

Variation in rostral dentition and telson setation in a saltmarsh population of *Palaemonetes varians* (Leach) (Crustacea: Decapoda: Palaemonidae)

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Received 29 August 1998; in revised form 29 January 1999; accepted 12 February 1999

Key words: Decapoda, Palaemonetes, saltmarsh, morphological variation, telson, rostrum

Abstract

A study was undertaken on the variability of rostral dentition and telson setation in a saltmarsh population of *Palaemonetes varians* (Leach), collected from the Douglas Estuary, Cork Harbour, Ireland. Both these morphological characters are thought to be of taxonomic value, but have been little studied. A comparison with literature data indicates a latitudinal trend with a higher frequency of six dorsal teeth at higher latitudes. However, more studies are needed to validate this trend. Only a minor amount of individuals deviated from harbouring two ventral sub-terminal setae on the telson, hence this character could be used to separate some of the European members of the genus.

Introduction

Historically, rostral dentition in palaemonid shrimps has been considered as a species specific character, with some taxa described solely on the basis of differences in the number of dorsal and/or ventral rostral teeth. However, numerous species are known to show some degree of variation in terms of the profile or dentition of the rostrum (Holthuis, 1952). Hence, recent keys and species diagnoses have relied more on other morphological characters, although knowledge of the variation in rostral dentition does aid in species recognition.

Information regarding rostral variability in the majority of palaemonids is usually restricted to a short statement regarding the total range and perhaps the most frequent combination of dorsal and ventral teeth, often on the basis of only a few specimens. In contrast, rostral variation has been well studied in the genus *Palaemonetes* Heller, dating back as far as Weldon (1890) who studied *Palaemonetes varians* Leach in Plymouth (U.K.). Further studies on *P. varians* were undertaken by Brožzek (1912) and Gurney (1923). Other species of the genus have also been studied: *P. pugio* Holthuis (Duncker, 1900 as *P. vulgaris* (Say)), *P. antennarius* (H. Milne Edward) (Brožzek, 1908 as *P. varians*), *P. australis* Dakin (Serventy, 1938) and *P. zariquieyi* Sollaud (Sanz, 1988).

Although rostral dentition has not been used to differentiate between the European species of *Palaemonetes*, systematic importance has been accorded to the number of sub-terminal, plumose setae on the ventral side of the telson, although Gurney (1923) after studying the variation of this character in *P. varians*, considers this to be of no specific or generic importance. Nevertheless, the number of setae has been used in recent keys to the genus in Europe (Azzouna, 1994; Noël, 1993).

The present study aims at characterizing the variation in both rostral dentition and telson setation in a saltmarsh population of *P. varians*.

Material and methods

Palaemonetes varians individuals were collected by dip-net from upper estuarine saltmarsh pans in the Douglas Estuary, Cork Harbour, Ireland during a 1 week period in September 1997. These pans are only subjected to tidal inundation on a monthly basis and



Figure 1. Diagram of carapace, showing measurements taken. (a) Post-orbital carapace length, (b) rostral length, (c) distance between apex of rostrum and base of first tooth in bifid specimens, (d) distance between apex of rostrum and base of first tooth in non-bifid specimens.

some only quarterly, and during the summer months considerable evaporation takes place with all but the largest pools drying out. Due to the combined action of tidal inundation, evaporation and shallow water depths (<0.2 m), considerable fluctuations in temperature, dissolved oxygen and salinity take place on an hourly to daily basis.

A total of 510 individuals were collected. These were sexed by means of the presence or absence of an appendix masculina on the second pleopod (see Fleming, 1969), which according to Antonopoulou & Emson (1992) is present on males with a carapace length greater than 3 mm. Individuals with obvious signs of rostral damage or regeneration were excluded from measurements.

The following morphological measurements were taken: post-orbital carapace length (from the orbital socket to the posterior end of the carapace, Figure 1), rostral length (from the apex of the rostrum to the orbital socket, Figure 1) and the distance from the rostral apex to the base of the last dorsal tooth (Figure 1). Total length equals the sum of post-orbital carapace length and rostral length. All measurements were taken with the aid of an ocular micrometer fitted to a binocular microscope and are given in mm.

Specimens were classed as having a bifid or nonbifid rostral apex on the basis of the presence or absence of a sub-apical, small dorsal tooth (Figure 1). The telson of all specimens was dissected out and after clearing in a weak lactophenol solution was viewed with a high power microscope. Number and position of the ventral, sub-terminal setae was scored. Broken setae were not considered a separate category, but were included in the appropriate category together with intact setae.

