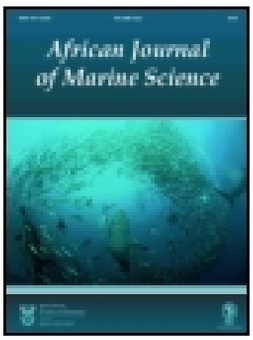

South African Journal of Marine Science

ISSN: 0257-7615 (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tams19

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To cite this article: W. K. Florence , P. A. Hulley , B. A. Stewart & M. J. Gibbons (2002) Genetic and morphological variation of the lanternfish *Lampanyctodes hectoris* (Myctophiformes: Myctophidae) off southern Africa, South African Journal of Marine Science, 24:1, 193-203, DOI: 10.2989/025776102784528466

To link to this article: https://doi.org/10.2989/025776102784528466

Published online: 08 Apr 2010.

S. Afr. J. mar. Sci. 24: 193–203
2002

GENETIC AND MORPHOLOGICAL VARIATION OF THE LANTERNFISH *LAMPANYCTODES HECTORIS* (MYCTOPHIFORMES: MYCTOPHIDAE) OFF SOUTHERN AFRICA

W. K. FLORENCE, P. A. HULLEY†, B. A. STEWART‡ and M. J. GIBBONS**

Genetic and morphological variation within the southern African population of *Lampanyctodes hectoris* was analysed. A total of 15 enzymes, encoding 22 isozyme loci, was examined (n = 327); seven were polymorphic. The percentage of polymorphic loci ranged from 13.6 to 27.3%. The mean heterozygosity was generally low and ranged from 0.003 to 0.005. Genetic divergences between specimens from four areas along the west coast of southern Africa were negligible, genetic distance values (D) ranging from 0 to 0.00011. The results showed the population of *L. hectoris* to be genetically invariant. Principal Component Analysis was performed separately on ratios of 13 morphometric and 6 meristic variables (n = 446), and there was evidence of extensive overlap between fish from all areas. However, discriminant analysis suggested some morphological variability within this population. Although genetically the population of *L. hectoris* seems to be homogenous, morphologically it appears to be variable. A combination of these results suggests that there is no clear genetic basis for the slight morphological differentiation within the population.

Key words: Agulhas Bank, Benguela Current, lanternfish, Namibia, population genetics

Lampanyctodes hectoris, the "Cape onderbaaidjie", is one of the most common lanternfish around southern Africa, and is distributed from northern Namibia (at least 20°S) to Port Elizabeth, South Africa (34°S, 26°E). It is a pseudoceanic species, being confined to waters of the continental shelf and slope (Hulley 1981) around southern Africa, Australia and New Zealand.

Off South Africa, lanternfish are caught as part of the bycatch of the commercial anchovy *Engraulis capensis* and sardine *Sardinops sagax* fisheries (Hulley and Prosch 1987). Landings of pelagic fisheries are subject to considerable interannual variation (Kawasaki 1992), causing a measure of instability to those sectors of the fishing industry that deal with (especially) fishmeal production. This could prompt fishers to embark on a search for alternative resources, and *L. hectoris* appears to be abundant enough to be considered as just such an alternative.

If a directed attempt to fish *L. hectoris* were to be made, knowledge of its biology and ecology is required. There have been a number of studies on its distribution (Shelton 1986, Hulley and Lutjeharms 1995), feeding (Prosch 1986), growth (Hewitson and Cruickshank 1993), reproduction (Prosch 1991) and ecosystem role (Armstrong *et al*. 1991, Jarre-Teichmann *et al*. 1998, Shannon and Jarre-Teichmann 1999), but there have been no attempts to examine the subpopulation structure of local stocks. Information on the latter is essential if an eventual fishery is to be managed in a sustainable manner.

The aim of this study is to investigate the population structure of *L. hectoris* off southern Africa using a combination of morphological/meristic and genetic (allozyme) analyses. Studies that combine the two methodologies maximize both information content and usefulness (Hillis 1987) and are preferred over a single-method approach. Allozyme electrophoresis permits the examination of many independent characters/loci, and a large comparative database for fish exists (e.g. Ward *et al*. 1994, Hilbish 1996). Although allozymes do not directly reflect the variation exhibited in DNA (Avise 1994, Hillis *et al.* 1996), allozyme electrophoresis derives acceptably precise estimates of genetic parameters, ensuring its continued widespread use (Ward *et al.* 1994).

MATERIAL AND METHODS

Samples of *L. hectoris* were collected off southern Africa by demersal and pelagic trawls. The samples were assigned to one of four geographic areas (Leslie and Grant 1990), based on the four major hydrographic and faunal provinces that can be identified along the southern African coast (Shannon 1985):

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Manuscript received January 2001; accepted July 2001

Table I: Abbreviations of meristic counts and morphological measures of *L. hectoris*

Abbreviation	Character
	Meristic
DR	Number of dorsal fin rays
AR	Number of anal fin rays
AOa	Number of *AOa* photophores (left and right)
AOp	Number of *AOp* photophores (left and right)
GRUL	Number of gill rakers on upper limb (left)
GRLL	Number of gill rakers on lower limb (left)
	Morphological
SL	Standard length
HL	Head length
HD	Head depth
BD	Body depth
UJL	Upper jaw length
CPL	Caudal peduncle length
CPD	Caudal peduncle depth
PRED	Predorsal length
PREAD	Pre-adipose length
PREP	Prepectoral length
PREV	Preventral length
PREA	Pre-anal length
ED	Eye diameter
SNL	Snout length

Area 1 – Kunene River to Orange River, an area sometimes influenced by the warm, south-flowing Angola Current in the north and permanently by the cold, north-flowing Benguela Current in the south; Area 2 – Orange River to Cape Columbine, an area influenced by the cold, north-flowing Bengeula Current; Area 3 – Cape Columbine to Cape Infanta, an area of mixing between the Agulhas Current and the Benguela Current; and Area 4 – Cape Infanta to Cape Recife, an area influenced by the warm south- and west-flowing Agulhas Current. The boundary between Areas 1 and 2 also represents the political border between Namibia and South Africa, which manage their fisheries separately.

