Marine Biology (1994) 119: 541–547

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Geographic variation in *Loligo forbesi* in the Northeast Atlantic Ocean: analysis of morphometric data and tests of causal hypotheses

Received: 10 January 1994 / Accepted: 11 February 1994

Abstract Geographic variation in the squid *Loligo forbesi* was investigated using multivariate analysis of morphometric and meristic characters in samples of squid taken from 13 localities in the Northeast Atlantic Ocean. Two character sets, body morphometrics and beak morphometrics, indicated similar patterns of variation, with squid from the Azores differing markedly from those on the continental shelf. No consistent pattern was apparent in meristic data. Partial Mantel tests indicated that similarity matrices for morphological data were significantly correlated with distance matrices for (a) geographic proximity, (b) whether the capture site was on the continental shelf or the Azorean bank, and (c) (beak data only) average sea-surface temperature at site of capture. Partial Mantel tests on allozyme data for the same individuals support hypothesis (b). The results suggest that *L. forbesi* in the Azores may reasonably be regarded as a distinct stock, differing significantly from *L. forbesi* on the continental shelf.

Introduction

The veined squid *Loligo forbesi* occurs throughout the Northeast Atlantic Ocean, and supports an important commercial fishery, particularly in Spain and Portugal. Its range extends from the Faroe islands to the west coast of Africa and includes the Mediterranean and the Azores archipelago in the mid-Atlantic (Roper et al. 1984). In the southern part of its range, it co-occurs with the congeneric *L. vulgaris*, which is also of considerable importance to fisheries.

The application of multivariate analysis of morphometric data to studies on taxonomy and geographic variation is well-established for vertebrates (Thorpe 1984; Thorpe and Baez 1987; Butler et al. 1989; Thorpe and Brown 1989; Creech 1992). Collection of morphometric data from soft-bodied animals presents additional difficulties. Nevertheless, there are published studies on morphometric variation in squid. Kashiwada and Recksiek (1978) found morphometric differences between spring- and autumn-spawning populations of *Loligo opalescens*, Kristensen (1982) examined geographic variation in *Gonatus fabricii*, and Augustyn and Grant (1988) compared *L. vulgaris vulgaris* and *L. vulgaris reynaudii* using morphological, meristic and allozyme characters and concluded that the differences were of subspecific rather than specific nature.

Boyle and Ngoile (1993) examined morphometric variation in *L. forbesi* from Scottish waters. They found significant differences between *L. forbesi* from the North Sea, Northeast Atlantic and Rockall fishery areas (International Council for the Exploration of the Sea, ICES, Fishery Subdivisions IV, VI a and VI b), but the status of these differences was unclear, since samples within areas were not homogeneous. More recently, Pierce et al. (1994) have shown that there are seasonal changes in the body form of *L. forbesi*, probably related to maturation, which remain apparent when differences in body size are taken into account.

There is evidence that *L. forbesi* from the Azores may differ from those on the continental shelf. The species

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Communicated by J. Mauchline, Oban

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reaches a markedly larger adult size in the Azores (Martins 1982). Also, Brierley et al. (1983) have demonstrated significant differences in allozyme distributions between specimens from the Azores and British waters.

Currently there are no published morphometric or allozyme data on *Loligo forbesi* from the Spanish and Portuguese mainland coasts, and studies of British populations have been based on a restricted number of sites. Consequently, the status of any difference between Azores and British specimens remains uncertain. Geographic variation is ubiquitous, and the existence of differences between two areas is in itself unremarkable (Thorpe 1987 a). Data from across the entire range are needed to establish the pattern of variation and to allow testing of causal hypotheses.

The present paper describes the results of a new study of morphometric variation in *Loligo forbesi* across its geographic range. Results of a parallel genetic study focusing on allozyme variation are presented in Brierley et al. (1994).

Materials and methods

In September to December 1991, squid samples were collected from 13 localities across the known range of *Loligo forbesi*. Sampling sites are detailed in Table 1. Samples from overseas were transported frozen to Aberdeen. The Spanish sample, from Vigo, was augmented by individuals collected in April 1992 to increase the sample size. Since more males than females were obtained and there are sexual differences in body form, we concentrate here on data from males. If a sample contained < 30 males, all males were used, otherwise a size-stratified sub-sample of at least 30 males was selected.