Rostral formulae are given as:

post-orbital tooth + dorsal series + sub-apical tooth ventral series

Results

Within the population studied the overall female: male ratio was 1:1.26, with on average females being larger than males (Table 1). Both the post-orbital carapace length (Table 1, t-test 5.897, p < 0.001) and rostral length (Table 1, *t*-test 5.377, p < 0.001) were significantly larger in females than in males, as a consequence the total length was also significantly larger in females than in males (Table 1, *t*-test 5.744, p < 0.001). The frequency distribution of size classes, as measured by post-orbital carapace length, in both sexes also appears different (Figure 2), with males exhibiting a smaller total spread and a lower standard deviation (Table 1). Hence, in subsequent analyses both sexes were kept separate. In terms of the relationship between rostral length and post-orbital carapace length, the following linear regression equation was found to fit the data best in females: rostral length = 0.160 + 0.952× post-orbital carapace length, adjusted R^2 =0.903, p < 0.001; and in males: rostral length = 1.419 + 0.704× post-orbital carapace length, adjusted R^2 =0.545, p < 0.001.

Of the total number of individuals, 58.85% exhibited a bifid rostral apex, with in females and males this percentage being 58.10 and 59.43% respectively (Table 2). In females, both the post-orbital carapace length and the rostral length were larger in individuals with a bifid rostral apex versus a non-bifid apex (Table 2), whilst in males only the rostral length was significantly larger in bifid rostral apex specimens and not the post-orbital carapace length (Table 2).

The full range of variation in rostral dentition in the studied population is illustrated in Figures 3 and 4. In all individuals a single post-orbital dorsal tooth was present, with the exception of two specimens (Figure 4M, N), in addition one of these harboured no

Table 1. Morphometric details of population.

	Mean	Standard error	Standard deviation	Min.	Max.
Females (n=222)					
Post-orbital carapace length (mm)	5.709	0.098	1.461	2.220	9.370
Rostral length (mm)	5.596	0.098	1.463	2.060	9.370
Total length (mm)	11.306	0.194	2.888	4.290	18.410
Males (<i>n</i> =281)					
Post-orbital carapace length (mm)	5.058	0.060	1.009	3.330	8.410
Rostral length (mm)	4.992	0.061	1.016	1.110	8.570
Total length (mm)	10.071	0.116	1.942	6.190	16.980



Figure 2. Frequency histogram of post-orbital carapace length in females (top) and males (bottom).

dorsal teeth at all (Figure 4N). Other striking peculiarities included no dorsal rostral teeth (Figure 4A, E) and the bifid development of a dorsal tooth (Figure 4J). Regenerating rostra are illustrated in Figure 3T–W, with in addition Figure 3D possibly representing an advanced stage of regeneration.

	Bifid rostral apex	Non-bifid rostral apex	t	
Females				
n	129	93		
Percentage of females	58.10	41.90		
Post-orbital carapace length (mm)	5.984 (1.321)	5.329 (1.564)	-3.284^{**}	
Rostral length (mm)	5.867 (1.377)	5.221 (1.504)	-3.270**	
Males				
n	167	114		
Percentage of males	59.43	40.57		
Post-orbital carapace length (mm)	5.103 (0.946)	5.043 (1.227)	-0.462^{ns}	
Rostral length (mm)	5.095 (0.993)	4.840 (1.034)	-2.084^{*}	



Figure 3. Rostral variation. (A) Female, 5.71 mm post-orbital carapace length; (B) female, 6.82; (C) male, 4.28; (D) female, 6.19; (E) female, 6.03; (F) male, 4.13; (G) male, 4.76; (H) male, 6.67; (I): male, 4.92; (J) male, 3.97; (K) male, 5.71; (L) male, 5.08; (M) male, 3.97; (N) female, 7.94; (O) female, 5.87; (P) female, 8.57; (Q) female, 6.35; (R) female, 5.87; (S) male, 4.76; (T) male, 4.50; (U) male, 5.80; (V) female, 4.20; (W) female, 10.30. Scale bar indicates 2 mm.

