

Comparison of the life cycles of two populations of the polychaete *Perinereis cf. cultrifera* from the Bay of Algiers (Mediterranean Sea)

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SUMMARY: The benthic phases of the life cycles of two populations of the polychaete *Perinereis cultrifera* from the Bay of Algiers were investigated using field surveys. We found no differences in the life cycle of the two populations. In the Bay of Algiers, *P. cultrifera* reproduces without epitokal modifications. The lifespan of the species probably does not exceed two years. The reproductive period spans most of the year but is more intense in spring from March to May when the sea-water temperature starts rising. A few mature individuals were collected at the end of summer and in winter. The oocytes take 9 to 12 months to mature and their diameter at maturity is approximately 200 µm.

Keywords: Annelida, Polychaeta, Nereididae, life cycle, population dynamics, reproduction.

RESUMEN: COMPARACIÓN DE LOS CICLOS VITALES DE DOS POBLACIONES DEL POLIQUETO PERINEREIS CF. CULTRIFERA DE LA BAHÍA DE ARGEL (MAR MEDITERRÁNEO). – Se investigaron las fases bentónicas del ciclo vital del poliqueto *Perinereis cultrifera* de la bahía de Argel usando muestreos de campo. No se encontraron diferencias en el ciclo vital de las dos poblaciones. En la bahía de Argelia *P. cultrifera* se reproduce sin modificaciones de la epitoca. El periodo de vida de esta especie probablemente no excede los dos años. El periodo reproductivo se extiende durante la mayor parte del año, pero es más intenso en primavera, de marzo a mayo, cuando la temperatura del agua del mar empieza a subir. Se recolectaron unos pocos individuos maduros al final de verano y en invierno. Los oocitos necesitan entre 9 y 12 meses para madurar y su diámetro cuando están maduros es de aproximadamente 200 µm.

Palabras clave: Annelida, Polychaeta, Nereididae, ciclo vital, dinámica de poblaciones, reproducción.

INTRODUCTION

The polychaete *Perinereis cultrifera* (Grube, 1840) occurs along the northwestern coasts of Europe and the Mediterranean. In Algeria this species is known as the “worm with antennae and legs” or the “green worm”, and is commercially collected from natural populations by semi-professional bait harvesters supplying a variety of local outlets. Bait

harvesters commonly use bleaching liquid (10% in sea water) or a KMnO₄ (0.5 to 1% in sea water) solution to force individuals out of their algal mat.

Observations by Scaps *et al.* (2000) and Rouabah and Scaps (2003a) indicate that a complex of species may be referred to *P. cultrifera*. Reproduction in the English Channel and the Atlantic is of an epitokous type and has been observed from May to June and sometimes July (Fauvel, 1916; Herpin, 1925; Fage

and Legendre, 1927; Durchon, 1951, Cazaux, 1965; Scaps *et al.*, 1992). In the Arcachon Basin (Cazaux, 1965) and on the north coasts of Brittany (Scaps *et al.*, 1992), *P. cf. cultrifera* has a 3-year life span.

In the Mediterranean Sea, specimens assigned to *P. cultrifera* have been described as being atokous in Marseille (Perès and Rancurel, 1948) and on the west coast of Algeria in the Bay of Algiers (Durchon, 1957; Marcel, 1962). In the Bay of Algiers reproduction takes place all year round but is more intense from July to November (Marcel, 1962). However, more recent studies in the Mediterranean Sea have shown that reproduction of individuals of *P. cf. cultrifera* is of an epitokous type in the Venice Lagoon in Italy (Ansaloni *et al.*, 1986), at Salammbô near Tunis (Zghal and Ben Amor, 1989) and at Annaba on the east coast of Algeria near the Tunisian border (Rouabah and Scaps, 2003b). Sexually mature individuals were found in May at Salammbô (Zghal and Ben Amor, 1989) and in March in the Venice Lagoon (Ansaloni *et al.*, 1986). At Annaba, *P. cf. cultrifera* has a 3-year life cycle and spawning occurs in late April/early May (Rouabah and Scaps, 2003b). Thus, in the Mediterranean Sea specimens assigned as *P. cultrifera* can reproduce with or without the morphological modifications characteristic of epitoky.

In a previous study we described the population structure and life cycle of the epitokous form of *P. cf. cultrifera* on the east coast of Algeria (Rouabah and Scaps, 2003b). It is now necessary to describe the life cycle of the atokous form of *P. cf. cultrifera* on the west coast of Algeria. To achieve this we studied the life cycles of two populations of the atokous form of *P. cf. cultrifera* separated by 50 km in the Bay of Algiers. The results will allow us to compare the life cycles of the two forms of *P. cf. cultrifera* from the Algerian Mediterranean coasts which are impossible to distinguish morphologically. They will also allow us to compare our results with the old and incomplete observations of Marcel (1962) in order to determine whether there have been modifications in the life cycle of the species over a period of more than 40 years.

