Hydrobiologia **449:** 179–186, 2001.
J.P.M. Paula, A.A.V. Flores & C.H.J.M. Fransen (eds), Advances in Decapod Crustacean Research.

Morphometric comparison between Mediterranean and Atlantic populations of *Pontophilus norvegicus* (Decapoda, Crangonidae)

S. De Grave[1] & D. Diaz[2]
[1]*Oxford University, Museum of Natural History, Oxford, OX1 3PW, U.K.*
Fax: + 44-1865-272970; E-mail: sammy.degrave@oum.ox.ac.uk
[2]*Institut de Ciències del Mar-CSIC, Passeig Joan de Borbó, 08039 Barcelona, Spain*

Key words: Crangonidae, *Pontophilus*, morphometrics, Atlantic, Mediterranean

Abstract

A multivariate comparison of morphometric differences was undertaken on populations of *Pontophilus norvegicus* from four Atlantic and one Mediterranean locations. Multiple discriminant analysis revealed clear morphometric differences between Atlantic and Mediterranean populations, with the Atlantic populations exhibiting a low degree of separation. The underlying variables responsible for this discrimination are shown not to have any operational taxonomic utility and, hence, no sub-specific status is attached to the respective populations.

Introduction

Pontophilus norvegicus (Sars, 1861) is a widespread benthic crangonid shrimp in the eastern Atlantic Ocean, ranging from the Cantabrian Sea and the Gulf of Gascogne in the south (Lagardère, 1970; Rodríguez-Marín, 1993) to Iceland and Spitzbergen (Hansen, 1908) in the north. In the western Atlantic Ocean, it has been recorded from Greenland south to Maryland, U.S.A. (Williams, 1984; Squires, 1990). The species also occurs in the Mediterranean, where it is considered to be a glacial relict (Abelló & Vallarades, 1985); Mediterranean locations include Mallorca (Forest, 1965), Ligurian Sea (Relini-Orsi & Relini, 1972), Catalan Sea (Abelló & Vallarades, 1985; Cartes, 1993), the Sicilian Channel (Pipitone & Tumbiolo, 1993) and possibly the Adriatic Sea (Stevcic, 1990).

As regards depth, the species occurs from 50 to 1450 m in the Atlantic (Sivertsen & Holthuis, 1956), but is most common between 200 and 500 m (Smaldon, 1979). In the Mediterranean, it occurs in depths of 392–2261 m (Abelló & Vallarades, 1985; Cartes, 1993).

Following the original discovery of the species in the Mediterranean, Forest (1965) suggested that the specimens from Mallorca exhibited morphological differences in the relative lengths of the sub-orbital spines, rostral length and the antennal scale, compared with the Atlantic specimens figured by Kemp (1910). These differences were attributed to the smaller size of the specimens studied, compared to Kemp's material. Although Abelló & Vallarades (1985) concluded that no apparent morphological differences exist between Atlantic and Mediterranean specimens, they suggested that a morphometric and/or biochemical study may shed some light on possible regional differences. More recently, d'Udekem d'Acoz (1999) suggested that this matter deserved closer scrutiny and offered the suggestion of potential sub-specific differences between Atlantic and Mediterranean populations.

A review of Mediterranean/Atlantic vicariant forms in Decapoda is provided by d'Udekem d'Acoz (1999), who lists more than 40 taxa. However, the precise taxonomic status of many of the forms is poorly understood, with some forms allocated full specific or subspecific status (e.g. *Chaceon inglei* Manning & Holthuis vs. *C. mediterraneus* Manning & Holthuis), whilst others are simply recorded as vicariant forms of infraspecific rank (e.g. *longipes* form of *Macropodia tenuirostris* (Leach). In many of these taxa, intermediate populations in the Gibraltar area are know, raising doubt as to their separate taxonomic status. In contrast, several taxa have a discontinuous distribution, potentially limiting gene flow due to geographical isolation.

