



Seasonality in the reproductive biology of a shelf-dwelling galatheid (Crustacea: Decapoda): an example from a Western Mediterranean population of *Munida iris rutllanti*.

Antonio SANZ-BRAU, Francesc MEZQUITA and Sebastián SANZ.

Universitat de València - Departament de Microbiologia i Ecologia

Dr. Moliner, 50. E-46100 Burjassot (Spain)

Fax: (34) 9 63 98 30 99; e-mails: francesc.mezquita@uv.es; sebastian.sanz@uv.es

Abstract: A glance at the literature is enough to establish that seasonality of the reproductive features is not a general trend among galatheid decapods. The most important factor determining population dynamics is the depth at which each species dwells. A program was carried out to study the reproductive biology of the shelf-dwelling *Munida iris rutllanti* using all the captures landed by commercial trawlers in the València Harbour area (W. Mediterranean, Spain). The program lasted from February 1986 to October 1987, during which time 5116 specimens were collected. The following biological features were recorded: size of individuals, percentage of ovigerous females and sex ratio. All this information was then analysed using a number of statistical approaches, including time-series analyses. Most of these features greatly vary with time, indicating that the reproductive dynamics of this population is seasonal in nature. These conclusions are supported by an analysis of the seasonal changes in size class frequencies. The relationships between variables are outlined, allowing us to draw inferences regarding other populational traits, such as time of recruitment or life span.

Résumé: Rythme saisonnier de la reproduction d'un galathéidé (Crustacea : Decapoda) : l'exemple d'une population de *Munida iris rutllanti* en Méditerranée Occidentale. Selon la littérature la périodicité de la reproduction n'est pas générale chez les décapodes galathéides. La dynamique des populations est essentiellement sous l'influence de la profondeur à laquelle vivent les espèces. La biologie de la reproduction de *Munida iris rutllanti* a été étudiée grâce à des récoltes réalisées par des chalutiers aux alentours du port de Valence (Méditerranée Occidentale, Espagne), entre février 1986 et octobre 1987. Les caractéristiques suivantes ont été déterminées : taille des animaux, pourcentage des femelles ovigères et sex-ratio. Ces données ont été traitées par différentes méthodes statistiques, incluant des séries temporelles. La plupart de ces caractéristiques changent suivant la saison, ce qui montre que la dynamique de la reproduction est de type saisonnier. Ces conclusions sont confirmées par les résultats de l'analyse de l'évolution des fréquences de tailles. Leurs relations avec d'autres variables permettent de dégager d'autres caractères liés à la dynamique des populations tels que la longévité et l'arrivée des nouvelles recrues.

Keywords: *Munida iris rutllanti*, Galatheids, Seasonality, Reproductive biology, Western Mediterranean.

Introduction

Most galatheids, at least as adults, are benthic organisms. Ecological exclusion and habitat fragmentation along a

bathymetric gradient, ranging from shallower waters to abyssal plains (Wenner, 1982; Williams, 1984; Harnoll et al., 1992; Fariña & Pereiro, 1995) seem to be the likely key to explain the galatheid distribution. Environmental factors such as temperature, light intensity and food availability (factors affected by depth) are important parameters which influence the reproductive dynamics of crustaceans in

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general (Sastry, 1983). Although a simplistic life history cannot be outlined, some trends can be inferred from the data collected by several authors (Zariquiey-Álvarez, 1968; Wenner, 1982; Williams, 1984; Zeldis, 1985; Hartnoll et al. 1992). Thus, seasonal patterns have been shown in species inhabiting shallower waters (*Galathea squamifera* Leach, 1814, *Munida curvimana* A. Milne-Edwards & Bouvier, 1894), continental shelf (*Munida iris* A. Milne-Edwards, 1880, *M. intermedia* A. Milne-Edwards & Bouvier 1899, *M. gregaria* (Fabricius, 1795)) or even continental slope (*M. sarsi* Huus, 1935) whereas they are less obvious in species from abyssal plains (*Munida tenuimana* Sars, 1872, *M. microphthalma* A. Milne-Edwards, 1880, *Munidopsis* spp.). Nevertheless, the nature of the mechanisms involved in these seasonal patterns is not clear. The dynamics and trophic regime of larvae, which are both influenced by the depth at which adults dwell, seem to play a major part (examples from the genus *Munidopsis*, see Wenner (1982) and Sastry (1983) for an overview on decapods). Furthermore, abyssal species can also display seasonal breeding periods in some groups of decapods other than galatheids (Hartnoll et al., 1987).

The geographic latitude is another, superimposed factor. Many works and reviews point to the fact that the bathymetric range of a given species varies along its latitudinal range (Williams, 1984; González-Gurriarán & Olaso, 1987; García-Raso, 1989; Freire et al., 1992; Hartnoll et al., 1992; Fariña & Pereiro, 1995).