MATERIAL AND METHODS

Study sites

Individuals were collected from two localities on the Algerian Mediterranean coast. Pointe Pes-

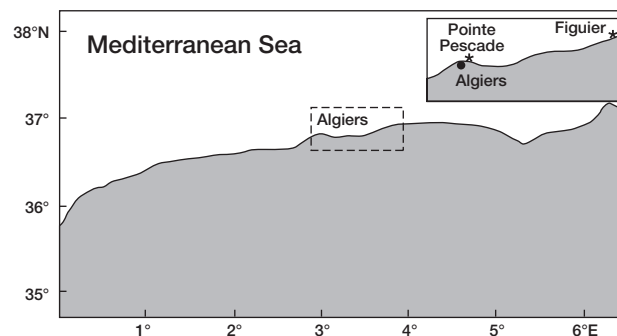


FIG. 1. – Map of North Africa showing the location of the sampling sites near Algiers in Algeria.

cade and Figuiier are located in the west and the east Bay of Algiers respectively (Fig. 1). The two sites are separated by 50 km. Worms were found within the *Rhodophyceae*, in algal-covered hard bottoms. Rocks are metamorphic at Pointe Pescade and are composed of gneiss and quartzite, whereas at Figuiier they are volcanic and composed of rhyolite. The maximum tides are small (0.5 m for Pointe Pescade and 1 m for Figuiier).

Collection of individuals

Monthly samplings were conducted from January 2005 to December 2005. The individuals occur in the low intertidal zone and extend down into the sublittoral, so the intertidal and shallow sublittoral hard bottoms were sampled methodically by scraping algae and looking for individuals. The time spent collecting worms in the field was between 3 and 5 hr per tide. In total 1447 worms were collected and examined. At each sampling occasion, air and sea-water temperature were measured. Air temperature was also measured at night.

Relationships between body weight and partial body weight

Since the collected worms were frequently broken by the occurrence of autotomy and by mechanical breaks during sampling, we determined the partial weight of individuals that had been placed in formaldehyde and wiped. The use of partial weights gives a better representation of all individuals in the natural population and prevents the massive rejection of many worms broken during sampling. As described by Desrosiers *et al.* (1988) for *Nereis virens*, the weight was determined from a histogram (Fig. 2) in which breaking points are “ranked”. In order to take into account the totality of the individuals we

measured the partial weight of the first 36 chaetigerous segments. Intact specimens were used to calculate the relation between whole body wet weight and partial body weight.

$$W = 1.6262 P + 0.0135 \quad (n = 73, r^2 = 0.9273)$$

(where W: whole body weight, P: partial body weight)

Size distribution

Monthly whole body weight distribution histograms were plotted. The worms ranged in weight from 0.016 to 0.540 g; the weight of each worm was tabulated using a class interval of 0.05 g. The size-class interval was chosen according to Scherrer (1984).

Reproductive cycle

For the study of the reproductive cycle, the individuals were fixed in the laboratory with formaldehyde and examined in order to determine the presence or absence of morphological modifications characteristic of epitoky (Bauchot-Boutin and Bobin, 1954) and sexual products in the coelom. A short incision was made in the body wall at about the twentieth chaetigerous segment and a drop (~1 ml) of the coelomic fluid was taken out with a Pasteur pipette and examined under a binocular microscope. When possible, forty oocytes were measured using a calibrated eye-piece graticule. The longest and shortest length of oocytes were determined, and the average value was used as an estimate of oocyte size. Males were recognised by the presence of sperm plates in the coelomic fluid and mature ones by the presence of sperm aggregates. Those animals without sexual products were considered to have an undetermined sex.

RESULTS

Temperature of the study sites

The evolution of monthly sea-water and air temperature (Fig. 3) was similar for the two sites during the study period. Air temperature ranged from 4°C in January to 31°C in July when measured during low tide and from 3°C in January to 25°C in June and July when measured at night. Sea-water temperature measured during low tide fluctuated from 10°C in

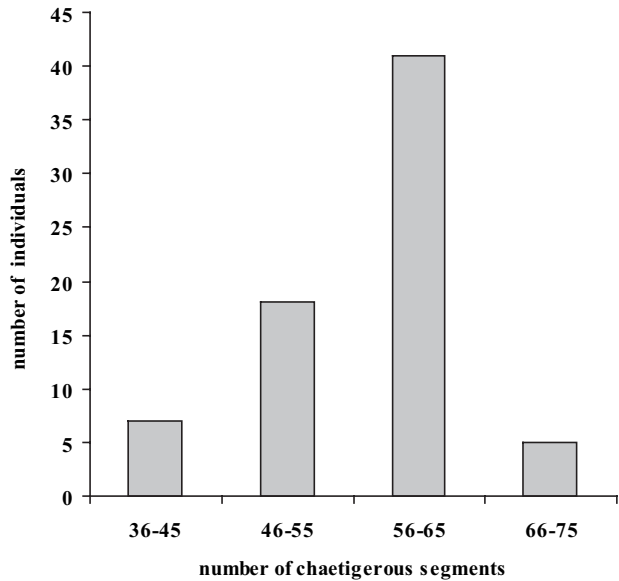


FIG. 2. – Histogram in which breaking points are ranked (n = 73).

February to 25°C July. There was a clear temperature increase in the summer and a reverse trend in the winter.