The samples were immediately blast-frozen or preserved in liquid nitrogen on board ship. In the laboratory, the specimens were stored in a -80°C ultra-deepfreeze prior to examination. Allozyme and morphological data were based on a total of 327 and 286 thawed samples respectively. A further 160 preserved specimens from the collections at the South African Museum collection were included in the morphological analysis.

Meristic and morphometric data

A total of 14 morphometric measurements (Table I) was made on thawed and preserved specimens from each area (Area 1 – 78 specimens, Area 2 – 102 specimens, Area 3 – 149 specimens, Area 4 – 117 specimens). Measurements followed Nafpaktitis (1973), and were made to the nearest 0.1 mm under a binocular dissecting microscope using digital callipers. In all, six meristic counts were also made using a binocular dissecting microscope (Table I). Counts and measurements, other than *AOa* and *AOp* (see Hulley 1986 for definitions), were made where possible on the left side of all fish.

In this study, Principal Component Analysis (PCA) and Discriminant Functions Analysis (DFA) were used to examine morphological variation. PCA acts as a data-reduction method and attempts to explain variation in multi-dimensional space, whereas DFA maximizes differentiation in pre-determined groups. Morphological divergence among populations of a species is usually limited to small changes in shape and size; it seldom involves changes in body structure. Principal components from morphometric data are therefore interpreted as patterns of covariance in size and shape.

Where the mean size of fish among samples differs appreciably, the size differences may dominate the results of a morphometric study. These differences in size may not be a true reflection of regionalism, but rather a reflection of sampling bias. The best method of eliminating any such bias has been debated for a number of years. The simplest way to eliminate any bias caused by size is to express all morphological variables as a function of size, in the present case standard length (*SL*). Although the use of ratios in multivariate analyses has been criticized by some authors (Atchley *et al*. 1976, Albrecht 1978, Atchley and Anderson 1978, Humphries *et al*. 1981), it has been defended by others (Corruccini 1977, Dodson 1978, Hills 1978, Johnson *et al*. 1983). On balance, it was decided to use ratios in this study because they met certain criteria. First, all individuals used were adults, immediately eliminating allometric changes in shape between the larval and the juvenile and adult stages. Second, the slopes of all regression lines fitted to relationships between ratio and size had insignificant slopes, indicating that growth was isometric. This was supported by a preliminary PCA, which generated a high Eigenvalue for Principal Component 1 (PC1) and had approximately equal loadings for each character. This was a strong indication that, for the size range of fish used in the study, growth was mainly isometric.

Meristic and morphometric variation among specimens from the four areas was calculated using the factor analysis module from the STATISTICA V.5 statistical software package (STATSOFT 1996). The meristic and morphometric data were analysed sepa-

Table II: Enzyme (commission numbers), locus abbreviations, and tissue-buffer combinations.Details of the buffers can be found in text

Enzyme	Locus	Buffer	Tissue
Adenylate kinase (2.7.4.3)	*ak-1*	3	M
Creatine kinase (2.7.3.2)	*ck-1*	1	M
	ck-2	1	M
	ck-3	1	L, H
Esterase (3.1.1.1)	*est-2*	1	L, H
	est-3	1	L, H
	est-5	1	L, H
General Protein	*gp-2*	4	M
	gp-3	4	M
	gp-5	4	M
Glucose dehydrgenase	*gdh-1*	2	M
Glucosephosphate isomerase (5.3.1.9)	*gpi-1*	1	M
Glucose-6-Phosphate	*g-6-p-1*	2	M
Isocitrate dehydrogenase (1.1.1.42)	*idh-2*	3	M
Lactate dehydrogenase (1.1.1.27)	*ldh-1*	1	M
Malate dehydrogenase (1.1.1.37)	*mdh-1*	3	M
Malic enzyme (1.1.1.40)	*me-2*	2	M
Peptidase (3.4.11) (Glycyl leucine as substrate)	*gl-1*	2	M
	gl-2	2	M
Phosphoglucomutase (2.7.5.1)	*pgm-1*	1	M
Phosphogluconate dehydrogenase (1.1.1.44)	*pgd-1*	2	M
Superoxide dismutase (1.15.1.1)	*sod-1*	2	M

H = Heart tissue
L = Liver tissue
M = Muscle tissue

rately. Classification functions were calculated using the jack-knife method, which eliminates unbiased group assignment. A discriminant function coefficient for each variable and each individual was also calculated. Mahalonobis distances were measured between samples from the four areas. The factor scores of PC1 and PC2 for each individual were plotted on a two-dimensional plot. Significant differences between slopes of the "most discriminatory variables" based on the morphometric measurements were tested using analysis of covariance.