Table 1. Continuous variables and their abbreviations

Carapace length (CL)
Rostral length (RL)
Length of basal rostral spines (BASAL)
Distance between endpoint of rostrum and endpoint of sub-orbital spine (SUBORB)
Distance between orbit and insertion of first and last tooth on dorsal carina of carapace (CARINA1, CARINA2)
Distance between orbit and insertion of first tooth and second on first lateral carina (CARINA3, CARINA4)
Distance between orbit and insertion of tooth on second lateral carina (CARINA5)
Length, width of antennal scale (SCALEL, SCALEW)
Dorsal length of somites 1–6 (SOM1–6)
Maximum width and depth of pleuron 2 (PLEUR2W, PLEUR2D)
Length of telson (TELSON)
Insertion point of anterior and posterior dorsal spines (TELANT, TELPOST)
Length, width of chelae of first pereiopod (CHELAEL, CHELAEW)
Length of propodus of fourth and fifth pereiopod (PROP4, PROP5)
Length, width of uropodal endopod (ENDOL, ENDOW)
Length, width of uropodal exopod (EXOL, EXOW)

Table 2. Discrete variables and their abbreviations

Sex
Rostrum falling short, equal to or overreaching eye (ROSTRUM)
Rostrum falling short of, level with or overreaching proximal segment of antennular peduncle (ANTPED)
Number of teeth on dorsal carina (DORSAL)
Tubercle on dorsal carina present or absent (TUBERCLE)
Number of teeth on first lateral carina (LATFIRST)
Number of teeth on second lateral carina (LATSECOND)
Antennal scale tooth falling short, level with or overreaching antennal scale (SCALETOOTH)

The present study aims at elucidating potential sub-specific differences of Mediterranean from Atlantic populations of *P. norvegicus* by using morphometric measurements and the multivariate method of Multiple Discriminant Analysis (MDA).

Materials and methods

Shrimps (N = 189) were studied from one Mediterranean and four Atlantic locations: (1) Spain – NW Mediterranean (41° 04 N, 1° 45 E–41° 17 N 2° 50 E, 366–769 m, 16 males, 32 females), (2) Faroe Islands – Scotland (61° N, 7° E – 60° 42 N 4° 15 E, 300–500 m, 13 males, 20 females), (3) Lødingen & Ullsfjord, Norway (68° 20 N 15° 30 E, 200–270 m, 7 males, 20 females), (4) south of Ireland (51° 53 N 11° 59 W–56° 23 N 09° 18 W, 570–1000 m, 4 males, 33 females) and (5) off the western seaboard of U.S.A. and Canada (44° 49 N 61° 41 W–42° 16 N 69°56 W, 172–848 m, 7 males, 37 females). Individuals were grouped into these arbitrary regions, as some finer resolution regions did not harbour enough specimens to satisfy MDA assumptions.

For each individual, 30 different characters (continuous variables, Table 1) were measured, and categorical data recorded from a further eight characters (discrete variables, Table 2). Absent, regenerating or damaged body parts sometimes reduced the total number of variables for individual shrimps, these were treated statistically as missing data. Observations were made using a stereo microscope fitted with an ocular micrometer. Measurements were made with an accuracy of 0.05 mm, whilst discrete variables were recorded as counts or assigned dichotomous codes.

Within-regional analyses were carried out on the raw data to identify outliers using linear least-squares regression analyses with carapace length as the independent variable (Spotte, 1997). Individual measure-

Table 3. Position of group centroids in Discriminant Analysis

	Root 1	Root 2	Root 3	Root 4
Sexes combined				
NW Mediterranean	−4.215	−0.177	−0.177	0.006
Faroe-Scotland	2.287	0.103	−1.258	0.610
Norway	1.462	−0.173	−0.759	−0.948
Ireland	0.704	1.652	0.733	0.005
U.S.A.–Canada	1.549	−1.160	0.901	0.107
Females only				
NW Mediterranean	−5.857	0.528	0.116	0.006
Faroe-Scotland	2.488	−0.146	2.075	0.962
Norway	1.952	0.399	1.001	−1.295
Ireland	0.375	−2.055	−0.625	0.002
U.S.A.–Canada	2.533	1.228	−1.038	0.226