Reproductive biology

The evolution of mean oocyte diameter for females during the study period was similar for the two sites (Fig. 4). We noticed a steady increase of the mean oocyte diameter from January to March, with mean maximal values of 212.79 and 208.13 µm for females from Pointe Pescade and Figuiet, respectively. Then, from April to June the mean oocyte diameter was relatively constant. From June (Pointe Pescade) or July (Figuiet) to December, two well-defined groups of females were identified, one bearing large oocytes with a diameter higher than 100 µm and the other bearing oocytes with a diameter lower than 100 µm. Thus, in June or July, a new group of females with small oocytes started to emerge. In December females bearing large oocytes disappeared. Oocytes took between 9 to 12 months to develop fully (Fig. 4).

The diameter of mature oocytes was about 230 µm (range: 200-250 µm). The maximum number of mature females (from 41.17 to 64.00% of all the females) (Tables 1 and 2) bearing large oocytes (diameter larger than 200 µm) was found from March to May, indicating that this period corresponds to the most intense period of spawning. A few isolated mature females were found from September to October and in Feb-

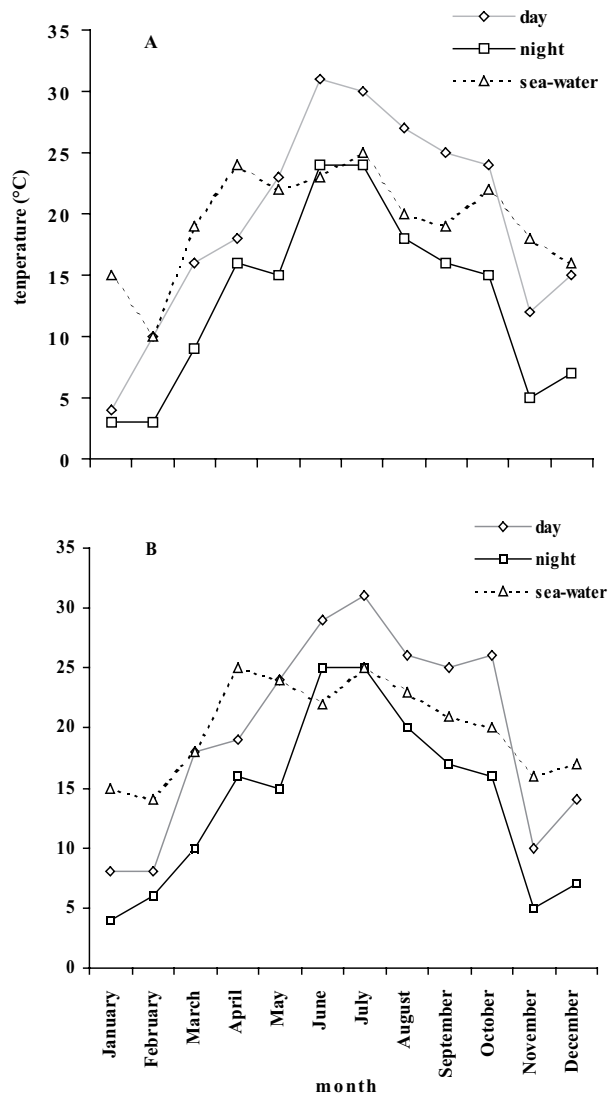


FIG. 3. – Monthly sea-water and air temperature during low tide and air temperature at night. A: Pointe-Pescade, B: Figuiet.

ruary at Pointe Pescade and in June-July and October-November at Figuiet, indicating the presence of a sporadic reproduction. No mature females were found in late summer (July-August for Pointe Pescade and August-September for Figuiet) and in winter (December-January for Pointe Pescade and from December to February for Figuiet), indicating that individuals do not reproduce during that period.

For both sites and during the whole study period we did not find large mature individuals of both sexes showing morphological modifications characteristics of epitoky. In consequence, individuals from the two sites reproduce exclusively by atoky and neither of the sexes appears to survive after spawning.

The comparison of the monthly surface sea-water temperature (Fig. 2) with oocyte size (Fig. 3) for the

