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Population dynamics of *Scolelepis squamata* (Annelida: Polychaeta) from a Northwest African beach

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Abstract: The sedentary polychaete *Scolelepis squamata* (Müller, 1868) has a wide geographical distribution, but its population dynamics is less known. This species is relatively abundant at Skhirat beach on the Moroccan Atlantic coast where its population dynamics was studied between December 1985 and March 1988 in terms of abundance, distribution on the shore, sexual maturation, recruitment period, growth and life span. The mean density ranged from 130 to 2800 ind.m^{-2} over the year according to the periods and successful of spawning and recruitment. Sexual maturation, which covered over 10 months of the year, began at the end of winter, reached a maximum in April-June and ended in autumn. The population exhibited a demographic strategy which included four recruitment periods per year, the summer recruitments were more important than those in spring and autumn. Prostomium growth was irregular and varied between 0.08 and 0.21 mm per month. The average life span was estimated at one year for individuals recruited in summer. Mean annual biomass was 5.57 g.m^{-2}, mean annual production was 11.28 g.m^{-2}.y^{-1} and mean P/B ratio was 2.03 y^{-1}.

Résumé : *Dynamique de population de* Scolelepis squamata *(Annelida : Polychaeta) d'une plage Nord-ouest africaine*. Le polychète sédentaire *Scolelepis squamata* (Müller, 1868) présente une large distribution géographique, mais peu de travaux ont été dédiés à sa dynamique de populations. Relativement abondante sur la plage de Skhirat sur la côte atlantique marocaine, une étude de dynamique de population a été menée de décembre 1985 à mars 1988 en termes d'abondance, de distribution sur l'estran, de maturation sexuelle, de période de recrutement, de croissance et de longévité. La population présente des densités moyennes comprises entre 130 et 2800 ind.m^{-2} dont la variabilité est en rapport avec le déroulement et le succès des pontes et des recrutements. La maturation sexuelle qui s'étale sur plus de 10 mois dans l'année commence à la fin de l'hiver, atteint son maximum en avril-juin et se termine en automne. La stratégie démographique développée par la population montre quatre périodes de recrutement par an, les recrutements estivaux étant les plus importants par rapport à ceux de printemps et d'automne. La croissance du prostomium est irrégulière et varie entre 0,08 et 0,21 mm par mois. La longévité moyenne a été estimée à une année pour les individus recrutés en été. La biomasse annuelle moyenne était de 5,57 g.m^{-2}, la production annuelle moyenne était de 11,28 g.m^{-2}.an^{-1} et le rapport P/B moyen était de 2,03 an^{-1}.

Keywords: *Scolelepis squamata*; Distribution; Sexual maturation; Recruitment; Growth; Moroccan beach

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Introduction

Scolelepis squamata (Müller, 1868) is a sedentary spionid Polychaeta occurring on sandy beaches of Morocco. It has a wide geographical distribution with a latitudinal range from 58°N to 35°S. This species has been recorded along the coast of the Wadden Sea, the North Sea (Eleftheriou & McIntyre, 1976; Degraer et al., 2003), the Mediterranean Sea, the North Pacific, the North and South Atlantic Ocean and the Indian Ocean (Souza & Borzone, 2000).

On Moroccan beaches, according to Salvat's zonation scheme (Salvat, 1964), *S. squamata* principally occurs in the retention zone (i.e. the zone reached by all tides which loses its water through the action of gravity at low tide but maintains its retention water) (Bayed, 2003). However, occasionally, it can be observed in the resurgence zone (below the retention zone) (Bayed, 1991). According to the tidal level, *S. squamata* lives usually between MHWN and mid-tide, but also occurs in lower level on beaches and was sampled in subtidal zone (Knott et al., 1983; Souza & Borzone, 2000). *S. squamata* inhabits vertical tubes in fine, medium or coarse sand (Bayed, 1991; Van Hoey et al., 2004). This species is generally considered as a microphagous deposit-feeder, feeding at the sand-water interface using the palps or directly with the mouth, but it can be a suspension feeder in response to water flow (Dauer, 1983). This opportunistic change in feeding behaviour is considered as a well adaptation to environmental conditions on beaches (Pardo & Amaral, 2004). *S. squamata* is a prey for other polychates (e.g. *Eteone longa* Fabricius, 1980) (Kruse & Buhs, 2000), fishes (e.g. *Pleuronectes platessa* Linaeus, 1758) (Beyst et al., 2002) and birds.

On sandy shores, *S. squamata* constitutes benthic communities and assemblages with crustacean species: e.g. community of *S. squamata-Eurydice pulchra* (Leach, 1815) on the upper zone of Belgian sandy beaches (Van Hoey et al., 2004), assemblage of *S. squamata-E. pulchra* and assemblage of *S. squamata-Lekanesphaera teissieri* (Boquet & Lejuez, 1967) in the retention zone on Moroccan sandy Beaches (Bayed, 1991). *S. squamata* can reach very high densities (more than 20000 ind.m^{-2}) on a Southern Brazil beach (Souza & Borzone, 2000), high densities (more than 4000 ind.m^{-2}) on a Moroccan sandy beach (Bayed, 1991) and medium densities (around 500 ind.m^{-2}) on sandy beaches along the coasts of Scotland (Eleftheriou & McIntyre, 1976) and Belgium (Degraer et al., 2003). *S. squamata* dominates generally other species of macroinfauna in the areas of beaches where it occurs and can represent more than 70% of total abundance (Barros et al., 2001).

Within its large geographical distribution and its high abundance on sandy beaches, few works have been dedicated to its population dynamics (Joyner, 1962; Souza & Borzone, 2000) although the knowledge of the population dynamics of dominant species in communities is important to understand the responses of animals to some environment changes and to evaluate their role in trophic food web. In this context, this study represents the first one conducted in the eastern Atlantic Ocean on *S. squamata*. The aim of this work was to study its population dynamics by examining the reproductive cycle, recruitment, growth, life span (longevity) and annual productivity on a Moroccan sandy beach and to compare the results to those obtained by Souza & Borzone (2000) on a population of a southern Brazil beach.

Material and Methods

Site description and sampling

The studied population of *S. squamata* was from Skhirat beach (33°52'N, 7°03'W), located at 25 km to the south-west of Rabat (Fig. 1). The tide is semidiurnal with amplitude varying between 2.5 and 3.0 m during spring tides and between 1.3 and 1.4 m during neap tides. The beach in the sampled area was approximately 60 m wide with a mean slope of 4.7° and was sheltered from direct wave action by a break-water wall.

