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# Variations in Paragnath Number of the Different Morphs of the Polychaete *Perinereis* Cf. *Cultrifera* in Relation to Geographical Location and Type of Reproduction

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**Abstract:** Bristleworms assigned to *Perinereis cultrifera* can reproduce by epitoky or atoky according to the location of the populations. Variation in the number and distribution of paragnaths has been investigated in two populations of the atokous form from Algiers Bay and two populations of the epitokous form from the English Channel and the Algerian Mediterranean east coast respectively. Significant inter-population variation was revealed. The atokous forms from the bay of Algiers constitute an homogeneous group for all the paragnath groups whereas the epitokous forms from the English Channel and the Mediterranean Sea present a great heterogeneity in the number of paragnaths in most of the groups. The three distinc groups of populations identified during this study can be assigned to cryptic species.

**Key words:** *Perinereis cultrifera* · paragnath number · Mediterranean Sea · English Channel

## INTRODUCTION

The polychaete *Perinereis cultrifera* (Nereididae) was described for the first time by Grube [1] from the Adriatic Sea. It occurs along the north-western coasts of Europe and the Mediterranean. This species has also been described in the Indian Ocean and the Pacific [2-4]. Observations by Scaps *et al.,* [5] and by Rouabah and Scaps [6] indicate that a complex of species may be referred to *P. cultrifera*. The spawning season, mode of reproduction, age at maturity and biometric characteristics of animals assigned to *P. cultrifera* differ largely according to the geographical location of the populations. Reproduction in the English Channel and the Atlantic is of an epitokous type [7-10] as in the Mediterranean Sea at Salammbô near Tunis, at Annaba on the Algerian Mediterranean coast near the Tunisian border and in the Venice Lagoon in Italy [11, 12, 6]. In the English Channel and the Atlantic, reproduction occurs from April to June and sometimes July [7, 8, 10, 13]. At Salammbô, sexually mature individuals can be found in May [12]. At Annaba spawning occurs at the end of April early May [6]. *P.* cf. *cultrifera* reproduces in March in the Venice Lagoon [11]. On the north coasts of Brittany and at Annaba in the Mediterranean, *P.* cf. *cultrifera* has a 3-year life cycle but some individuals may reproduce in their fourth year in Brittany [6, 10]. However, in Algiers Bay, the reproduction has been described as atokous [14], occurring throughout the year but being more intense from July to November, individuals had a 1.5 year life cycle.

Whereas the mode of reproduction (atoky, epitoky) distinguish two forms of *P.* cf. *cultrifera*, the biometric characteristics (weight, number of segments) reveal three types:

- The epitokous form of the English Channel and the Atlantic, characterized by a large segment number (up to 120) and a high weight (3.0 to 6.0 g) [9, 10],
- The atokous form of the Algiers Bay, in which the segment number is below 80 [14],
- The epitokous form of the Mediterranean Sea, characterized by a high segment number (up to 120) and a small weight (0.24 to 0.85 g) [6, 12].

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The aim of this study was to assess interpopulation variation in the number and distribution of paragnaths in epitokous and atokous forms of *P*. cf. *cultrifera* from the English Channel and the Mediterranean Sea in the context of the presence of cryptic species. This species bears small chitinous teeth, called paragnaths, on the eversible section of the buccal tube (the proboscis). Paragnaths lie in various groups (numbered I-VIII) with the number in each group being rather variable. As described for other species of nereidid polychaete use is made of paragnaths to distinguish species [15-17].

## MATERIALS AND METHODS

Adults worms were collected by hand in a restricted area from three localities in Algeria and one in France (Fig. 2). Individuals were collected from the St-Aubin-sur-Mer beach on the English Channel (StA, Fig. 2) and from pointe Pescade (Pp, Fig. 2) and Figuier (Fg, Fig. 2) in the the bay of Algiers and St-Cloud (StC, Fig. 2) close to the town of Annaba near the Tunisian border (30 km). The three last sites are located on the Algerian Mediterranean coast. In St-Aubin, worms build U or Y-shaped burrows in calcareous cobbles essentially in the *Fucus serratus* zone. Worms were found with the *Rhodophyceae* in the Algerian Mediterranean coast.