Munida iris rullanti Zariquiey-Álvarez, 1952, is a shelf-dwelling galatheid decapod, which was described as a subspecies of *Munida iris* by Zariquiey-Álvarez (1952). The subdivision of *M. iris* into two subspecies is based on morphological characteristics such as ornamentation of pereopod, maxillipeds and chelipeds, and it also reflects difference in the geographical range of *Munida iris* populations. For instance, *Munida iris iris* A. Milne-Edwards, 1880 is widely distributed along Western Atlantic shores (Coelho & Ramos, 1972; Wenner, 1982; Williams, 1984; Pohle, 1988), whereas *Munida iris rullanti* dwells on Eastern Central Atlantic coasts with some populations in westernmost areas of the Mediterranean Sea, such as the Alborán Sea or the Spanish coast near Sant Antoni Cape (Zariquiey-Álvarez, 1952, 1968; García-Raso, 1989; Sarda & Palomera, 1981; Guillén, 1990). Some authors consider these two subspecies as distinct species (Noël, 1992) according to the same criteria (Noël, unpublished).

Pèrs (1985) stressed that *Munida iris rullanti* is of special interest within the Mediterranean biota, because it occurs along the bathyal zone of the North African margin (from Gibraltar to Cap Bon in Tunisia) and is included into a group of species having an "Atlantic origin" (Pèrs op. cit., p. 226). According to this author, this group of species shares not only the same history but also ecological

characteristics, since they are all associated with muddy beds and are more or less eurybathic in character.

The presence of *Munida iris rullanti* was not recorded by either Castellón & Abelló (1983) or Sarda & Palomera (1981) along the Catalan shore, or Forest (1965) in the Balearic Islands. Then the València Harbour area is probably the northernmost area of this species' range along the Mediterranean coasts of the Iberian Peninsula and, even more, within the Western Mediterranean. The extreme geographical position of this area within the range of *M. iris rullanti*, makes this zone of particular interest from a biogeographical and ecological point of view.

The extent to which geographical and ecological factors influence the dynamics of *M. iris rullanti* populations has yet to be evaluated. In fact, data available on the biology of this subspecies is rather scarce. The sexual dimorphism of the subspecies and other biometric data were discussed in Sanz-Brau & Sanz-Santos (1993), and the predation on *M. iris rullanti* was also documented in Sanz-Brau & Morte (1992).

The aim of the present work is to survey populations of *M. iris rullanti* off València Gulf collected by commercial trawlers in València Harbour, in an attempt to clarify the seasonality in population dynamics. In our study area, the subspecies was found ranging in muddy beds on the outer part of continental shelf, at a depth varying from 100 to 200 meters. The subspecies is quite common in the Gulf of València area. Although there are no fisheries in this area trading with this species, *M. iris rullanti* is caught by trawlers which fish shrimps in similar habitats, such as *Aristeus antennatus* (Risso, 1816), *Aristeomorpha foliacea* (Risso, 1827) and *Parapenaeus longirostris* (Lucas, 1846). In the deepest parts of its bathymetric range, populations of *M. iris rullanti* seem to overlap with those of *Munida intermedia*, often being caught together. *Munida iris rullanti* is known to be an important prey for fishes which live at the same depth, such as the sharks *Galeus melastoma* Rafinesque, 1810 and for *Scyliorhinus canicula* (Linnaeus, 1758), but is also seldom preyed on by fishes inhabiting shallower waters (Sanz-Brau & Morte 1992).

Materials and methods

In order to study the main phases of the annual cycle of *M. iris rullanti*, a sampling project was started in 1986. 67 samples were collected during the period of time ranging from 13 February 1986 to 20 October 1987. These samples, collected from commercial trawlers operating from València Harbour (Fig. 1), did not allow to achieve a comprehensive information on population size, since data on lower size classes might be underestimated. However, the large number of samples collected in a regular way over a long

period of time allowed to test the hypothesis of seasonality in the reproduction of *M. iris rutilanti*.

A total number of 5116 specimens were processed. For subsequent analysis, samples were pooled into twenty consecutive monthly periods, except for August 1986, for which samples are lacking. *Munida iris rutilanti* is only of minor commercial interest, and is often sold together with *Munida intermedia* and *Macropipus tuberculatus* (Roux, 1830) from which it was sorted at the laboratory, then fixed with 70% ethanol. Sex and ovigerous state of females were checked and noted on each specimen. Carapace length (viz. distance between the ocular arch and the posterior dorsal edge of the cephalothorax) was taken, as it is a good estimator of individual's size, following the criteria set out by Hartnoll et al. (1992). All measurements were made with dial callipers to the nearest 0.1 mm. Specimens were grouped into 0.5 mm length classes to study length-frequency distributions.