Besides variation in the number of dorsal and ventral teeth and the presence or absence of the smaller sized sub-apical dorsal tooth, considerable variation is also apparent in the position of the teeth in relation to



Figure 4. Rostral variation. (A) Female, 8.57 mm post-orbital carapace length; (B) female, 8.25; (C) male, 5.87; (D) female, 7.94; (E) male, 5.71; (F) male, 5.71; (G) female, 5.40; (H) female, 2.38; (I) female, 6.35; (J) male, 3.81; (K) female, 6.35; (L) female, 3.81; (M) male, 6.03; (N) female, 8.73. Scale bar indicates 2 mm.

each other and in relation to the orbital angle and the rostral apex, and in the depth and inclination of the rostrum (Figures 3 and 4). These aspects were however not quantified, as they are thought to be of no systematic importance.

Tables 3 and 4 present the frequency of occurrence and the post-orbital carapace length of the various combinations of dorsal and ventral rostral teeth in the studied population, with the dorsal post orbital tooth excluded. Only specimens which harboured a post-orbital tooth and at least one tooth in the dorsal series were included, representing 98.63% of the total population. Abnormal specimens and regenerat-



Figure 5. Variation in telson setation. (A, B) Female, 5.87 mm post-orbital carapace length; (C) male, 5.56; (D) male, 3.97; (E) male, 4.29; (F) female, 5.87; (G) female, 7.46; (H) female, 7.94; (I) male, 6.35; (J) male, 5.71; (K) male, 6.67. Scale bar indicates 1 mm (A) or 0.4 mm (B–K)

ing rostra were excluded from this compilation. The most frequently encountered combination for females (Table 3) and males (Table 4) is (1+4+1)/2 for bifid and (1+4+0)/2 for non-bifid rostra.

Although these tables are unsuitable for statistical analysis, it appears that the number of either dorsal or ventral teeth does not increase with post-orbital carapace length, nor does there appear to be a large deviation from the overall mean size in each of the classes (Tables 3 and 4).

A significant difference exist in the insertion point of the apical tooth of non-bifid versus bifid rostra, with this distance being much shorter in both males and females exhibiting a bifid apex (Table 5). Some bias is present in these percentages, due to the fact that if the apical tooth is situated more than a certain distance away from the apex, the rostrum will not be perceived as being bifid. However, only a few such cases were encountered and in these the small size of the apical tooth in bifid rostra versus a larger tooth in non-bifid rostra was used as the deciding factor.

The general form of the telson is illustrated in Figure 5A and its apical portion in Figure 5B. Of the 510 specimens examined, 11 specimens (2.15%) had broken apices and were not considered further. The majority of specimens (491 individuals, i.e. 98.40%) harboured a pair of ventral sub-terminal setae (Figure 5B), with a considerable number having one or both of these setae broken (Figure 5C).

Overall, only eight specimens (1.60%) harboured supernumerary setae. Of these, five individuals harboured three setae, with the single supernumerary seta situated in the center (Figure 5D) or close to one of the other setae (Figure 5E-F, I-J). A single case each of four setae (Figure 5G), six setae (Figure 5K) and eight setae (Figure 5H) was encountered. As can be seen from Figure 5, variation was also observed in the position, number and shape of the sub-terminal spines, with Figure 5J clearly representing a highly aberrant situation. Variation in the number and alignment of one or both pairs of dorsal telson spines (Figure 5A) was also observed, however this was not quantified, as no systematic importance has been attached to this character in European *Palaemonetes*.

Discussion

Although Gurney (1923) acknowledged that local populations of *P. varians* are isolated for long periods and are subject to intense selection, he believed that a study of variation in rostral dentition was greatly offset by the large amount of labour involved. Nevertheless, information regarding this variability can be considered to be of some taxonomic value. In addition, if geographical comparisons or ecological factors, such as the influence of habitat are to be discussed, more information is needed, as very few studies have been made so far.

Using the data of Weldon (1890) and Brožzek (1908, 1912), Gurney (1923) concluded that rostral dentition is not influenced by geographic location or salinity. As Brožzek (1908) included the freshwater species *P. antennarius* (see Sollaud, 1930) under the material of *P. varians*, this comparison is partly invalid. Hence, only the data of Weldon (1890) from Plymouth; Gurney (1923) from Norfolk, Essex and Suffolk; Evans (in Gurney, 1923) from Firth of Forth, Scotland and Brožzek (1912) from Copenhagen can be used. As all these populations are from estuarine locations, a comparison between freshwater and estuarine populations can no longer be made.

