015	–
	100	0.989	0.985	0.980	0.990	0.975	0.976	0.984	0.990	0.985	1.000
	–1000	0.006	0.010	–	–	–	0.006	–	–	–	–
	2N	178	196	148	200	198	164	188	196	200	92
Ldh–B	100	1.000	1.000	0.953	1.000	1.000	1.000	1.000	0.995	1.000	1.000
	80	–	–	0.027	–	–	–	–	0.005	–	–
	70	–	–	0.020	–	–	–	–	–	–	–
	2N	178	196	148	200	198	164	188	196	200	92
Mdh–3	120	–	–	–	–	–	–	–	–	–	0.043
	100	–	–	–	–	–	–	–	–	–	0.011
	80	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.946
	2N	178	196	148	200	196	164	188	196	200	92
Me	112	–	–	–	0.010	–	–	–	0.005	0.011	–
	107	0.022	0.036	0.061	0.030	0.045	0.018	0.037	0.051	0.030	0.054
	100	0.978	0.949	0.919	0.930	0.934	0.970	0.957	0.908	0.940	0.902
	95	–	0.010	0.020	0.025	0.015	0.012	0.005	0.020	0.020	0.033
	90	–	0.005	–	0.005	–	–	–	0.015	0.005	–
	2N	178	196	148	200	198	164	188	196	200	92
Mpi	108	–	–	–	–	–	–	0.006	0.006	–	–
	104	–	–	0.007	0.010	0.020	–	–	0.005	–	–
	102	0.135	0.146	0.139	0.177	0.173	0.146	0.114	0.165	0.120	0.076
	100	–	–	–	–	–	0.006	–	0.015	–	–
	97	0.725	0.620	0.604	0.636	0.617	0.604	0.625	0.655	0.705	0.826
	95	–	–	0.014	0.005	0.005	0.043	0.017	–	0.015	–
	93	0.129	0.229	0.222	0.162	0.184	0.171	0.205	0.170	0.145	0.087
	87	0.011	0.005	0.014	0.010	–	0.024	0.034	0.005	–	0.011
	2N	178	192	144	198	196	164	176	194	200	92
Pgd	65	–	–	–	–	–	0.006	–	–	–	–
	62	0.011	–	–	–	–	–	–	–	–	–
	60	0.989	0.969	1.000	1.000	1.000	0.994	1.000	1.000	1.000	1.000
	40	–	0.031	–	–	–	–	–	–	–	–
	2N	178	196	148	200	198	164	188	196	200	92

Table 4 (continued)

Locus	Allele	Sample number									
		1	2	3	4	5	6	7	8	9	10
Pep–D	110	–	–	0.007	0.010	–	0.006	0.016	–	0.005	–
	108	0.265	0.240	0.215	0.210	0.176	0.213	0.231	0.199	0.230	0.217
	103	0.571	0.547	0.542	0.540	0.596	0.494	0.532	0.591	0.515	0.555
	100	–	0.010	–	–	0.005	0.018	0.005	0.005	–	–
	98	0.165	0.203	0.236	0.235	0.223	0.268	0.215	0.204	0.245	0.228
	85	–	–	–	0.005	–	–	–	–	0.005	–
	2N	170	192	144	200	188	164	186	186	200	92
Pgm–A	150	0.006	–	0.007	0.005	–	–	0.005	–	–	–
	140	0.057	0.046	0.034	0.050	0.030	0.055	0.032	0.011	0.045	0.022
	130	–	–	–	–	–	0.006	0.005	0.005	–	–
	120	0.989	0.903	0.939	0.900	0.914	0.890	0.936	0.888	0.930	0.913
	100	–	–	0.007	–	–	–	0.005	–	0.005	0.011
	97	0.034	0.051	0.014	0.045	0.051	0.043	0.011	0.066	0.010	0.054
	77	0.066	–	–	–	0.005	0.006	0.005	–	0.010	–
	2N	176	196	148	200	198	164	188	196	200	92
Pgm–B	102	0.006	–	0.014	0.005	0.010	0.006	0.005	–	0.040	–
	97	0.972	0.908	0.953	0.910	0.919	0.951	0.931	0.949	0.885	0.935
	95	0.022	0.092	0.034	0.080	0.071	0.043	0.064	0.051	0.075	0.065
	92	–	–	–	0.005	–	–	–	–	–	–
	2N	178	196	148	200	198	164	188	196	200	92
Sod	–100	0.978	0.995	1.000	0.995	0.990	0.988	1.000	0.990	0.990	0.989
	–500	0.022	0.005	–	0.005	0.010	0.006	–	0.010	0.010	0.011
	–1000	–	–	–	–	–	0.006	–	–	–	–
	2N	178	196	148	200	198	164	188	196	200	92