Table 4. Summary statistics for Discriminant Analysis

	Eigenvalue	% of variance	Cumulative %	Canonical correlation
Sexes combined				
Root 1	6.58	78.9	78.9	0.93
Root 2	0.90	10.8	89.7	0.69
Root 3	0.66	7.9	97.6	0.63
Root 4	0.20	2.4	100.0	0.41
Females only				
Root 1	11.35	79.0	79.0	0.96
Root 2	1.55	10.7	89.7	0.78
Root 3	1.09	7.6	97.3	0.72
Root 4	0.38	2.7	100.0	0.53

ments (outliers) were re-measured (if possible) and values corrected prior to subsequent analysis and only excluded from further analyses, if their values still exceeded 3 standard deviations (SD) in regression residual plots. All continuous variables were then divided by carapace length to minimise size effects. Carapace length was used as the variable indicating body size, as it is relatively unaffected by variation induced by growth and maturation (Lovett & Felder, 1989) and preservation fluid induced effects. Three sets of data in proportional form were retained as unstandardised values. These were rostral length (RL), already expressed as a ratio to carapace length and the insertion points of the anterior and posterior telson spines (TELANT, TELPOST), both distances measured from the proximal end of the telson and expressed as a percentage of telson length. Prior to further analysis, proportions were arcsin transformed to achieve univariate normality, with the exception of telson length (TELSON), which was arctan transformed, as several values exceeded unity.

Sexual variation was analysed first, using one-way ANOVA tests. Following this, the data set was subjected to Multiple Discriminant Analysis (MDA), a technique also known as canonical variate analysis. MDA finds linear combinations of variables (roots), that maximise differences among a priori defined groups (in this case regions), with the hit ratio (percentage correctly classified) providing a goodness of fit measure. In all MDA analyses, all variables were entered simultaneously, with the relative contributions of each variable assessed on the basis of the structure correlations (discriminant loadings), rather than the discriminant coefficients, as the former are considered more valid in interpreting the discriminating power of the independent varaibles. This technique has been successfully used in the discrimination of sibling species in *Alpheus* (Duffy, 1996), stock discrimination of lobsters (Cadrin, 1995) and to assess geographical variation in *Periclimenes* (Spotte, 1997).

Results

Several discrete variables were found not to exhibit any variation amongst regions, and hence they were excluded from further analysis. These were the number of teeth on the dorsal and both lateral carina, which in all individuals numbered four, two and one, respectively. On the dorsal carina, a small tooth was present close to the base of the rostrum followed by three large teeth. This small tooth has been overlooked in many earlier descriptions (e.g. Kemp, 1910), but its presence is identified in more recent descriptions (Williams, 1984; Squires, 1990).

Regarding carapace lengths, the across-region mean values for males was 8.60 mm (SD 1.82) and 10.21 (SD 2.87) for females, with this difference being statistically significant (one-way ANOVA, $F_{1,184}13.011$, $p<0.001$). A within-region analysis revealed that significant differences in carapace length of both sexes were only present in the Faroe-Scotland ($F_{1,28}14.251$, $p<0.005$) and U.S.A.-Canada ($F_{1,42}20.263$, $p<0.001$) populations, with in both instances males being on average smaller than females. An across-region analysis (sexes separate) revealed that significant differences existed in carapace

length of males ($F_{4,42}$5.020, p<0.005) and females ($F_{4,134}$31.329, p<0.001). Further post-hoc testing (Dunnett T3 test, p<0.05) demonstrated that males from the U.S.A. to Canada population are significantly larger than males from the Ireland population, whilst females from the U.S.A. to Canada population are significantly larger than from any of the other populations and females from the Ireland population are significantly smaller than females from either the Faroe-Scotland or the Norway populations.

Following standardisation with carapace length, all other variables were tested for sexual variation. Discrete variables were tested with Mann–Whitney tests, which revealed no sexual difference (all Z values <1.574). Continuous variables were assessed with one-way ANOVA tests, with the following variables, on average, being larger in males than in females: RL, BASAL, SUBORB and TELANT (all $F_{1,184}$> 5.820, p< 0.05), whilst the following variables, on average, were larger in females than in males: SOM1, SOM6 and PLEUR2W (all $F_{1,184}$> 6.083, p<0.05).