Electrophoretic data

Genetic variation at 22 isozyme loci was examined in 327 specimens (Area 1 – 47 specimens, Area 2 – 80 specimens, Area 3 – 119 specimens, Area 4 – 81 specimens) on a 13% horizontal starch gel. Four electrophoretic buffer systems were used: (1) Electrode – pH 8.1, 60 mM lithium hydroxide and 300 nM boric acid, Gel – pH 8.5, 30 mM tris, 5 mM citric acid, 0.6 mM lithium hydroxide and 30 mM boric acid (Ridgway *et al.* 1970); (2) Electrode – pH 8.7, 180 mM tris, 100 mM boric acid and 4 mM NaEDTA, Gel – 1–4 dilution of electrode buffer (Markert and Faulhaber 1965); (3) Electrode – pH 6.9, 150 mM tris and 50 mM citric acid, Gel – 1 to 29 dilution of electrode solution (Whitt 1970); and (4) Electrode – pH 8.6, 100 mM tris and 772 mM glycine, Gel – 1–4 dilution of electrode buffer (Richardson *et al*. 1986).

Proteins were extracted from muscle, heart and liver tissue with 2–3 drops of 0.01 M tris homogenizing buffer, pH 8.0. Tissue and buffer were homogenized with sterilized sand, using a glass rod in 1.5 mℓ microfuge tubes. Water-soluble proteins were separated from the homogenate by centrifugation at 2 500 g for 5 minutes. The supernatant was blotted onto filter-paper wicks, which were inserted into a horizontal starch gel. Red food dye was used as a marker. Gels were run in a refrigerator at 4°C for 3–5 h at 30–50 mA. Thereafter, they were divided horizontally into 3 or 4 slices and stained for enzymatic activity by applying specific chemical reagents to a 2% agar overlay (Shaw and Prasad 1970). Details of the enzyme buffer combinations, locus abbreviations, the tissue giving the best results and the loci examined for each study are presented in Table II. The nomenclature of enzyme loci and allele designations follows Allendorf and Utter (1979). Alleles were denoted according to their mobility relative to the most commonly observed allele.

The allelic and genotype frequencies were computed from the allozyme data using BIOSYS v1.7 software (Swofford and Selander 1981). Genotype frequencies were pooled for each locus prior to Chi-square analysis to determine whether they were in Hardy-Weinberg equilibrium. Levene's correction for small sample sizes was used. The percentage of polymorphic loci in each population was determined. Loci were considered polymorphic if the frequency of the most common allele did not exceed 0.99. Nei's (1978) unbiased estimate was used to calculate the mean heterozygosity (H) for each population. The degree of genetic differentiation among the populations was determined by calculating the F statistics (Wright 1965). These included: $F_{(IS)}$, the mean departure from random mating; $F_{(IT)}$, inbreeding relative to the entire population; and $F_{(ST)}$, the genetic differentiation among subpopulations. The mean unbiased genetic identity (I) and genetic distance (D) among the populations were calculated from the allele frequencies according to Nei (1978).

