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Morphological variation in *Nereis* (*Neanthes*) *virens* (Polychaeta: Nereididae) populations

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The intraspecific variation in the number and distribution of paragnaths in ten populations of *Nereis* (*Neanthes*) *virens* collected throughout its range was examined. Significant differences among populations are found in the total number of paragnaths and in each paragnath group. The unweighted pair-group method using arithmetic averages cluster analysis revealed three distinct clusters separating Canadian populations, Europe/USA populations and the Japanese population, suggesting the implication of either restricted gene flow, selection on paragnath patterns or phenotypic plasticity. Comparison with a previous genetic study suggests that morphological variants represent ecotypes of the single, widely distributed *N. virens* species.

INTRODUCTION

The nereidid polychaete *Nereis* (*Neanthes*) *virens* (Sars, 1835) occurs on both sides of the North Atlantic and North Pacific (Breton et al., 2003). Previous studies have revealed important ecological and physiological differences within and among North American and European populations (reviewed in Desrosiers et al., 1994). These findings coupled with morphological evidence have led some authors to conclude that *N. virens* is a complex of closely related species (Khlebovitch et al., 1980). Khlebovich et al. (1980) have distinguished *N. virens* (North America and Europe), *N. brandti* (Malmgrem, 1865) (Pacific waters) and *N. grandis* (Stimpson, 1853) (Denmark, England, Canada) on the basis of paragnath number, mode of reproduction and larval behaviour. *Nereis brandti* is separated from *N. virens* and *N. grandis* due to a larger size and a higher number of paragnaths in all groups (Khlebovich et al., 1980). On the other hand, *N. grandis* is undistinguishable from *N. virens* by the number of paragnaths but differs in terms of mode of reproduction (only males are epitokous *N. grandis* whereas both sexes are swimming during reproduction in *N. virens*) and larval behaviour (the larvae of *N. grandis* have no pelagic phase whereas *N. virens* larvae have a short one) (Khlebovitch et al., 1980; but see Bass & Bradfield, 1972).

A recent genetic study has revealed extremely low genetic variability at two mitochondrial and ten allozyme loci among 12 populations of *Nereis* (*Neanthes*) *virens* encompassing the known geographic range (Canada, USA, Scotland, England, the Netherlands, Germany, Russia, Japan), suggesting that it is a single, widely distributed species (Breton et al., 2003). These results are thus inconsistent with life history trait differences or with morphology-based taxonomy. Since differences in reproductive mode and larval behaviour have been observed within other polychaete species, it may not be an appropriate taxonomic character (Fong & Garthwaite, 1994). The use of paragnath number as a taxonomic character may also be inappropriate, given that it may be a response of phenotypic plasticity to different environmental or biotic constraints (Garcia-Arberas & Rallo, 2000). The purpose of this study was to: (i) evaluate the levels of morphological variation in the same *N. virens* populations (i.e. by studying the number of paragnaths in each group of the pharynx); and (ii) compare the results with previous genetic data.

MATERIALS AND METHODS

A total of 169 *Nereis* (*Neanthes*) *virens* individuals was collected between May 1992 and September 2000 from ten localities throughout its range (Table 1). The samples were stored in 95% ethanol, with the exception of specimens from Japan which were preserved in formalin for ten years. The number and distribution of paragnaths in the ten groups (I, II left, II right, III, IV left, IV right, VI left, VI right, VII/VIII and V) figured by Fauchald (1977) were examined under a binocular microscope. Groups I–IV form the posterior belt on the retracted proboscis whereas groups V–VII/VIII form the anterior belt (Fauchald, 1977). The data were analysed statistically using STATISTICA (Softstat, Inc. 1995).

Means, ranges and standard deviations of paragnath numbers in each group for all populations are shown in Table 1. The number of paragnaths in each one of the ten groups vary within and among populations. Means and ranges are broadly similar to values reported previously (Fauchald, 1977; Chambers & Garwood, 1992), except for individuals from Japan which have a greater number of paragnaths in all groups.