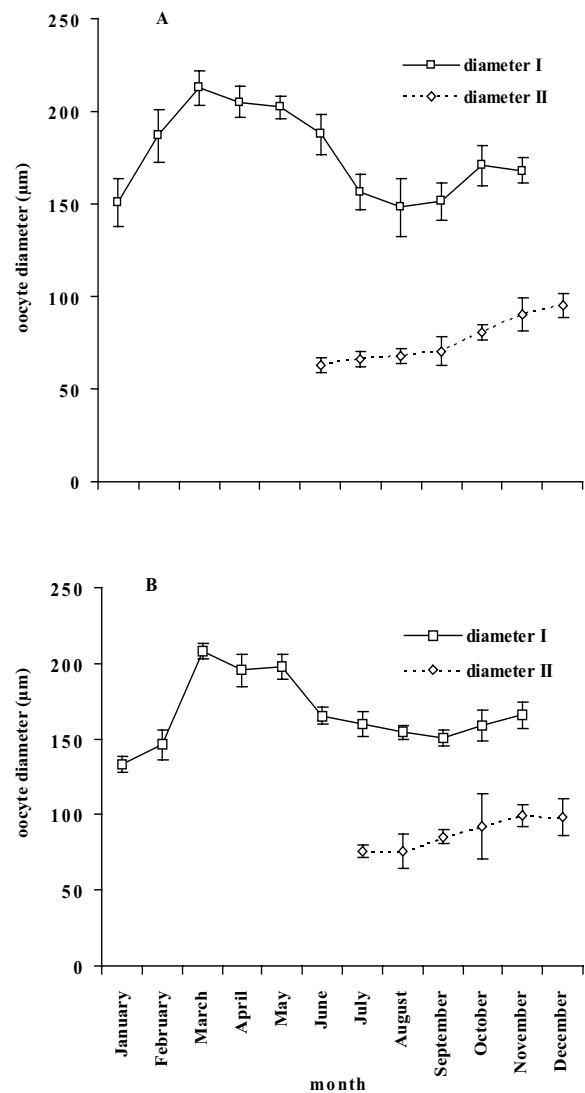


FIG. 4. – Evolution of oocyte size from January to December 2005. Each data point represents mean \pm standard deviation. Diameter I corresponds to the diameter of oocytes of females bearing large oocytes while diameter II corresponds to the diameter of oocytes of females bearing small oocytes when two groups of females can be identified. A: Pointe Pescade, B: Figuiet.

two populations studied shows that the main spawning period occurs in spring (from March to May) when the sea-water surface temperature starts rising.

The monthly proportion of sexually differentiated individuals of both sexes was similar for the two sites (Fig. 5A and B). However, from September to January the proportion of males was lower than that of females. This is probably due to the fact that this period corresponds to the moment when the reproduction is less intense and that it was more difficult to recognise sperm plates than small oocytes. In February and March the proportion of males was almost equal to that of females. From April to August the

TABLE 1. – Monthly proportion of mature females from January to December at Pointe Pescade.

	N1	N2	N1/N2	% of mature females
January	0	33	0	0
February	1	8	0.12	11.11
March	7	10	0.70	41.17
April	8	11	0.73	42.10
May	11	11	1	50.00
June	2	12	0.17	14.28
July	0	13	0	0
August	0	8	0	0
September	1	14	0.07	6.66
October	2	10	0.20	16.66
November	1	16	0.06	5.88
December	0	20	0	0

N1: number of females with an oocyte diameter >200 µm; N2: number of females with an oocyte diameter <200 µm.

TABLE 2. – Monthly proportion of mature females from January to December at Figuiér.

	N1	N2	N1/N2	% of mature females
January	0	30	0	0
February	0	11	0	0
March	11	10	1.10	52.38
April	7	8	0.87	46.66
May	13	12	1.77	64.00
June	1	16	0.06	5.88
July	1	14	0.07	6.66
August	0	17	0	0
September	0	14	0	0
October	1	15	0.06	6.25
November	1	18	0.05	5.26
December	0	8	0	0

N1: number of females with an oocyte diameter > 200 µm; N2: number of females with an oocyte diameter < 200 µm.

proportion of males and females fluctuated greatly. The proportion of sexually differentiated individuals was maximal from March to June (approximately 60%), corresponding to the most intense period of reproduction. In July and August, the proportion of sexually differentiated individuals decreased, indicating the end of the most intense period of reproduction and the death of mature atokous individuals. From September to November the proportion of sexually differentiated individuals was constant (approximately 40%). From November to February we noticed a second decrease in the proportion of sexually differentiated individuals. From February to March, the proportion of sexually differentiated individuals increased to its maximal value; this was probably due to the sexual differentiation of the individuals of the second generation.

The percentage of sexually differentiated individuals showed a positive correlation with sea-water temperature (Pointe Pescade, R:0.82; Figuiér, R:

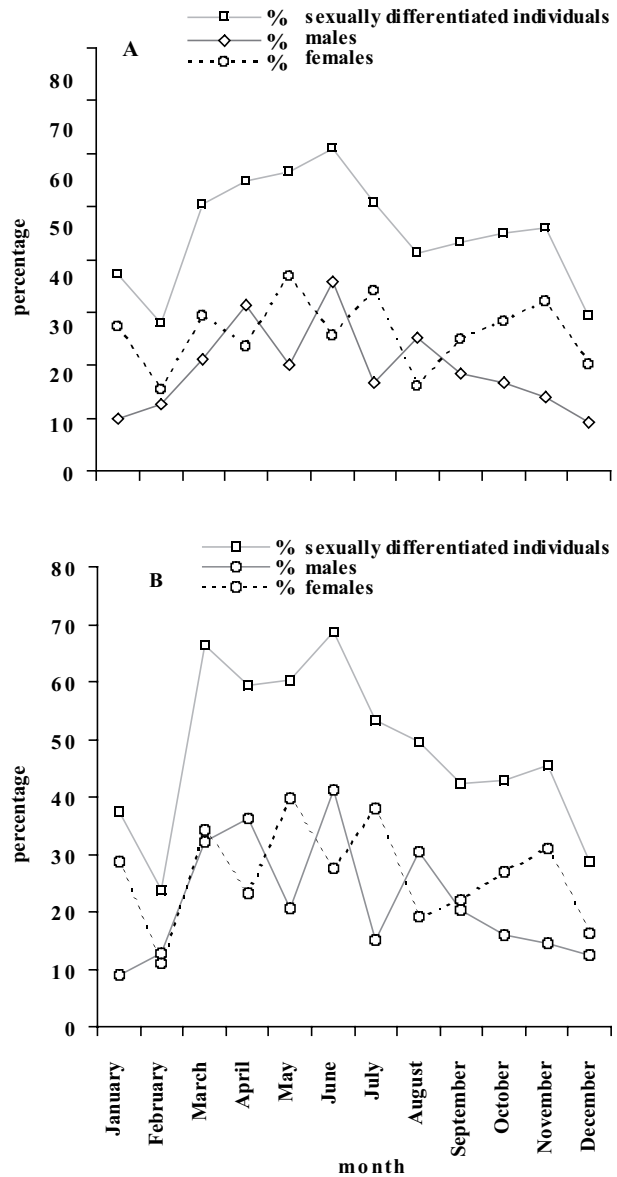


FIG. 5. – Monthly proportion of sexually differentiated individuals, females and males from January to December 2005. A: Pointe-Pescade, B: Figuiér.

0.65). The maturation of gametes varied according to the fluctuations of sea-water temperature.

Population dynamics

The monthly variation of mean individual whole body weight during the study period was similar for the two sites (Fig. 6 and 7). The mean whole body weight of individuals varied with time. The mean whole body weight for all individuals increased from February to March (Fig 6A and 7A) but showed a gradual decrease from March to July. In August the decrease in body weight was greater.

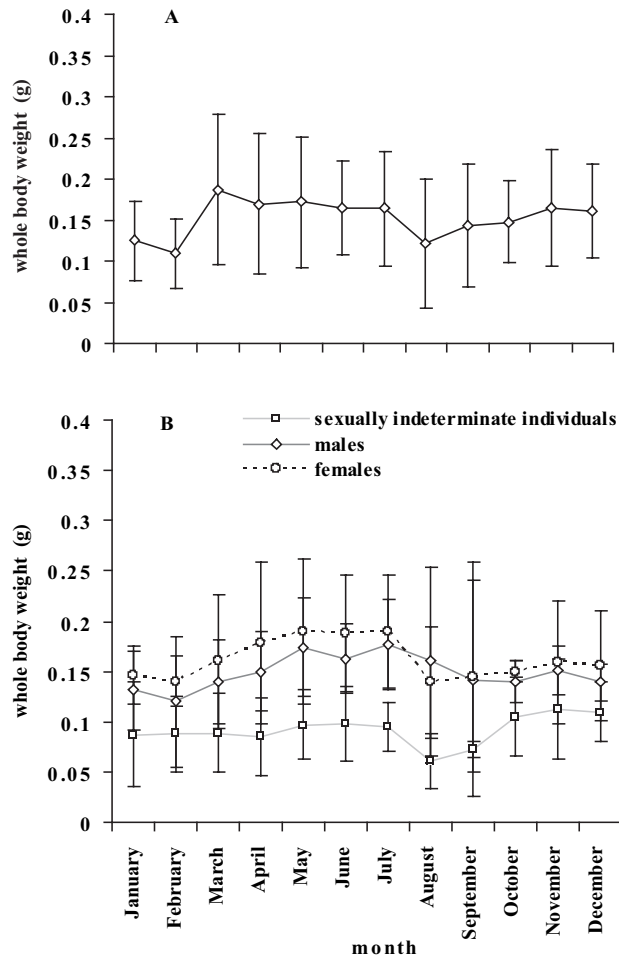


FIG. 6. – Monthly variation between January and December 2005 of mean individual whole body weight at Pointe Pescade. A: for all individuals, B: for the sexually indeterminate and differentiated individuals. Each data point represents mean \pm standard deviation.

From August to September the mean whole body weight of individuals increased and then remained more or less stable during the autumn and early winter (September-December). During the winter (December-February) the mean whole body weight of individuals decreased, the decrease being greater in February.

The mean weight of sexually indeterminate individuals (Fig. 6B and 7B) was more or less stable (approximately 0.1 g) throughout the year, except in August when we noticed a strong decrease corresponding probably to the recruitment of new individuals. Patterns of weight variation were similar for females and males. Male weight was lower than female weight, except in August (Fig. 6B and 7B). From February to July the mean weight of sexually differentiated individuals increased. From July to August the weight of sexually differentiated individuals decreased, probably indicating the end of the