Size frequency distributions (SFD) of each sex and for each month were tested for normality using the Kolmogorov-Smirnov test and also for the homogeneity of variances using the Levene test. For each sex, variation in mean size with respect to time was analysed using multi-sample Kruskal-Wallis test, and monthly samples were compared by pairs using Mann-Whitney U-test. We carried out within-month comparisons of the average size of males and females using the Mann-Whitney U-test. Comparisons between the size of ovigerous and non-ovigerous females were performed by an identical statistical approach. Monthly deviations from a 1:1 males / females ratio were studied by χ^2 test of goodness of fit (Sokal & Rohlf, 1995).

The temporal periodicity of the sex ratio, female size, male size, difference in size between sexes and percentage of ovigerous females were examined by means of autocorrelation analysis (SPSS Inc., 1994). Its significance and meaning is deduced from the patterns that occur in shape, together with those correlation coefficients that fall outside confidence limits. Both correlation and cross-correlation analyses were used to establish the relationship between parameters. Although not very frequently used, time-series analysis techniques give good results in populational studies, when a possible seasonality or periodicity effect is suspected (Begon et al., 1996; Guerao, 1995). Modal decomposition of the size-class histograms was performed with the program MIX following Macdonald & Green (1988) by fitting normal components to the data.

Results

I. Number and average size of individuals

The number and the average size of both males and females individuals collected each month are shown in Table 1.

Minimum and maximum individual size (length of cephalothorax) recorded for males was 9.4 and 21.9 mm respectively, and for females 10.0 and 21.2 mm respectively, whereas temporal fluctuations of the average size of both males and females ranged from 15.91 to 17.62 mm as a maximum.

Kolmogorov-Smirnov tests gave no significant deviations from normality ($p > 0.01$) of the SFD in any month and for any sex, but the variances were not homogeneous as resulting from a Levene test ($p < 0.01$). The results of Kruskal-Wallis tests lead to the rejection of the null hypothesis of the equality of averages over the study period ($\chi^2 = 170$, $p < 0.0001$ for females; $\chi^2 = 99.01$, $p < 0.0001$ for males). Recorded differences in size between individuals from different months were not erratic. In females, comparisons between months using Mann-Whitney U-test showed that individuals from summer periods (June - September 1986 and June - October 1987) were significantly larger than those from the rest of the study period. Females from January 1987 were significantly smaller than the rest. In males, specimens from summer (July - September 1986 and June - October 1987) and December 1986 were significantly larger than those from spring (April 1986 and April - May 1987). Males from January 1987 were significantly smaller than those from other months. Fig. 2 shows some of these results. Pattern in size variation is more clearly defined in females than in males, and this suggests a periodicity in the temporal evolution of these two parameters (males' and females' monthly average size). In this sense, size of females clearly behaves as a periodical variable, as inferred from the autocorrelogram in Fig. 3.

The difference recorded in size between males and females was not constant over time (see Fig. 2 and Fig. 4) and varies according to the season as it is shown in Fig. 3. Comparisons by Mann-Whitney U-test showed that differences ($p < 0.01$) took place within the autumn and winter months (February 1986 and the period October 1986 - March 1987).

II. Size frequencies

Length frequency distributions (Fig. 2) and their modal decompositions (Fig. 5) show that recruitment took place mainly in February - April for males and females in both the studied years. A striking decrease in the number of individuals is observed in the largest females during October. This trend was obvious in 1986, and corresponds to a decrease in the percentage of ovigerous females. In contrast, such a drastic event was not observed for males.

III. Sex ratio

The χ^2 test indicated significant deviations ($p < 0.01$) from a 1:1 males / females ratio during the following months:

Table 1. Data collected per month according to the sex. Mean size of length of cephalothorax (mm) \pm standard deviation and number of individuals (in parentheses).

Tableau 1. Données mensuelles en fonction du sexe : longueur moyenne du céphalothorax (mm) \pm écart type, nombre d'individus (entre parenthèses).