The weights of individuals from the English Channel differ markedly from those of the Mediterranean Sea (average mean fresh towel-dried weight of 2.54±0.99 g for the English Channel and 0.747±0.326 g for the Mediterranean Sea). Worms reproduce by epitoky in St-Aubin [10] and St-Cloud [5, 6, 18] and by atoky in Figuier and pointe Pescade (this study).

From 30 to 46 intact worms were collected at each site and were transported, live, to the laboratory. Live worms were persuaded to evert their proboscis by dipping them in 95% alcohol ; they then died usually with the proboscis everted. A few specimen died with the proboscis totally or partially retracted, but this was easily remedied by generating pressure some distance behind the head. The number of setigerous segments was counted and the number of paragnaths in each group was assessed under a binocular microscope (the scar left by recent loss of a paragnath was scored as if that paragnath was still present).

Specimens for examination by SEM were fixed in 5% formaldehyde in sea-water and dehydrated via an ethanol series. After critical point drying, they were mounted on copper stubs with double sided tape, sputtered with gold and observed with a scanning electron microscope JEOL-JEM100CX+ASID 4-D.

In order to appreciate if there exist some interrelationships between the size of the worm expressed as the number of segments and the number of paragnaths in each group linear correlation matrices were constructed.

A one-way analysis of variance (ANOVA) was used to compare means of the number of setigerous segments, means of the number of paragnaths in each group and means of the total number of paragnaths of the four populations. This analysis was followed by application of the Fisher's least significant difference (LSD) procedure [19].

A multivariate analysis of variance (MANOVA) was used to compare the whole of the groups of paragnaths of the four populations. This analysis was followed by mutivariate tests (Wilk's lambda, Lawley-Hotelling's trace and Pillai's trace) in order to test the equality of vectors of means of the number of paragnaths of the different groups between the four populations [20, 21].

In order to get a partition of the individuals in groups as homogeneous as possible, a hierarchical classification of the four populations of *Perinereis cultrifera* was performed using the simple link method and the Manhattan distance [22, 23]. All statistical analyses were performed using the statistical software Minitab [24].

## RESULTS

The maximum number of segments from the two atokous populations of the bay of Algiers (pointe Pescade and Figuier) is similar and is below 75. The maximum number of segments from the epitokous form from the English Channel (St-Aubin-sur-Mer) and the Mediterranean Sea (St-Cloud) is similar and is up to 125 segments (Fig. 3). The mean number of segments from the two atokous populations of the bay of Algiers (Pointe Pescade: 57.76±10.94; Figuier: 57.13±10.61) is significantly lower than that of the two epitokous populations from the English Channel (89.93±17.80) and the Mediterranean Sea (86.70±15.16).

The paragnaths are disposed in two belts: An anterior one (groups I-IV) (posteriorly situated when the proboscis is fully everted) of simple cones or forwardly directed, sickle shaped teeth and a posterior one (groups V-VIII) of long, strongly curved teeth directed backwards and towards the lumen of the gut (Fig. 1c). The genus *Perinereis* is characterized by the presence of conical and transversal paragnaths. In the four populations, there is a single large transverse paragnath in group VI (Fig. 1a).

No allometric relationship was found between the size of the worms and the number of paragnaths in any group. So the size of the worms is unimportant in respect