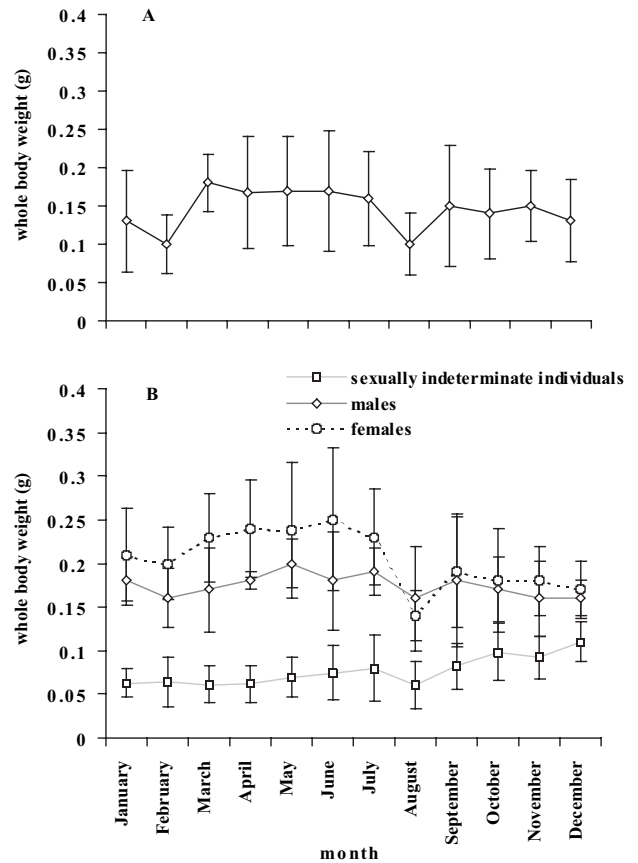


FIG. 7. – Monthly variation between January and December 2005 of mean individual whole body weight at Figuier. A: for all individuals, B: for the sexually indeterminate and differentiated individuals. Each data point represents mean \pm standard deviation.

most intense period of reproduction and the death of the big atokous individuals.

Since most specimens were incomplete, whole body weights were estimated from the equation using partial body weight (see Methods). The weight frequency histograms of individuals collected from January 2005 to December 2005 from Pointe Pescade and Figuier are shown in Figures 8 and 9, respectively. They are very similar for the two studied sites. In March, the population consisted of two cohorts, one of small, undifferentiated individuals and one of large, sexually differentiated individuals. In April and May we observed the same cohorts but with a displacement towards the right indicating the growth of individuals. From May to June we observed the disappearance of the large breeding individuals due to death. From June to September, we noticed a peak of small individuals corresponding to the appearance in mass of new recruits. This phenomenon was more marked for individuals collected at Pointe Pescade than for those collected at Figuier. From October to February, undifferentiated individ-

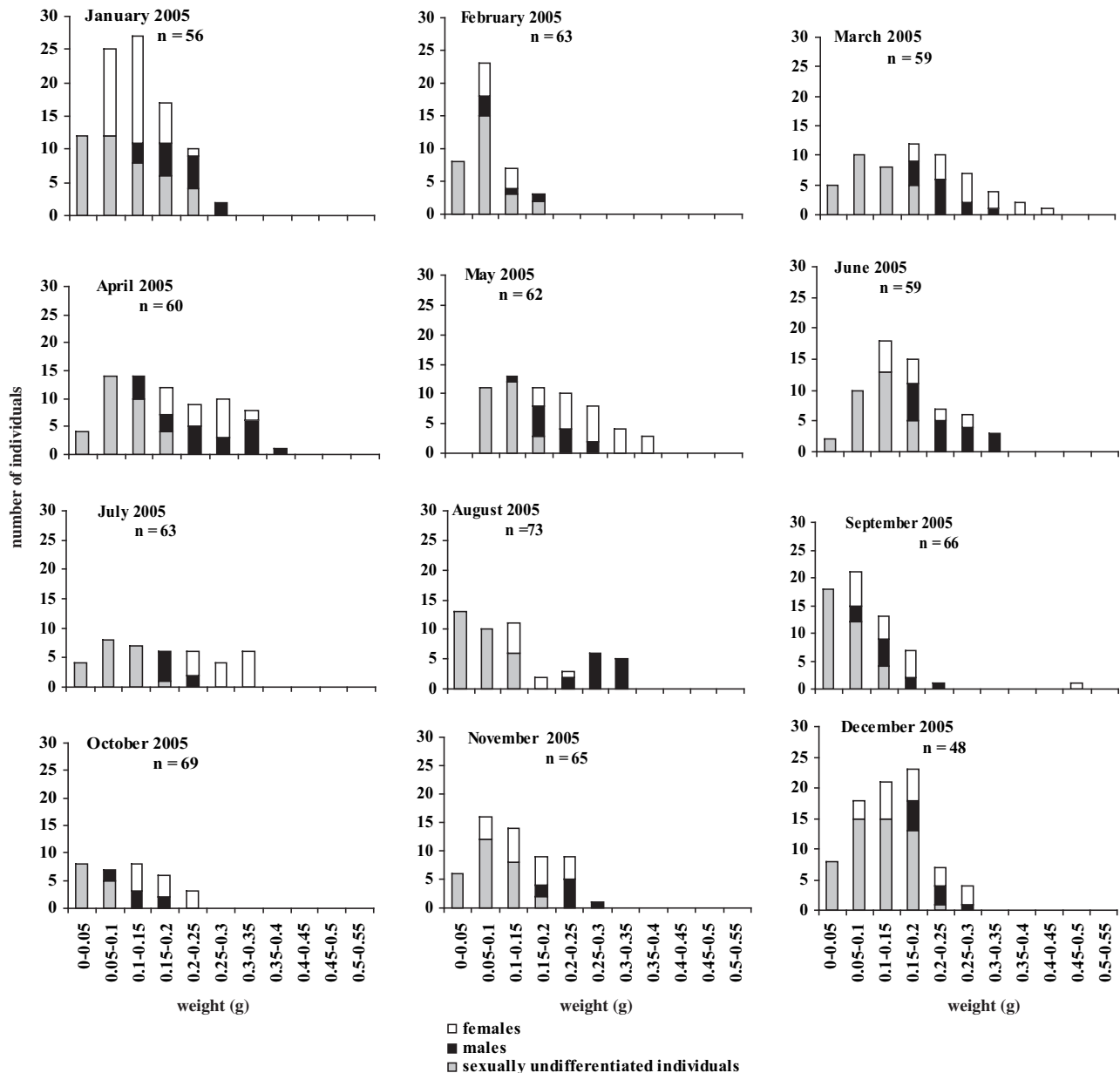


FIG. 8. – Size-frequency distribution based on whole body wet weight from January to December 2005 at Pointe Pescade.

