Cah. Biol. Mar. (2013) 54 : 593-603

Reproductive cycles and recruitment in *Ophiomastix venosa* and *Ophiocoma scolopendrina*, two co-existing tropical ophiuroids from the barrier reef of Toliara (Madagascar)

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Abstract: The reproductive cycles and recruitment of two co-existing ophiuroids species, *Ophiocoma scolopendrina* and *Ophiomastix venosa,* were investigated on the barrier reef of Toliara (Madagascar) from February 2000 to April 2001. The two species inhabit the boulder tract of the barrier reef. *O. scolopendrina* reproduces continuously, has planktotrophic larvae, and new recruits are seen year-round while *O. venosa* has a clear annual reproductive cycle. In the latter, spawning occurs during the austral summer (from November to February), larvae are lecithotrophic, and new recruits (individuals less than 4 mm disk diameter) were seen mostly from February to May. It is hypothesized that differences in reproductive strategies shown by the two species are linked to local environmental conditions and species adaptations. The tolerance to emersion shown by *O. scolopendrina* allows it to successfully colonize regularly emerged areas. As for *O. venosa,* while adults live in permanently immersed tidal channels, juveniles were often seen as symbiont of *O. scolopendrina,* which allows them both to resist emersion and to increase the species recruitment area.

Résumé : *Cycles de reproduction et recrutement chez* Ophiocoma scolopendrina *et* Ophiomaxtix venosa, *deux espèces d'ophiures sympatriques du Grand récif de Tuléar (Madagascar).* Les cycles reproductifs et le recrutement de deux espèces d'ophiures coexistant sur la barrière de corail de Tuléar (Madagascar), ont été étudiés de février 2000 à avril 2001. Les deux espèces, *Ophiocoma scolopendrina* et *Ophiomastix venosa*, vivent sur la levée détritique de la barrière de corail. *O. scolopendrina* se reproduit continuellement, a une larve planctotrophe et les nouvelles recrues (individus dont le diamètre du disque est inférieur à 4mm) sont trouvées toute l'année alors qu'*O. venosa* a un cycle reproductif annuel clair. Chez cette dernière, la ponte se déroule durant l'été austral (de novembre à février), les larves sont lécitotrophes, et les nouvelles recrues sont observées principalement de février à mai. L'hypothèse émise est que les différences de stratégies reproductives montrées par les deux espèces sont liées aux conditions environnementales locales et aux adaptations des deux espèces à ces conditions. La tolérance à l'émersion montrée par *O. scolopendrina* permet de coloniser avec succès des zones régulièrement émergées. Chez *O. venosa*, les adultes vivent au niveau des canaux immergés de manière permanente et les juvéniles sont souvent observés comme symbiote d'*O. scolopendrina,* au niveau des zones émergées, ce qui leur permet de résister à l'émersion et d'augmenter la zone de recrutement de l'espèce.

Keywords: Reproduction • Echinodermata • Ophiuroid • Reef ecology • Intertidal ecology

Introduction

Ophiocoma scolopendrina (Lamarck, 1816) and *Ophiomastix* venosa Peters,1851 are two intertidal ophiuroids commonly distributed in the whole tropical Indo-West Pacific Ocean. In Madagascar, the two species closely co-occur in the boulder tract of the Toliara barrier reef where they are the two most abundant ophiuroids (Fourgon et al., 2007). There, juveniles of *O. venosa* were even observed to live as symbiont of *O. scolopendrina* (Fourgon et al., 2007) in a way similar to that already reported in Okinawa by Hendler et al. (1999) for the pair *Ophiomastix annulosa*/*O. scolopendrina*. Nothing is known on the reproductive habits neither of *O. scolopendrina* nor of *O. venosa*, although reports occur on their larval development that is planktotrophic in the former (Mortensen 1937) and lecithotrophic in the latter (Fourgon et al., 2005).

Ophiuroids have been described to adopt different reproductive strategies depending on the species and the geographical area (Hendler, 1991). One may think that such strategy in a given population is evolving to maximise its fitness through selective pressures, which may influence various aspects of the reproduction, among which the pattern of the reproductive cycle. The present paper aims to investigate the reproductive strategy - in term of reproductive cycle, spawning period and recruitment - of two closely co-existing ophiuroid species (*O. scolopendrina* and *O. venosa*).

Materials and Methods

Samplings were made on the boulder tract of the Great Reef of Toliara (Madagascar), where rocky domes and tidal channels alternate. Individuals of *Ophicoma scolopendrina* and *Ophiomastix venosa* were hand-collected monthly from February 2000 to April 2001 either on the rocky domes (*O. scolopendrina*) or in the tidal channels (*O. venosa*). The temperature of the water was measured each month. After each sampling, collected individuals were brought alive to the laboratory and their disk diameters were measured using a sliding caliper. Adult individuals were collected for gonadal studies (disc diameters ranging from 1.6 to 2.0 cm) among which 20 individuals of the two species were dissected -10 males and 10 females - and their gonads isolated. Gonads from each individual were dried (60°C for 48 h) then weighted, and the gonad index (GI) was calculated (GI = (gonad dw / total body dw) x 100).

Investigations on reproductive cycles were also performed from histological analyses. Gonads of 30 specimens of the two species (60 individuals in total) were fixed monthly in Bouin's fluid for 48 h and stored in 70% ethanol until use. They were then dehydrated, embedded in paraffin, cut in 7 µm thick sections, and stained with Masson's Trichrome (Gabe, 1968). Sections were performed on one gonad per individual only (it had been checked that development is synchronous in all gonads from single individuals). Additional staining procedures were done on ovaries using the Schiff reagent method, which is known to colour yolk material in ophiuroids (Moloney & Byrne, 1994). The growth of female gametes was followed by measuring the diameter of 50 oocytes from each investigated gonad. This was done using a light microscope mounted with a micrometer eyepiece (two perpendicular measurements were made for each oocyte [only profiles including the nucleus were measured] and the mean value was considered). In testis the occurrence and relative importance of spermatocytes, spermatids and spermatozoa was noted. This allowed to recognize several male and female gonadal stages and to calculate the monthly maturity indices ($MI = \Sigma(n.F) / N$, where F is the gametogenic stage, n the number of individuals in the stage F and N the total number of organisms in the sample) (Yoshida, 1952). The maturity index (MI) represents the monthly mean gonadal stage calculated after transforming the maturity stage of each individual to a circular scale. The obtained MI values were converted as circular data and represented graphically using polar coordinates: each monthly mean value is represented as a vector in a circle where the vector direction points to the corresponding gonadal stage and the vector length represents the homogeneity of the sample (the longer the vector, the higher the homogeneity) (Spirlet et al., 1998).