Faunal samples were taken at seven stations at 3.5 m intervals along a transect perpendicular to the shoreline between MHWN and MLWN (Fig. 1). Sampling was performed monthly from December 1985 to March 1988 (except for October 1986, January 1987 and September 1987). Four replicates of 1/16 m^2 (0.25 m^2 in total) of sand were collected at low tide at each station by digging with a spade to a depth of 30 cm. Sand was sieved through a 1 mm mesh size. The material retained on the sieve was fixed in 5% formaldehyde. Further, the sampled organisms were identified and counted. For each station, separate sediment sample was collected with a 3.5 cm diameter core to determine the sediment grain size and its total organic matter content (loss to ignition, 450°C, 6 h). To estimate the porosity of the sand and its water content, a known volume of sediment was sampled with a 3.5 cm diameter core at each station. The wet samples were weighed, dried and then weighed again. Water content was obtained by calculating the difference between wet and dry weights. The dried sediment was put into a known volume of water in a burette. The difference between the two levels of water was the volume of the sand grain. The total porosity was estimated by calculating the difference between the known volume of sampled sediment and the volume of the sand grain (Cherkaoui, 1989). The seawater temperature and salinity were measured during each sampling campaign, between 8 h and 10 h GMT, in a representative zone of the

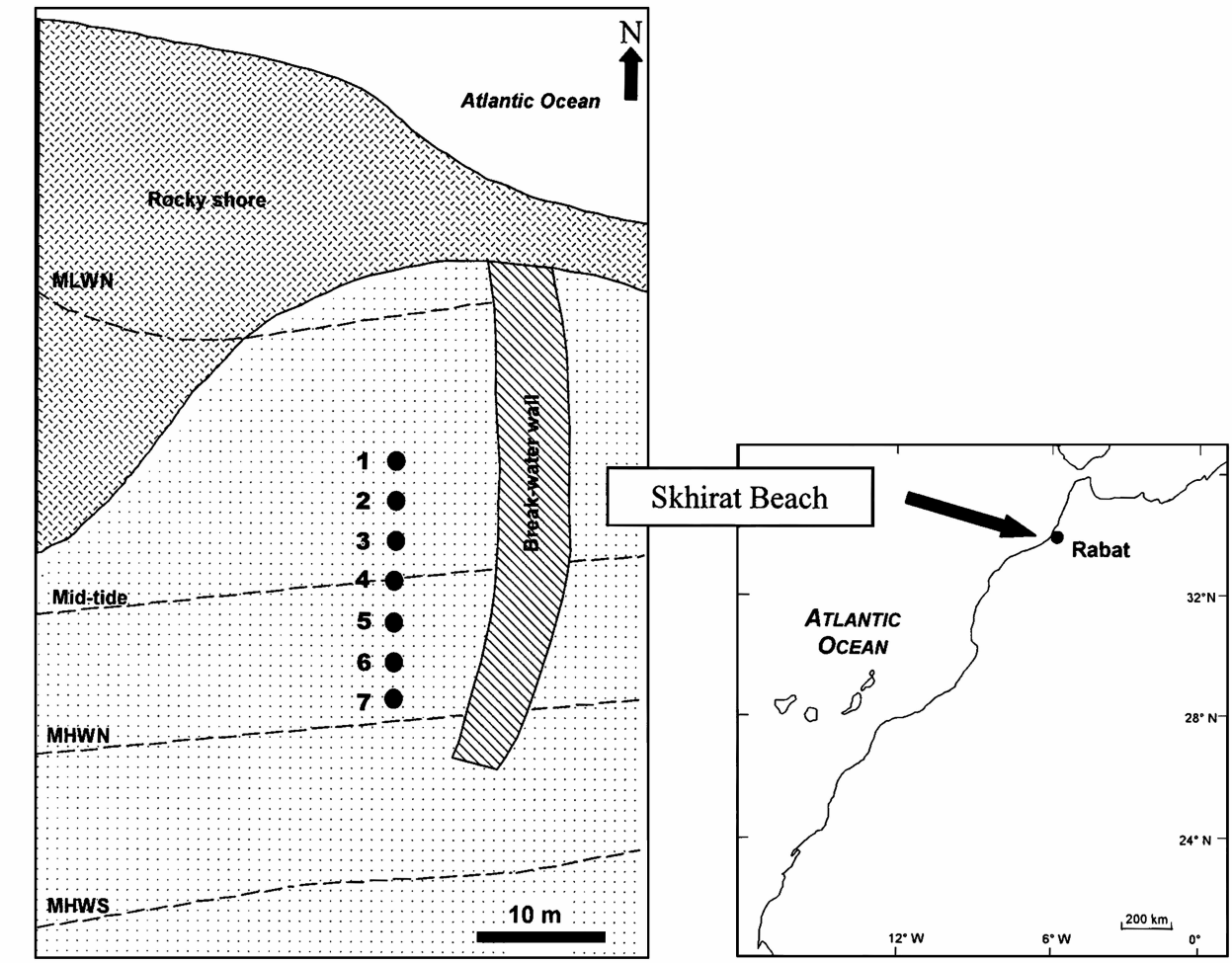

Figure 1. Geographic location of Skhirat Beach and the position of the sampling stations (numbered from 1 to 7) on the shore.
Figure 1. Localisation géographique de la plage de Skhirat et positionnement des stations de prélèvement (numérotées de 1 à 7) sur la plage.

beach at low tide in the waves to a depth of 50 cm near the sampling transect. In this area, samples of seawater were taken to determine suspended particulate carbon, chlorophyll a and phaeopigment levels in the coastal waters. In the laboratory, the seawater samples were analyzed according to Aminot & Chaussepied (1983).

Choice of the characteristic length (metric variable)

The total length of animals was not considered because sampled individuals were usually missing some posterior parts of the body. The total number of setigers was not considered also because our laboratory observations shown that *S. squamata* can regenerate up to 10 posterior setigers over a one month period. Therefore different measurements were taken on anterior part of the body of *S. squamata* with the attempt to determinate the most appropriate metric variable for the estimation of the animal growth. Four parameters were measured to the nearest 0.008 mm from 50 intact individuals chosen among sampled animals at Skhirat beach in December 1985. These were:

Length of the prostomium up to the first pair of eyes (L_1);

Length of the entire prostomium (L_2);

Width of the prostomium at the level of the first pair of eyes (L_3);

Width of the body at the level of the second setiger (L_4).

In order to study correlation between weight and length, an allometric relationship $W=kL^b$ was used, where W = animal dry weight in mg, k = proportionality coefficient, L = length in mm and b = constant. The correlation between log W and log L was tested using the correlation coefficient of Pearson. Total dry weight was obtained for each individual after drying at 80°C for 24 hours.

Secondary production of the population was estimated by the increment summation method based on the production of each cohort at successive dates (Boysen-Jensen, 1919; Dias & Sprung, 2003).

$P_{t,t+1} = \text{antilog}((\log N_t + \log N_{t+1})/2) \times (W_{t+1} - W_t)$

$P_{t,t+1}$: cohort production between dates t and t+1;

N_t and N_{t+1}: number of individuals of the cohort at dates t and t+1;

W_t and W_{t+1}: mean weight of individuals of the cohort at dates t and t+1

Cohort analysis

Measurements of the metric variable chosen (L_2: length of the entire prostomium, see results) were grouped in 0.1 mm interval classes and presented as frequency histograms. The cohort analysis required the modal decomposition of the histograms. The number of Gaussian components was determined using the method of Bhattacharya (1967) and the data were analysed according to Hasselblad's method (Hasselblad, 1966), which represents a maximum likelihood optimization method. The above analyses were performed using Normsep software developed by Tomlinson (1971).