To ensure standardization of effects of storage, all squid were kept frozen (−20 °C) prior to measurement. After thawing, morphometric data were collected and structures required for meristic data were removed and fixed in 10% buffered formalin.

Table 1 Sampling sites of *Loligo forbesi*. All samples were collected in 1991 unless otherwise stated. No *L. forbesi* were found off the Algarve, Barcelona or the Canaries. Sample sizes (*N*) and mean and range of body sizes (pen length, *PL*) are given for males only

Sites	Collection dates	(*N*)	PL
British Isles			
Aberdeen	2, 4, 10, 19, 20, 27 Sep. 3, 22 Oct.	(45)	229 (103–369)
Moray Firth	13 Sep.	(19)	234 (135–332)
Shetland	3 Oct.	(29)	293 (189–389)
Sule Skerry	31 Oct.	(29)	156 (101–203)
Rockall	21 Sep., 30 Oct.	(23)	407 (191–574)
Faroe Bank	11 Nov.	(33)	259 (150–415)
Irish Sea (south)	10 Sep.	(20)	229 (150–326)
Isle of Man	5 Dec.	(9)	319 (209–417)
English Channel	9 Oct.	(20)	203 (154–308)
Spain			
Vigo	18, 19 Sep., 20 Apr. 1992	(22)	235 (88–370)
Portugal			
Lisbon (North)	26 Sep., 2, 7 Oct., 7 Nov.	(18)	355 (110–520)
Lisbon (South)	19, 21, 25 Oct.	(15)	120 (86–145)
Azores	25 Sep., 11, 15, 25 Oct.	(29)	476 (280–621)

The morphometric and meristic characters analysed were selected and modified from those recommended by Roper and Voss (1983) and those used in previous studies (Clarke 1962, 1986, Augustyn and Grant 1988, Boyle and Ngoile 1993, L. Coelho personal communication, A. Guerra personal communication). The general aims were to derive two or more sets of independent characters (see Thorpe 1985 a, b, 1987 a, b). Morphometric characters should describe shape as fully as possible. Reliable measurements are however limited on soft-bodied animals such as cephalopods, and it is impractical to use a formal characterization of shape such as the Box-truss method (Creech 1992). To minimize variation in measurements due to worker differences (Pierce et al. 1994), measurements for each character set were made by one person (except for upper beaks, for which two persons made measurements).

Seventeen morphometric characters were used (Fig. 1): fin length, fin width, head length, head with, lengths of Right Arms 1, 2, 3, and 4, length of the right tentacle and tentacle club, diameter of the largest sucker on the right tentacle club, mantle circumference, length of the right gill and right funnel cartilage length, nuchal cartilage length, pen length and pen width. Measurements on arms, tentacle, gill and pen were made after removing the structure from the squid. Pen length (PL) was selected as a size indicator in preference to dorsal mantle length. No measurements were made on body parts which appeared to be damaged or to have suffered previous damage (e.g. missing arm tips, re-grown arms).

Five meristic characters were selected. The third arm, right ventro-lateral buccal lappet, right tentacle club and right gill were removed during dissections and fixed in buffered formalin. Meristic data were later collected as follows: number of suckers on the buccal lappet, number of rows of suckers on the tentacle club, number of denticles on the largest sucker ring on the tentacle club (NDTC) and Arm R3 (NDA3), number of gill lamellae (NGL).

Beaks were dissected out and stored in 70% ethanol. Five measurements were made on the upper beaks: hood length, rostral length, wing length, crest length and height (Fig. 2). Each upper beak was placed on its side on a microscope slide on the stage of a photographic enlarger, set to achieve $\approx \times 10$ magnification. Measurements were made on the projected image on the base plate of the enlarger using a ruler, adjusting the focus for each measurement. Results for each beak were calibrated with reference to the projected size of a 2 cm scale. Six measurements were made on the lower beaks using callipers (Fig. 2): hood length, rostral length, rostral gap, shoulder height, oblique length (LBOL). Measurement of a projected image was found to be impractical for lower beaks due to their shape.