Comparisons between GI values were done using one-way ANOVA after arcsine transformation of data (Zar, 1996). The Watson U^2 non-parametric test was used to compare male and female MI values (Fisher, 1993; Zar, 1996). Correlation between day length, water temperature, GI and MI were made using the non-parametric angular-linear rank correlation statistic U_n (Fisher, 1993).

To characterize the recruitment periods, monthly samplings were done from March 2000 to February 2001 using quadrats of 1 m^2. Samplings were performed on a rocky dome and in the neighbouring tidal channel. In each site, 8 quadrats were randomly placed along a line perpendicular to the shore. This allowed to get at least 200 individuals of each species at each collecting period. The disk diameter of all individuals was measured and their size-frequency distributions were analysed using the C.A.MAN program (Böhning et al., 1992). The information generated by C.A.MAN were used as initial values and introduced in MIX program (Macdonald & Pitcher, 1979) in order to check their significance using chi-square test. A p-value above 0.05 was considered to significantly explain the overall size-frequency distribution in term of component normal distributions.

Results

Gonads in the two species are close to inter-radial bursae in which gametes are emitted. There are up to 16 gonads per bursa in *O. venosa*, and up to 40 in *O. scolopendrina*. When mature, ovaries of *O. venosa* are green in colour while those of *O. scolopendrina* are pinkish.

Gonad indices

The gonad index of *O. venosa* showed an annual cycle (Fig. 1A). The male and female indices were significantly different (the female GI is higher throughout the sampling period except in February 2001; one-way ANOVA, $p < 0.001$) although the two indices were significantly correlated (Pearson correlation, $r = 0.82$, $p < 0.01$). The lowest GI values for both male and female were obtained in April 2000 (0.18 % and 0.35%, respectively) and the higher values in December 2000 in females (1.7%) and in February 2001 in males (1.8%). From April to October 2000 the GI values remained significantly constant (one-way ANOVA, $p > 0.05$).

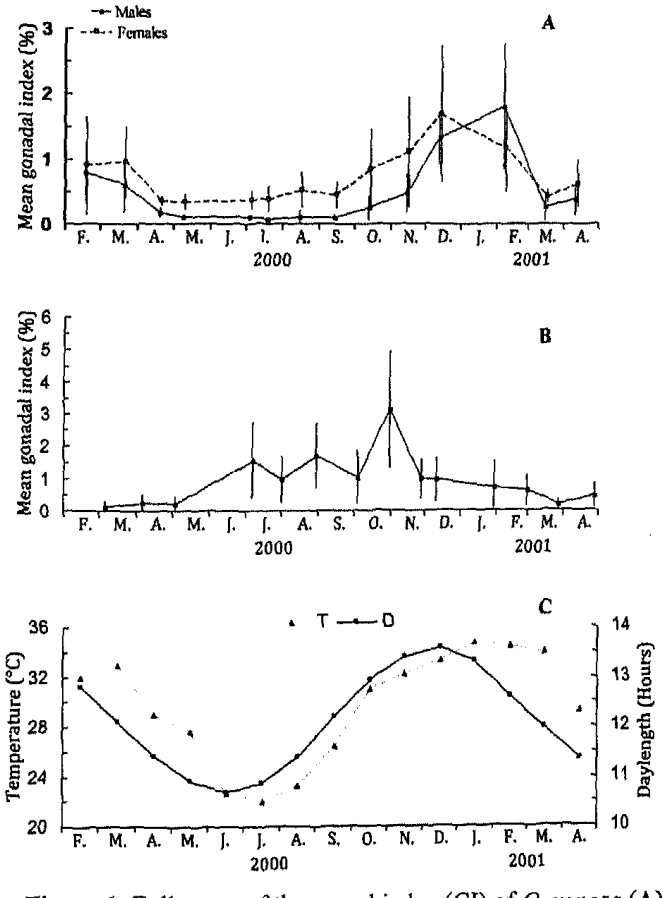

Figure 1. Follow up of the gonad index (GI) of *O. venosa* (**A**) and *O. scolopendrina* (**B**), and of changes in water temperature (T) and day length (D) recorded during the study period (**C**). Data for males and females were pooled for *O. scolopendrina* as no significant difference between sexes was observed in this species.

The gonad index of *O. scolopendrina* also showed annual variations (Fig. 1B). Yet, there was no significant difference between males and females (pooled on Fig. 1B) at any time of the sampling period (one-way ANOVA, $p = 0.15$). The GI was low in March 2000 (0.14%) and did not significantly change until May. It then rose to 1.54% in July, remained significantly constant until October where it peaked to 3.13% then fell to 0.98% the month after.

Gonad histology

For both species, oogonia and spermatogonia occur at the periphery of the entire gonad. While testis could be totally filled up by mature spermatozoans, ova were never seen in the ovarian lumen indicating that oocyte maturation should take place in relation with spawning. Oocyte sizes and oocyte staining properties were the main criteria used to document ovarian cycle in the two species. As for the testis, we mainly considered the relative proportions of gonadal cells.

Ophiomastix venosa. Monthly changes in gonad histology were rather well marked in *O. venosa* indicating the occurrence of an annual gonadal cycle. Previtellogenic oocytes are PAS negative and range from 20 to 225 µm in diameter; vitellogenetic oocytes contain PAS positive material (yolk material) and range from 175 to 300 µm in diameter; premature ovocytes are intensely PAS+ and range from 275 to 485 µm in diameter. Five different maturity stages were recognized for both male and female gonads.

Stage I: Recovering (Fig. 2A & F). Recovering ovaries appear as small pocket-like structure lined by previtellogenic oocytes. Recovering testes are small sacs with spermatogonia lining the organ wall. In both sexes the organ lumen is mostly empty with small amounts of phagocytic cells and degenerating oocytes or spermatozoans, the latter sometimes forming yellow strands with brownish spots.

Stage II: Growing (Fig. 2B & G). In growing ovaries, previtellogenic oocytes multiply intensively and invade the gonad lumen though there is no sign of vitellogenic activity. An inner layer of spermatogonia from which columns of spermatocytes project centrally is seen in testes where a few spermatozoans may already be observed in the lumen. Small amounts of phagocytes may still be present in both ovaries and testes.