Sexual maturation and spawning periods

During the reproductive period, males and females of *S. squamata* can be distinguished by the coloration of the reproductive region of their bodies: whitish for the mature males and greenish for the mature females. Full ovigerous females, defined as those in which the coelomic cavities in all or most of the segments in the reproductive region were full of oocytes (Joyner, 1962), were monitored by measuring their oocytes diameter (longed axis) (Gudmundsson, 1985; Souza & Borzone, 2000). Between April 1986 and August 1987, a minimum of eight full ovigerous females were chosen and about thirty oocytes, obtained by dissecting animals, were measured for each female, using a micrometer eyepiece mounted on a stereomicroscope. The data on diameter of the oocytes were grouped in 10 µm interval classes and presented as frequency histograms.

The gonadal activity (resting, maturation, spawning and resumption) also affects the weight of individuals. In order to evaluate these weight changes, the dry weight for a 'standard' individual of *S. squamata* (considered as a representative mature animal) was calculated. The calculation of the weight for a given length (length of prostomium (L_2), see results) was based on the allometric relationship established between dry weight and the characteristic length, obtained monthly from 50 sampled individuals.

Results

The table 1 gives annual mean values obtained at each station for the sediment parameters and for the density of *S. squamata*. According to the classification of Chassé & Glémarec (1976), the sediment was a well sorted medium sand, with a sorting index (Trask, 1932) varying from 1.2 to 2.2. Along the sampled transect, the mean value of median grain size at each station increased from the lower to the upper levels varying between 221 µm and 226 µm from stations 1 to 3 and between 283 µm to 296 µm from stations 4 to 7 (Table 1). The standard deviations were also varying in the same way: from 14 µm to 24 µm in the lower levels, and from 41.5 µm to 51.0 µm in the upper levels. No obvious significant difference has been observed between stations. The spatial variability of the mean dry weight organic matter content of the sediment ranged from 1.45% (station 1) to 1.68% (station 4) (Table 1) and no significant difference pointed out between stations. Mean water content decreased from lower levels of the beach (19-20% in stations 1-3) to the upper levels (11.5% in station 7). The mean porosity showed low value of 43.0% in station 4 and

Table 1. Sediment properties in the sampled stations with the indication of density and relative abundance of *Scolelepis squamata* at Skhirat beach.

Tableau 1. Propriétés du sédiment dans les stations échantillonnées avec indication de la densité et de l'abondance relative de *Scolelepis squamata* sur la plage de Skhirat.

Stations	Median grain Size (µm) Mean ± SD	Organic matter content (%) Mean ± SD	Mean Water content (%)	Mean porosity (%)	Density ($N.m^{-2}$) Mean ± SD	Relative abundance
1	221 ± 24.0	1.45 ± 0.24	19.00	44.8	136 ± 222	2.8
2	221 ± 22.5	1.50 ± 0.20	19.50	44.4	60 ± 44	0.6
3	226 ± 14.0	1.50 ± 0.09	20.00	43.6	230 ± 279	6.5
4	283 ± 41.5	1.68 ± 0.26	18.50	43.0	1310 ± 1329	31.1
5	278 ± 49.0	1.51 ± 0.40	17.75	43.8	1348 ± 1222	52.1
6	281 ± 51.0	1.54 ± 1.23	13.00	45.0	102 ± 180	2.6
7	296 ± 46.5	1.60 ± 0.28	11.50	45.8	164 ± 279	4.2

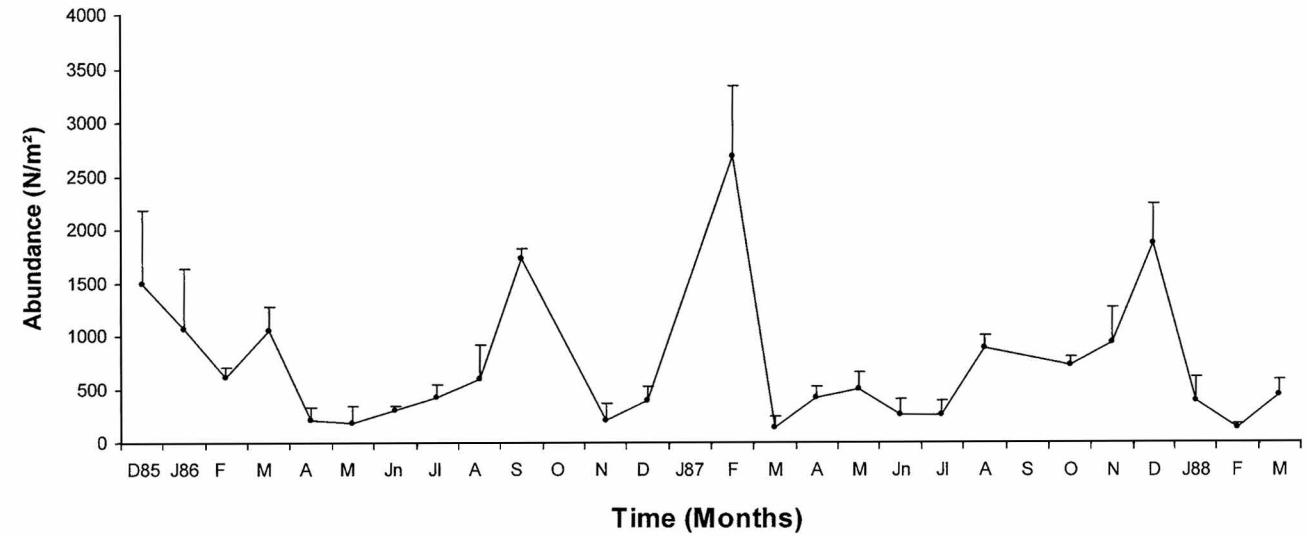

Figure 2. Temporal variation of the population densities of *Scolelepis squamata* at Skhirat Beach between December 1985 and March 1988. Error bars represents the standard deviation.

Figure 2. Variation temporelle de la densité de la population de *Scolelepis squamata* de la plage de Skhirat entre décembre 1985 et mars 1988. Les barres verticales représentent l'écart type.

regularly increased to lower level (44.8% in station 1) and to upper intertidal zone (45.8% in station 7).

The temporal variability of the mean median grain size did not show periodicity, but maximum values were observed in August (420 µm in 1986 and 394 µm in 1987) and the minimum ones were recorded between December 1985 and March 1986, in July 1986 and in February and November 1987 with values varying from 200 µm to 230 µm. Mean dry weight organic matter content of the sediment varied from 0.51% (February 1986) to 2.62% (May 1987) and seasonally peaks occurred in spring (March 1986, March and May 1987) and in autumn-early winter 1986 and 1987. Mean water content and porosity showed a periodical and seasonal but opposite scheme. The first parameter was minimal in June (11.2%) and maximal in December (22.6%), whereas porosity was minimal in November-December (42.0%) and maximum in April-May (47.7%) (Cherkaoui, 1989). Temperature and salinity of the seawater near the shore showed periodicity and seasonal variations and ranged from 13.4°C in January to 28.0°C in July and from 30 in winter to 36 in summer respectively. Suspended particulate carbon exhibited a seasonal variations with maximum in June-August (1.30 $mg.L^{-1}$) and minimum in December (0.72 $mg.L^{-1}$). Chlorophyll a and phaeopigment levels showed also a seasonally trends with very low values from January to March (less than 0.3 $\mu g.L^{-1}$) and two maximum in May-July (3.8-4.0 $\mu g.L^{-1}$) and in October-November (6.3-6.8 $\mu g.L^{-1}$) separated by a minimum in August (3.0 $\mu g.L^{-1}$) (Cherkaoui, 1989).