Morphometric and meristic data were screened for errors using bivariate plots and regression analyses to detect outliers. Errors were corrected by reference to the original data sheets and beaks were remeasured if necessary. Further analyses used BMDP statistical software (Dixon et al. 1990). All body measurements and three meristic variables (NDTC, NDA3, NGL) were positively linearly related with size (PL). Beak measurements were also related to body size. Beak measurements showed a negative allometric increase with respect to PL, but were linearly related to LBOL.

Body measurements and the three size-dependent meristic variables were corrected for size using pooled within-group regressions on PL. Beak measurements were corrected for size using pooled within-group regressions on LBOL.

Each data set was then entered into a canonical variates analysis. Analyses were repeated including and excluding size variables (PL, LBOL). Three morphometric variables (tentacle length, tentacle club length and sucker diameter) were dropped from the final analysis due to the large number of missing values. Results were plotted using SURFER (Golden Software Inc.).

Partial Mantel tests were employed to test observed patterns of geographic variation against putative causes (Brown et al. 1991, Manly 1991, Thorpe and Baez 1993, A. Malhotra personal communication).

The observed patterns of variation examined were (1) body dimensions ($N = 248$), (2) beak dimensions ($N = 248$), and (3) allozymes ($N = 247$; data from Brierley et al. 1994). These observed (dependent) "variables" are similarity matrices among individuals from the 13 populations. The software used a maximum of 250 individu-