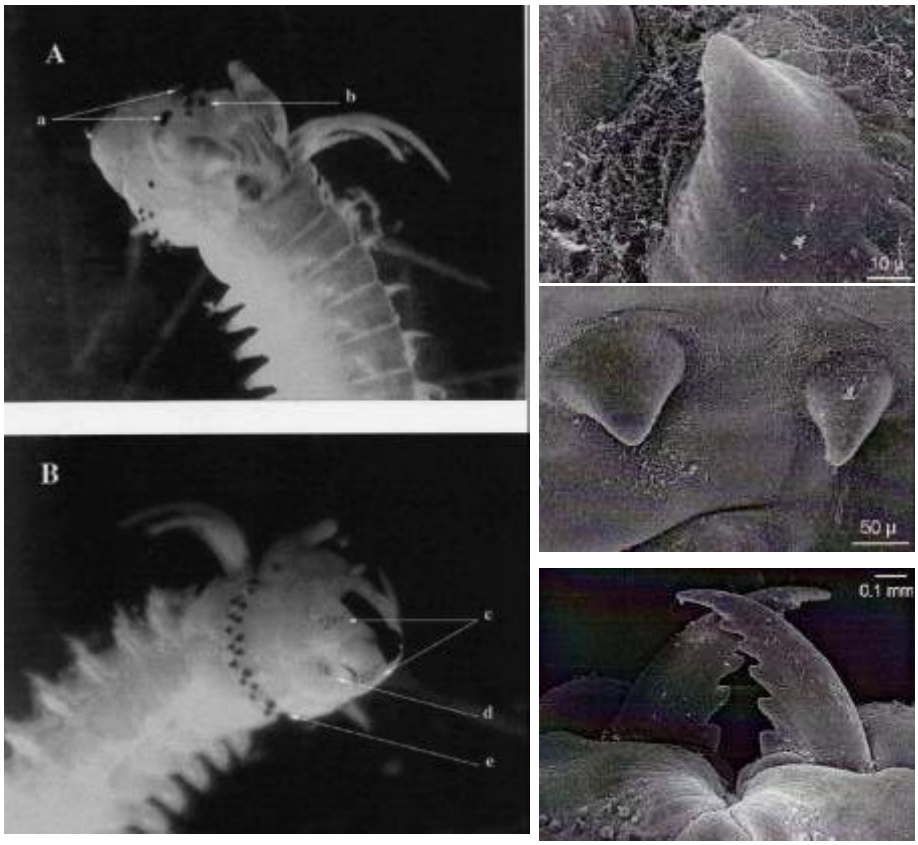


Fig. 1: Photonic microscope micrographs and scanning electron micrographs of *Perinereis cultrifera*. A: dorsal view of the everted proboscis: groups of paragnaths on the maxillary ring (I, II and II') are not visible on the photograph, pharyngeal ring: IV (b), a single transversal paragnath is located on group VI right and VI left respectively (a); B: ventral view of the everted proboscis: groups of paragnaths, maxillary ring: III (d), IV right and IV left (c); pharyngeal ring: VII-VIII (e); C: morphology of a paragnath from group II; D: two paragnaths from group VII-VIII (ventral side of the pharyngeal ring) showing wear marks on the end; E: jaws.

of intra-individual variations in paragnath number. Histograms of distribution of paragnaths are unimodal and approximately symmetrical (data not shown). Data on paragnath numbers in the four populations are set out in Table 1.

Although highly variable in number from one individual to another, in each individual paragnath number and distribution is nevertheless referable to a basic pattern comprising certain groups of denticles with consistent intergroup symmetry. Although a strong interrelationship exists between the numbers of paragnaths in the left-right pairs II and IV, they are not rigorously equal. Mean differences between symmetrical arrangements of paragnath groups (|IIr-III| and |IVr-IVl|) are comprised between 0.10 (|IVr-IVl| atokous form from Figuier) and 1.73 (|IVr-IVl| epitokous form from the English Channel) (Table 1). Asymmetry is much more important in epitokous forms from the English Channel and the Mediterranean Sea (measures of asymmetry comprised between 1.13 and 1.73) than in atokous forms from the bay of Algiers (measures of asymmetry comprised between 0,10 and 0,25) (Table 1).

The analysis of variance shows a very high significant difference ($p < 0.001$) between the four populations for each group of paragnaths (Table 2). Table 3 lists the homogeneous populations on the basis of the values of the least significant difference. The atokous forms from the bay of Algiers constitute a homogeneous population for all the paragnath groups. The epitokous form from the English Channel do not constitute an homogeneous population with the epitokous form from the Mediterranean Sea for most of its paragnath groups (exception is the paired group IV).