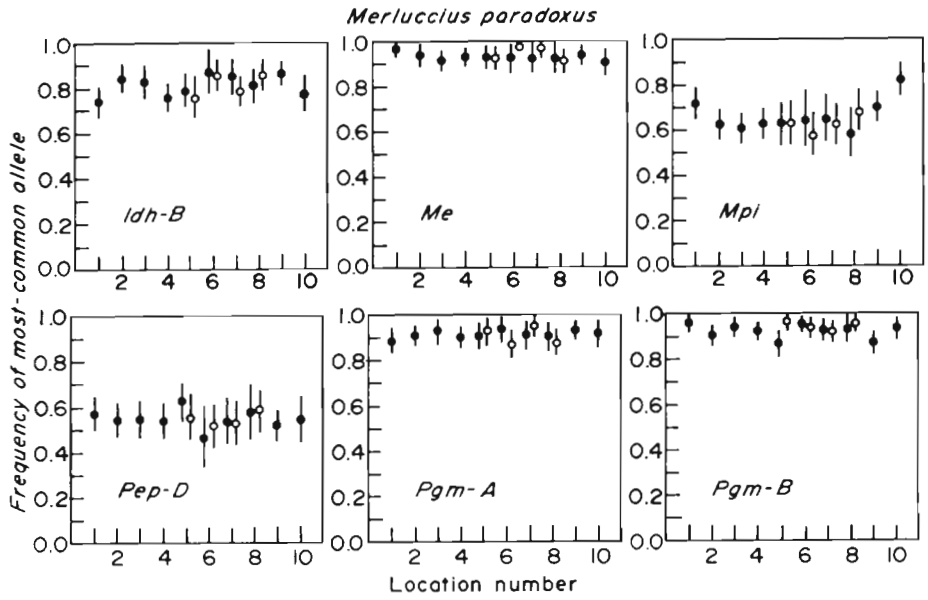

Fig. 3. Frequencies of most common alleles in samples of *Merluccius paradoxus*. (●) Frequencies of males; (○) frequencies of females. Vertical bars represent 4 binomial standard errors and approximate a 96 % confidence interval. Location numbers as in Table 1 and Fig. 1

Pgm-A, and *Pgm-B*, were sufficiently polymorphic for statistical analysis (Fig. 3). Individuals were sexed in Samples 5 to 8. Significant departures from Hardy-Weinberg expectations were detected for *Idh-B* among males in Sample 8 ($G_1 = 3.92$, $p < 0.05$) and among pooled individuals in the same sample ($G_1 = 5.52$, $p < 0.05$). Significance was detected for *Ldh-B* in Sample 3 ($G_1 = 8.89$, $p < 0.01$), for *Mpi* in Sample 7 among individuals pooled over sexes ($G_1 = 4.39$, $p < 0.05$). Significant departures were also observed for *Pgm-B* in Sample 4 ($G_1 = 12.07$, $p < 0.01$) and among males in Sample 5 ($G_1 = 5.12$, $p < 0.05$).

A single significant difference between sexes was detected for *Pgm-B* ($G_1 = 6.92$, $p < 0.055$). Significant

allele-frequency heterogeneity was detected among locations in South Africa for *Mpi* ($G_8 = 19.15$; $p < 0.05$). This significance appears to be due to an aberrant frequency in the eastern-most sample. There were no significant differences for the other enzymes and the sum of G over loci was not significant. A significant degree of allele-frequency heterogeneity was also detected among Namibian samples for *Idh-B* ($G_4 = 10.03$, $p < 0.05$) and for *Pgm-B* ($G_4 = 10.22$, $p < 0.05$). The sum of G over loci for this comparison was also significant ($G_{32} = 49.54$, $p < 0.05$). The between-regions comparison was significant for *Idh-B* ($G_1 = 6.99$, $p < 0.01$), but the summed value of G was not.

A slightly different picture emerges using approximate F ratios to test for heterogeneity at the different nested levels. These results suggest that the degree of heterogeneity among the Namibian samples ($F_{32,8} = 1.46$, ns) and that among South African samples ($F_{23,24} = 1.57$, ns) was no greater than the genetic heterogeneity between sexes within each sample. The results further indicated that the degree of allele-frequency heterogeneity between regions was no greater than that among samples collected within each region ($F_{8,64} = 0.82$, ns).

The gene diversity analysis showed that sample heterozygosities ranged from 0.059 to 0.068 and averaged 0.065. This represented 98.9 % of the total genetic variability on average. Allele-frequency differences between sexes represented 0.3 %, differences among samples within regions represented 0.7 % and differences among regions represented 0.1 % of the total genetic variability. The average genetic distance between pairs of samples was 0.0007 and there was no geographic structure in the distribution of genetic distances among samples.