year	month	males	females			
			ovigerous	non-ovigerous	total females	
1986	February	17.17 \pm 1.90 (130)	17.09 \pm 1.08 (40)	16.03 \pm 1.47 (65)	16.33 \pm 1.43 (105)	
	March	16.70 \pm 2.05 (128)	16.74 \pm 1.23 (11)	16.45 \pm 1.57 (68)	16.49 \pm 1.52 (79)	
	April	16.66 \pm 1.81 (118)	16.76 \pm 1.36 (18)	16.47 \pm 1.64 (65)	16.53 \pm 1.58 (83)	
	May	16.90 \pm 1.61 (131)	16.48 \pm 1.31 (89)	16.51 \pm 1.29 (46)	16.49 \pm 1.30 (135)	
	June	17.04 \pm 1.79 (86)	17.20 \pm 1.72 (38)	15.83 \pm 2.25 (3)	17.10 \pm 1.77 (41)	
	July	17.62 \pm 1.58 (55)	17.20 \pm 1.09 (45)	16.44 \pm 1.23 (8)	17.08 \pm 1.13 (53)	
	September	17.28 \pm 1.71 (110)	17.06 \pm 1.29 (90)	16.45 \pm 2.00 (12)	16.99 \pm 1.39 (102)	
	October	17.00 \pm 1.72 (149)	16.34 \pm 1.47 (37)	16.06 \pm 1.50 (31)	16.21 \pm 1.48 (68)	
	November	17.08 \pm 1.79 (195)	17.26 \pm 1.42 (19)	16.12 \pm 1.48 (111)	16.29 \pm 1.52 (130)	
	December	17.49 \pm 1.60 (212)	16.99 \pm 1.83 (17)	16.53 \pm 1.93 (100)	16.60 \pm 1.91 (117)	
	1987	January	16.57 \pm 1.69 (206)	17.73 \pm 1.38 (9)	15.83 \pm 1.41 (211)	15.91 \pm 1.46 (220)
		February	17.09 \pm 1.73 (111)	16.84 \pm 1.62 (27)	16.08 \pm 1.52 (76)	16.28 \pm 1.57 (103)
March		16.87 \pm 2.08 (221)	17.64 \pm 0.75 (24)	16.09 \pm 1.57 (100)	16.30 \pm 1.57 (184)	
April		16.36 \pm 1.94 (226)	17.68 \pm 1.26 (12)	16.13 \pm 1.57 (211)	16.21 \pm 1.59 (223)	
May		16.62 \pm 1.87 (148)	16.45 \pm 1.48 (96)	16.29 \pm 1.77 (55)	16.39 \pm 1.58 (151)	
June		17.17 \pm 1.84 (120)	16.99 \pm 1.71 (92)	16.52 \pm 2.03 (10)	16.95 \pm 1.74 (102)	
July		17.51 \pm 1.65 (112)	17.45 \pm 1.54 (98)	17.81 \pm 0.93 (8)	17.47 \pm 1.50 (106)	
August		17.30 \pm 2.22 (66)	17.51 \pm 1.43 (38)	17.28 \pm 1.29 (5)	17.48 \pm 1.40 (43)	
September		17.45 \pm 1.81 (117)	17.52 \pm 1.32 (77)	15.92 \pm 2.71 (5)	17.42 \pm 1.47 (82)	
October		17.00 \pm 1.69 (203)	17.07 \pm 1.45 (72)	16.56 \pm 1.63 (73)	16.81 \pm 1.56 (145)	
total		16.99 \pm 1.83 (2844)	17.03 \pm 1.47 (949)	16.20 \pm 1.59 (1323)	16.54 \pm 1.59 (2272)	
mm		9.4	12.5	10.0	10.0	
max		21.9	21.2	21.2	21.2	

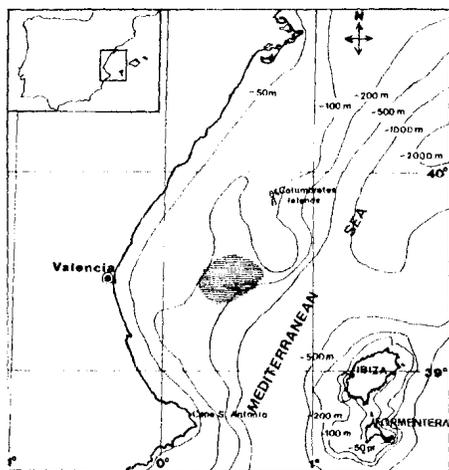


Figure 1. Location map of the studied area.
Figure 1. Carte de la zone étudiée.

March, June, October, November and December 1986, and October 1987. This information is summarised within Fig. 2. A slight trend seems to exist, and indicates that males are more abundant than females in late autumn. However, samples collected in winter 1986 did not behave similarly in winter 1987, and do not allow us to show a clear periodicity (Fig. 3).

IV. Ovigerous females

Ovigerous females were recorded throughout the whole period of the study (see Table 1, Fig. 2). The percentage of ovigerous females underwent pronounced changes with time, as shown in Fig. 4. From June to September of both 1986 and 1987, it increased to almost 90% of the females. The autocorrelagram associated with this parameter is shown in Fig. 3. A significant correlation is observed with a delay of exactly 12 months, an annual cycle.