The mean monthly density varied from 130 $ind.m^{-2}$ in May 1986 to 2800 $ind.m^{-2}$ in February 1987 (Fig. 2). For each year, three peaks of densities seem to be observed. The peak of beginning of spring (March-May) is weaker than the one of the end of summer (August-September) and the one of winter (December-February) Along the sampling transect, most individuals of S. squamata were concentrated in a narrow band corresponding to stations 4 and 5 where mean densities were 1310 $ind.m^{-2}$ and 1348 $ind.m^{-2}$ respectively representing more than 83% of the sampled individuals (Table 1).

The variable L_2 (length of the prostomium) generated the best correlation with dry weight ($r = 0.91$, $p < 0.01$) compared to L_1 ($r = 0.82$, $p < 0.05$), L_3 ($r = 0.75$, $p < 0.05$) and L_4 ($r = 0.67$, $p < 0.05$) and was thus considered as the characteristic length. The relationship established for the Skhirat beach population between W and L_2 was:

$$W = 0.122\ L_2^{3.52}$$

Sexually mature males and females were present for a period of 10 months (Fig. 3). They appeared in January-February and involved only a small percentage of the population (< 5%). Sexual maturation was maximal in April-June (mature animals were about 66-89% of the whole population in 1986 and 67-78% in 1987). The number of mature individuals subsequently dropped drastically towards the middle of summer in July (matures animals were 16% in 1986 and 21% in 1987) followed by an appreciable return of gonadal activity in August-September with an increase in mature males and females corresponding to less than 30% of the population. This reproductive cycle ceased between November and

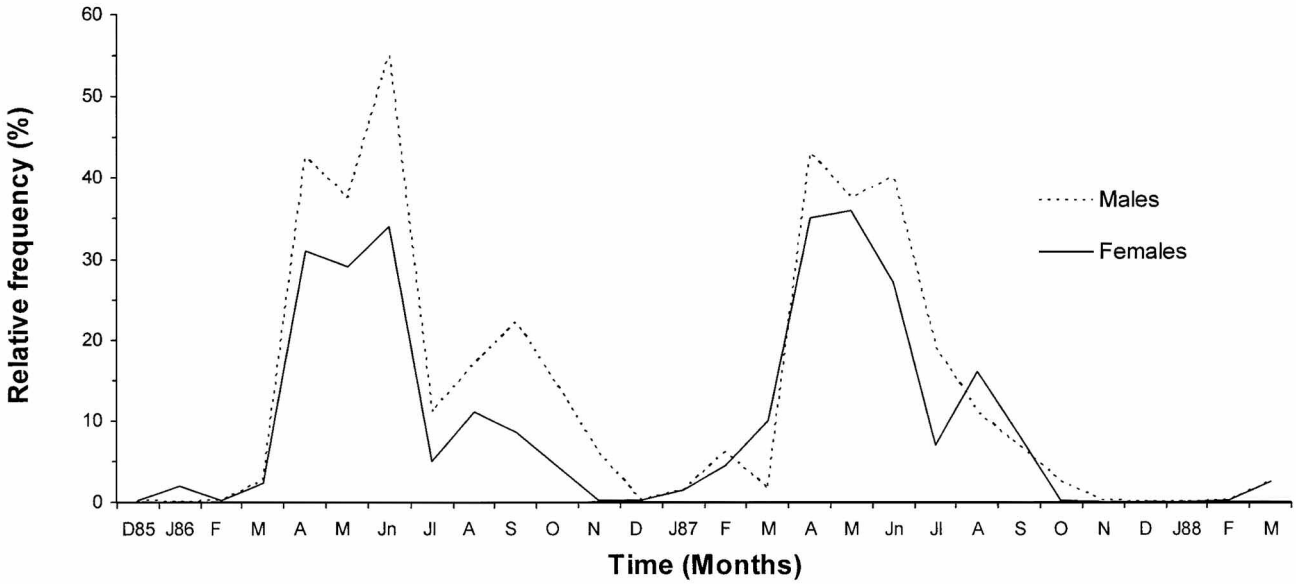

Figure 3. Temporal variation in the relative frequency of mature male and female individuals of *Scolelepis squamata* at Skhirat Beach between December 1985 and March 1988.

Figure 3. Variation temporelle de la fréquence relative des individus mâles et femelles matures de *Scolelepis squamata* sur la plage de Skhirat entre décembre 1985 et mars 1988.

December. In the general trends, the relative frequency of mature males was greater than that of females.

Monitored between April 1986 and August 1987, the mean diameter of measured oocytes varied between 130-160 µm (values ranged from 40 to 200 µm) and oocytes with diameter more than 40 µm were not present from October 1986 to January 1987. The size-frequency distributions of the oocytes diameter (Fig. 4) were generally centred on a main mode from April to July 1986 and in March, July and August 1987. The return of gonadal activity in August-September 1986 was shown by the appearance of a lower mode (70-110 µm). In February and from April to July 1987, samples having two distinct modes were both related to the increase of the mature female's number.

To use the dry weight of a 'standard' individual, three values of L_2 were tested (1.0, 1.5 and 2 mm). The latest value showing the highest amplitude of variations was retained. Maximum dry weight was reached between the end of spring (May 1986) and the onset of summer (June 1987) with respectively 32 mg and 34 mg (Fig. 5). When these massive reductions of dry weight were related to spawning periods, it appears that the population of Skhirat beach presented a period of major spawning extending from late spring to early summer. Other peaks with less drastic decreases observed may correspond to periods of minor spawning recorded at the early spring in 1986 and 1987, in autumn 1986 and in winter 1988.

Modal analysis of the histograms revealed the occurrence of two to four modes per monthly sampling period from December 1985 to March 1988 (Fig. 6). The periods of recruitment can be grouped into three seasons: spring, summer and autumn. Spring recruitment (SP86 observed in May 1986 and SP87 observed in May 1987) as well as autumn recruitment (A86 observed in December 1986 and A87 observed in November 1987) was each represented by a single mode (cohort). The summer recruitment is the major one gave rise to two groups of young individuals, which corresponded to the modes, observed respectively in July and August (SM_1 86 and SM_2 86 in 1986 and SM_1 87 and SM_2 87 in 1987) which were identified through modal analysis. Each of these modes can be considered to be a distinct cohort. The 1986 recruits were more numerous than their 1987 counterparts.