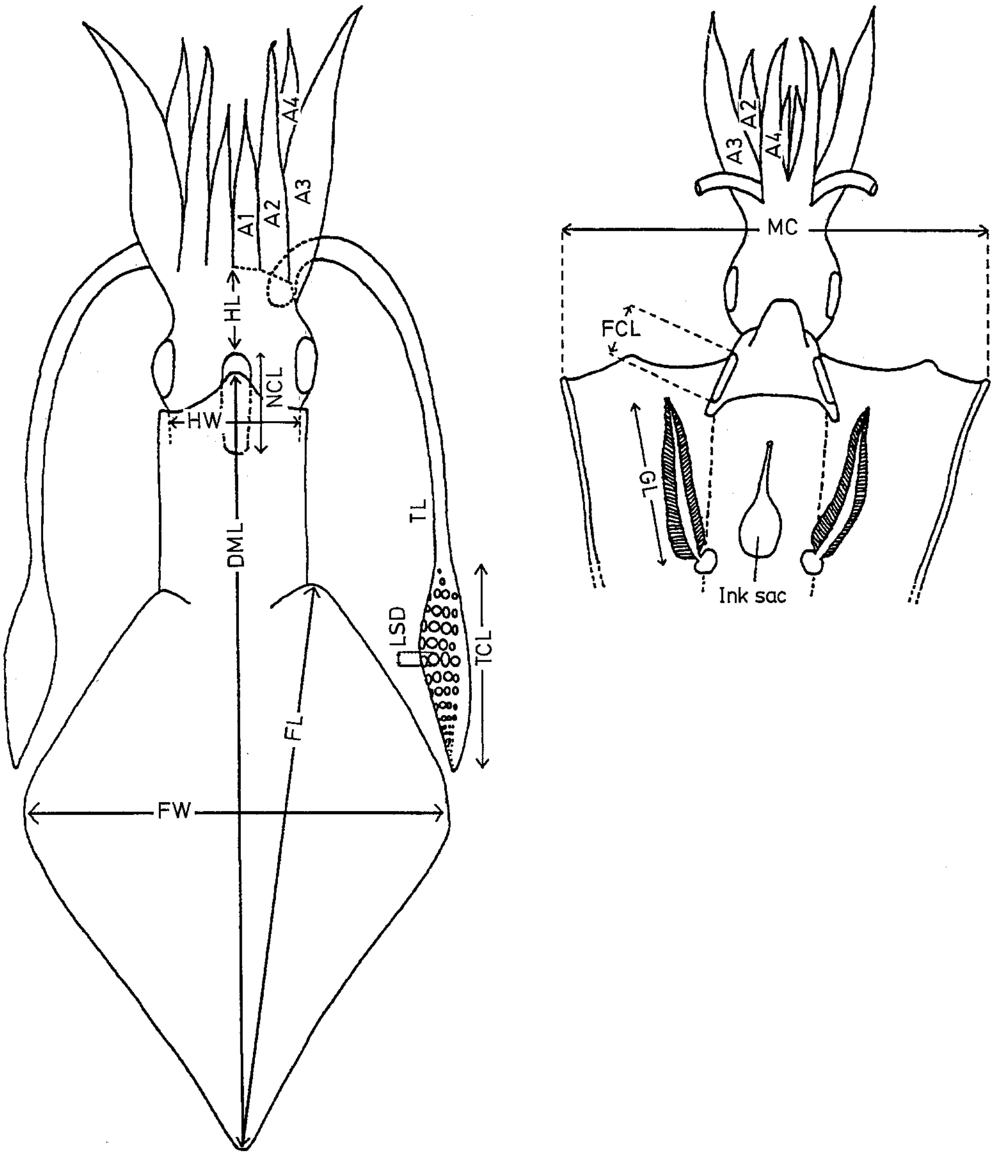

Fig. 1 *Loligo forbesi.* Morphometric measurements used. (*A1–A4* lengths of Right Arms 1 to 4; *DML* dorsal mantle length. This character is measured externally, the alternative body size measurement, pen length, is equivalent, but is taken after removing pen from interior dorsal mantle surface. *FCL* funnel cartilage length; *FL* fin length; *FW* fin width; *GL* gill length; *HL* head length; *HW* head width; *LSD* largest sucker diameter; *MC* mantle circumference; *NCL* nuchal cartilage length; *TCL* tentacular club length; *TL* tentacle length. Pen width is not illustrated)

als, selected at random from each of the 13 populations. In the case of the morphological data sets, the similarity matrices were Mahalonobis distances (derived from individual canonical variate scores), and in the case of the allozyme data it was mismatch distance (derived from allele frequencies at six polymorphic loci). The independent "variables" against which they were simultaneously tested were also distance matrices. They were (1) geographic proximity, (2) average sea surface temperature at site of capture, (3) average water salinity at site of capture, (4) whether the capture site was on the Continental Shelf or the Azorean bank. Data on average sea-surface temperatures and salinities were taken from Tchernia (1980) and ICES (unpublished data 1980 – 1990).

The probability of association between an observed pattern of geographic variation and a putative cause was established by randomization procedures (Manly 1991) using, in this case, 5000 randomizations. As four hypotheses are considered simultaneously, a Bonferroni correction was applied and $P<0.013$ was considered significant.

Results

Considered separately, ANCOVAs showed significant between-area variation ($P<0.001$) for all variables except for NDTC. There was considerable variation in mean body size (PL) of *Loligo forbesi* between samples, although there was extensive overlap between the size ranges of most samples (Table 1). The largest individuals were from the Azores, while large specimens were also obtained from Lisbon (north) and Rockall. The smallest squid were in the Lisbon south and Minch (Sule Skerry) groups.

Mean group scores on the first canonical variate for analysis of morphometric data are summarized in Table 2. There are some differences between "size-in" and "size-out" results, but the Azores sample is clearly distinct (Fig. 3). The Faroe sample appears at the opposite end of the spectrum of values, although there is no consistent north–south trend, and the two Lisbon samples appear to be rather different from each other.

The Azores sample is to some extent separated in the size-in analysis of meristic data, but no clear pattern of separation is apparent in the size-out results for meristics (Table 3).