Given these sexual differences, two Multiple Discriminant Analyses were run; one on both sexes combined, but excluding any variables which exhibited significant sexual differences and one on females only, including all variables. As MDA requires a minimum within-region sample size of 20, a separate analysis could not be run on males only. MDA analysis on both sexes combined (Fig. 1) shows that Root 1 separates the NW Mediterranean population from the Atlantic populations as a whole, with along this root, overlap between the Atlantic populations being evident. Nevertheless, the position of all group centroids (Table 3) is significantly different from each other (Fig. 1), probably caused by the small separation of the Atlantic populations along the second root. Summary statistics demonstrated that the first root accounted for the majority of variance explained (Table 4), with the second root only accounting for an additional 10.8%. Examination of the structure correlation matrix (Table 5) reveals that four variables are highly loaded on the first root: TUBERCLE, TELSON, SOM and SCALEW, whilst nine variables exhibit their largest loading on Root 2. A classification matrix indicates that overall 88.2% of *a priori* grouped cases were correctly classified, with within-group classifications being: NW Mediterranean 100.0%, Faroes-Scotland 76.7%, Norway 70.4%, Ireland 89.2% and U.S.A.–Canada 93.2%. The MDA analysis on females only, essentially reveals the same structure in the data set, with the NW Mediterranean population separating from the Atlantic populations along Root 1 (Fig. 2), although a greater separation is evident between the Ireland and the U.S.A.–Canada populations on the Atlantic side (Fig. 2, Table 3). Similar eigenvalues and% variance explained are achieved (Table 4), whilst in the structure correlation matrix four variables are associated with the first root: TELSON, TUBERCLE, SCALEW and SOM1 (Table 6). A classification matrix indicates that overall 93.5% of a priori grouped cases were correctly classified, with within-group classifications being: NW Mediterranean 100.0%, Faroes-Scotland 88.2%, Norway 75.0%, Ireland 100.0% and U.S.A.–Canada 94.6%.

Table 5. Discriminant Analysis on sexes combined. Structure matrix of discriminant loadings. All variables entered simultaneously, largest absolute correlation between each variable and any discriminant function indicated by *

	Root 1	Root 2	Root 3	Root 4
TUBERCLE	0.380*	0.111	0.263	−0.107
TELSON	0.367*	0.054	−0.243	−0.154
SOM2	0.280*	−0.095	0.092	0.180
SCALEW	0.179*	−0.111	0.147	−0.146
ENDOL	0.171	0.488*	0.107	−0.242
PROP5	0.019	0.442*	−0.085	−0.139
EXOL	0.258	0.373*	0.024	−0.233
CARINA4	−0.092	0.319*	−0.053	0.286
SOM5	0.104	−0.299*	0.085	−0.161
PROP4	0.093	0.269*	−0.238	−0.118
SOM3	−0.079	−0.254*	−0.079	0.089
TELPOST	−0.070	−0.159*	−0.137	0.079
CARINA2	−0.063	0.143*	−0.027	0.042
CHELAW	0.335	0.197	−0.339*	−0.045
CARINA1	−0.194	0.118	0.254*	−0.156
EXOW	0.102	−0.129	0.221*	−0.027
PLEUR2D	−0.083	−0.170	0.210*	0.107
ROSTRUM	0.009	0.001	−0.112*	−0.101
CHELAEL	−0.119	0.418	−0.248	−0.541*
SCALEL	0.110	0.086	−0.059	−0.467*
CARINA3	−0.169	0.119	−0.010	0.420*
CARINA5	−0.036	−0.121	0.120	0.388*
SOM4	−0.070	−0.224	0.163	−0.350*
ENDOW	0.060	0.085	0.128	−0.255*
ANTPED	−0.048	−0.125	−0.160	0.196*

Discussion

When comparing geographically separated populations by means of a morphometric data set, factors