The multivariate analysis of variance, clearly shows a rejection of the hypothesis of equality of mean vectors between the three separate groups with very

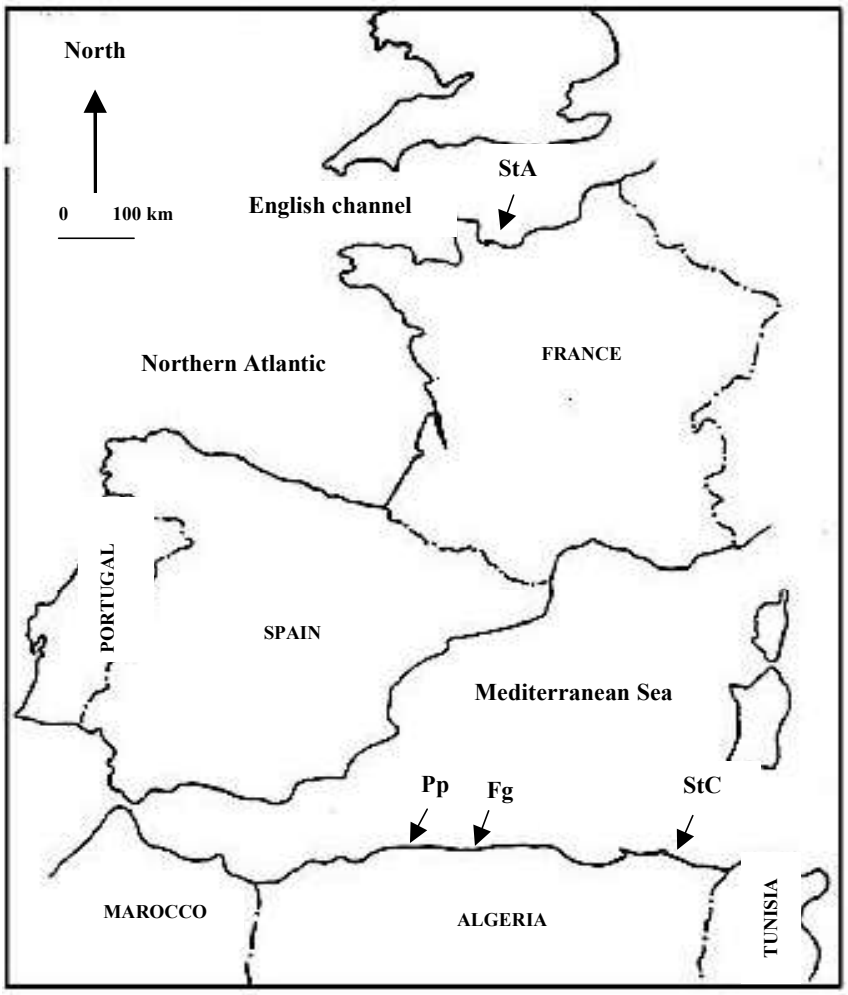


Fig. 2: Map of western Europe and north Africa showing location of sampling sites in the Mediterranean Sea (Figuier (Fg) and pointe Pescade (Pp) in the Algiers Bay and St-Cloud (StC) around Annaba) and the English Channel (St-Aubin-sur-Mer beach: StC).

Table 1: Mean values (x), standard deviations (SD) and ranges (R) in numbers of paragnaths comprising the various groups and the total number of paragnaths in the four populations

| | | I | IIr | IIl | III | IVr | IVl | V | VII-VIII | \|IIr-IIl\| | \|IVr-IVl\| | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pp N = 46 | x | 1.89 | 6.91 | 7.04 | 4.98 | 11.9 | 12.33 | 2.87 | 35.5 | 0.15 | 0.16 | 83.4 |
| | SD | 0.27 | 1.42 | 1.41 | 0.84 | 1.76 | 1.75 | 0.22 | 1.81 | 1.43 | 1.78 | 6.54 |
| | R | 1-3 | 3-12 | 3-12 | 3-12 | 7-18 | 7-18 | 2-3 | 31-45 | 0-3 | 0-2 | 56-105 |
| Fg N = 46 | x | 1.83 | 7.48 | 7.59 | 5.04 | 12.24 | 12.26 | 2.83 | 35.11 | 0.25 | 0.10 | 84.39 |
| | SD | 0.28 | 1.51 | 1.39 | 1.01 | 2.07 | 1.83 | 0.28 | 1.69 | 1.48 | 1.99 | 5.87 |
| | R | 1-2 | 3-14 | 1-10 | 1-8 | 5-18 | 5-18 | 2-3 | 26-40 | 0-3 | 0-5 | 56-105 |
| StC N = 30 | x | 2.37 | 15.80 | 15.40 | 9.33 | 15.90 | 15.43 | 2.53 | 63.87 | 1.56 | 1.20 | 141.1 |
| | SD | 0.61 | 2.14 | 2.51 | 2.09 | 2.35 | 2.19 | 0.86 | 3.73 | 0.17 | 0.18 | 8.11 |
| | R | 1-3 | 12-19 | 10-21 | 6-14 | 11-19 | 11-21 | 1-3 | 55-72 | 0-4 | 0-3 | 127-160 |
| StA N = 30 | x | 1.73 | 10.17 | 10.37 | 7.93 | 16.17 | 16.03 | 3.10 | 38.83 | 1.13 | 1.73 | 105.70 |
| | SD | 0.45 | 1.70 | 2.39 | 1.46 | 2.89 | 2.93 | 0.30 | 2.48 | 0.26 | 0.27 | 8.82 |
| | R | 1-2 | 7-14 | 7-18 | 3-11 | 10-21 | 10-21 | 3-4 | 33-43 | 0-6 | 0-6 | 81-116 |