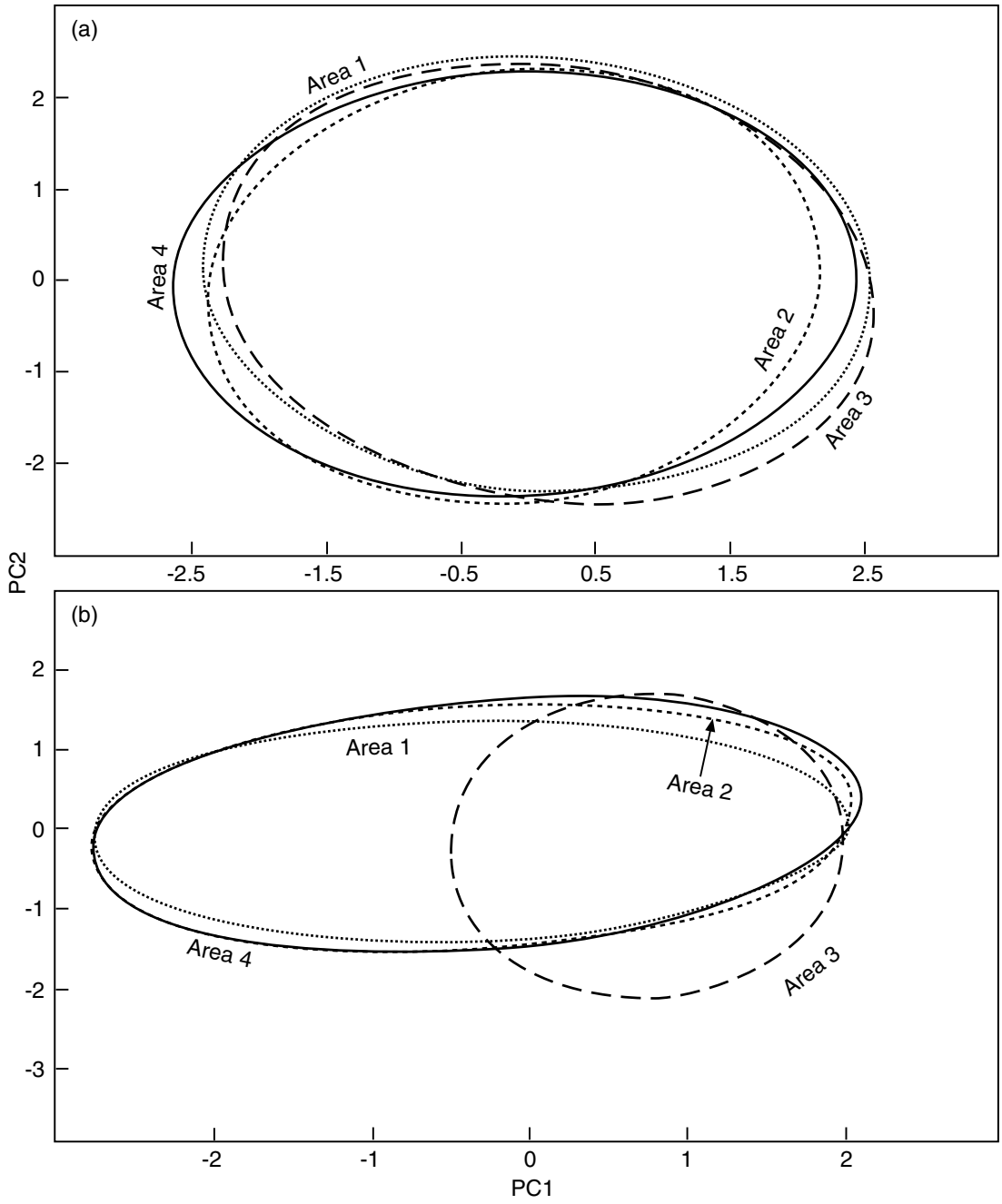

Fig. 1: Plot of 95% confidence intervals for the first and second principal components for (a) meristic and (b) morphometric data of *L. hectoris* from the four areas off southern Africa

Table III: Ranges, 95% confidence intervals (*CI*) and means of meristic counts of *L. hectoris* from four areas off southern Africa. Abbreviations as in Table I

Population group	*n*	Parameter	*DR*	*AR*	*AOa*	*AOp*	*GRUL*	*GRLL*
Area 1	78	Range	11–14	13–16	13–17	10–14	10–12	16–21
		95% *CI*	12.8–13.0	14.8–15.1	14.8–15.3	11.3–11.7	10.6–11.0	19.0–19.4
		Mean	13	15	15	12	11	19
Area 2	102	Range	11–14	14–16	13–17	10–14	10–12	16–21
		95% *CI*	12.7–12.9	15.0–15.2	15.0–15.4	11.3–11.6	10.6–10.9	19.1–19.5
		Mean	13	15	15	11	11	19
Area 3	150	Range	11–14	13–16	13–17	10–14	10–12	16–21
		95% *CI*	12.8–13.0	14.9–15.1	14.9–15.2	11.4–11.7	10.9–11.1	19.0–19.3
		Mean	13	15	15	12	11	19
Area 4	117	Range	11–14	12–16	13–17	6–14	10–12	18–21
		95% *CI*	12.7–12.9	14.9–15.2	15.0–15.4	11.2–11.6	10.6–10.9	19.2–19.5
		Mean	13	15	15	11	11	19

RESULTS

Meristic data

Table III lists the ranges, 95% confidence intervals (*CI*) and means for the meristic counts used in this study. The means of all meristic counts, except *AOp*, were identical for specimens from each area.

There was extensive overlap among samples for PC1 and PC2 (Fig. 1a). The relative contribution of the six principal components that discriminated between specimens is given in Table IV. The first two components contributed 48% collectively to the total variance between the four areas.

The stepwise discriminant analysis selected *GRUL* as the only character that distinguished between populations. A classification function (a linear combination of variables that best discriminate between areas) was calculated for each area. The classification functions were: Area 1 – Y = -80.5440 (*GRUL*) +14.5646; Area 2 – Y = -79.3230 (*GRUL*) +14.4763; Area 3 – Y = -82.3286 (*GRUL*) +14.7882; Area 4 – Y = -78.8986 (*GRUL*) +14.4495. The discriminant analysis module was used to classify each individual into the population group with the highest *a posteriori* probability, according to the classification function computed from all data. The percentage of individuals correctly classified for the population groups varied from 0 to 62% (Table V). The highest miscalculation was between geographically distant areas, indicating a general lack of regional differentiation. The Mahalanobis distances between areas (Table VI) ranged from 0.001 to 0.095. Specimens from Area 3 appeared to be relatively distant from the other three areas, whereas individuals from Area 2 were closer to those from Area 4 than they were to Areas 1 and 3.

Morphometric data

Table VII shows the ranges, 95% *CI* and means for the

Table IV: Eigenvalues and relative contributions of the six principal components generated from the meristic and morphometric data from *L. hectoris* from four areas around southern Africa

Principle component	PC1	PC2	PC3	PC4	PC5	PC6
			Meristic data			
Eigenvalue	1.69	1.20	1.13	0.71	0.65	0.62
Cumulative percentage	28.21	48.29	67.07	78.87	89.68	100
			Morphometric data			
Eigenvalue	3.04	1.59	1.38	1.10	0.95	0.86
Cumulative percentage	25.29	38.53	50.02	59.17	67.05	74.15

Table V: Percentage correct *a posteriori* classification of *L. hectoris* to groups using meristic and morphometric classification functions between the four areas around southern Africa