Comparing the number of dorsal teeth, the most frequently encountered number is four or five in the British (Gurney, 1923) and Irish specimens, and six in the specimens from Copenhagen (Brožzek, 1912). Al-

Dorsal teeth								
1	2 3		4		5			
cl	n	cl	n	cl	n	cl	n	cl
7.46	1	8.25	6	6.80	8	6.09	1	8.09
(1.57)		(-)		(1.47)		(1.16)		(-)
6.34	4	7.10	26	5.74	61	5.65	16	6.51
(-)		(1.39)		(1.29)		(1.24)		(1.28)
	1	6.35			2	5.87		
	(-)					(0.01)		
							1	3.81
								(-)
8.25	1	7.94	4	6.63	3	4.07		
(-)		(-)		(1.54)		(1.60)		
	3	5.87	24	5.37	44	5.06	11	5.81
		(0.82)		(1.70)		(1.41)		(1.40)
							1	3.81
								(-)
	1 cl (1.57) 6.34 (-) 8.25 (-)	$\begin{array}{c cccc} 1 & & & \\ \hline cl & n & \\ \hline (1.57) & & \\ 6.34 & 4 & \\ (-) & & \\ & & 1 & \\ (-) & & \\ 8.25 & 1 & \\ (-) & & \\ 3 & \\ \end{array}$	$\begin{array}{c c c c c c c c c c c c c c c c c c c $	$\begin{array}{c c c c c c c c c c c c c c c c c c c $	1 2 3 cl n cl n cl 7.46 1 8.25 6 6.80 (1.57) (-) (1.47) 6.34 4 7.10 26 5.74 (-) (1.39) (1.29) 1 6.35 (-) 1 6.35 (-) 1 8.25 1 7.94 4 6.63 (-) (-) (1.54) 3 5.87 24 5.37 (0.82) (1.70) (1.70) (1.70) (1.70) (1.70)	1 2 3 n cl n cl n cl n 7.46 1 8.25 6 6.80 8 (1.57) (-) (1.47) (1.47) (1.47) 6.34 4 7.10 26 5.74 61 (-) (1.39) (1.29) 1 6.35 2 (-) 1 6.35 2 (-) 2 (-) (-) (1.54) 3 3 (-) 3 5.87 24 5.37 44 (0.82) (1.70) 4 4 4	1 2 3 4 cl n cl n cl n cl 7.46 1 8.25 6 6.80 8 6.09 (1.57) (-) (1.47) (1.16) 6.34 4 7.10 26 5.74 61 5.65 (-) (1.39) (1.29) (1.24) 1 6.35 2 5.87 (-) (-) (1.54) (0.01) (0.01) 8.25 1 7.94 4 6.63 3 4.07 (-) (-) (1.54) (1.60) 3 5.87 24 5.37 44 5.06 (0.82) (1.70) (1.41) (1.41) (1.41)	1 2 3 4 cl n cl n cl n cl n 7.46 1 8.25 6 6.80 8 6.09 1 (1.57) (-) (1.47) (1.16) 6.34 4 7.10 26 5.74 61 5.65 16 (-) (1.39) (1.29) (1.24) 1 6.35 2 5.87 (-) (-) (1.54) (0.01) 1 8.25 1 7.94 4 6.63 3 4.07 (-) (-) (1.54) (1.60) 1 1 8.25 1 7.94 4 5.37 44 5.06 11 (0.82) (1.70) (1.41) 1 1

Table 3. Frequency of occurrence (*n*) and mean post-orbital carapace length (cl) (\pm S. D.) of encountered rostral formulae for female *P. varians* (*n*=222). Number of dorsal teeth refers to the dorsal series proper, exclusive of the post-orbital tooth which is present in all specimens and the sub-apical tooth which is considered separately as either present (bifid) or absent (non-bifid).

Table 4. Frequency of occurrence (*n*) and post-orbital carapace length (cl) (\pm S. D.) of encountered rostral formulae for male *P. varians* (*n*=281). Number of dorsal teeth refers to the dorsal series proper, exclusive of the post-orbital tooth which is present in all specimens and the sub-apical tooth which is considered separately as either present (bifid) or absent (non-bifid).