Pp: pointe Pescade ; Fg: Figuier ; StC: Saint-Cloud ; StA: Saint-Aubain-sur-Mer. N: number of individuals.

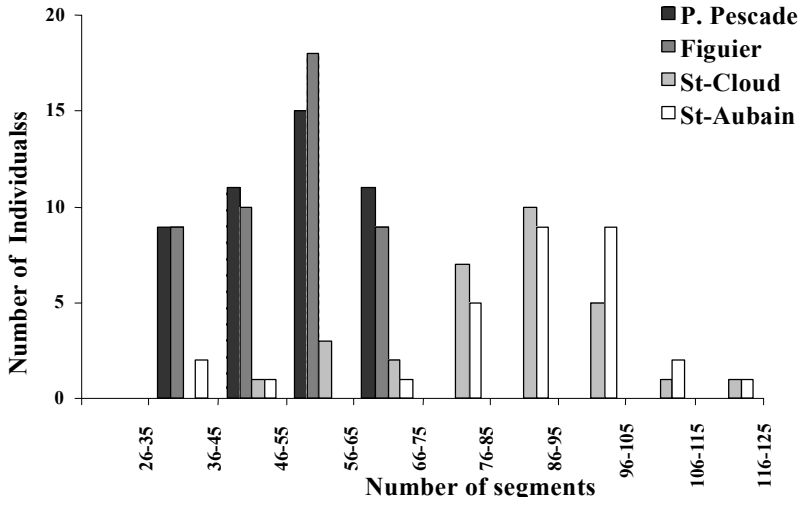


Fig. 3. Size-frequency distribution based on the number of segments

Table 2: Interpopulation comparisons of the mean number of paragnaths in each group and of the total number of paragnaths (ANOVA)

| Paragnath | Source of variation | dg | SSD | MS | F | P |
|---|---|---|---|---|---|---|
| Group I | difference between sites | 3 | 8.3352 | 2.7784 | 12.80 | *** |
| | residual variation | 148 | 32.1319 | 0.2171 | | |
| | total variation | 151 | | | | |
| Group Iid | difference between sites | 3 | 1709.04 | 569.68 | 134.49 | *** |
| | residual variation | 148 | 626.9 | 4.24 | | |
| | total variation | 151 | | | | |
| GroupIIg | difference between sites | 3 | 1503.46 | 501.15 | 128.67 | *** |
| | residual variation | 148 | 576.43 | 3.89 | | |
| | total variation | 151 | | | | |
| Group III | difference between sites | 3 | 514.91 | 171.64 | 85.00 | *** |
| | residual variation | 148 | 298.85 | 2.02 | | |
| | total variation | 151 | | | | |
| Group IVd | difference between sites | 3 | 572.21 | 190.74 | 29.26 | *** |
| | residual variation | 148 | 964.89 | 6.52 | | |
| | total variation | 151 | | | | |
| Group IVg | difference between sites | 3 | 435.21 | 145.07 | 23.56 | *** |
| | residual variation | 148 | 911.31 | 6.16 | | |
| | total variation | 151 | | | | |
| Group V | difference between sites | 3 | 4.8954 | 1.6318 | 6.71 | *** |
| | residual variation | 148 | 35.9928 | 0.2432 | | |
| | total variation | 151 | | | | |
| Groups VIIVIII | difference between sites | 3 | 18843.7 | 6281.2 | 883.59 | *** |
| | residual variation | 148 | 1052.1 | 7.1 | | |
| | total variation | 151 | | | | |
| Total | difference between sites | 3 | 3686.21 | 1228.7 | 244.52 | *** |
| | residual variation | 148 | 702.91 | 5.9 | | |
| | total variation | 151 | | | | |

dg: degree of freedom; SSD: sum of squares deviation ; MS: mean square ; F: Fisher F Value ; P: probability. (* * *): P<0.001.