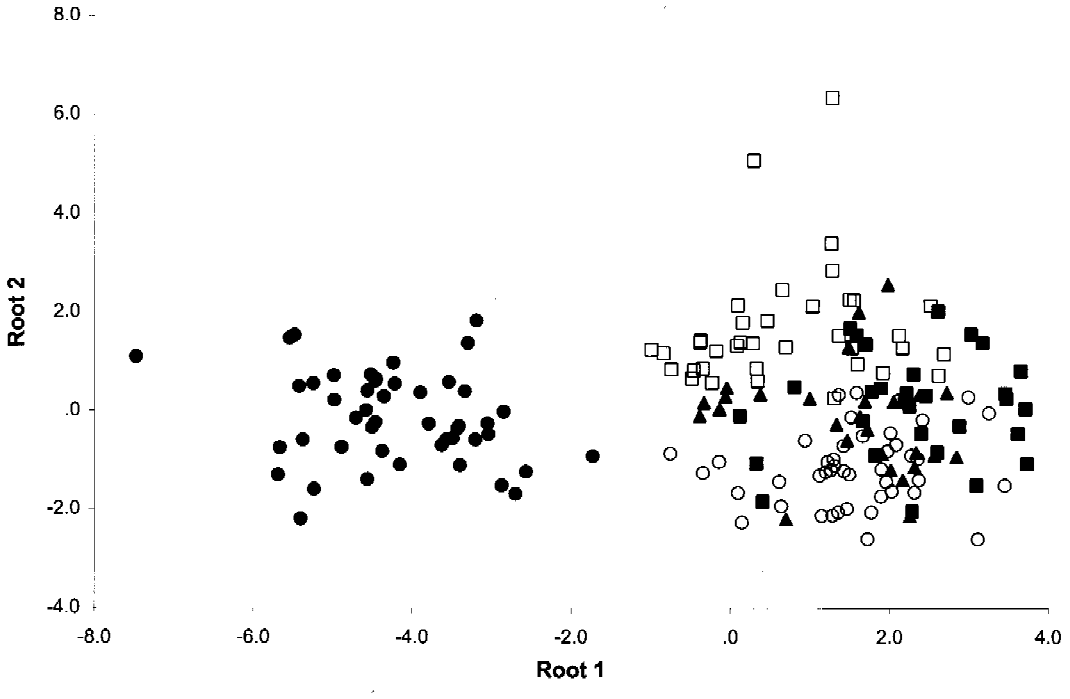

Figure 1. Scatterplot of MDA scores (first and second root only) for the five regions, both sexes combined. Symbols: NW Mediterranean (filled circle), Faroe-Scotland (filled square), Norway (filled triangle), Ireland (open square) and U.S.A.–Canada (open circle). Wilks's λ 0.035, χ^2 570.90, df 100, $p<0.001$