Population group	Number of specimens classified into populations				Percentage correctly classified
	Area 1	Area 2	Area 3	Area 4	
Meristic data					
Area 1	0	0	40	38	0
Area 2	0	0	50	52	0
Area 3	0	0	93	56	62
Area 4	0	0	55	62	53
Morphometric data					
Area 1	6	20	15	37	7.69
Area 2	9	35	15	43	34.31
Area 3	0	2	135	12	90.60
Area 4	9	31	20	57	48.72

Table VI: Mahalanobis distance between *L. hectoris* from four areas off southern Africa, based on meristic counts (above diagonal) and on morphometric measurements (below diagonal)

Population group	Area 1	Area 2	Area 3	Area 4
Area 1		0.006	0.040	0.011
Area 2	0.139		0.077	0.001
Area 3	4.082	4.558		0.095
Area 4	0.123	0.155	3.943	

morphometric characters used in this study. The mean morphometric measurements for specimens from Area 3 were larger than those for specimens from the other areas for characters *HL*, *UJL*, *PRED*, *PREAD*, *PREP*, *PREV* and *ED*, but were lower for characters *HD*, *BD*, *CPL* and *CPD*. Measurements for characters *PREA* and *SNL* were identical for specimens from Areas 1 and 3, but similar from Areas 2 and 4.

The plot of 95% *CI* of the individual factor scores for the morphometric data between PC1 and PC2 showed extensive overlap (Fig. 1b). The relative contribution of the six principal components that discriminated between the individuals is given in Table IV. The first two components contributed 38.5% to the total variance between the four areas.

The stepwise discriminant analysis selected *PREP*, *CPD*, *BD*, *UJL*, *SNL*, *PREA*, *PREAD*, *ED*, *HL* and *PREV*, in order of importance, as the characters that best distinguished among the populations. The classification functions are summarized in Table VIII and should be read as the sum of the products of variable and coefficient. The percentage of individuals correctly classified for the population groups varied from 7.69 to 90.6% (Table V). This function did not discriminate well among fish from different areas, except for Area 3, where 90% of specimens coming from this area were correctly reassigned. The greatest overlap was between geographically distant areas, indicating very weak regional differentiation. The Mahalanobis distances between areas (Table VI) ranged from 0.123 to 4.558. Fish from Area 3 appeared to be the most distant from the other three areas and Area 1 was closer to Area 4 than it was to either Area 2 or Area 3. The plots of the most discriminatory variables against *SL* exhibited significant differences between areas for seven variables (Table IX). Fish from Area 3 tended to have longer upper jaws and larger eyes than those from the other areas. These fish also had larger distances between their fins and smaller caudal peduncle depths, implying that they are stronger swimmers with more muscle tissue between their fins and streamlining near the tail area.

Electrophoretic data

Of the 22 isozymes screened, 15 were monomorphic (*ck-2*, *ck-3*, *gdh-1*, *gl-1*, *gl-2*, *gpi-1*, *g-6-p-1*, *idh-2*, *ldh-1*, *sod-1*, *est-1*, *est-1*, *gp-1*, *gp-2* and *gp-3*) and seven were polymorphic (Table X). Alleles varied from two to three in polymorphic loci. No single locus was polymorphic in all areas. Significant departures from Hardy-Weinberg proportions were detected for *est*-3 ($\chi^2 = 52.69$, $p < 0.01$) in Area 1, *pgd-1* ($\chi^2 = 109.01$, $p < 0.01$) in Area 2, *pgd-1* ($\chi^2 = 20.70$, $p < 0.01$) and *est-3* ($\chi^2 = 213.01$, $p < 0.01$) in Area 3, and *pgd-1* ($\chi^2 = 53.00$, $p < 0.01$) in Area 4. Identity values (*I*) were 1.00 for all four areas, and genetic distances (*D*) ranged from 0 to 0.00011 (Nei, 1978; Table XI).

The percentage of polymorphic loci ranged from 13.6 to 27.3%. The mean heterozygosity was generally low and ranged from 0.003 to 0.005 (Table XII). The mean number of alleles per locus ranged from 1.1 to 1.3 (Table XII). Pairwise $F_{(ST)}$ between all samples from the four areas ranged from 0.003 to 0.029, whereas the mean, over loci, $F_{(ST)}$ was 0.011 (Table XIII). The mean, over loci, $F_{(IS)}$ was 0.339 and mean, over loci, $F_{(IT)}$ was 0.347.

DISCUSSION

The results of this study show that *L. hectoris* in the four hydrographic areas are genetically homogenous, but that they display some morphological variability.

Table VII: Ranges, 95% confidence intervals (*CI*) and means of body measurements of *L. hectoris* from four areas off southern Africa. Abbreviations as in Table I