DISCUSSION

Within-sample variation

It is difficult to interpret the significant allele-frequency differences that we found between the sexes of both hake species. For *Merluccius capensis,* we made a total of 60 comparisons between sexes over the 6 polymorphic enzymes and found significant differences between sexes at 5 locations. With a significance level set at $p = 0.05$ we would expect 3 of these comparisons to be significant by chance alone because of our finite sample sizes. It is still possible, but unlikely, that all 5 significant differences could be within the possibility of sampling error. For *M. paradoxus,* we detected only 2 significant differences between sexes out of 24 comparisons, one of which would be expected by chance alone.

If in fact these allele-frequency differences are not just due to sampling errors, there are 2 possible explanations. The first hypothesis centers on the population biology of these hakes and is that the subsamples were drawn from mixed but genetically differentiated subpopulations of each sex. This hypothesis may have some merit because females grow faster, mature later and live longer than males, and because females are larger they tend to inhabit deeper water than males of the same age (Inada 1981). Such behavior tends to isolated the sexes from one another so that catches from deep waters consist primarily of large females and those from shallower waters consist for the most part of smaller males for each species (pers. comm.; R. Leslie, Sea Fisheries Research Institute). If this hypothesis is true, we might expect to find a significant degree of genetic heterogeneity among samples from different areas and a consistent deficit of heterozygotes in samples pooled between sexes. Neither of these predictions, however, were apparent in our samples. The degree of genetic heterogeneity among samples was small (see later), and there were no consistent deficits of heterozygotes in samples pooled between sexes.

The second possibility is that some kind of sex-specific selection is operating. Since large mature females inhabit the deepest water, there may be environmental factors such as hydrostatic pressure, temperature or environmental heterogeneity which act as selective forces on various genotypes (e.g. Hilbish et al. 1982, Siebenaller et al. 1982). One selective model that has received much attention is heterozygote advantage in which we might expect to find an excess of heterozygotes at loci under selection, i.e. those loci showing significant allele-frequency differences between sexes. This was not the case, however, for *Merluccius capensis.* None of the samples showing significant differences between sexes showed a significant departure from Hardy-Weinberg expectations or a consistent excess (or deficit) of heterozygotes. Another possibility is that there is some kind of directional selection operating on fish found in different habitats. In such a model, we would expect to find that the frequency of one allele or another is consistently greater in one of the sexes. This, however, was also not apparent in the allele frequency data (Fig. 2).

Significant allele frequency differences between sexes in the same sample have also been reported for 2 other marine fishes. Mork et al. (1985) found significant differences for 4 enzymes in Atlantic cod *Gadus morhua* at 2 locations. The enzymes showing the significant differences, however, did not deviate significantly from Hardy-Weinberg expectations and there was no obvious explanation for the sex differences. In another study, significantly different allele frequencies between sexes were observed for witch flounder *Glyp-*

tocephalus cynoglossus in a single sample located in the Gulf of St. Lawrence, Canada (Fairbairn 1981). This difference was accompanied by a significant heterozygote deficit and Fairbairn (1981) postulated that the difference between sexes had arisen by selection for rare alleles in females. Alternatively, the difference may have arisen by chance because no other significant differences between sexes were observed in that study. Without applying *ad hoc* explanations to individual samples, there does not seem to be a general explanation for allele frequency differences between sexes, a not infrequent occurrence in marine fishes.

Geographic variation

Marine fishes in general tend to show very little genetic subdivision between geographic stocks (e.g. Ryman et al. 1984, Shaklee 1984) because there is a very large potential for gene flow between areas by the passive drift of larvae in ocean currents and by active migration of adults. Gene flow, when it occurs, acts as a strong homogenizing force on geographically separated stocks or populations (Waples 1987). Another reason that marine fishes are characterized by a general lack of population subdivision is that genetic drift is negligible at the very large population sizes that are typical of marine fishes. Even for populations that become completely isolated from one another, at least N (= population size) generations must pass before any substantial divergence is likely (Kimura 1955). Nonetheless, genetic subdivisions among regional stocks of marine fishes have been reported, which appear to be the result of ancient allopatric subdivision rather than the result of differentiation *in situ* (Grant 1987).

Our allozyme data show that there is only a small amount of genetic divergence between the stocks of each species of hake. Genetic distances between samples were remarkably small, generally less than 0.001, and more than 98% of the total genetic diversity on average was found within locations for both species. Nonetheless, there was a significant degree of allele frequency heterogeneity between the Namibian and South African stocks of *Merluccius capensis* which appear in both the nested contingency-table analysis and the analysis using approximate F-ratios. Most of the regional heterogeneity, about 80% of the G-statistic summed over loci, was due to regional differences in the allele frequencies of *Ck-A*. None of the other polymorphic loci showed the same degree of geographic differentiation for this comparison.