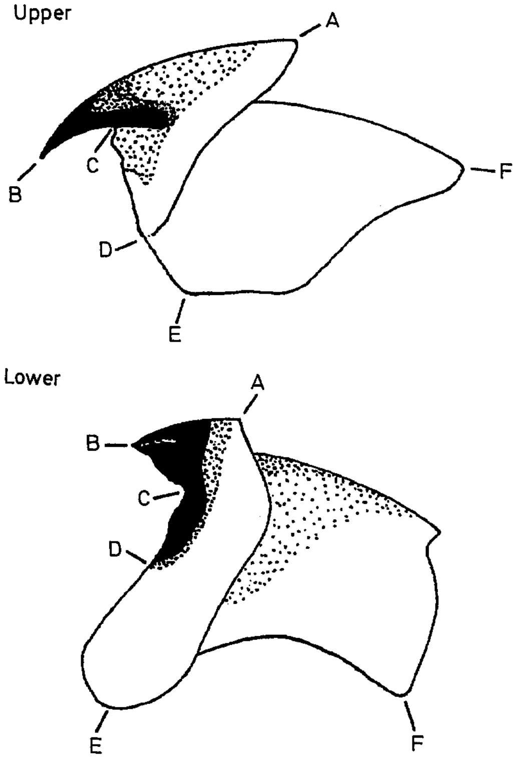

Fig. 2 *Loligo forbesi*. Measurements on beaks. Upper beaks: all measurements were made on a projected image; hood length ($A-B$), rostral length ($B-C$), wing length ($C-D$), crest length ($B-F$), height ($A-E$). Lower beaks: all measurements were made on beak itself; hood length ($A-B$), rostral length ($B-C$), rostral gap ($B-D$), shoulder height ($D-E$), oblique length ($B-F$)

The analysis of the beak data supports the separation of the Azores samples from other samples, although the separation is reduced in the size-out analysis (Table 3, Fig. 4). The discriminant analysis results indicate that the differences between samples were primarily in upper beak measurements.

Mahalonobis distances based on body dimensions were significantly correlated with distance, temperature and continental shelf hypotheses ($P=0.0002$). Mahalonobis distances based on beak dimensions were significantly correlated with distance ($P=0.0038$) and continental shelf ($P=0.0002$) hypotheses. Mismatch distances based on allozyme data were significantly correlated only with the continental shelf hypothesis ($P=0.0002$).

Table 2 *Loligo forbesi*. Canonical variates analysis for morphometric data. Scores for first canonical variable, evaluated at group means, for four analyses. $N_{1,2}$ and $N_{3,4}$ are sample sizes for the first and second pairs of analyses, which are: 1, size-in, all variables; 2, size-out, all variables; 3, size-in, excluding tentacle measurements; 4, size-out, excluding tentacle measurements

Site	Analyses					
	($N_{1,2}$)	1	2	($N_{3,4}$)	3	4
Aberdeen	(31)	1.34	1.05	(36)	1.32	1.09
Moray Firth	(10)	0.74	0.77	(12)	0.76	0.80
Shetland	(23)	0.03	0.22	(24)	0.14	0.40
Sule Skerry	(12)	1.58	0.51	(16)	1.36	0.31
Rockall	(14)	0.25	1.17	(20)	−0.49	0.65
Faroe Bank	(19)	1.31	1.71	(29)	1.06	1.23
Irish Sea	(16)	1.16	0.92	(18)	1.03	0.74
Isle of Man	(8)	0.12	0.64	(9)	0.10	0.63
English Channel	(17)	−0.13	−0.71	(17)	0.13	−0.63
Vigo	(13)	−1.06	−1.18	(17)	−0.29	−0.68
Lisbon (North)	(9)	−1.72	−1.09	(11)	−1.57	−1.05
Lisbon (South)	(11)	2.19	1.06	(13)	2.04	0.90
Azores	(20)	−5.47	−4.73	(26)	−4.95	−4.20

Table 3 *Loligo forbesi*. Canonical variates analysis for meristic and beak data. Scores for first canonical variable, evaluated at group means, for four analyses. $N_{1,2}$ and $N_{3,4}$ are sample sizes for the first and second pairs of analyses, which are: 1, size-in, meristics; 2, size-out, meristics; 3, size-in, beaks; 4, size-out, beaks

Site	Analyses					
	($N_{1,2}$)	1	2	($N_{3,4}$)	3	4
Aberdeen	(34)	0.94	0.25	(43)	0.65	0.25
Moray Firth	(14)	0.67	0.32	(23)	0.71	0.32
Shetland	(27)	−0.02	0.01	(27)	−0.26	0.27
Sule Skerry	(17)	1.76	−1.13	(18)	1.53	0.10
Rockall	(18)	−1.76	−0.20	(18)	−0.93	0.36
Faroe Bank	(18)	0.30	−0.35	(30)	0.90	1.53
Irish Sea	(13)	0.85	0.50	(18)	0.15	−0.42
Isle of Man	(8)	−0.66	0.07	(9)	−0.31	0.01
English Channel	(15)	1.08	0.86	(15)	0.91	−0.03
Vigo	(12)	−0.12	0.47	(20)	0.48	0.34
Lisbon (North)	(14)	−0.75	0.37	(17)	−2.05	−0.91
Lisbon (South)	(1)	–	–	(14)	1.87	−0.29
Azores	(20)	−2.61	−0.70	(22)	−4.78	−2.73