Character	Area 1 (n = 78)			Area 2 (n = 102)			Area 3 (n = 149)			Area 4 (n = 117)		
	Range	95% *CI*	Mean	Range	95% *CI*	Mean	Range	95% *CI*	Mean	Range	95% *CI*	Mean
HL	0.27–0.32	0.29–0.30	0.29	0.27–0.33	0.29–0.30	0.29	0.27–0.35	0.30–0.30	0.30	0.27–0.33	0.29–0.30	0.30
HD	0.10–0.15	0.12–0.13	0.13	0.10–0.15	0.12–0.13	0.13	0.10–0.15	0.12–0.12	0.12	0.10–0.15	0.12–0.13	0.12
BD	0.16–0.22	0.19–0.20	0.19	0.16–0.22	0.19–0.20	0.19	0.14–0.22	0.17–0.18	0.18	0.14–0.44	0.19–0.20	0.20
UJL	0.20–0.25	0.22–0.23	0.23	0.20–0.26	0.22–0.23	0.23	0.21–0.26	0.24–0.24	0.24	0.20–0.77	0.22–0.24	0.23
CPL	0.16–0.26	0.20–0.21	0.21	0.16–0.26	0.20–0.21	0.21	0.17–0.23	0.19–0.20	0.19	0.16–0.26	0.20–0.21	0.21
CPD	0.07–0.10	0.08–0.09	0.08	0.07–0.10	0.08–0.08	0.08	0.06–0.09	0.08–0.08	0.08	0.07–1.00	0.08–0.08	0.08
PRED	0.37–0.45	0.42–0.43	0.43	0.39–0.47	0.42–0.43	0.43	0.39–0.47	0.43–0.44	0.43	0.39–0.49	0.42–0.43	0.43
PREAD	0.73–0.85	0.78–0.79	0.79	0.73–0.85	0.78–0.79	0.79	0.77–0.84	0.80–0.81	0.80	0.73–0.85	0.79–0.79	0.79
PREP	0.28–0.33	0.30–0.31	0.30	0.28–0.35	0.30–0.31	0.30	0.29–0.35	0.32–0.32	0.32	0.28–0.35	0.30–0.31	0.31
PREV	0.40–0.80	0.43–0.45	0.44	0.40–0.80	0.43–0.45	0.44	0.42–0.48	0.44–0.45	0.45	0.40–0.80	0.43–0.45	0.44
PREA	0.60–0.66	0.62–0.63	0.63	0.58–0.66	0.63–0.63	0.63	0.59–0.66	0.62–0.63	0.63	0.58–0.66	0.62–0.63	0.63
ED	0.07–0.10	0.09–0.09	0.09	0.07–0.11	0.09–0.09	0.09	0.07–0.11	0.09–0.09	0.09	0.07–0.11	0.09–0.09	0.09
SNL	0.02–0.04	0.03–0.04	0.04	0.02–0.04	0.04–0.04	0.04	0.03–0.05	0.03–0.04	0.04	0.02–0.05	0.04–0.04	0.04

Table VIII: Classification functions based on morphometric data for *L. hectoris* from four areas off southern Africa. Abbreviations as in Table I

Character	Area 1	Area 2	Area 3	Area 4
PREP	-311.87	-310.91	-259.40	-317.61
CPD	2 800.74	2 785.44	2 709.99	2 794.57
BD	1 456.25	1 466.53	1 365.12	1 463.14
UJL	-386.80	-391.65	-342.87	-382.95
SL	277.64	365.81	161.04	307.34
PREA	3 019.49	3 027.63	2 970.36	3 014.08
PREAD	1 969.32	1 970.15	2 005.83	1 980.19
ED	2 785.76	2 770.84	2 712.42	2 777.07
HL	550.95	551.08	581.42	561.08
PREV	-19.34	-21.42	-28.45	-20.67

Morphological variation

Although the principal components extracted for both the meristic and morphometric characters showed extensive overlap among all areas, the discrimant analysis indicated that fish from Area 3 were slightly different. This difference cannot be attributed to sampling artifacts, because the size structure of the sampled populations was similar across all areas, and all samples contained >75 individuals (n = 149, Area 3).

Morphological differences among populations are normally related to factors such as temperature and salinity, or food availability (Barlow 1961, Wootton 1990). Therefore, it might be expected that fish from Areas 2 and 4 would be most dissimilar, because the temperature of the water in those two areas differs the most. However, although Areas 1, 2 and 4 differ in their biophysical environments, each is characterized by relative uniformity throughout the year (Shannon 1985, Brown *et al*. 1991, Hutchings *et al*. 1991). By contrast, Area 3 is characterized by substantial variability across all environmental features (Shannon 1985, Brown *et al*. 1991, Hutchings *et al*. 1991), suggesting that environmental instability, *per se*, might be influencing morphology. It is not possible to test this hypothesis using the dataset here, but it would require individuals to be resident in the area, either throughout their life or post-metamorphosis.

Although morphological changes can be induced by the environment at the larval stage (Tåning 1918, Wootton 1990), the local current systems are dynamic and are essentially longshore (Shannon 1985). As a consequence, the currents are unlikely to allow the accumulation of larvae along any one region of the coast, especially as they are thought to have a planktonic lifespan of "only a few days" (P. A. Shelton, pers. comm., in Prosch 1991). Indeed, this species is believed to take advantage of the current systems to ensure the optimal distribution of larvae around the

Table IX: Linear relationship ($y = mx + c$) between morphometric variables plotted against *SL* as an independent variable for *L. hectoris* from four areas off southern Africa.The slopes of lines for each population were compared using ANCOVA: *F*-ratio and probabilities indicated. Abbreviatons as in Table I