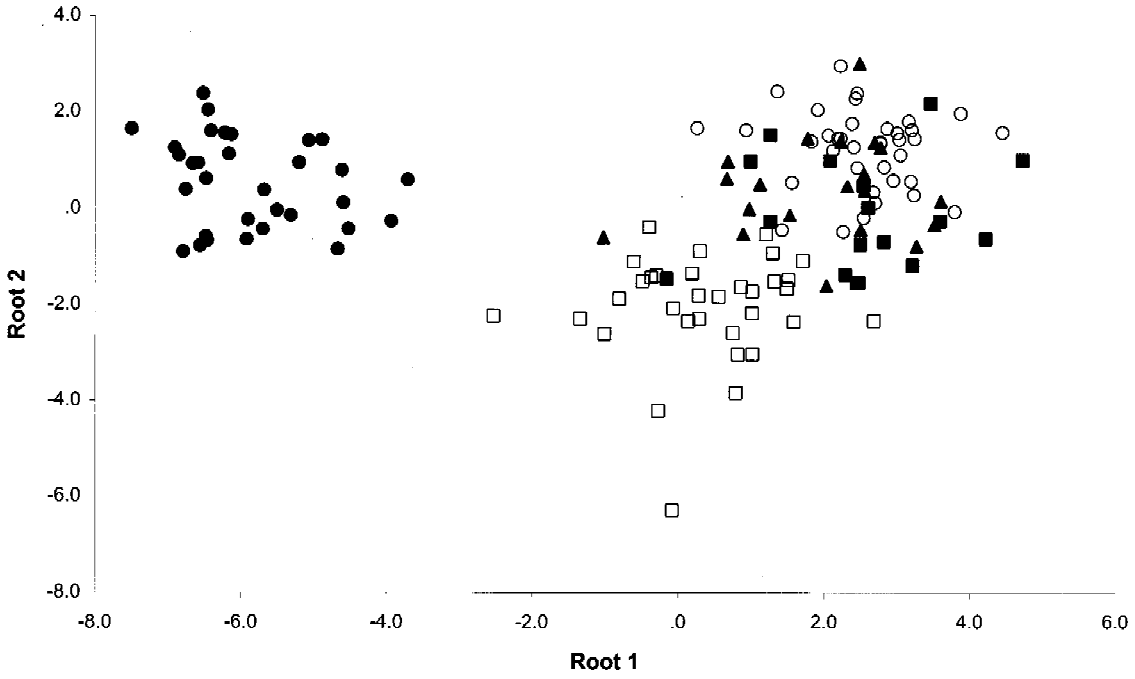

Figure 2. Scatterplot of MDA scores (first and second root only) for the five regions, females only. Symbols: NW Mediterranean (filled circle), Faroe-Scotland (filled square), Norway (filled triangle), Ireland (open square) and U.S.A.–Canada (open circle). Wilks's λ 0.011, χ^2 539.17, df 128, $p<0.001$.

Table 6. Discriminant Analysis on females only. Structure matrix of discriminant loadings. All variables entered simultaneously, largest absolute correlation between each variable and any discriminant function indicated by *

	Root 1	Root 2	Root 3	Root 4
TELSON	0.299*	−0.181	0.227	−0.213
TUBERCLE	0.237*	−0.160	−0.141	−0.062
SCALEW	0.139*	0.026	−0.123	−0.024
SOM1	0.096*	0.029	−0.076	−0.095
ENDOL	0.120	−0.411*	−0.046	−0.213
BASAL	−0.054	−0.384*	0.083	−0.122
EXOL	0.183	−0.373*	0.049	−0.232
PROP5	−0.033	−0.336*	0.036	−0.245
SOM6	0.127	−0.318*	−0.120	−0.175
SUBORB	−0.214	−0.275*	0.119	−0.086
CARINA4	−0.103	−0.264*	0.045	0.131
RL	−0.079	−0.248*	0.100	−0.034
TELPOST	−0.069	0.242*	0.215	0.082
PLEUR2W	−0.017	0.213*	−0.158	0.071
SOM3L	−0.045	0.176*	0.118	0.026
ANTPED	−0.012	0.167*	0.114	0.098
CARINA2	−0.044	−0.124*	−0.009	−0.001
CHELAEW	0.242	−0.219	0.327*	0.019
CARINA1	−0.117	−0.056	−0.205*	−0.174
PROP4	0.023	−0.143	0.167*	−0.126
EXOW	0.093	0.032	−0.157*	−0.092
CARINA3	−0.141	−0.086	0.004	0.453*
CHELAEL	−0.105	−0.301	0.138	−0.405*
CARINA5	−0.010	0.084	−0.127	0.339*
TELANT	0.054	0.235	0.233	0.290*
SCALEL	0.068	−0.046	0.057	−0.278*
SOM2	0.211	−0.057	0.002	0.248*
SOM4	−0.033	0.193	−0.079	−0.237*
ENDOW	0.047	−0.076	−0.088	−0.228*
SOM5	0.119	0.209	−0.072	−0.222*
PLEUR2D	−0.055	0.130	−0.171	0.199*
ROSTRUM	0.012	0.024	0.080	−0.164*

Table 7. Presence-absence of tubercle on dorsal carina of carapace per region, expressed as a percentage

	Presence	Absence
NW Mediterranean	83.3	16.7
Faroe-Scotland	13.3	86.7
Norway	14.8	85.2
Ireland	8.1	91.9
U.S.A.–Canada	6.8	93.2

such as sexual dimorphism, allometric growth and state of maturity can exert some influence on the observed differences (Mamuris et al., 1998). In addition, in the present data set, many of the collections contained few small and/or juvenile specimens, perhaps related to deployed mesh size and/or sampling gear selectivity in the different regions. The present study attempted to minimise additional variances through size standardisation, data transformation and by performing separate MDA analysis.