Growth was studied through the temporal variations of the mean length of each cohort in the cohort analysis (Fig. 7). Growth of the different cohorts was relatively irregular and was curtailed in December-March for SM_1 85 and in August-November for SM_1 86 and SM_2 86. The maximum growth rates were recorded for the spring 1987 cohort (SP87) with a mean of 0.21 mm per month. These rates appeared to drop subsequently, based on growth of cohorts SM_1 86 (0.13 mm.month^{-1}), SM_2 86 (0.08 mm.month^{-1}) and A87 (0.08 mm.month^{-1}). There were differences between 1986 and 1987 with a maximal growth in winter for 1986 cohorts (mean growth is about 0.16 mm per month) and in summer for 1987 cohorts.

Mean life span was estimated using the appearance and disappearance of modes in the cohort analysis. It varied

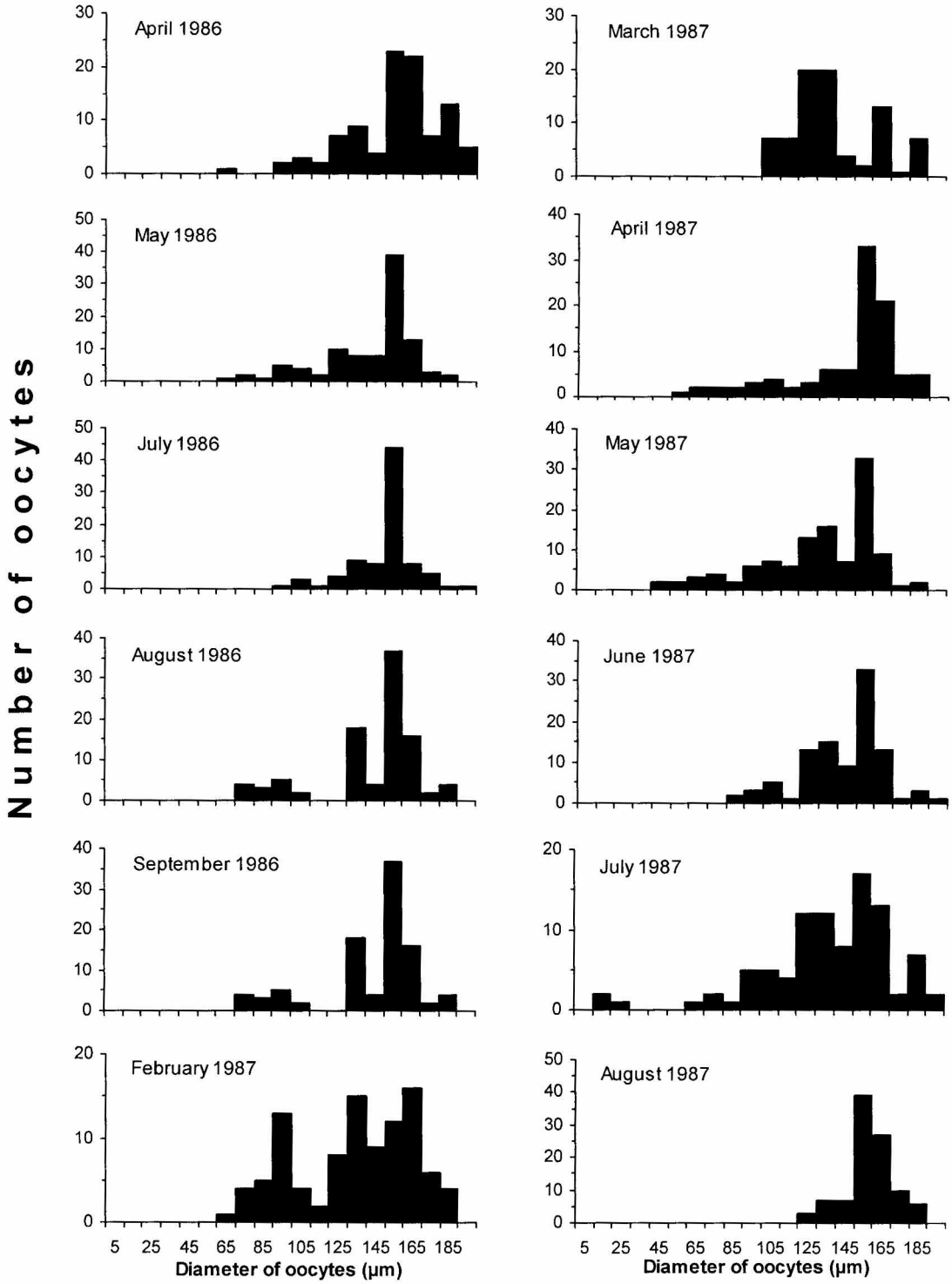

Figure 4. Size distribution frequency of oocytes recovering from the annual maturation period of *Scolelepis squamata* at Skhirat Beach between April 1986 and August 1987.

Figure 4. Distribution des fréquences de taille des ovocytes pendant la période annuelle de maturation de *Scolelepis squamata* à la plage de Skhirat entre avril 1986 et août 1987.

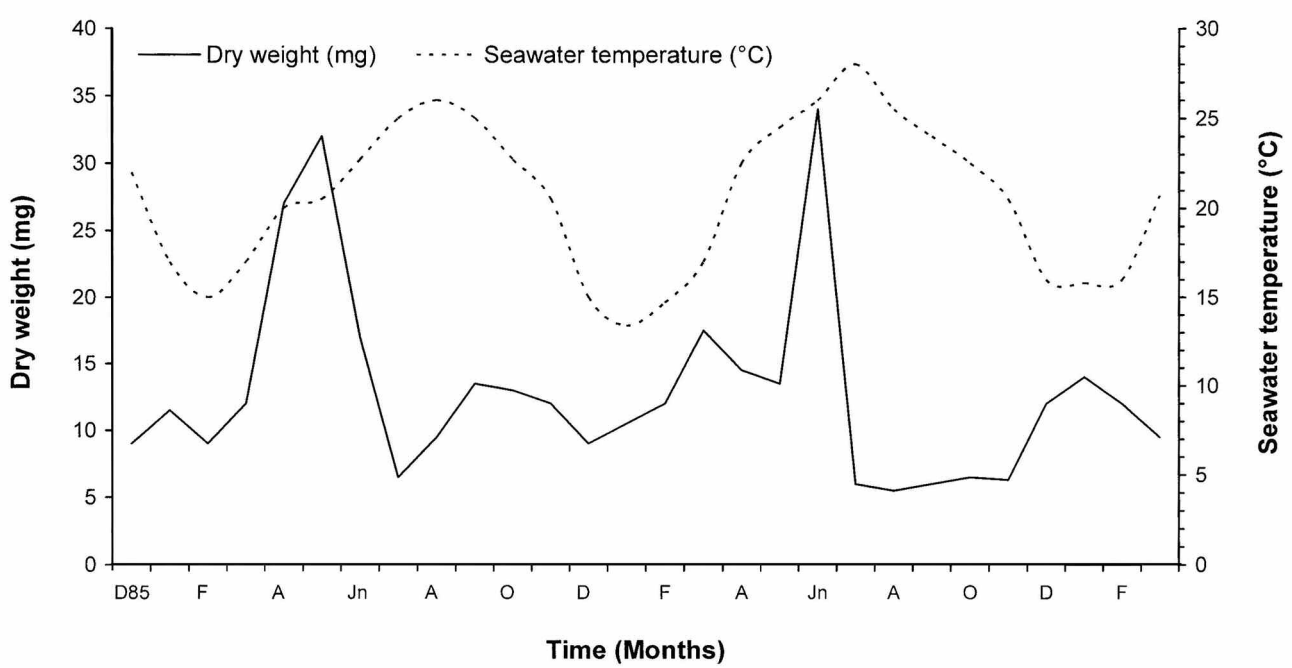

Figure 5. Temporal variation in dry weight for the 'standard' individual of *Scolelepis squamata* at Skhirat Beach between December 1985 and March 1988. The variations in sea water temperature are also shown.