uals and new recruits united due to a growth of the new recruits. From February to March we noticed the appearance of a second cohort of large, sexually differentiated individuals, indicating the beginning of the reproduction period. We can therefore conclude that the longevity of the species in the Bay of Algiers is 2 years.

It should be also noted that, with the exception of May for individuals collected at Pointe Pescade and April for those collected at Figuier, we observed the presence of small undifferentiated individuals, indicating that sporadic reproduction can occur during most of the year.

DISCUSSION

The benthic phases of the life cycles of the two studied populations of *P. cf. cultrifera* in the Bay of Algiers are similar. The life span of the species probably does not exceed 2 years and individuals reproduce exclusively by atoky. The reproduction can take place all year round but is more intense from March to May. The oocytes take 9 to 12 months to mature and their diameter at maturity is approximately 200 μm .

Our results confirm previous observations of the mode of reproduction of *P. cf. cultrifera* in the Bay of

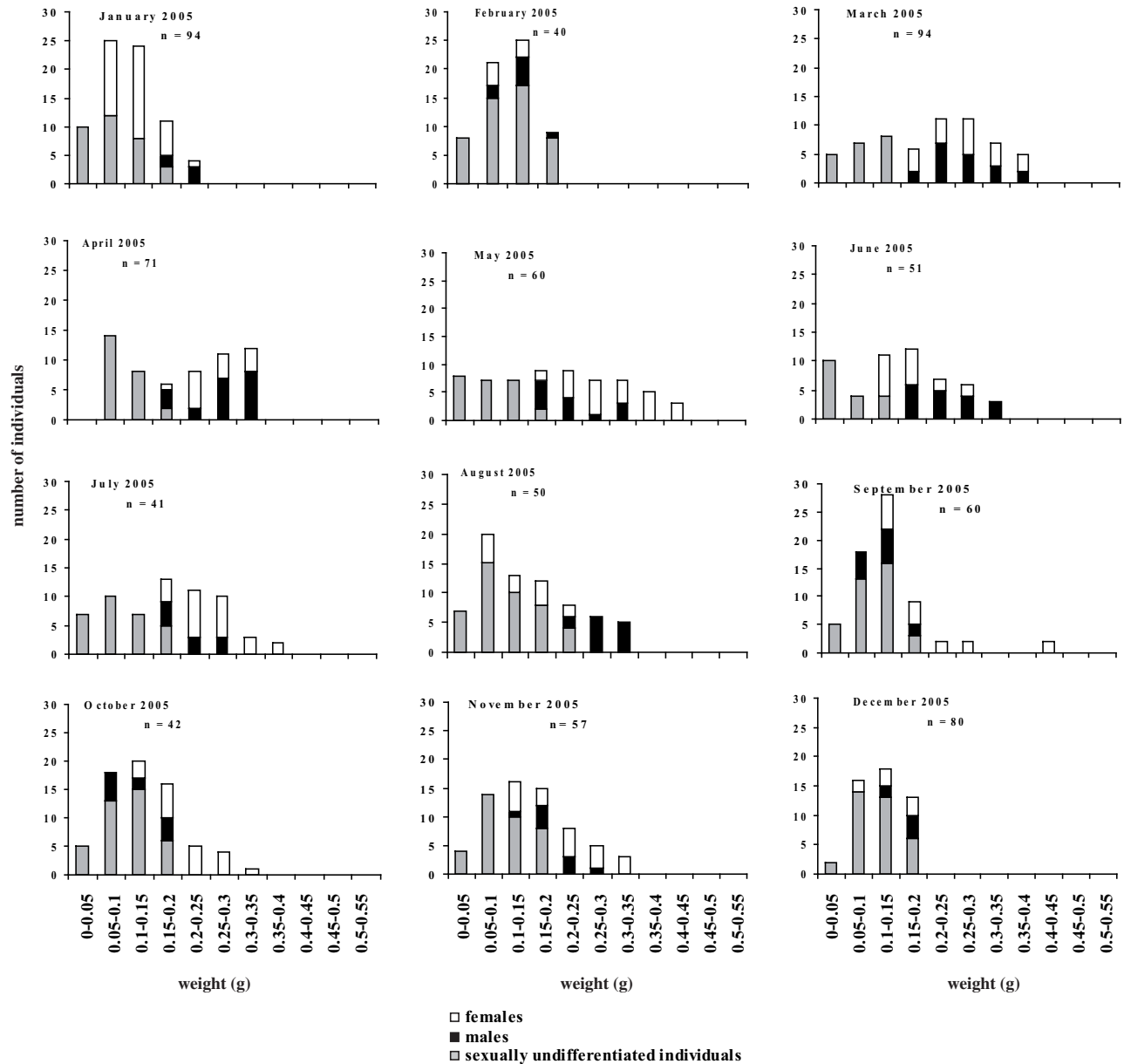


Fig. 9. – Size-frequency distribution based on whole body wet weight from January to December 2005 at Figuer.