Population group	*m*	*c*	r^2	*F*-ratio	*p*
PREP				4.26	<0.01
Area 1	0.25	2.62	0.86		
Area 2	0.20	5.58	0.66		
Area 3	0.27	2.15	0.89		
Area 4	0.24	3.21	0.91		
CPD				3.68	<0.05
Area 1	0.08	0.01	0.69		
Area 2	0.08	0.18	0.63		
Area 3	0.08	-0.27	0.78		
Area 4	0.10	-0.92	0.86		
BD				1.91	>0.05
Area 1	0.19	-0.15	0.75		
Area 2	0.19	-0.01	0.62		
Area 3	0.23	-1.88	0.84		
Area 4	0.24	-2.68	0.86		
UJL				5.94	<0.01
Area 1	0.17	2.73	0.85		
Area 2	0.15	4.34	0.63		
Area 3	0.18	2.50	0.92		
Area 4	0.17	2.69	0.91		
SNL				6.89	<0.01
Area 1	0.03	0.23	0.48		
Area 2	0.02	0.75	0.33		
Area 3	0.03	0.31	0.51		
Area 4	0.03	0.18	0.60		
PREA				0.19	>0.05
Area 1	0.62	0.37	0.95		
Area 2	0.48	7.38	0.73		
Area 3	0.64	-0.64	0.98		
Area 4	0.61	0.74	0.98		
PREAD				3.16	<0.05
Area 1	0.75	1.60	0.98		
Area 2	0.60	9.64	0.73		
Area 3	0.77	1.10	0.97		
Area 4	0.74	2.46	0.97		
ED				0.67	>0.05
Area 1	0.07	0.77	0.67		
Area 2	0.06	1.59	0.73		
Area 3	0.07	0.72	0.78		
Area 4	0.07	0.66	0.78		
HL				1.27	>0.05
Area 1	0.26	2.02	0.87		
Area 2	0.19	5.20	0.66		
Area 3	0.26	1.82	0.92		
Area 4	0.25	2.45	0.93		
PREV				3.05	<0.05
Area 1	0.36	4.03	0.45		
Area 2	0.31	6.46	0.82		
Area 3	0.42	1.41	0.77		
Area 4	0.38	2.82	0.91		

Table X: The distribution of alleles over seven polymorphic loci among *L. hectoris* from four areas off southern Africa (*n* = sample size). Locus codes as in Table II

Locus	Area 1	Area 2	Area 3	Area 4
pgm-1				
n	40	79	119	81
A	1.000	0.968	0.979	0.975
B	0.000	0.025	0.017	0.012
C	0.000	0.006	0.004	0.012
ak-1				
n	40	79	116	81
A	1.000	1.000	1.000	0.994
B	0.000	0.000	0.000	0.006
pgd-1				
n	40	55	110	81
A	1.000	0.982	0.977	0.981
B	0.000	0.018	0.023	0.019
mdh-1				
n	40	64	106	80
A	1.000	0.992	0.995	0.988
B	0.000	0.008	0.005	0.013
ck-1				
n	40	70	107	81
A	0.988	1.000	0.995	1.000
B	0.013	0.000	0.005	0.000
me-2				
n	40	55	107	81
A	0.975	1.000	0.991	1.000
B	0.025	0.000	0.009	0.000
est-3				
n	40	40	107	81
A	0.950	1.000	0.991	1.000
B	0.050	0.000	0.009	0.000

region (Shelton 1986, Hulley and Lutjeharms 1995). If morphological changes are not induced at the larval stage, then they could still develop at post-metamorphosis. Such has been suggested by Leslie and Grant (1990), who demonstrated regional differences in the morphology of the anglerfish *Lophius vomerinus* off southern Africa, (in the absence of genetic variation). Those authors hypothesized that the sedentary nature of that essentially benthic species could result in the result of the development of environmentally induced morphological changes that would lead to regional differentiation. It is difficult to invoke a similar argument for *L. hectoris,* because there is no evidence to suggest that the species is similarly sedentary and because the geographic structure of the morphologically differentiated populations shows no distinct pattern. In their study of *L. vomerinus,* Leslie and Grant (1990) noted that the pattern in the morphology reflected the geography and the oceanography and was essentially clinal. However, the slight morphological differences

Table XI: Coefficient of unbiased genetic identity (I – above diagonal) and unbiased genetic distance (D – below diagonal) between *L. hectoris* from four areas off southern Africa

Population group	Area 1	Area 2	Area 3	Area 4
Area 1		1.00000	1.00000	1.00000
Area 2	0.00011		1.00000	1.00000
Area 3	0.00000	0.00000		1.00000
Area 4	0.00000	0.00000	0.00000	

Table XII: Mean number of alleles per locus, percentage of loci that were polymorphic, and the mean heterozygosity among *L. hectoris* from four areas off southern Africa

Population group	Mean number of allelles	Percentage polymorphic loci	Mean heterozygocity
Area 1	1.1	13.6	0.003
Area 2	1.2	13.6	0.004
Area 3	1.3	27.3	0.005
Area 4	1.2	18.2	0.005

in *L. hectoris* observed between the areas in this study cannot be explained in the same way.

Genetic variation

L. hectoris exhibits very low levels of allozyme variation when compared with studies conducted on other marine teleosts. Planes (1998) summarized the results of some 230 genetic studies of marine teleosts and found the mean of estimated heteorozygosities to be 0.054 (range 0–0.180), and the mean percentage polymorphism to be 20.08% (range 0–75%). The values of heterozygosity for *L. hectoris* ranged between 0.003 and 0.005, whereas the mean percentage polymorphism ranged from 13.6 to 27.3%. Although these values fall within the range common to marine teleosts, they are nevertheless extremely low. They are also lower than those reported for either *L. vomerinus* (0.1256; Leslie and Grant 1990) or *E. capensis* (0.115; Grant 1985) off southern Africa, and are less than the values reported for the Cape hake *M. capensis* (0.063) and *M. paradoxus* (0.065; (Grant *et al*. 1987).