It is difficult to account for this regional heterogeneity. Assuming that allozyme variation is largely neutral to natural selection and that the geographic distributions of alleles are due to population events, one explanation is that ancestral populations of hake were geographically subdivided and isolated in some way. There were several episodes of oceanic cooling in the Pleistocene which may have subdivided and displaced populations of hake northward to either side of the southern African subcontinent. A similar biogeographic model appears to explain genetic subdivision between eastern and western populations of several North Pacific Ocean fishes in which coastal Pleistocene glaciation and oceanic cooling in the central North Pacific Ocean apparently acted as a barrier to migration isolating eastern and western populations (Grant et al. 1983, Grant & Utter 1984, Grant et al. 1987). In Pacific herring, for example, the average genetic distance between the 2 major groups was 0.039 (40 loci), whereas the average genetic distance between locations within groups was only 0.003. The small amount of overall divergence between the groups of hake suggest that this explanation is unlikely.

If the regional differentiation in *Merluccius capensis* was due to historical population events we would expect, first of all, that all of the loci in a species would be affected to the same extent and that each locus would show a similar amount of divergence (Allendorf & Phelps 1981). Our observation that *Ck-A* shows a significantly greater degree of geographic differentiation than other loci suggests that this locus may be under selection. It is, however, notoriously difficult to make a formal test of a selective hypothesis with allele-frequency data alone (Ewens & Feldman 1976). Secondly, if paleo-oceanographic events subdivided populations of one species of fish in southern Africa, then they would have similarly affected other species in the same area. Genetic studies of southern African anchovies *Engraulis capensis* (Grant 1985a), pilchards *Sardinops ocellata* (Grant 1985b) and *M. paradoxus,* however, do not show corresponding degrees of genetic subdivision over this area.

Our genetic results are somewhat ambiguous over the question of whether Namibian and South African hakes represent 1 or 2 stocks. Ihssen et al. (1981) point out that 'observed electrophoretic difference is a sufficient but not necessary condition for 2 groups of fish to be genetically differentiated' and suggest that population, morphometric and meristic data also be used to infer stock structure. There are minor morphological differences between Namibian and South African stocks of both species. North of the Orange River, the anal fin of *Merluccius capensis* is entirely white and that of *M. paradoxus* is black in color, and this difference is used by research biologists to separate species in the field (E. Macpherson, Instituto de Investigaciones Pesqueras, Barcelona). In this area, this difference between species consistently parallels other differences such as gill tubercle (van Eck 1969) and otolith

morphology (Botha 1971). At the Orange River and to the south, however, both species tend to have gray anal fins with black edges. In this southern area, gill arch tubercle morphology is used to identify species. The geographic variation in anal fin color may reflect genetic differences not detectable with electrophoretic methods or may reflect environmental influences on a genotype capable of variable expression. Either interpretation suggests that there is at least a small degree of regional subdivision between these 2 stocks.

Many species of hake show seasonal longshore migrations driven by annual cycles of cooling and warming. Generally hakes migrate poleward during summer and toward the equator in winter (Inada 1981, Bailey et al. 1982). Such migratory systems should of course be managed as a single panmictic population over the whole geographic range of migration. The extent of longshore migration in the southern African hakes appears to vary from region to region. There have been no tagging studies to investigate patterns of migration because hakes do not survive capture and release well (Fritz 1959). Therefore we can only infer migrational patterns from seasonal and geographic variation in density. An analysis of densities by age show that the greatest concentrations of adult fishes for *Merluccius capensis* and *M. paradoxus* tend to be located off Cape Point and off the mouth of the Orange river (Payne et al. 1986). The densities of younger fishes, however, tend to be geographically more evenly distributed. The northward flowing Benguela Current on the west coast undoubtedly has an homogenizing effect by passively transporting planktonic eggs, larvae and small juveniles. There is no indication of seasonal longshore movements in the concentrations of South African hakes. In contrast, there appears to be at least some seasonal longshore movement of hake stocks in the Namibia region. The greatest concentrations of *M. capensis* tend to be located between 17° and 19°S in summer and autumn but in the vicinity of Walvis Bay (22° to 24°S) in late winter and early spring (Anon. 1986). This movement corresponds with seasonal movement of the boundary between the warm Southern Equatorial Current and the cold upwelled Benguela Current (Inada 1981).

We thus conclude that there is restricted movement of adults between Namibian and South African waters. On the other hand, there may be passive northward movement of eggs and larvae by the Benguela Current. Nonetheless, our finding of a small, but measurable, degree of genetic differentiation between Namibian and South African waters for *Merluccius capensis* suggests that the amount of gene flow between these areas is restricted to at least some degree. These results endorse the present policy of managing Namibian and South African stocks of *M. capensis* as 2 separate units. Although there was no evidence for genetic subdivision between stocks of *M. paradoxus*, the most conserative approach would also be to treat Namibian and South African stocks as separate units.

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