RESULTS AND DISCUSSION

The differences among populations for the total number of paragnaths and the number of paragnaths in each group are significant (Kruskal–Wallis test; $P \leqslant 0.01$). The population from Japan, with the highest mean total number of paragnaths, differs significantly from all other

Table 1. Nereis (Neanthes) virens. *Means, ranges and standard deviations of paragnath numbers in each group for the different populations.*

Sampling sites		Proboscide groups										
		I	IIL	IIR	III	IVL	IVR	VIL	VIR	VII/VIII	V	Total
Canada	M	1.3	6.0	6.1	8.8	14.4	14.2	1.2	1.1	15.5	0	68.5
(St Fabien, Qc)	±SD	0.4	1.6	1.5	1.9	2.5	2.1	0.4	0.3	2.2	0	13.0
N=24	R	1–2	3–9	3–8	6–13	11–20	8–17	1–2	1–2	12–21	0	60–77
Canada	M	1.2	7.0	6.8	9.3	16.2	15.5	1.5	1.4	17.4	0.1	76.2
(Bic, Qc)	±SD	0.4	1.3	1.5	1.9	1.5	1.9	0.8	1.0	2.8	0.3	13.3
N=22	R	1–2	4–10	5–10	7–13	13–19	10–19	1–4	1–4	12–24	0–1	64–90
Canada	M	1.2	5.5	5.5	8.6	14.6	14.3	1.1	1.3	15.5	0	67.4
(Forestville, Qc)	±SD	0.4	1.4	1.6	1.8	2.0	2.2	0.3	0.4	2.4	0	12.6
N=20	R	1–2	2–8	3–9	6–13	11–20	8–19	1–2	1–2	12–21	0	52–85
Canada	M	1.0	7.7	7.8	9.1	15.1	14.6	1.2	1.2	17.0	0	74.7
(Miguasha, Qc)	±SD	0	1.4	1.4	1.7	1.5	1.6	0.4	0.4	1.7	0	10.2
N=10	R	1	6–10	6–10	7–12	12–17	12–17	1–2	1–2	15–19	0	70–82
Canada	M	1.2	4.4	4.5	9.4	14.2	14.8	1.2	1.2	20.9	0.06	71.8
(P–E–I)	±SD	0.4	1.4	1.1	1.4	1.9	1.9	0.4	0.4	2.5	0.24	11.7
N=17	R	1–2	2–7	2–7	7–12	10–17	10–18	1–2	1–2	16–25	0–1	60–82
USA	M	1.8	7.3	7.4	11.8	18.8	17.8	1.7	1.6	27.6	0.1	95.8
(Maine)	±SD	0.4	1.7	1.7	1.8	3.8	3.9	1.3	0.9	5.1	0.3	22.1
N=16	R	1–7	3–10	5–11	9–16	13–26	12–25	1–5	1–4	19–37	0–1	72–124
Scotland	M	1.6	7.1	7.1	11.6	18.3	18.8	1.5	1.7	31.8	1.1	100.7
(St Andrews)	±SD	0.8	1.8	1.8	1.8	3.4	3.5	0.6	0.8	2.3	0.6	18.5
N=30	R	1–4	4–11	4–11	7–18	12–28	14–28	1–3	1–4	28–35	0–3	85–122
England	M	1.3	6.2	6.8	9.6	18.5	18.7	1.2	1.9	21.4	0	85.6
(Blyth)	±SD	0.5	2.0	1.5	1.5	4.0	3.5	0.4	0.7	3.0	0	17.2
N=10	R	1–2	3–10	4–9	7–11	10–25	13–25	1–2	1–3	17–26	0	63–99
Germany	M	2.0	8.9	8.4	12.0	21.9	21.7	1.7	1.6	24.6	0.7	103.4
(Wadden Sea)	±SD	0.0	2.4	0.5	1.6	2.7	4.4	0.5	0.5	3.6	0.5	16.8
N=7	R	2	6–12	8–9	10–15	18–25	13–26	1–2	1–2	19–28	0–1	95–114
Japan	M	8.2	11.4	11.5	19.1	26.1	25.6	2.8	2.9	69.2	2.0	178.7
(Otsuchi Bay)	±SD	2.4	3.0	2.2	3.3	3.3	4.3	1.2	1.4	5.7	2.0	29.0
N=13	R	6–14	8–19	9–17	12–24	20–31	17–32	0–5	0–5	61–82	0–5	158–217
Range in Fauchald (1977)		0–7	1–8	1–8	4–14	5–27	5–27	0–5	0–5	—	0–4	—
Chambers & Garwood (1992)		0–2	4–10	4–10	7–14	11–23	11–23	1–3	1–3	17–36	0–1	—