Figure 5. Variation temporelle du poids sec d'un individu standard de *Scolelepis squamata* sur la plage de Skhirat entre décembre 1985 et mars 1988. Les variations de la température de l'eau sont également fournies.

depending on recruitment period, but remained similar from one year to another for the same type of cohorts (Fig. 7 and 8). The spring 1986 cohort (SP86) disappeared very early (about three months), whereas that of 1987 (SP87), which exhibited maximal growth rates, disappeared in November 87 after seven months. The summer cohorts SM_1 and SM_2 disappeared in March and May-June respectively of the following year. The summer 1986 cohorts (SM_1 86 and SM_2 86) exhibited the longest life spans (10-12 months), whereas the autumn cohort (A86), disappearing in July 87, did not exceed the age of 8-9 months.

Mean annual biomass (dry weight) of *S. squamata* of Skhirat beach was 5.57 $g.m^{-2}$ (5.66 $g.m^{-2}$ in 1986 and 5.48 $g.m^{-2}$ in 1987) with very higher values in summer (15.32-17.63 $g.m^{-2}$) corresponding to main recruitments. Mean annual production was 11.28 $g.m^{-2}.y^{-1}$ and was higher for 1987 (13.93 $g.m^{-2}.y^{-1}$) than 1986 (8.63 $g.m^{-2}.y^{-1}$). Mean P/B ratio was 2.0 y^{-1} with calculated values of 1.52 for 1986 and 2.54 for 1987.

Discussion

The distribution of *S. squamata* along the sampled transect at Skhirat beach was characterized by a high concentration of animals in a narrow band localized at mid-tide level (stations 4 and 5) where maximal density were reached representing approximately 85% of the population. According to sediment properties evaluated with this study (median grain size, organic matter content, water content, porosity), the variations of measured parameters between stations were lower and could not explain the spatial distribution of the species. Other environmental factors not detected in the present study seem to be involved in this distribution. Indeed, on other Moroccan exposed beaches, the densities were lower (Bayed obs.) and the maximum of abundance of the species was reached at upper levels than in Skhirat beach (Bayed, 2003). On the Brazilian beach of Atami (South Atlantic Ocean), *S. squamata* was concentrated in a band in the middle intertidal beach and its abundance was related to mean grain size and morphodynamic indices. However, the species occurred also in the subtidal zone (Souza & Borzone, 2000). On other Southern Brazilian beaches, the peak of abundance of *S. squamata* occurred in resurgence zone (Barros et al., 2001). On North Sea shores, the maximum density of *S. squamata* population of Whitstable beach, England, occurred in a narrow zone just below MHWN (Joyner, 1962) as the case of Belgian beaches where the peak of abundance of this species was located in the upper intertidal zone in a fine to medium sand (Van Hoey et al., 2004). *S. squamata* reached higher densities on ultra-dissipative beaches than on low

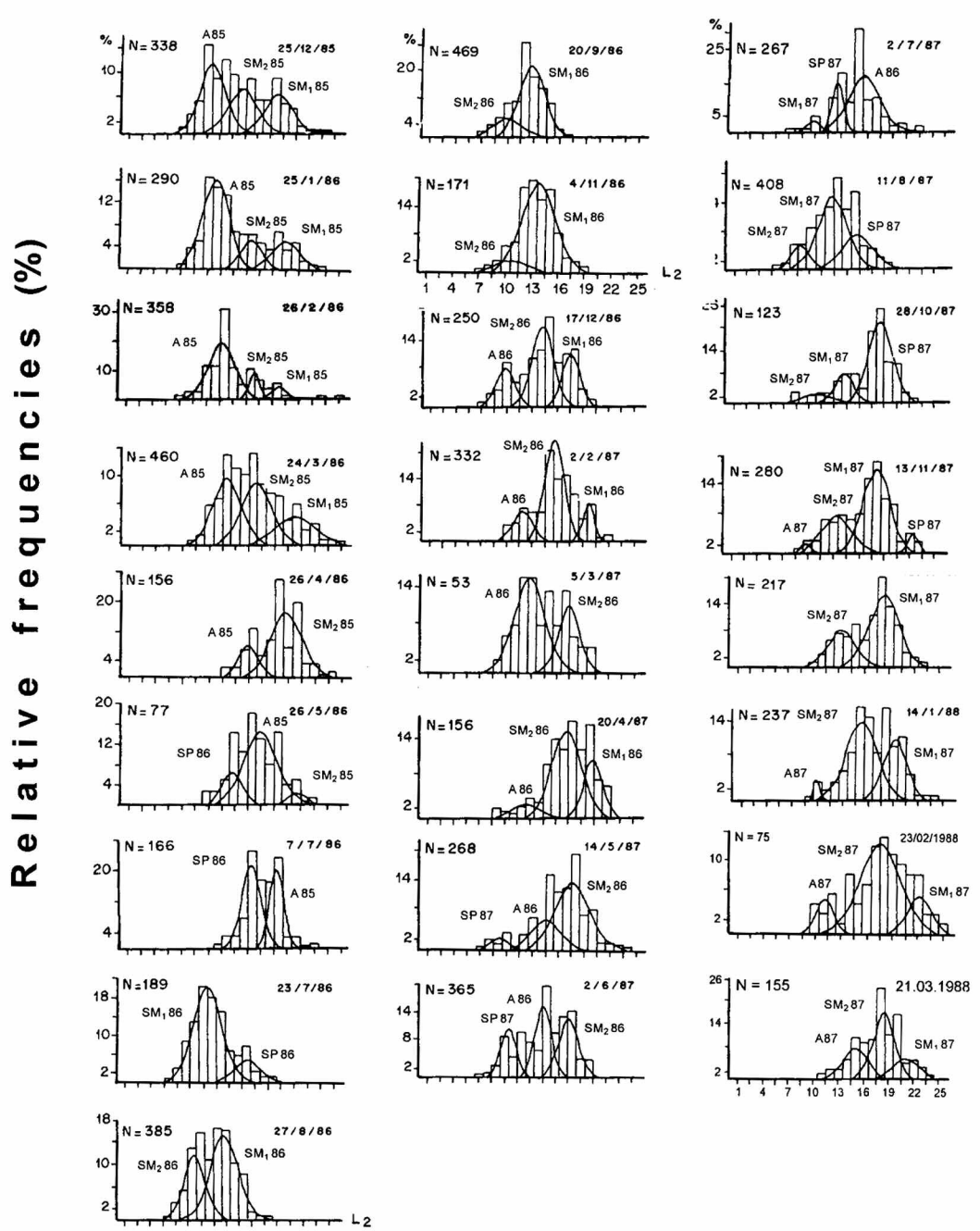

Figure 6. Size frequency histograms for the population of *Scolelepis squamata* sampled at Skhirat Beach between December 1985 and March 1988. The values of L_2 given on the x-axis are of the multiple of 10 of the real value in mm. SM_1 and SM_2 = summer recruitments; A = autumn recruitment; SP = spring recruitment; 85, 86 and 87 = years; N = number of measured individuals