Stage III: Regenerative spawning (Fig. 2C & H). There is an intense vitellogenic activity in stage III ovaries where previtellogenetic, vitellogenetic and premature oocytes co-occur, being rather densely packed. Testes also contain densely packed cells (spermatozoans) that occlude the lumen while a basal layer of spermatogonia and columns of developing spermatocytes are still visible. Yet spaces

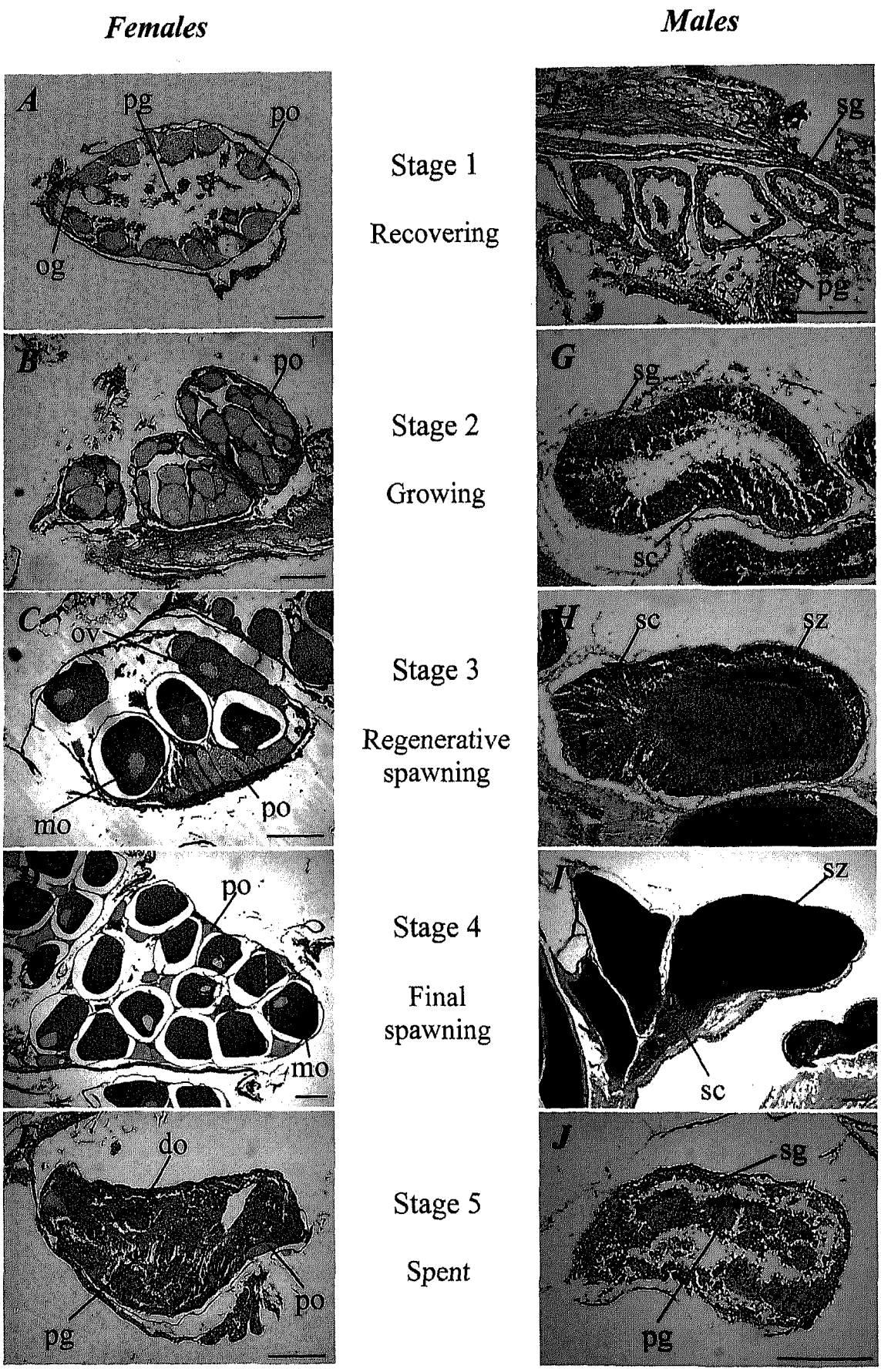

Figure 2. *Ophiomastix venosa.* Histology of the ovaries (**A-E**) and testes (**F-J**) showing the five maturity stages. See text for further description. do, degenerating oocyte; mo, mature oocyte; og, oogonia; ov, oocyte in vitellogenesis; pg, phagocytes; po, previtellogenic oocyte; sc, spermatocytes; sg, spermatogonia; sz, spermatozoa.

between oocytes in some ovaries (as well as a more diffuse aspect of the spermatozoan mass where some empty spaces occur by place) indicate that partial spawning already takes place in both sexes. However developing gametes are much more numerous than those that were spawn and stage III are characterized by an increase in gonad size.

Stage IV: Final spawning (Fig. 2D & I). Stage IV ovaries mostly contain premature oocytes as well as some previtellogenetic oocytes which indicate a strong reduction or even a stop of the ovarian vitellogenetic activity. Similarly, spermatogonia and spermatocytes are rarely visible in testes meaning that spermatogenesis almost stopped. Premature oocytes as well as spermatozoans are from closely packed to loosely arranged depending of the intensity of former spawning events. Due to gamete release, stage IV gonads progressively decrease in size.

Stage V: Spent (Fig. 2E & J). Spent ovaries and testes have a shrunken appearance. A few previtellogenic oocytes may be seen in ovaries as well as small patches of spermatogonia at the level of the testis wall. The lumen in both ovaries and testes is filled with phagocytic cells and degenerating gametes.

The relative monthly frequencies of the male and female maturity stages of *O. venosa* gonads are illustrated on Fig. 3, and the changes in their monthly maturity index are presented using circular data on Fig. 4. The latter provides a quantitative follow up of the maturity stages recorded throughout the study period. These figures show that *O. venosa* has a well-marked annual reproductive cycle. Data analysis also underlines that significant differences occur between sexes, since the maturity stages in testes always appeared from one to six months later than the corresponding ones in ovaries (Watson U^2 nonparametric test; $P < 0.05$). The spent stage was rarely observed in females, while being the dominant stage in males from April to July 2000 (Fig. 4). From March to August 2000 and in March and April 2001, ovaries are mostly at the recovering or growing stages (Fig. 4). These stages in