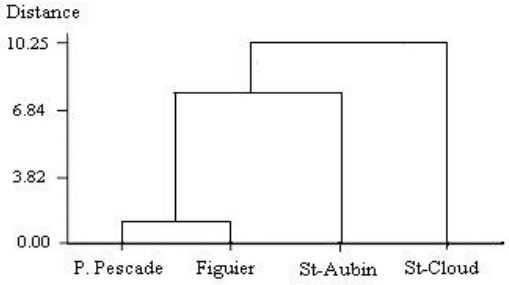


Fig. 4: Hierarchical cluster analysis classification of the four studied *Perinereis cultrifera* populations. Dendrogram of the Manhattan distances

Table 3: Homogeneous populations on the basis of the values of the least significant difference

| | Site | | | |
|---|---|---|---|---|
| Mean | P. Pescade | Figuier | St-Aubain | St-Cloud |
| Group I | 1.89 | 1.83 | 1.73 | 2.37 |
| Group II d | 6.91 | 7.48 | 10.17 | 15.80 |
| Group IIg | 7.04 | 7.59 | 10.37 | 15.40 |
| Group III | 4.98 | 5.04 | 7.93 | 9.33 |
| Group IVd | 11.90 | 12.24 | 16.17 | 15.90 |
| Group IVg | 12.33 | 12.26 | 16.03 | 15.43 |
| Group V | 2.87 | 2.83 | 3.10 | 2.53 |
| Groups VII-VIII | 35.50 | 35.11 | 38.83 | 63.87 |
| Total | 83.40 | 84.39 | 105.70 | 141.20 |

highly significant differences ($p < 0.001$) (Table 4). The dendrogram of Manhattan distance (Fig. 4) confirms the existence of three separate groups. The first group is

Table 4: Multivariate tests used in order to test the equality of mean vectors of the number of paragnaths in the different groups of paragnaths

| Test | Fobs | P |
|---|---|---|
| Wilk's lamda | 44.832 | *** |
| Lawley-Hotelling's trace | 129.402 | *** |
| Pillai's trace | 16.382 | *** |

F: Fisher F Value ; P: probability. (* * *): P<0.001.

Table 5: Manhattan distances matrix between the different groups of populations on the basis of the distribution of the different groups of paragnaths

| | Group 1 | Group 2 | Group 3 |
|---|---|---|---|
| Group 1 | 0.000 | 3.3296 | 5.2485 |
| Group 2 | | 0.000 | 4.2961 |
| Group 3 | | | 0.000 |

composed of the two atokous populations from the bay of Algiers whereas the second group represents the epitokous population from the English Channel (St-Aubin-sur-Mer) and the third group is relative to the epitokous population from the Mediterranean Sea (Saint-Cloud). The distances between the different groups are 3.3296 (G1/G2), 4.2961 (G2/G3) and 5.2485 (G1/G3) respectively (Table 5).

## DISCUSSION

This study about variations in paragnath number of the different morphs of the polychaete *Perinereis* cf. *cultrifera* in relation to geographical location and type of reproduction reveals the existence of a great variability in the size of the individuals and in paragnath number in the different groups on the proboscis. The weight of individuals from the epitokous population of the English Channel (2.54 ± 0.99 g) is much more important than those of the atokous and epitokous populations from the Mediterranean Sea (0.747 ± 0.326). The maximal number of segments (up to 125) is similar between the two epitokous forms from the English Channel and the Mediterranean Sea and is significantly larger than those of the atokous forms of Algiers Bay (below 75). Moreover, concerning the distribution of paragnaths on the proboscis, the atokous forms from the bay of Algiers constitute an homogeneous group for all the paragnath groups whereas the epitokous forms from the English Channel and the Mediterranean Sea present a great heterogeneity in the number of paragnaths in most of the groups. Cluster analysis performed on Manhattan distance separated the populations in three distinct groups. Individuals from atokous populations of the bay of Algiers cluster together whereas individuals from epitokous populations from the English Channel and the Mediterranean Sea constitute two distinct groups.