Extensive variation in morphometric variables existed between the studied Mediterranean population and the Atlantic populations as a whole. In addition, within the Atlantic populations studied the Faroe-Scotland and the Norwegian populations were most similar, whilst the south of Ireland and the U.S.A.–Canada populations were most dissimilar. This is supported by not only the MDA scores along the first two roots, but also the centroids of the regions and the percentage correctly re-classified individuals in the original groups.

The variables of primary importance in separating the Mediterranean and Atlantic populations as a whole, were related to telson length, the presence vs. absence of a tubercle on the dorsal carina of the carapace and the width of the antennal scale. However, the relatively low discriminant loadings on Root 1 of these variables (Tables 5 and 6), suggests that other variables may represent additional sources of variance. This is also the case for the separation of the Atlantic regions themselves, on which a strong influence of a score of variables associated with the second root is exerted. As the visibility of non-standardised, non-transformed variables is a necessary prelude to taxonomic, operational utility; the encountered differences in both the length of the telson and the width of the antennal scale (both transformed and standardised in the MDA analysis) should be interpreted as statistical constructs with no operational utility (Spotte, 1997). In contrast, the presence vs. absence of a tubercle has palpable reality and could be an operational variable. Although, it is more frequently present in the Mediterranean than in the Atlantic populations, 16.7% of Mediterranean individuals still lack a tubercle (Table 7) and hence this variable can also be discounted as being of operational utility. None of the other variables, with potential operational utility (e.g. carapace spines, rostral length) were identified by the MDA analyses as having any discriminatory power.

In general, morphological variability amongst different geographical populations is attributed to different genetic structure of populations and/or different environmental conditions prevailing in each geographic region. Certainly, the known Atlantic distribution of *P. norvegicus* only extends to the Bay of Biscay (Rodríguez-Marín, 1993), with the closest Mediterranean population being in the Catalan Sea (Abelló & Vallarades, 1985, 1988). At the present time, due to this geographical isolation and prevailing current patterns along the southern European coastline, gene flow and larval exchange between the Atlantic and Mediterranean population is, in all likelihood, severely restricted, if existent at all. Adaptations to environmental conditions may also play a role in this Atlantic-Mediterranean separation, as Lagardère (1970) formulated the hypothesis that along the eastern Atlantic seaboard, the amplitude of depth distribution becomes progressively lower with decreasing latitude, due to the upper limit of occurrence becoming progressively deeper; suggested to be in response to both temperature and substrate preferences (Lagardère, 1970). Although the depth range of the species extends from 50 to 1450 m in the Atlantic, it is most common between 200 and 500 m (Smaldon, 1979), whilst in the Mediterranean, Abelló & Vallarades (1985, 1988) consider the species to be a glacial relict species, typical of the bathyal zone (1020–1815 m) in the western Mediterranean, although it occurs here at higher temperatures than in the Atlantic. These differences in depth preferences and temperature regimes, and possibly substrate differences between the Atlantic and Mediterranean parts of the *P. norvegicus* range may thus play a role in the morphological variability between the regions.

Morphological variability between the Atlantic regions is much slighter, probably as a result of the absence of, present-day, geographical barriers and the resultant higher potential of larval exchange.

Given the present dataset, it can be concluded that the Mediterranean and Atlantic populations exhibit significant morphological differences as a result of geographical isolation with resultant limited gene flow and larval exchange. Although the populations are potentially approaching the subspecies stage in the evolutionary continuum of speciation, they at present do not appear to exhibit sufficient diagnostic morphological characters to be considered as subspecies, rather the results should be interpreted as geographical variation. As such, it is suggested that sub-specific status is presently not awarded to the populations.

Acknowledgements

The following curators entrusted us with specimens in their care: R. B. Manning, K. Reed (Smithsonian Institution, Washington), G. W. Pohle (Huntsman Marine Science Centre, New Brunswick), P. Clarke, M. Lowe (The Natural History Museum, London), W. Vader (Tromso Museum) and J. Sørensen (Kaldbak Marine Biological Laboratory), for which they are gratefully acknowledged. E. Rodríguez-Marín, C. Pipitone, P. Abelló, J. C. Sorbe and G. Gudmundsson provided much appreciated information. H. Wilkins and A. Myers provided constructive criticism on an earlier version of the manuscript.

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