Although the sampling method did not allow us to get information on dynamics of lowest-size classes (smaller animals are not usually caught), it should also be pointed out that these "lost" classes did not include the sexually mature fraction of the population at all. The histogram of Fig. 6 reveals that the two lower size classes are lacking the ovigerous state. Ovigerous females increase in proportion as we move towards higher size classes. The smallest ovigerous female observed in this study had a length of 12.5 mm, which may correspond to the initial size for spawning, although the average size of ovigerous females was 17.03 ± 1.47 mm.

Ovigerous females tend to be bigger than the rest of females. Significant differences, as obtained using Mann-Whitney U-tests, occurred in many monthly samples. A significant relationship ($r = 0.8349$; $P < 0.001$) was found between the average size of females of a given month and the percentage of females that were ovigerous (see Fig. 7).

Discussion

The percentage of ovigerous females of *Munida iris rullanti* follows a pronounced seasonal pattern. This should not come as a surprise: a look in literature indicates that the shallower the species lives, the more obvious the seasonal character in reproduction is. Deeper-living galatheids such as the populations of *M. tenuimana* from Porcupine Bay studied by Hartnoll et al. (1992) do not show clear temporal patterns in their reproductive traits, whereas the populations of *M. sarsi* (which dwells in shallower waters) from the same area show stronger seasonal trends. One must bear in mind that this study deals with populations dwelling on the outer continental shelf, therefore the water column above is more productive than the open sea and, moreover, this production undergoes important changes throughout the year (Estrada et al., 1985). This implies seasonal changes in food availability, which usually has important effects on synchrony of recruitment in benthic decapods with planktotrophic larvae (Sastry, 1983). Zeldis (1985) found that the shell-dwelling *M. gregaria* in New Zealand also showed strongly seasonal patterns in its population dynamics.

I. Life-span, overlap of generations and recruitment

Following accurate methodology, Zeldis (1985) was able to discriminate among annual cohorts of *Munida gregaria*, and found that members of a cohort can survive as benthic adults some 2-3 years on average. Since new offspring were produced once a year, cohorts from different years were found coexisting, at least to a certain extent. Our data on ovigerous females indicate that, even if a basal number of females carry eggs all the year long (5 to 15%), a clear

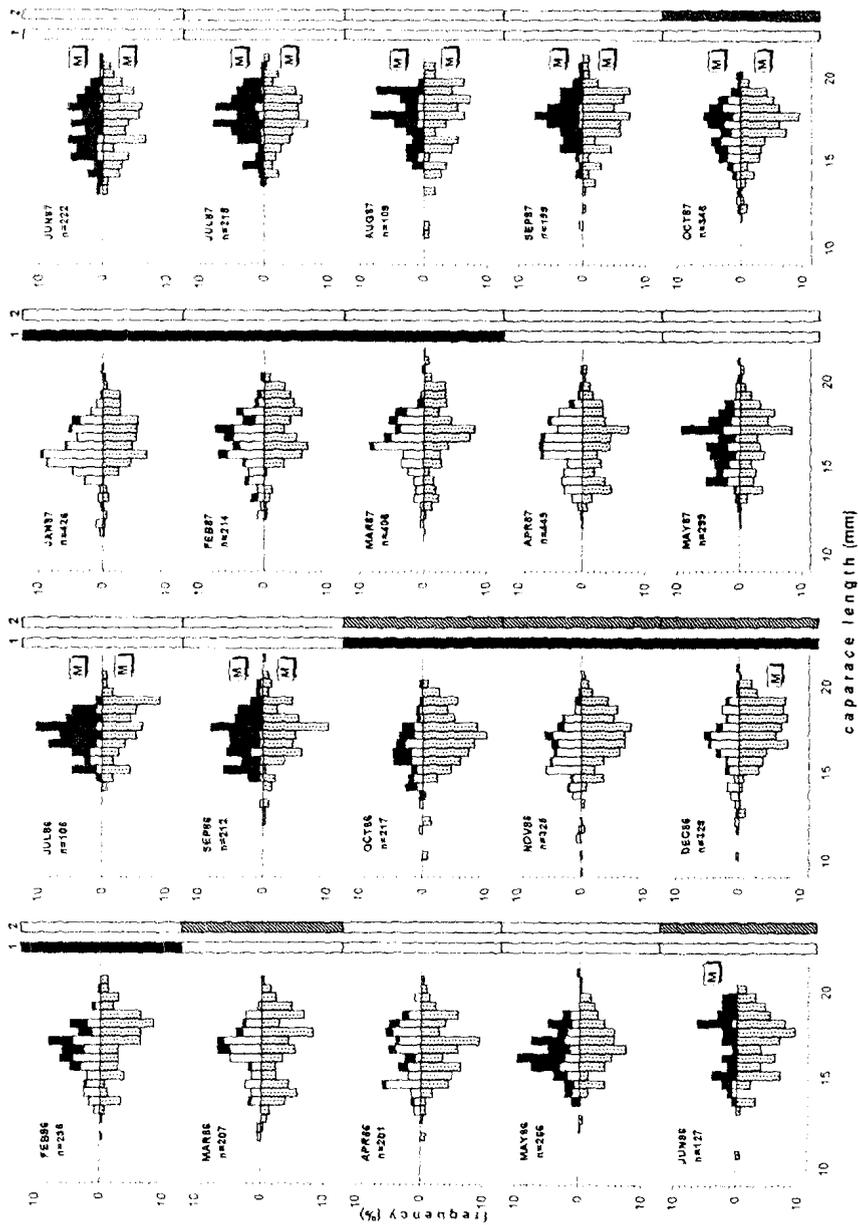
maximum is found in summer. Subsequently, a spawning peak is likely to occur in late summer-early autumn. This suggests that the concept of an «annual cohort» is valid in our case. If these cohorts could only survive one year, the population would be greatly disrupted in the late summer, as the old cohort would have to disappear before the newly produced offsprings had reached the benthic phase. This pattern has not been detected in our population, although the average size of individuals becomes lower in autumn. Subsequently, we can conclude that individuals of *M. iris rullanti* in this area can survive more than one year as benthic adults, meaning that cohorts overlap. In this sense, some different modes indicating cohorts can be observed in size-frequency distributions and their modal decomposition.