Figure 6. Histogrammes de fréquences de taille de la population de *Scolelepis squamata* échantillonnée sur la plage de Skhirat entre décembre 1985 et mars 1988. Les valeurs de L_2 indiquées sur l'axe des x sont des multiples de 10 de la valeur réelle en mm. SM_1 et SM_2 = recrutements estivaux ; A = recrutement automnal ; SP = recrutement printanier ; 85, 86 et 87 = années ; N = nombre d'individus mesurés.

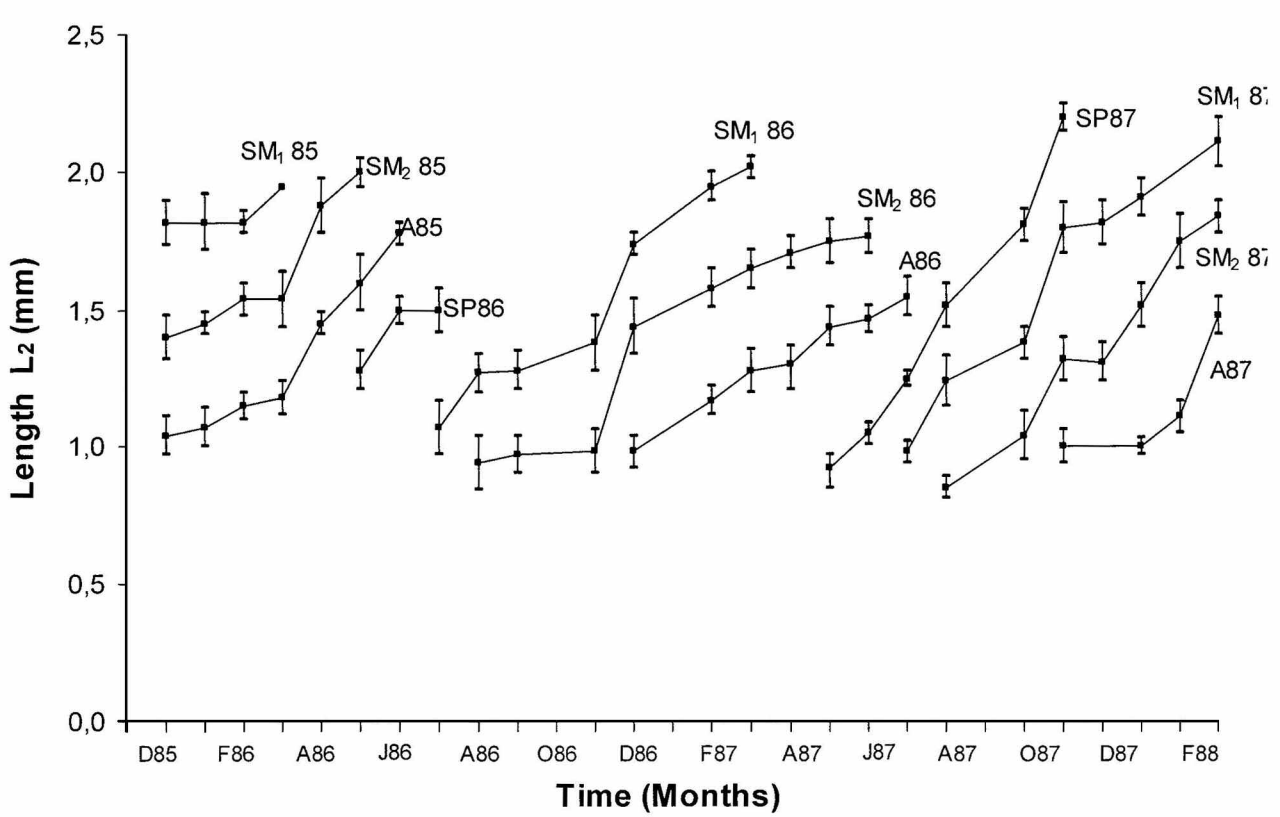

Figure 7. Growth curves for the different cohorts identified in the population of *Scolelepis squamata* sampled from Skhirat Beach between December 1985 and March 1988. Error bars represent the standard deviation. See Fig. 6 above for explanations.

Figure 7. Courbes de croissance des différentes cohortes identifiées pour la population de *Scolelepis squamata* sur la plage de Skhirat entre décembre 1985 et mars 1988. Les barres verticales représentent l'écart-type. Voir figure 6 pour les abréviations.

tide bar/rip beaches where the peak of density was lower and occurred in lower level of the beach (Degraer et al., 2003).

The sexual maturation period was long and lasted 10 months with a major peak in April-June and a minor peak in August-September. The oocyte diameter survey giving quantitative information about the state of maturation of the gonads of females (Souza & Borzone, 2000) was combined in this study with the mature animal's frequency. The oocytes observed from April to September in 1986 and from February to August in 1987 present mean diameter varying from 130 to 160 µm. At the end of each reproductive period (August-September) for both 1986 and 1987, oocytes attained their largest size of about 157-160 µm. In European populations, the oocytes mean diameter is greater: 180-200 µm in Brittany, France (Cherkaoui obs.) and 190-270 µm at Whitstable, Great Britain (Joyner, 1962). In the latest site, the reproductive period began in early March and extended to later than July and the highest percentages of full females occurred between April and June (Joyner, 1962). For a Southern Brazilian population, the season of reproduction was probably continuous, the oocyte diameters ranged from 90 to 150 µm and the full ovigerous females were present throughout the year with two peaks in February and August (Souza & Borzone, 2000).

Examination of the variation in dry weight of a 'standard' individual allowed the identification of small drops in dry weight attributable to short spring (1987) and autumn (1986) spawning periods, besides the main summer spawning (1986 and 1987). There was a good agreement between the drop in dry weight and the decrease in the percentage of mature individuals in summer and autumn while the short spawning period in spring was not reported from the examination of the mature individuals. However, for a European population, Joyner (1962) reported that the spawning period was long and that some individuals may reproduce before the occurring of highest percentages of full individuals.