Ventral teeth	Dorsal teeth											
		1		2		3		4		5		6
	n	cl	n	cl	n	cl	n	cl	n	cl	n	cl
Bifid apex												
1	3	5.50	1	6.03	7	5.35	5	5.24				
		(0.64)		(-)		(0.86)		(0.80)				
2	2	5.95	7	4.99	27	5.10	82	5.06	28	5.03	3	5.18
		(0.56)		(1.02)		(1.11)		(0.96)		(0.93)		(0.33)
3					1	5.24						
						(-)						
5									1	4.76		
										(-)		
Non-bifid apex												
1			4	6.07	8	6.78	5	5.33				
				(0.23)		(2.05)		(0.86)				
2	2	6.03	4	5.32	24	5.11	54	4.69	12	4.69		
		(0.45)		(0.82)		(1.20)		(0.96)		(1.07)		
3									1	3.97		
										(-)		

Table 5. Mean (\pm S.D.) of insertion point of apical dorsal tooth, expressed as a percentage of rostral length (** p < 0.001)

	Bifid rostral apex	Non-bifid rostral apex	t
Females	4.32 (2.93)	35.11 (9.29)	35.311**
Males	4.24 (1.61)	34.54 (8.47)	45.141**

though it is not clearly stated in the previous studies, it is assumed that the number of dorsal teeth includes the post-orbital tooth, but not the smaller sub-apical tooth in the bifid rostral condition. Gurney (1923) stated that six dorsal teeth is more common in Scotland and along the east coast, than in Plymouth (Weldon, 1890), with the exception of the Suffolk specimens. In the present study six dorsal teeth occurred in 13.1% of specimens, which is higher than the 5-6% encountered in Plymouth and Suffolk, but lower than the 34-37% along the east coast of the UK and the 28-33% in Copenhagen. Although these figures suggest a latitudinal trend, with higher numbers of teeth in the dorsal series with increasing latitude, it should be noted that the sample sizes of Gurney (1923) and Brožzek (1912) are small compared to those of Weldon (1890) and the present study, a fact which may influence the actual numbers derived.

In terms of ventral teeth, Gurney (1923) mentioned that it is exceptional to find more or less than two teeth, whilst in Weldon (1890) specimens 68.85% harboured two ventral teeth; Brožzek (1912) does not discuss the number of ventral teeth. In the present study 86.7% of all specimens harboured two ventral teeth. Clearly, this number represents the normal condition in *P. varians*, regardless of location.

With respect to the bifid condition of the rostral apex, Weldon (1890) found 52.8% of all specimens exhibited a bifid apex, Brožzek (1912) 73.1% and the present study 58.8% with Gurney (1923) stating that a small apical tooth is present in more than half of the individuals. Although these figures may be indicative of a latitudinal difference, with the most northern population exhibiting this condition more frequently, more work needs to be done on this aspect before a conclusion can be drawn.

Although the number of ventral sub-terminal setae has been shown to be of systematic importance, at least to discriminate the European members of the genus (Azzouna, 1994; Noël, 1993), only Gurney (1923) appears to have studied the variation of this character. Gurney's study was based on 30 specimens, 11 (i.e. 6.7%) of which harboured at least one supernumerary seta, with as much as four additional setae encountered in one specimen. In the present study only 1.6% of all specimens harboured supernumerary setae, with a single additional setae being most frequent in these. Variation in the number and position of the sub-terminal spines was also observed, which was also infrequently present in the material of Gurney (1923). The much lower percentage of specimens with supernumerary setae in the present study is in all likelihood caused by the much larger sample size, although the possibility that the population studied by Gurney (1923) exhibits a higher incidence of supernumerary setae can not be totally discounted. Although Gurney (1923) attributed the presence of supernumerary setae to the retention of larval setae (see Fincham, 1979), which may indeed account for the presence of a single, additional seta; it is also likely that regeneration plays a role in this. The latter is supported by the fact that a considerable number of specimens with supernumerary setae, exhibited an asymmetrical development of the telson's apex, which is consistent with regeneration after partial damage.

Based on the results in the present study, it can be concluded that only minor variation exists in the number of ventral sub-terminal setae and that if this character is also proven to be stable in the other European members of the genus, it can be reliably used to discriminate between at least some species of the genus. Although some evidence is present that a latitudinal trend occurs in the number of dorsal teeth, with six being much more frequent in more northern European latitudes, more studies are needed in intermediate locations to either accept or confirm this trend.

Acknowledgements

H. Wilkins and C. d'Udekem d'Acoz are acknowledged for critically reading the manuscript.

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