N, number, M, mean; SD, standard error; R, range. P-E-I, Prince Edward Island.

populations (Tukey test; $P \leqslant 0.01$). Populations from Scotland, Germany and USA differ significantly from the remaining populations (Tukey test; $P \leqslant 0.01$) in having a greater total number of paragnaths (Table 1).

The unweighted pair-group method using arithmetic averages cluster analysis using Euclidean distances shows three distinct clusters in *Nereis* (*Neanthes*) *virens* separating Maine and European populations from a Canadian cluster and the Japanese population (Figure 1). These results are consistent with ecological and physiological interpopulation differences observed previously (Desrosiers et al., 1994), but clearly contrast with those obtained from a genetic study of the same populations, except for the close relationships among the Maine and European populations (Breton et al., 2003). This supports the hypothesis that North Sea coast populations may be recently derived from a North American one (Reise et al., 1999). The most unusual aspect of our data is the clear morphological divergence of the Japanese population. According to Khlebovich et al. (1980), the individuals from Japan belong to the species *Nereis brandti* (Malmgrem, 1865), which is found in shallow marine soft-bottoms of the eastern and western Pacific coasts. However, it is still questionable whether *N. brandti* is in fact a true species or an ecotype of the environmentally plastic *N. virens* species. Indeed, mitochondrial sequences from Breton et al. (2003) indicated that this Japanese population is genetically similar with European and North American *N. virens* populations. This may imply either: (1) selection on paragnath patterns; (2) restricted gene flow; (3) phenotypic response to environmental constraints; or (4) hybridization and mtDNA introgression between *N. virens* and *N. brandti* in Pacific waters. Additional sampling and analyses of morphological, ecological, physiological

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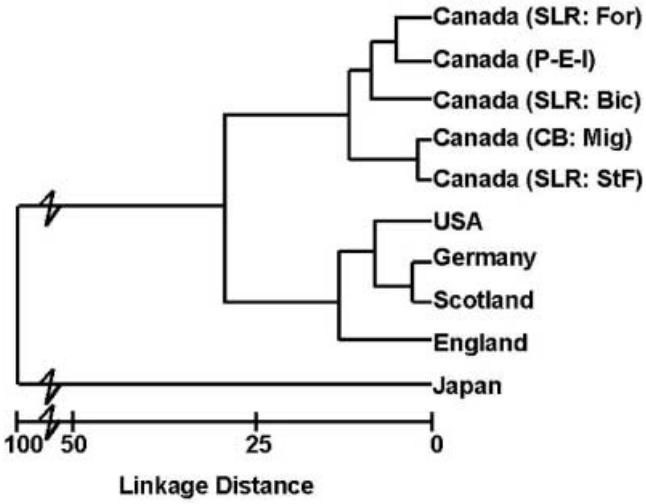

Figure 1. *Nereis (Neanthes) virens*. Unweighted pair-group average cluster analysis using Euclidean distances. [Site abbreviations: *SLR* St-Lawrence River (*For* Forestville, *StF* St-Fabien), Quebec; *CB* Chaleur Bay (*Mig* Miguasha), Quebec; *PEI* Prince Edward Island, Canada.]

and genotypic data would be helpful to verify if *N. brandti* can be recognized as a valid species. Similarly, the lack of genetic variability observed previously suggests that records of *N. grandis* may refer to *N. virens* (Breton et al., 2003). Given that we lack robust anatomical characters that can be used to clearly differentiate the three species and that a previous genetic study has not contributed to solving the question, it seems more conservative to conclude that *N. virens* is a single, widely distributed species. We propose that the use of molecular markers with a greater resolving power would be helpful to better assess intra- or interspecific levels of genetic diversity in the putative *N. virens* species complex.

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