Comparative information on the population genetics of myctophids is scarce. The results reported here for *L. hectoris* differ appreciably from those obtained for *Triphoturus mexicanus* along the Pacific coast of the Americas (Afanas'yev *et al*. 1989). The mean heterozygosity (and percentage polymorphism) of *T. mexicanus* populations along the coasts of California and Peru was 0.158 (75%) and 0.125 (88%) respectively. The discrepancies between the two species can be explained in part by the fact that Afanas'yev *et al.* (1989) only used eight pre-selected polymorphic loci in their study, compared to the 22 used in the present study.

The results show a general lack of genetic divergence between the fish from all areas (D = 0–0.00011). It could be argued that this reflects the fact that populations were sampled during the non-breeding period, which for *L. hectoris* is winter–spring (Prosch 1991, Olivar *et al*. 1998). If samples had been collected during the spawning season, it is possible that genetic differences between the populations in the different areas might have been observed. Such an argument is based on the premise that fish from different stocks spawn in discrete areas and then disperse to mix with fish from other stocks during the non-breeding period (Waples and Teel 1990). This argument is not seriously considered here because, to the authors' knowledge, myctophids do not aggregate in large numbers over discrete spawning grounds. Further, even for species of fish that do show this type of behaviour in the region (e.g. clupeoids), the number of individuals that move between spawning grounds is clearly enough to homogenize genetic structure (Grant 1985).

The lack of genetic divergence between the fish from different areas is consistent with their conspecific status. The genetic divergence between the four areas is also consistent with the D values for *L. vomerinus* around southern Africa (D = 0.0005–0.0010; Leslie and Grant 1990). Grant *et al*. (1987) reported average D values of 0.0006 and 0.0007 for *M. capensis* and *M. paradoxus* respectively, whereas Grant (1985) reported an average D value of 0.0002 for *E. capensis*. Naish (1990) detected no genetic structuring within populations of the Cape horse mackerel *Trachurus*

Table XIII: Summary of F-statistics over the seven polymorphic loci for *L. hectoris* from four areas off southern Africa

Locus	$F_{(IS)}$	$F_{(IT)}$	$F_{(ST)}$
pgm-1	-0.022	-0.016	0.006
ak-1	-0.006	-0.002	0.005
pgd-1	0.660	0.662	0.005
mdh-1	-0.010	-0.006	0.003
ck-1	-0.010	-0.004	0.006
me-2	-0.021	-0.009	0.012
est-3	1.000	1.000	0.029
Mean	0.339	0.347	0.011

trachurus capensis in the region.

It is generally accepted that natural selection, random genetic drift and gene flow are responsible for the genetic structure of populations that are geographically widely distributed. The results of this study have been interpreted in terms of random drift and gene flow, because there is much evidence to suggest that these factors are more important in influencing variation in allele frequency among populations (Waples 1987). The extent of genetic variation can therefore be explained in three ways. First, fish numbers within the southern African population are large enough to ensure that genetic divergence through random drift is not advanced enough to be detectable. The estimated biomass of *L. hectoris* off southern Africa is of the order of no less than 1 million tons (PAH, unpublished data). Second, there is little evidence of strong physical boundaries to gene flow between the areas (Shannon 1985). The extent of adult migration in *L. hectoris* has not been studied, so the lack of genetic differentiation among fish from these areas may be assumed to be the result of the large dispersal potential at the egg and larval stages (Hulley and Lutjeharms 1995). However, with the limited knowledge on migration of *L. hectoris* it cannot be ascertained, with certainty, whether larval drift or adult movement is more important. A recent study of mitochondrial DNA in anchovy has suggested that local populations of *Engraulis* became extinct some ten to hundreds of thousands of years ago (W. S. Grant, International Centre for Living Aquatic Resources Management [ICLARM] unpublished data). This extinction was attributed to a deterioration in the physical environment, and it means that the present population of *E. capensis* is likely to have been founded fairly recently. Such an altered environment might also have affected *L. hectoris*, and the low levels of variability observed in this species could be attributed to a major population bottle-neck in population size (and limited subsequent migration into the region).

The combined results presented in this study show that the slight morphological variation among stocks of *L. hectoris* does not have a clear genetic basis. This implies that the morphological differentiation among the areas may be attributable to environmentally induced factors (Leslie and Grant 1990). It would therefore be appropriate to manage the southern African populations of *L. hectoris* as a single population unit.

ACKNOWLEDGEMENTS

We thank the scientific personnel on board the F.R.S. *Algoa* and F.R.S. *Africana* for their assistance with the collection of samples from South African waters, and to Messrs D. C. Boyer (National Marine Information and Research Centre, Namibia) and C. Sparks (Cape Technikon, Cape Town) for the material off Namibia. Ms M. van der Merwe, Ms L. Hoenson and Mr M. Bougart are thanked for helping with the collections at the SA Museum, and Dr R. W. Leslie (Marine & Coastal Management) is thanked for his assistance with the statistical analyses. Mr S. Daniels (University of Stellenbosch) is thanked for his invaluable advice on allozymes. We are grateful to Drs W. S. Grant (ICLARM, Malaysia) and J. Paxton (Australian Museum, Sydney) for their comments on an earlier draft of the manuscript. Financial support was provided by the Royal Society, London, and the National Research Foundation, through the South African Network for Coastal and Oceanic Research.

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