The two peaks of dry weight observed in April-May 1986 and June 1987 for the Moroccan beach were attributed to the favourable conditions of the habitat which

permitted an increase in the somatic weight (somatic growth) and a development of gametogenesis activity accompanied by an increase in gonadal weight. This may related with food availability, evaluated by the organic matter content of the sediment, combined with an increase in the seawater temperature. Hence, we noticed that each of the two peaks of dry weight was preceded by a peak of organic matter content: 2.19% in March 1986 and 2.62% in May 1987. This observation is also valid for the small peaks of January and September 1986, of March 1987 and of January 1988 that coincided with prompt peaks of the organic matter, but of least importance (0.64%-1.78%).

Sexual maturation in *S. squamata* population of Skhirat beach was probably triggered by an increase in temperature recorded at the end of winter-early spring following the period of minimum winter temperature (Bhaud, 1981). The resumption of the maturation after the main spawning was observed when temperature decreased (Bhaud, 1981) after the maximum of July. At Whitstable in Great Britain, the onset of sexual maturation in *S. squamata* was observed at the late winter (Joyner, 1962) when the temperature increased. It is possible that in addition to external factors such as temperature, internal factors may also affect the triggering of the maturity (Joyner, 1962).

Periods of recruitment observed in spring, summer and autumn 1986 were also reported in 1987: spawning in February 1986 and March 1987 related to the recruitment in spring (seen in samples in May), spawning in June-July related to the recruitment in summer (seen in samples in July and August respectively) and spawning in October related to the recruitment in autumn (seen in samples in December 1986 and November 1987 respectively). The summer recruitment was represented by two distinct cohorts, whereas the spring and autumn ones were represented each by one cohort. It results in the occurrence of two, three or four modes by month. In a Brazilian population, two cohorts occurred and two recruitment periods were observed (April and October) which appeared in samples two months later than the occurrence of peaks of the ovigerous females (Souza & Borzone, 2000). In the Moroccan population, the lag between maximum occurrence of mature females and recruitment was of 1 month for the spring cohort, of 1-2 months for summer cohorts and of 2-3 months for autumnal cohorts. It suggests variable duration of larval development and growth of recruits according to the seasons. These phases were shorter in spring and summer and may influenced by the increase of temperature and by the development of the phytoplanction during this period measured by the occurrence of high values of Chlorophyll a (Cherkaoui, 1989).

Temporal variation of the abundance in Skhirat beach was related to recruitment and two major maxima were recorded. The peaks observed in September 1986 and in August 1987, after the summer recruitments, were less than peaks recorded in February and in December 1987, after the autumnal recruitments. The spring recruitments (May of each year) did not produce significant changes in the abundance. This trend may relate to the higher interstitial temperature of the sand recorded at low tides during July and August (Bayed, 1991). During summer season, on some Moroccan sandy beaches, lot of individuals of many species of the retention zone left to the lower levels of the beach and some others species of saturation zone migrated to the subtidal zone (Bayed, 1991). May be a part of the recruited population did not settle in the sampled zone, in this case the mean abundance of the sampled population did not correspond to the recruit population. On a Brazilian shore, a lag of 2-4 months between recruitment periods and dates of peaks of abundance was observed for the same species (Souza & Borzone, 2000). The inter-annual variations of the importance of the three peaks of abundance observed each year (beginning of spring, end of summer, winter) and of the mean densities (564 ind.m^{-2} in 1986 and 876 ind.m^{-2} in 1987) were in relation to a successful recruitment (Souza & Borzone, 2000).

Growth of cohorts was irregular and did not appear to be seasonal. The spring 1987 cohort (SP87) present the maximum growth rate (0.21 mm per month). In 1986, the maximum growth occurred in winter for 1986 cohorts (0.16 mm per month), whereas in 1987, the maximum growth occurred in summer for 1987 cohorts. Life span was shorter for the spring cohorts (3 and 7 months respectively for SP86 and SP87), maximal for the summer cohorts (10-12 months for SM_1 86 and SM_2 86 respectively) and intermediate for the autumnal cohort (8-9 months for A86). No obvious relation has been observed between growth rate and life span. For the population of *S. squamata* of the South of Brazil for which life span varied between 6 and 8 months for the cohorts recruited in autumn (April) and spring (October) respectively, the reproductive effort would be at the origin of the shorter life span (Souza & Borzone, 2000).

The mean P/B ratio value of 2.0 y^{-1} obtained for the *S. squamata* population of Skhirat beach was lower than a Brazilian population with a value of 2.7 y^{-1} (Souza & Borzone, 2000). These authors, while using the ash free dry weight (AFDW), found a biomass of 0.21 g.m^{-2} and a production of 0.57 g.m^{-2}.y^{-1}. Mean values calculated from works mentioned by Souza & Borzone (2000) on secondary production for other species of the family Spionidae (Table 2) were varying between 0,14 to 8,20 gAFDW.m^{-2} and from 0.5 to 7.90 gDW.m^{-2} for the biomass, whereas for the production values varied from 0.20 to 4.62 gAFDW.$m^{-2}y^{-1}$ and from 3.0 to 43.40 gDW.m^{-2} y^{-1}. In These cases, the mean of P/B ratio ranged from 1.0 y^{-1} to 6.7 y^{-1}. Variations of secondary production from populations of a

Table 2. Secondary production of different species of family Spionidae; except for the Moroccan population of *Scolelepis squamata*, all values for the other species were obtained or calculated from Souza and Borzone (2000) data. P: production of ash free dry weight or *dry weight, B: mean biomass of ash free dry weight or *dry weight

Tableau 2. Production secondaire de différentes espèces de la famille Spionidae ; excepté pour la population marocaine de *Scolelepis squamata*, toutes les valeurs pour les autres espèces ont été calculées ou fournies de Souza et Borzone (2000). P : production annuelle du poids sec libre de cendre ou *du poids sec, B : biomasse moyenne du poids sec libre de cendre ou *du poids sec.

	P ($g.m^{-2}.y^{-1}$)	B ($g.m^{-2}$)	P/B (y^{-1})	Observations
Spiophanes kroyeri	0.20	0.14	1.4	
Spiophanes bombyx	1.71	0.38	3.1	Mean calculated values
Parapinospio pinnata	4.53	1.89	2.4	
Polydora quadrilobata	1.50	8.20	1-1.5	
Prionospio caspersi	4.62	0.94	6.0	Mean calculated values between consecutive years
Scolelepis gaucha	1.33	0.26	6.7	Mean calculated values from 4 populations
Streblospio benedecti	3.00*	0.50*	5.4	
Streblospio shrubsolii	15.65*	3.55*	4.4	
Marenzelleria viridis	43.40*	7.90*	5.3	Mean calculated values between 2 years
Scolelepis squamata (Brazilian population)	0.57	0.21	2.7	
Scolelepis squamata (Moroccan population)	11.28*	5.57*	2.0	This study

same species were related to the stability of sediments during recruitment periods for *Scolelepis gaucha* Orensanz & Gianuca, 1974 to environmental stress for *Prionospio caspersi* (Laubier, 1962) and to differences in successful recruitment for *Marenzelleria viridis* (Verrill, 1873) (Souza & Borzone, 2000).

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