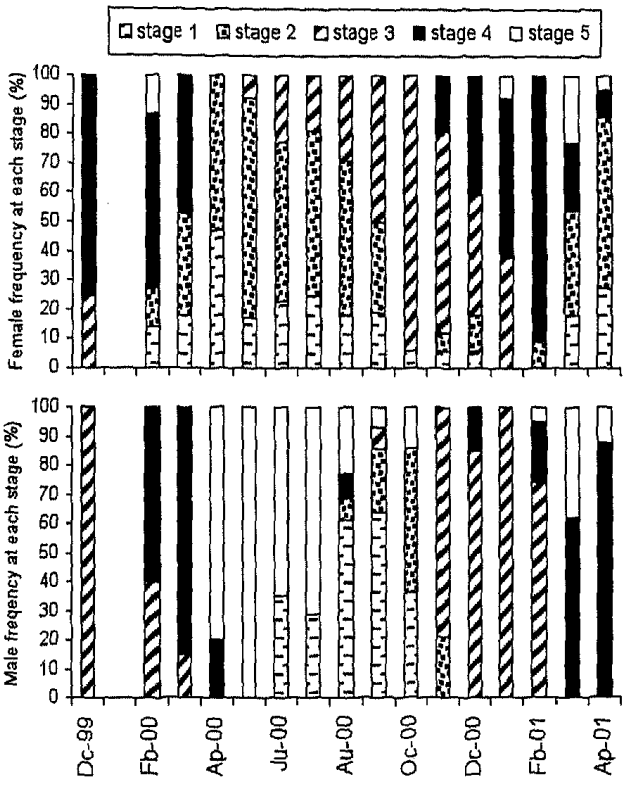

Figure 3. *Ophiomastix venosa*. Relative frequencies of the different gonadal stages for males and females from December 1999 to April 2001 (for description and illustration of stages 1-5, see text and fig 2.

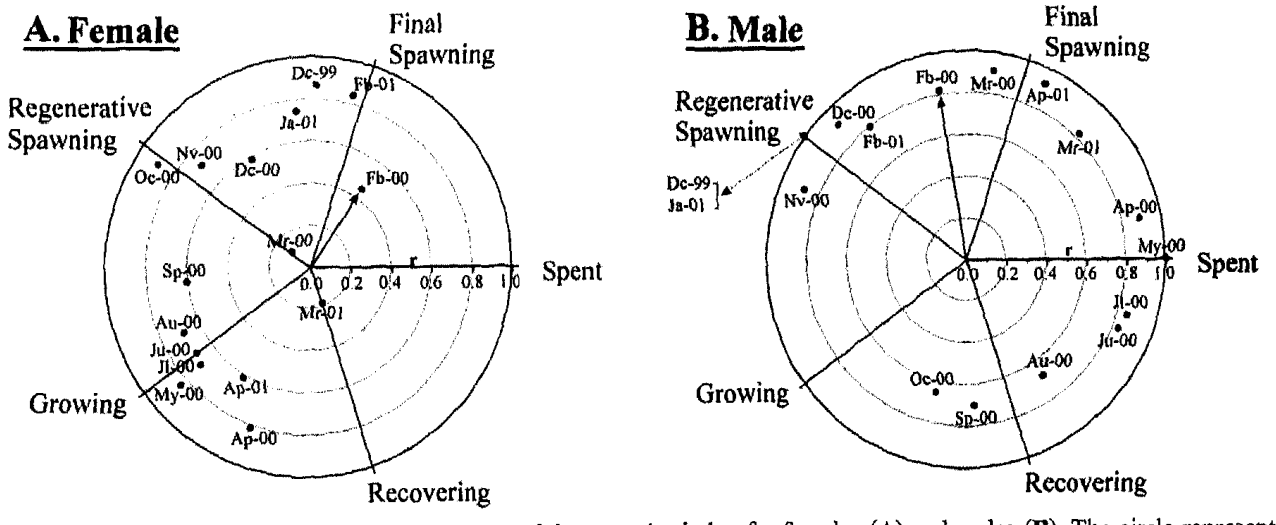

Figure 4. *Ophiomastix venosa*. Polar representation of the maturity index for females (**A**) and males (**B**). The circle represents the gametogenic cycle with the five identified maturity stages. One vector only is represented in both graphs and its direction points to the maturity stage, and r is the vector length, which is proportional to the homogeneity of the samples.

males lasted from June to October 2000 and from August to November 2000. Females able to spawn were found throughout the study period except in April 2000. If we consider the spawning season as the period where gonad stages III and IV are dominant in both males and females, then it lasted from December 99 until February 2000 and from November 2000 until February 2001. This is also the period where larger oocytes were found in the ovaries (Fig. 5A). Homogeneity in maturity stages is greater in males than in females (Fig. 4, length of the vector close to 1), and females are particularly poorly synchronized in March 2000 and March 2001 (Fig. 4, length of the vector close to 0), which corresponds to the end of the spawning season. Considering at once the number of gonads per individual (ca. 150), the mean diameter of premature oocytes (ca. 350 mm), and the number of premature oocytes in a ripe ovary (ca. 150), one may roughly estimate that fully mature, adult females of *O. venosa* (disk diameter ca. 20 mm) should hold at least 22 10^3 premature oocytes.

Ophiocoma scolopendrina. Gonad activity in *O. scolopendrina* is strikingly different than in *O. venosa* as gametogenesis is continuous in the former and occurs year-long (except for some period of rapid gonad recovering). Although gametogenesis varies in intensity during the year (which leads to gonad size variations), no growing stage could be recognized: achieved gametes (*i.e.*, premature oocytes and spermatozoans) occur at any period of the year and spawning takes place as soon as they appear in the gonad. We thus were able to describe only two stages for *O. scolopendrina* gonads: a mature-spawning stage and a recovering stage. As in *O. venosa*, the oocytes of *O. scolopendrina* are PAS negative when previtellogenetic (range: 10 to 30 µm in diameter), PAS positive when vitellogenetic (range: 25 to 50 µm in diameter), and intensively PAS positive when premature (range: 40 to 100 µm in diameter).

Mature gonads (Fig. 6A, B, E & F). Mature gonads are characterized by continuous gametogenesis and spawning: ovaries always contain oocytes at every stage of development, and testes always include spermatogonia, spermatocytes and spermatozoans. Depending on recent spawning episodes, gametes can be either densely packed or loosely arranged. When gametes were loosely arranged, small amounts of phagocytes can be found between them.

Recovering gonads (Fig. 6C, D, G & H). Recovering gonads have a shrunken appearance. Their lumen is either empty or filled with phagocytes; some unspent gametes may still occur. In most cases, lines of either oogonia or spermatogonia are seen along the gonad wall. In more advanced gonads, oogonia and previtellocytes co-occur in ovaries as well as spermatogonia and spermatocytes in testes.