Recruitment in this population probably takes place in late winter and spring months. The histograms show a more left-skewed distribution during this period and display several modes. Knowing that lower size classes can be biased by sampling, we cannot provide definitive assumptions, however other approaches such as the modal decomposition and its temporal follow-up seem to reinforce the previous conclusion. The trends discussed below also suggest this inference could be the most acceptable scenario.

II. Sex-ratio and male-to-female size departures

Overall sex ratio was 2844 males (55.59%) for 2272 females (44.41%). This means a greater frequency of the former sex over the latter ($\chi^2 = 63.9531$, $P < 0.0001$). Similar overall values were obtained by Hartnoll et al. (1992) for *M. sarsi* in Porcupine Bay (55% males), although they found monthly ratios which were more extreme than ours. In the same study, *M. tenuimana* overall sex ratio was about 50% males. Conversely, Wenner (1982) found significant deviations of sex ratio in favour of females in *M. longipes* A. Milne-Edwards, 1880 and *M. valida* Smith, 1883.

Sex ratio remains biased towards males during a few months, at the end of summer and beginning of autumn, following the hatching peak. There are two likely explanations of the prevalence of males after the hatching period: one possibility is the occurrence of a spawning migration in females and the other is a season and sex dependent mortality affecting mainly ovigerous females. Unequal sex ratios have been explained by differential mortality rates for both sexes in the shallow-dwelling decapods *Palaemon adspersus* (Rathke, 1837) and *P. elegans* (Rathke, 1837) (see Berglund, 1981; Comides et al., 1992). In organisms such as galatheids, females carry the eggs, and have additional energy expenditure associated with ventilation. Moulting after hatching has been described in *M. sarsi* females (Hartnoll et al. 1992). Thus, there is a greater energy expenditure and a reduced protection against cannibalism or predation. Bearing this information in mind,

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◀ **Figure 2.** Monthly length-frequency histograms. Frequencies are expressed as percentages of the total number of individuals found in the sample. Each interval represents a 0.5 mm class. Bars above the axis: frequency of females (empty portion of each bar represents non-ovigerous whilst solid portion ovigerous females). Bars below the axis: frequency of males. Mann-Whitney U-tests are partly indicated for each sex. For the females, months noted with "M" (maximum) indicate those in which individuals were significantly larger than all others. For males, individuals for the months noted with "M" were not significantly bigger than all others, but only than individuals from spring (April 1986 and April - May 1987). Vertical bars represent differences in size between sexes (bar 1) and sex ratio (bar 2). Bar 1: filled bars indicate months in which differences in size are significant at 0.01 level. Bar 2: filled bars represent months in which deviations from 1:1 sex-ratio are significant at 0.01 level or lower.

Figure 2. Histogrammes des fréquences mensuelles des longueurs en pourcentage. Intervalles de 0,5 mm. Au-dessus de l'axe, les femelles (en clair femelles non ovigères ; en noir femelles ovigères). Au-dessous de l'axe, les mâles. Les contrastes U de Mann-Whitney sont indiqués pour chaque sexe ; pour les femelles, "M" (maximum) indique les mois où les spécimens sont significativement plus grands. Pour les mâles le "M" indique les mois où les spécimens ont une taille plus grande qu'au printemps (avril 1986 et avril-mai 1987). Les barres verticales latérales indiquent l'évolution de la différence de taille entre les deux sexes (barre 1) et la sex-ratio (barre 2). Barre 1 : les barres pleines représentent les mois où les différences de longueur sont significatives à 0,01. Barre 2 : les barres pleines représentent les mois où les déviations de la sex-ratio 1:1 sont significatives à 0,01 ou moins.