Algiers by Gravier and Dantan (1928) and Durchon (1957) indicating that reproduction is of an atokous type. One of our study sites (Pointe Pescade) corresponds to the place where Marcel (1962) collected his individuals, which enabled us to carry out comparisons with more than 40 years of interval. In both cases, adults were small (maximum number of chaetigerous segments lower than 80) and reproduced exclusively by atoky, with a life span not exceeding two years. Reproduction could take place all year round but was more intense from July to November in 1962 and from March to May in 2005. We showed that the most intense period of reproduction was in

spring in 2005, when the sea-water temperature starts rising, and that maturation of gametes varies according to fluctuations in sea-water temperatures. Unfortunately, Marcel (1962) provided data of sea-water temperature only from January to June. The most intense reproduction period probably varies from one year to another according to the variations in sea-water temperature.

Our results obtained from the west coast of Algeria are in disagreement with those reported from the east coast of Algeria near the Tunisian border by Rouabah and Scaps (2003b), who found that individuals assigned to *P. cultrifera* reproduce exclusively by

epitoky, have a 3-year life span and reproduce only in late March or early April. Moreover, individuals are larger and heavier on the east coast (maximum segment number up to 125 and weight reaching 0.846 g before epitokous transformations) than on the west coast of Algeria (maximum segment number lower than 80 and weight reaching 0.540 g).

The mode of reproduction of *P. cf. cultrifera* has been examined at other sites in the Mediterranean Sea by other authors. Reproduction is reported to be of an epitokous type at Salammbô near Tunis (Zghal and Ben Amor, 1989) and in the Venice lagoon (Ansaloni *et al.*, 1986), whereas it is of an atokous type in the area of Marseille (Perès and Rancurel, 1948). Mature individuals were found in May at Salammbô (Zghal and Ben Amor, 1989) and in March in the Venice lagoon (Ansaloni *et al.*, 1986).

In addition, observations on the benthic phase of the life cycle of *P. cf. cultrifera* have been carried out in the English Channel and the Atlantic coast of France. Reproduction in the English Channel (Fauvel, 1916; Herpin, 1925; Durchon, 1951; Scaps *et al.*, 1992, 2000) and the Arcachon basin (Cazaux, 1965) is of an epitokous type and individuals assigned to *P. cultrifera* have a 3-year life span. In the Arcachon basin, the reproductive season is short and spawning occurs from late April to early June (Cazaux, 1965). In the English Channel specific observations made by Fauvel (1916), Herpin (1925) and Durchon (1951) indicated that reproduction takes place from May to June and sometimes July. More recently, Scaps *et al.* (1992) showed that on the north coast of Brittany reproduction may be more precocious and shorter, the spawning season occurring from late March to early April. Adults present in the English Channel and on the Atlantic coast of France are larger than those of the Mediterranean. Cazaux (1965) indicated that adults current have a weight of 3 g and 115-120 segments in Arcachon. On the north coast of Brittany, Scaps *et al.* (1992) found large individuals weighing between 3 and 6.6 g before epitokous modifications.

The observations related to the life cycle of individuals assigned to *P. cultrifera* in the various regions of its geographical distribution area thus reveal the existence of 3 types:

(i) The epitokous form of the English Channel and the Atlantic coast of France, characterised by a large weight (between 3 and 6.6 g before epitokous modifications) and a large segment number (up to 120 segments).

(ii) The atokous Mediterranean form of Marseille and the Bay of Algiers, in which the segment number is below 80 and the weight below 0.6 g.

(iii) The epitokous Mediterranean form of the east coast of Algeria, Salammbô near Tunis and the Venice lagoon, characterised by up to 125 segments and an intermediate weight between the above two (0.846 g before epitokous transformations).

The great variability of the mode of reproduction and of the biometric features leads us to discuss the problem of the validity of this species. Recently, Scaps *et al.* (2000) and Rouabah and Scaps (2003a) compared the epitokous form from the English Channel with that from the Mediterranean Sea. They found morphological (number of paragnaths at the surface of the proboscis, number of teeth per half jaw) and genetic (allozymes, general protein patterns) differences indicating that *P. cf. cultrifera* is a complex of species. At a smaller spatial scale, Maltagliati *et al.* (2001) reported morphological (number of paragnaths on the zones of the pharynx) and genetic (allozymes) divergence in *P. cf. cultrifera* from two habitats types (a brackish-water habitat and a adjacent marine site) at Elba Island in Italy and concluded that the two groups can be assigned to sibling species. Nevertheless, in a review about polychaete reproductive patterns, Giangrande (1997) reported that variability in the life cycles and life histories is often present in many species of polychaetes, especially those living in unpredictable habitats, and it is not always related to sibling species.

It would thus be interesting to use a prospective study of genetic markers to test whether the two forms present in the Mediterranean Sea (the atokous and the epitokous form) correspond to two different sibling species or to two distinct physiological races.

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