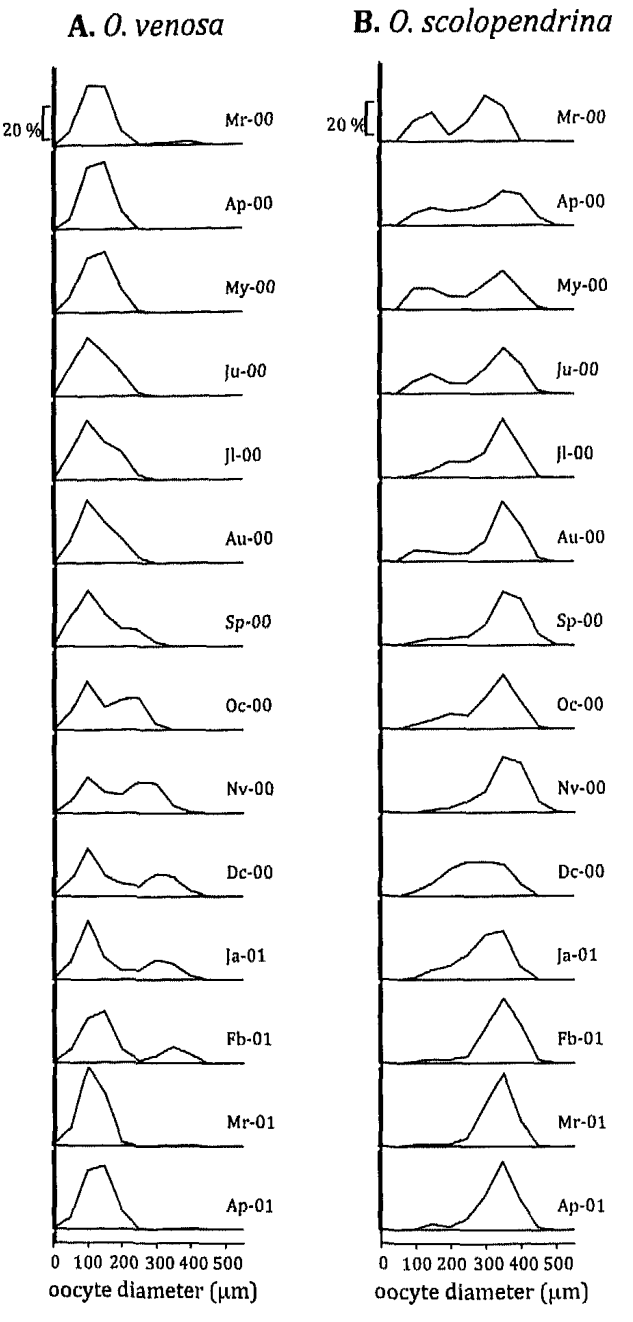

Figure 5. Oocyte size-frequency distributions of females of *O. venosa* (**A**) and *O. scolopendrina* (**B**).

Reproduction in *O. scolopendrina* is continuous, although short periods of gonad recovery have been observed. In agreement with that, large oocytes occur year-round in the ovaries of the species (Fig. 5B). Since only mature and recovery gonads can be described, it was rather easy to follow the change in proportion of mature individuals through the year (Fig. 7). Except for March 2000 (male individuals) and March 2001 (male and female individuals), mature individuals accounted for more than 80% in the studied population of *O. scolopendrina*. Considering at once the number of gonads per individual

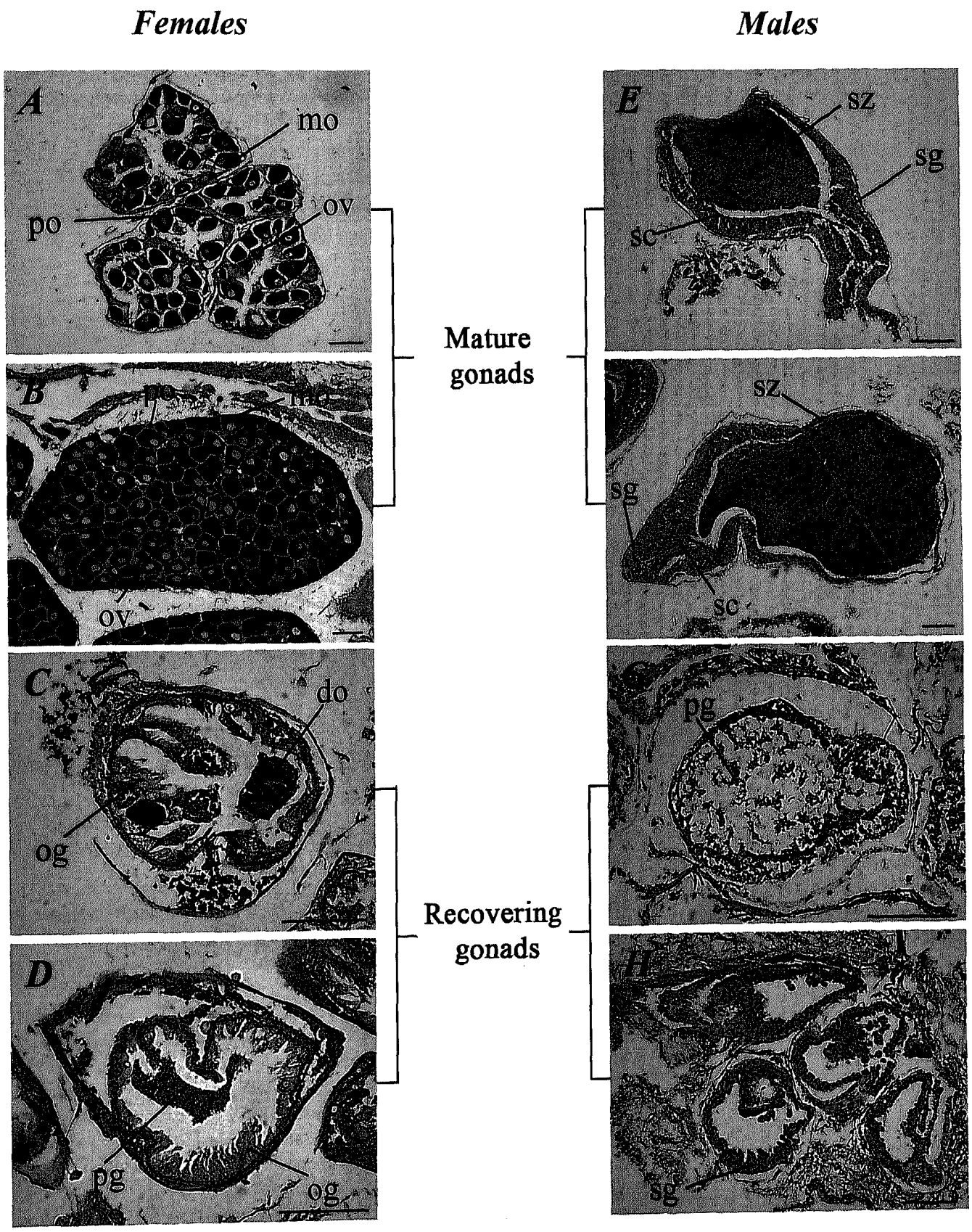

Figure 6. *Ophiocomina scolopendrina*. Histology of the ovaries (**A-D**) and testes (**E-H**) showing the mature and recovering stages. See text for further description. Do, denerating oocyte; mo, mature oocyte; og, oogonia; ov, oocyte in vitellogenesis; pg, phagocytes; po,