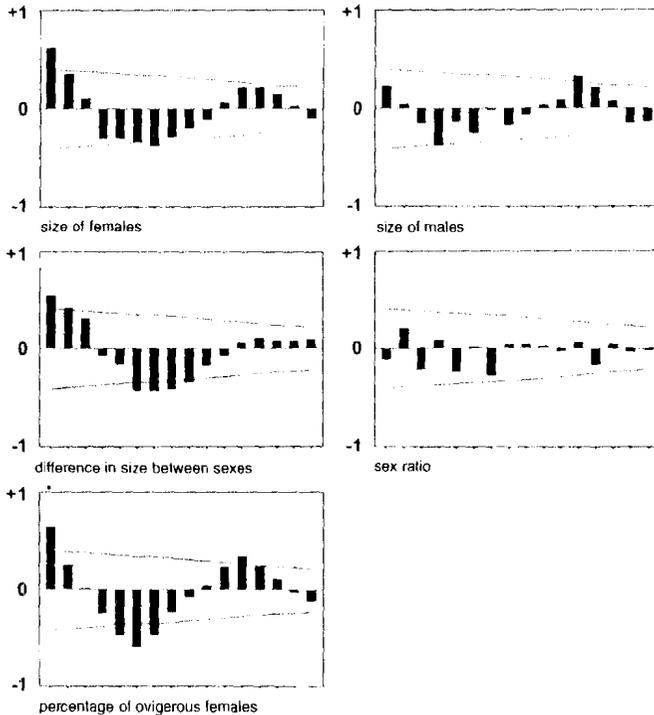


Figure 3. Autocorrelograms of several parameters. The vertical axis represents the autocorrelation coefficient whilst the horizontal axis represents the time-lag (months) with which the coefficient has been computed. Lines represent confidence intervals.

Figure 3. Autocorrelogrammes des divers paramètres. L'axe vertical indique le coefficient d'autocorrélation. L'axe horizontal représente le décalages de temps pour lesquels le coefficient d'autocorrélation a été calculé. Les lignes représentent l'intervalle de confiance.

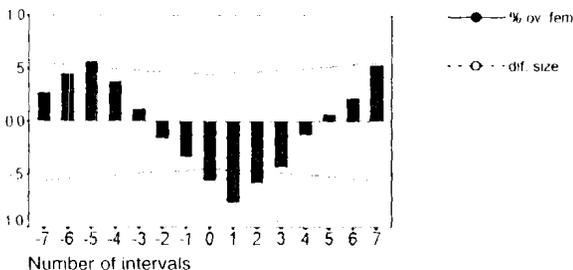
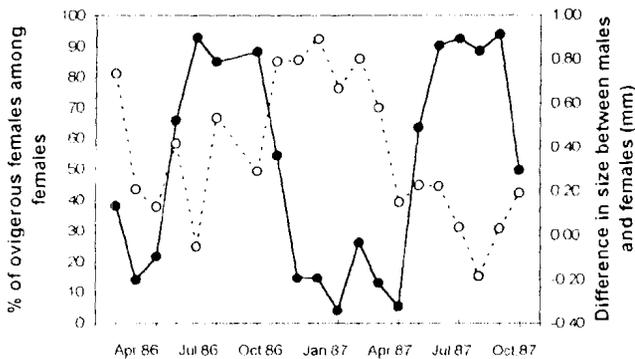


Figure 4. Parallel evolution of size differences between males and females (right axis) and percentage of ovigerous females on all females (left axis). A diagram of the crossed (lagged) correlations between these two parameters is also displayed.

Figure 4. Evolution parallèle des différences de longueur entre les mâles et les femelles (axe droit, pointillé) et pourcentage de femelles ovigères sur la totalité des femelles (axe gauche, ligne continue). On observe aussi une figure des corrélations croisées entre ces deux paramètres.

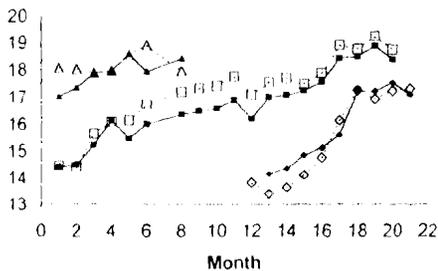


Figure 5. Temporal variations of the average size of males (white symbols) and females (black symbols) of *M. iris rullanti* within each age group as defined from the modal decomposition of size frequency distributions.