Discussion

The plasticity of body form in squid presents particular difficulties in carrying out morphometric studies. Firstly, measurements are likely to vary to some extent depending on handling, e.g. if the tentacles are stretched during measurement. A second consequence is that squid are easily damaged, particularly when caught in trawls, and in the present study many of the specimens of *Loligo forbesi* had lost tentacles or sustained other damage, reducing sample sizes for multivariate analysis. As far as possible, putative seasonal and maturity differences in body form were minimized by the choice of a restricted sampling period. Nevertheless, most samples contained individuals of a range of sizes and maturity states.

Analysis of two sets of morphometric characters, backed up by Mantel tests on allozyme data, supports the existence of a distinct stock of *Loligo forbesi* in the Azores, where individuals are both larger and differ in size-removed body shape. The size difference between Azores and continental shelf squid was previously documented by Martins (1982). It is unlikely that size differences can be accounted for simply in terms of the effect of water tem-

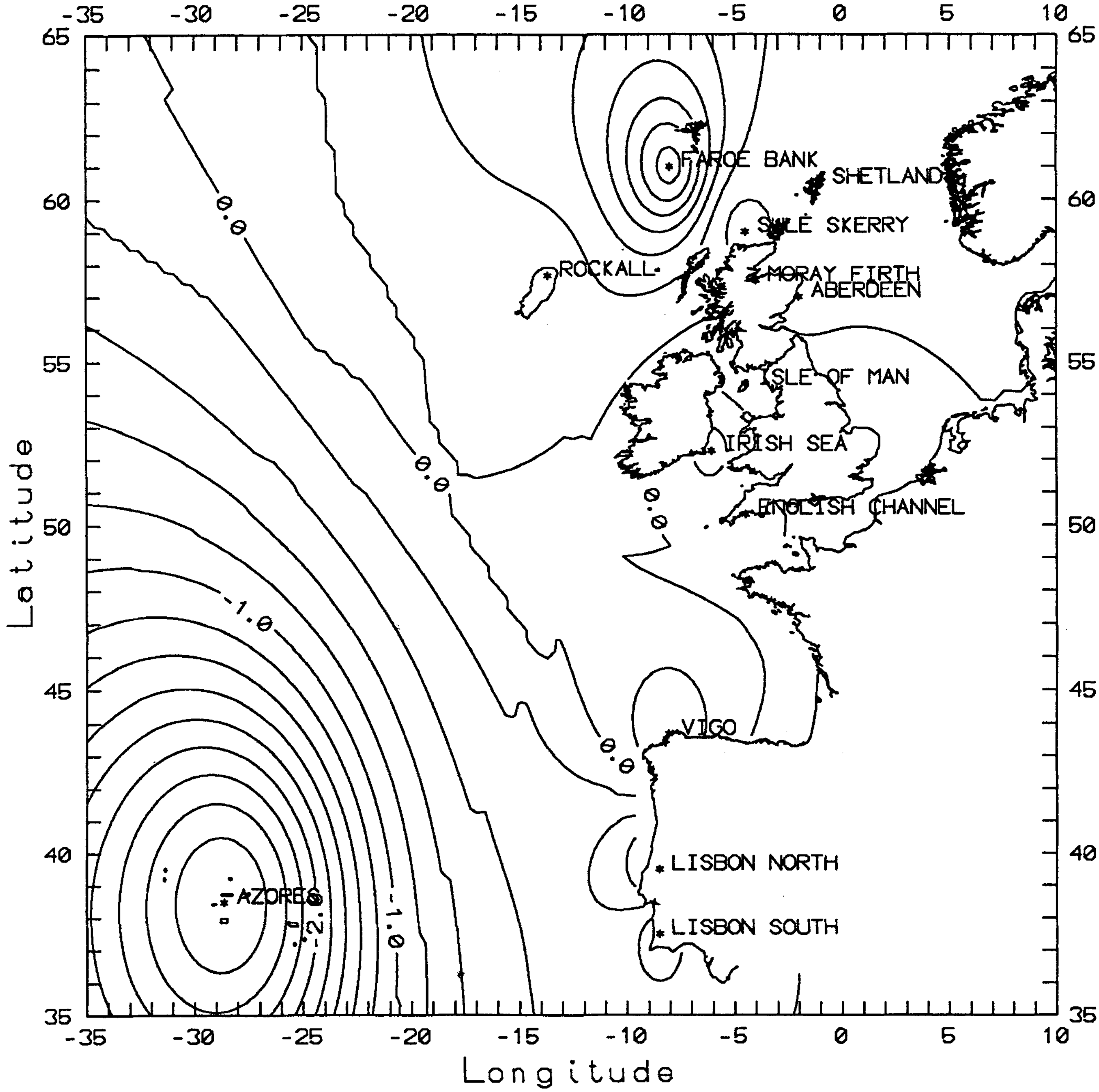

Fig. 3 *Loligo forbesi.* Contour map of group means of first canonical variate for morphometric data, excluding tentacle variables. Outlines of British and European mainland coasts are shown, also Azores island group and Rockall Bank

peratures on growth rate: summer sea-surface temperatures in the Azores reach 22 °C (Forsythe and Hanlon 1989) compared to ≈18.5 – 21 °C off the Iberian coast of Portugal (Alfonso Dias et al. 1992) and 12.5 – 13.5 °C for Scottish waters (Anonymous 1962). Some underlying genetic difference may, therefore, be proposed.

Although large squid were also obtained from Rockall and the Portuguese coast, these samples and that from the Spanish mainland coasts were morphologically much closer to the British coastal samples than to the Azores. Differences existed between samples from the continental shelf, as revealed by both univariate and multivariate analyses, but these differences are more difficult to interpret. Thus, the two Lisbon samples were at least as dissimilar as any other pair of samples from the continental shelf.

Congruence between independent character systems is more likely if the underlying cause of geographic variation is phylogenetic rather than ecogenetic (Thorpe 1987 a, c). The similarity between results of beak and body measurements may thus be held to support the existence of a phylogenetic difference. Meristic data from a small set of characters showed little clear pattern.