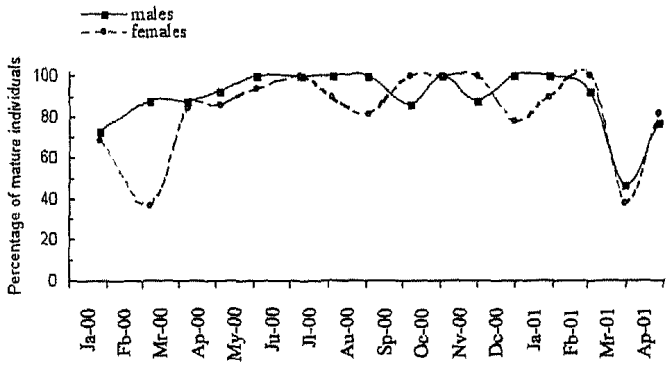

Figure 7. *Ophiocomina scolopendrina.* Percentage of matures males and females during the study period.

(ca. 300), the mean diameter of premature oocytes (ca. 70 µm), and the number of premature oocytes in a ripe ovary (ca. 4000), one may roughly estimate that fully mature, adult females of *O. scolopendrina* (disk diameter ca. 18 mm) should hold at least 12 10^5 premature oocytes.

Indices and environmental parameters

A marked annual variation was observed in seawater temperature and day length (Fig. 2C). Temperature variations actually fit the two seasons which prevail in the Toliara area, a warm and humid austral summer (from October to March) and a cool and dry austral winter (from April to September). Correlations between GI and MI of *O. venosa* and the two measured environmental parameters are represented in table 1. A significant positive correlation was observed between GI and temperature, and GI and day length for both male and female individuals. A significant correlation (C-association) was also observed between MI and these two parameters. These results reflect the observation that the period when a majority of males and females are able to spawn is restricted to the warmest and more enlightened months of the year. As for *O. scolopendrina*, there is no correlation between GI and temperature (Pearson correlation, $p > 0.05$) while GI is positively correlated with day length (Pearson correlation, $p < 0.01$).

Recruitment

Changes in size-frequency distributions of *O. venosa* and *O. scolopendrina* from March 2000 to February 2001 are illustrated on Fig. 8. For the two species, we considered as newly recruited individuals those whose disk diameter is less or equal to 4 mm. Recruits in *O. venosa* were present in all monthly samples except in November and December 2000 and in February 2001. In most samples they were rather scarce, representing less than 1.4% of the total population except from February to May 2000 where they accounted for 2.7 to 5.1%. Recruits in *O. scolopendrina* were seen yearlong. Their abundance was high in March to May and in October 2000, where they represented from 8.1 to 13.4% of the total population. In all the other months they accounted for maximum 5%.

Table 1. *Ophiomastix venosa.* Correlation between the reproductive indices and measured abiotic parameters.

	Temperature	Day length
GI-female	$r = 0.43$, $p < 0.01$	$r = 0.53$, $p < 0.01$
GI-male	$r = 0.67$, $p < 0.01$	$r = 0.61$, $p < 0.01$
MI-female	$D_n = 0.82$, $p < 0.01$	$D_n = 0.88$, $p < 0.01$
MI-male	$D_n = 0.74$, $p < 0.01$	$D_n = 0.88$, $p < 0.01$

Discussion

Ophiocoma scolopendrina and *Ophiomastix venosa* are the two most abundant ophiuroids on the Great Reef of Toliara and their populations stand very close to one another, but they display two very different reproductive strategies: the former reproduces continuously and recruits are found year-round while the latter has a clear annual reproductive cycle and recruitment period. Individuals of both species undergo successive spawning episodes during the breeding period and spawning seems to occur as soon as mature gametes appear in the gonad. Shed gametes are rapidly replaced by newly formed ones either year-round (*O. scolopendrina*) or during the whole regenerative spawning stage (*O. venosa*). That ophiuroids with prolonged breeding period continuously produce gametes during that period is not uncommon (Gage & Tyler, 1982; Selvakumuraswamy & Byrne, 1995; Falkner & Byrne, 2003). Yet the case of *O. scolopendrina* is somewhat particular as its breeding period corresponds to the entire year, which suggests that adult individuals in the investigated population produce gametes continuously during all their life.

Gametogenesis in *O. venosa* started shortly after spawning in females and began ca. six months later in males. Such a delay has already been noted in other ophiuroid species (Patent, 1969; Fenaux, 1970). As a consequence, while both males and females of *O. venosa* have a breeding period of about six months, they overlap for four months only (November to February), what corresponds to the austral summer.

The question here is why these two ophiuroid species, whose representatives co-exist and which are both successful in term of population density (they are the two most abundant ophiuroids in the boulder tract area of the Toliara reef; Fourgon et al., 2007) display so different reproductive strategies? Yet, while individuals of these two species are living in close vicinity, the exact location of their respective populations is not the same. Indeed *O. scolopendrina* inhabits dome areas whereas *O. venosa* is almost always seen in tidal channels (Fourgon et al., 2007). Strong tidal