It is possible that the observed differences in the paragnath number between the different populations studied reflect differences in diet and/or dominant mode of feeding, or are related to their respective habitat. Nevertheless, although the different populations of worms collected from the Algerian coasts of the Mediterranean Sea occupy the same environment (hard substratum covered with Rhodophyceae) the mode of reproduction and the size of individuals differ completely. Moreover, as no allometric relationship was found between the size of worm and paragnath number, there is no evidence for environmental influences on paragnath number. As demonstrated by Hateley *et al*., [25] on another nereidid polychaete *Nereis diversicolor*, it seems that paragnath pattern is inherited. Therefore, it seems that the presence of two distinct reproductive strategies (atoky and epitoky) is related to genetic differences (distincts species) rather than different ecological conditions.

In a previous attempt to distinguish the epitokous forms of *P*. cf. *cultrifera* from the Mediterranean Sea and the English Channel, Scaps *et al.* [5] and Rouabah and Scaps [26] reported morphological (number and morphology of paragnaths on the proboscis) and biochemical (allozymes, general protein band patterns obtained after one-dimensional electrophoretic procedure, two-dimensional electrophoresis of proteins) divergence and concluded that *P*. cf. *cultrifera* is a complex of species.

The biological features of the reproduction of *P*. cf. *cultrifera* are singular. According to Cazaux [27] who studied a population of *P*. cf. *cultrifera* from the Arcachon basin in the nortehrn Atlantic Ocean, the life cycle is bentho-pelagic with a brief semi-pelagic phase. Eggs are large (egg diameter 350 µm), lecitotrophic and demersal. Hatching occurs at the 3-setiger erpochaete stage. Larvae exhibit a little developed ciliary crown and often crawl on the bottom. At the end of the semi-pelagic phase, animals become sedentary at the 4-setiger erpochaete stage. Then, erpochaeta loose their ciliary crown and thus are completely benthic. The juvenile, benthic worm of 10 to 11 segments has the same life style as the adult. The absence of larval dispersion or its weak amplitude promotes the maintenance of the larvae in the biotope favorable to the adults and limits the possibilities of colonization of new habitats and promotes the geographic isolation of individuals.

Species are not static entities but evolve over time, giving birth to new species brought to follow an evolutionary history progressively then definitely independent of their sisters' species [28]. At the exception of the two populations of *P*. cf. *cultrifera* from the bay of Algiers separated by approximately 70 km, the other populations that we studied are separated by several hundreds of kilometers. Our results show that at a small spatial scale, individuals belonging to local populations (i.e. the two populations from the bay of Algiers) are very similar with regard to the number and distribution of paragnaths on the proboscis. At a larger spatial scale, populations show evident differences in the total number and numbers of paragnaths in the different groups as well as in the size of adults and the mode of reproduction. So, the three distinc groups of populations identified during this study can be assigned to cryptic species. According to Fong and Garthwaite [29], who studied a complex of species of another genus of nereidid polychaete (genus *Hediste*), when populations are separated by large geographical distances, it is impossible that such populations can exchange genes. The observed differences in the level of structuring genetic inter-populations can be attributed to differences in ability dispersion [30]. Given that population structure and genetic divergence are closely coupled, species that have different life-history traits can probably give rise to new species in different ways [31].

**Summary:** This study about variations in paragnath number of the different morphs of the polychaete *Perinereis* cf. *cultrifera* in relation to geographical location and type of reproduction reveals the existence of a great variability in the size of the individuals and in paragnath number in the different groups on the proboscis. Three distinct groups of populations were identified on the basis of paragnath distribution during this study. The first group is composed of the two atokous populations from the bay of Algiers whereas the second group represents the epitokous population from the English Channel and the third group is relative to the epitokous population from the Mediterranean Sea. The three distinc groups of populations identified during this study can be assigned to cryptic species.

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