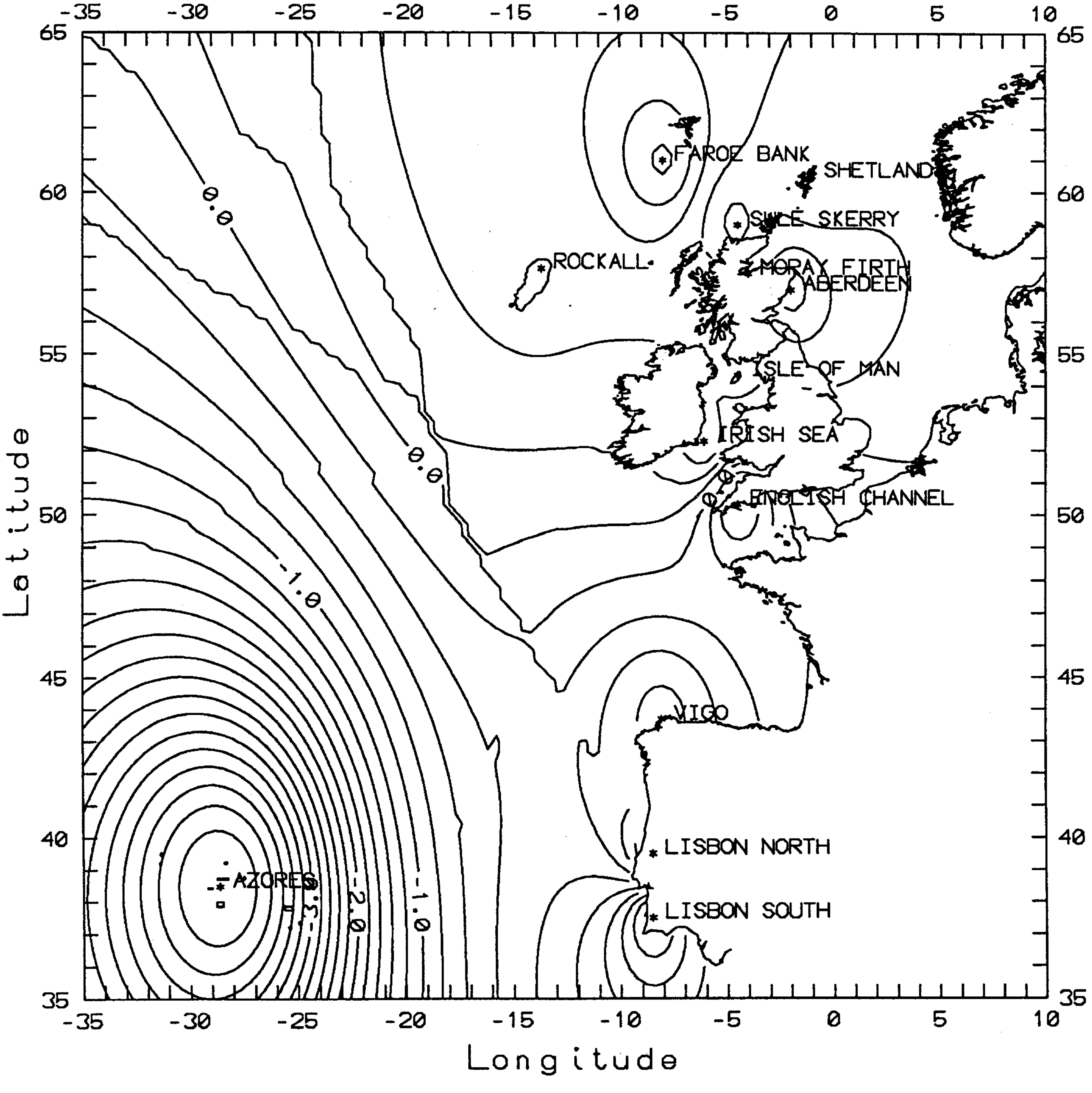

Fig. 4 *Loligo forbesi.* Contour map of group means of first canonical variate for beak data. Outlines of British and European mainland coasts are shown, also Azores island group Rockall Bank

Analysis of three independent datasets confirmed that population differences were consistent with Azorean squid being separated from all the other samples. However, morphometric differences were also correlated with geographic proximity, and body dimensions were correlated with average sea-surface temperature. It remains possible that the response to environmental factors is under genetic control.

The shortest distance between the Azores and the continental mainland is ≈ 1440 km, and deep water, with abyssal plains at 3500 to 5000 m depths, lies between the Azores and the British, European and African coasts. *Loligo forbesi* is a neritic species, occurring on the continental shelf at depths of 100 to 400 m (Roper et al. 1984), and is unlikely therefore to cross areas of deep water. Surface and sub-surface currents would not appear to favour movement from the mainland to the Azores (Worthington 1976). There is thus some basis for supposing that the Azores stock is reproductively isolated. It must be stressed however that squid are highly mobile (Boyle 1990), and almost nothing is known about migration in this species. Analysis of mitochondrial DNA has been applied to studies on stock structure and movements in fish and marine mammals (Baker et al. 1990, Bermingham et al. 1991) and offers a possible means to investigate stock structure and movements within the continental shelf populations of *Loligo forbesi* in more detail.

Acknowledgements We thank L. Key for assistance with data collection; E. Balguerias, F. Casas, M. Collins, M. Cunha, E. Gaard, J. Pereira, F. Porteiro, J. Quintela and P. Sanchez for assistance with collecting squid samples; and H. Dooley at ICES for provision of data on surface temperature and salinity. The procedure for morphometric data collection evolved from discussions and practical exercises involving the authors and L. Coelho, C. Martins, J. Pereira and F. Porteiro. C. Yau provided the drawings of beaks in Fig. 2. RST would like to thank B. F. J. Manly for the source code of his Mantel test program.

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