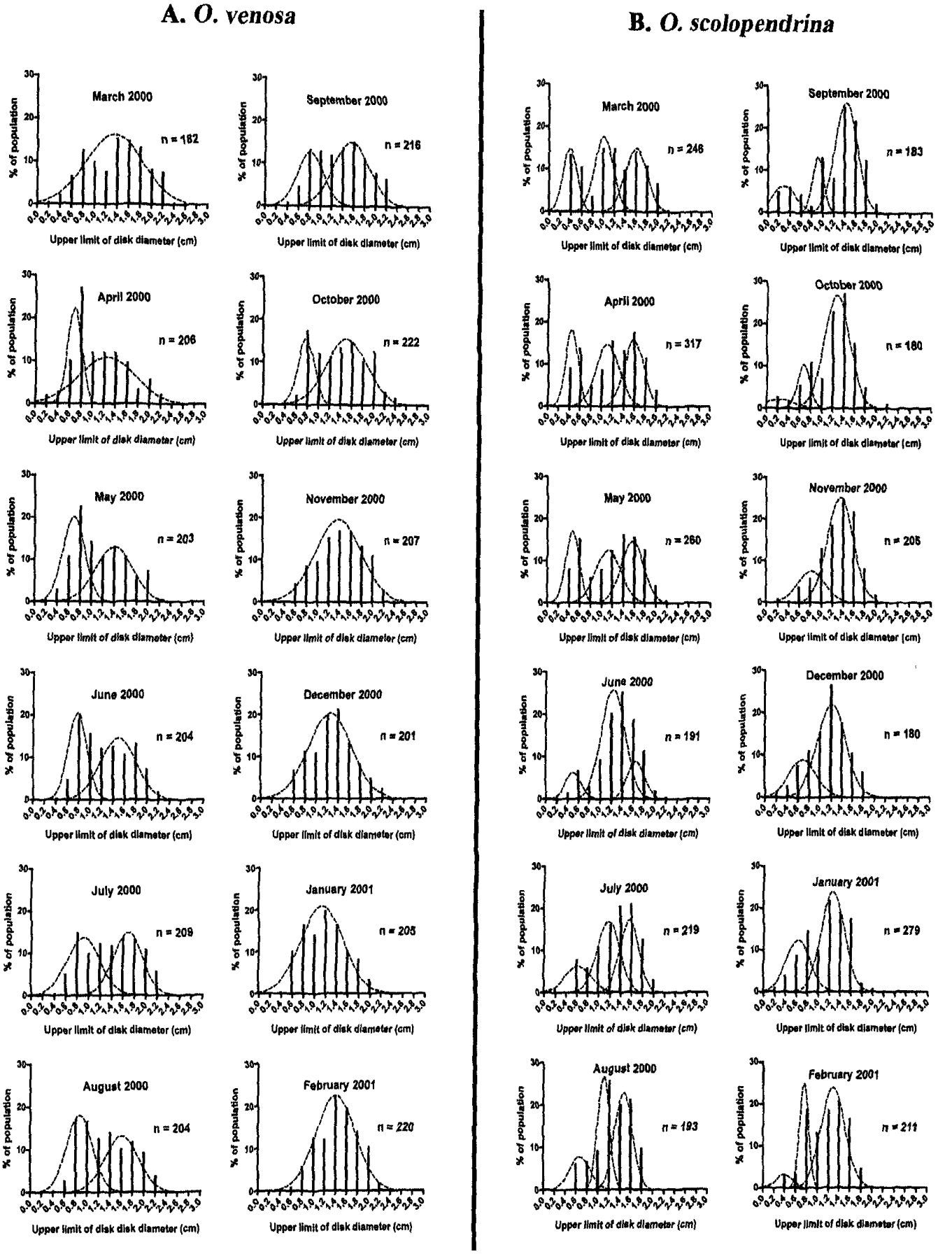

Figure 8. *Ophiomastix venosa* (Fourgon et al., 2007) & *Ophiocomina scolopendrina*. Disk diameter frequency distributions from March 2000 to February 2001. The normal components representing the cohorts are depicted. N = number of specimens.

currents occur in the channels that are permanently immersed. On the contrary, inhabitants of the domes are less hydrodynamically stressed. While being regularly emerged at low tide, they are submitted to more gentle currents either in rising or lowering tides. Moreover, the two species exhibit a different feeding biology. *O. scolopendrina* is rather opportunistic being both deposit- and suspension-feeder (Magnus, 1967; James & Pearse, 1969; Chartock, 1983). In the Toliara population, all individuals were seen catching neustonic particles during every rising tides, a food that is known to be highly energetic (Daumas & Thomassin, 1977). One may recall that, when emerged, *O. scolopendrina* display a particular arm curling behaviour, which allows them to retain water and remain wet during the period of hot air exposure (Fourgon et al., 2007). As a consequence of such arm arrangement, individuals immediately start feeding by raising their arms as soon as the water level increases. Clearly *O. scolopendrina* appears to be an opportunistic feeder to which, in addition, energy-rich neustonic food should be provided year-round. As for *O. venosa,* it was observed to be a deposit-feeder (Fourgon et al., 2006), thus depending on benthic food supply for the accomplishment of its biological processes.

According to Hendler (1991), the timing of the spawning period in echinoderms would constitute a compromise between optimal conditions for larval development and juvenile settlement on one side, and optimal gonad growth in the adults on the other side. There is clearly no need for such compromise in the investigated population of *O. scolopendrina*, as optimal conditions appear to be met all year long. Indeed reproduction and recruitment are continuous in that species, which implies that conditions for larval development and metamorphosis should be optimal too. One should note that *O. scolopendrina* has planktonic planktotrophic larvae (Mortensen, 1937) and that fully developed ophiopluteus are observed 20 days after fertilization (Fourgon, personal observations). The life-strategy of *O. scolopendrina* is to produce high number of gametes so that larvae always occur in great number in the area, which results in a high recruitment success. (Note that boulder tract domes are numerous all along the Toliara barrier reef [i.e., ca. 20 km] and that they always harbour dense populations of *O. scolopendrina.*) That *O. scolopendrina* almost exclusively occur in the dome area could result from the high interspecific competition for space that would occur between ophiuroids in reef channels (up to five ophiuroid species: *O. venosa*, *Ophioplocus imbricatus*, *Ophiocoma erinaceus*, *Ophiolepis cincta* and *Ophiocoma brevipes*, were observed in tidal channels against one or two in the dome area where *Ophioplocus imbricatus* sometimes co-occurred in few number with *O. scolopendrina*; Fourgon, personal observation). Yet, this would rather be the consequence of the high tolerance of *O. scolopendrina* to air-drying allowing individuals to colonize places where other species cannot survive.

The situation is different in *O. venosa* which has an annual gonad cycle. In that species gonad growth and spawning period correspond to the austral spring and summer, respectively, and new recruits are observed the following months (February to May). *O. venosa* has planktonic lecithotrophic larvae (Fourgon et al., 2005). Yet this appears not to be linked to its habitat as other channel inhabiting species have either a planktotrophic (e.g., *Ophiocoma erinaceus*; Mortensen, 1937) or a lecithotrophic (e.g., *Ophiolepis cincta*; Mortensen, 1938) planktonic larva. However, *O. venosa* is clearly the most abundant ophiuroid species in the channels; it is also the most abundant species observed on the Toliara barrier reef after *O. scolopendrina*. Given that it has a well-defined annual reproductive cycle and that it produces much larger oocytes, *O. venosa* clearly spawn much less gametes than *O. scolopendrina*. Fewer larvae thus appear in the water column where they would be seen for a few months only (3 against 12 for *O. scolopendrina* larvae). The success of *O. venosa* could partly rely on the short time their larvae require to metamorphose (8 days compared to at least 15 to 30 days in ophiuroids with planktotrophic larvae; Hendler, 1991). It could be due also to the fact that juvenile *O. venosa* occur on the dome area where they can survive providing they behave as symbiont of adult *O. scolopendrina*, a symbiosis allowing them to resist emersion (Fourgon et al., 2007). This clearly allows *O. venosa* to enlarge its recruitment area and to increase the number of adult individuals in the channel populations. Indeed, when becoming young adults, dome-inhabiting *O. venosa* necessarily either die or migrate towards the neighbouring tidal channel (adults of *O. venosa* were never seen free nor as symbiont in any dome area of the Toliara barrier reef).

Acknowledgments

The national fund for scientific research (FNRS - Belgium) and the university commission for development (CUD) provided substantial support for this work. J. Delroisse is supported by a doctoral research grant from the "National fund for Scientific Research (FNRS)". D. Fourgon was supported by a doctoral research grant from the "National Fund for Scientific Research".

References

Böhning D., Schlattmann P. & Lindsay B. 1992. Computer-assisted analysis of mixtures (C.A.MAN): statistical algorithms. *Biometrics*, **48**: 283-303.

Chartock M.A. 1983. Habitat and feeding observations on

species of *Ophiocoma* (Ophiocomidae) at Enewetak. *Micronesica*, **19**: 131-149.

Daumas R. & Thomassin B.A. 1977. Protein fractions in coral and zoantharian mucus, possible evolution in coral reef environment. *Proceeding 3rd international Coral Reef Symposium* (D.L. Taylor ed), pp. 517-523. Rosenstiel School of Marine and Atmospheric Science: Miami, Fl.

Falkner I. & Byrne M. 2003. Reproduction of *Ophiactis resiliens* (Echinodermata: Ophiuroidea) in New South Wales with observations on recruitment. *Marine Biology*, **143**: 459-466.

Fenaux L. 1970. Maturation of the gonads and seasonal cycle of the planktonic larvae of the ophiuroid *Amphiura chiajei* Forbes. *Biological Bulletin*, **138**: 262-271.

Fisher N.I. 1993. *Statistical analysis of circular data.* Cambridge University Press: Cambridge. 277 pp.

Fourgon D., Eeckhaut I., Vaïtilingon D. & Jangoux M. 2005. Lecithotrophic development and metamorphosis in the Indo-West Pacific brittle star *Ophiomastix venosa* (Echinodermata: Ophiuroidea). *Invertebrate Reproduction & Development*, **47**: 155-165.

Fourgon D., Jangoux M. & Eeckhaut I. 2007. Biology of a "babysitting" symbiosis in brittle stars: analysis of the interactions between *Ophiomastix venosa* and *Ophiocoma scolopendrina*. *Invertebrate Biology*, **126**: 385-395.

Fourgon D., Lepoint G. & Eeckhaut I. 2006. Assessment of trophic relationships between symbiotic tropical ophiuroids using C and N stable isotope analysis. *Journal of the Marine Biological Association of the United Kingdom*, **86**: 1443-1447.

Gabe M. 1968. *Techniques histologiques.* Masson: Paris. 1113 pp.

Gage J.D. & Tyler P.A. 1982. Growth and reproduction of the deep-sea brittlestar *Ophiomusium lymani* Wyville Thompson. *Oceanologica Acta* **5**: 73-83.

Hendler G. 1991. Echinodermata: Ophiuroidea. In: *Reproduction of Marine Invertebrates, vol. 6, Echinoderms and Lophophorates*, (A.C. Giese, J.S. Pearse & V.B Pearse eds), pp. 355-511. Boxwood Press: Pacific Grove, Ca.

Hendler G., Grygier M.J., Maldonado E. & Denton J. 1999. Babysitting brittle stars: heterospecific symbiosis between ophiuroids (Echinodermata). *Invertebrate Biology* **118**: 190-201.

James D.B. & Pearse J.S. 1969. Echinoderms from the Gulf of Suez and the northern Red Sea. *Journal of the Marine Biological Association of India*, **11**: 36-41.

Macdonald P.D.M. & Pitcher T.J. 1979. Age-groups from size-frequency data: a versatile and efficient method of analysing distribution mixtures. *Journal of the Fisheries Research Board of Canada*, **36**: 987-1001.

Magnus D.B. 1967. Ecological and ethological studies and experiments on the echinodermsof the Red Sea. *Studies in Tropical Oceanography*, **5**: 635-664.

Moloney P. & Byrne M. 1994. Histology and ultrastructure of the ovaries and oogenesis in the ophiuroid *Ophionereis schayeri*. In: *Echinoderms through time (Echinoderms Dijon)*, (B. David, A. Guille, J.P. Féral & M. Roux, eds), pp. 463-469. Balkema: Rotterdam.

Mortensen T. 1937. Contribution to the study of the development and larval forms of Echinoderms III. *Det Kongelige Danske Videnskabernes Selskabs Skrifter, Naturvidenskabelig og Mathematisk Afdeling*, **7**: 1-65.

Mortensen T. 1938. Contribution to the study of the development and larval forms of Echinoderms IV. *Det Kongelige Danske Videnskabernes Selskabs Skrifter, Naturvidenskabelig og Mathematisk Afdeling*, **7**: 1-59.

Patent D.H. 1969. The reproductive cycle of *Gorgonocephalus caryi* (Echinodermata; Ophiuroidea). *Biological Bulletin*, **136**: 241-252.

Selvakumaraswamy P. & M. Byrne. 1995. Reproductive cycle of two populations of *Ophionereis schayeri* (Ophiuroidea) in New South Wales. *Marine Biology*, **124**: 85-97.

Spirlet C., Grosjean P. & Jangoux M. 1998. Reproductive cycle of the echinoid *Paracentrotus lividus*: analysis by means of the maturity index. *Invertebrate Reproduction & Development*. **34**: 69-81.

Yoshida M. 1952. Some observation on the maturation of the sea urchin, *Diadema setosum*. *Annotationes Zoologicae Japonenses*, **25**: 265-271.

Zar J.H. 1996. *Biostatistical analysis.* 3rd ed. Prentice-Hall: Upper Saddle River, NJ.