Figure 5. Variation au cours du temps de la taille moyenne des mâles (symboles blancs) et des femelles (symboles noirs) de *M. iris rullanti* pour chacun des groupes définis par l'analyse modale

one can suppose that energy allocation on reproduction and the associated mortality risk is greater for females than for males in these animals (see also Berglund, 1981). On the other hand, recent studies discuss on female spawning migration behaviour to explain sudden deviations of sex-ratio toward males in marine decapods (e.g. Feire et al. 1991; Creasey et al. 1997). These migratory movements of ovigerous females would probably be addressed to reach a maximum in the reproduction success, for example by liberating free planktotrophic larvae in more productive areas. In any case, the decrease in the number of females of the studied population would lead to the observed pronounced differences between male and female size (as only big, mature female are leaving the population). These differences were far from evident during spring and summer months. It should be pointed out that female size follows better defined seasonal patterns than that of the male, and this may suggest that seasonality in size difference is due to unexpected changes affecting the growth of females, but not

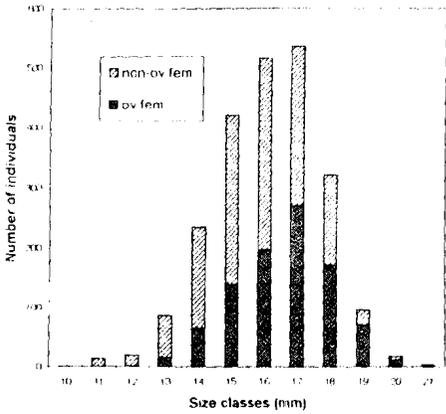


Figure 6. Overall distribution of the number of females in size classes. Bar indicates total number of females in a given class, lower (solid) portion representing ovigerous females and portion on top (hatched) indicating non-ovigerous females.

Figure 6. Distribution générale du nombre de femelles par classe de taille. La longueur totale des barres représente le nombre total des femelles dans une classe donnée, la partie sombre représente les femelles ovigères et la partie rayée représente les femelles non-ovigères.

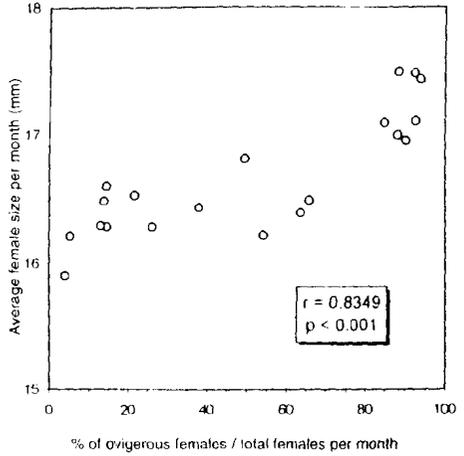


Figure 7. Percentage of ovigerous females on total number of females per month versus the mean size of females (mm) per month.

Figure 7. Pourcentage mensuel de femelles ovigères sur l'ensemble des femelles par mois, versus la taille moyenne mensuelle des femelles (mm).

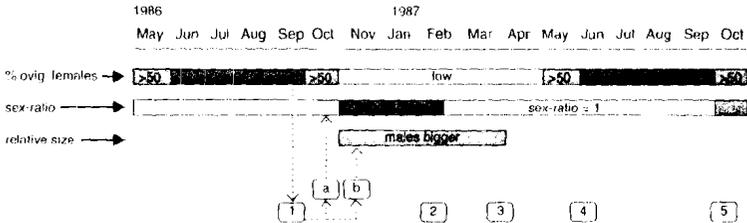


Figure 8 Diagram showing the main events observed between two breeding seasons of the studied population of *Munida iris rutlandi*. (1): towards the end of the breeding season, mortality or (and) migration affect the oldest females. As a result, two changes in the population structure are observed in the following months: a) there is a deviation of the sex ratio in favour of males, b) size difference between males and females appears. (2): the incorporation of abundant younger individuals with a balanced sex ratio into the population results in a new sex ratio close to 1. (3): The size difference observed between males and females disappears slowly, decreasing when old males die and the new generation grows. (4): the population enters the next breeding season with a balanced sex ratio and no size differences between sexes. (5): events similar to those described in 1(a) and (b) renew in the next breeding season.

Figure 8 Diagramme résumant les principaux événements qui surviennent entre deux périodes de reproduction dans la population étudiée de *Munida iris rutlandi*. (1) : vers la fin de la saison de ponte survient une mortalité ou (et) une migration des femelles les plus âgées. Il en résulte deux changements dans la structure de la population : (a) une modification de la sex-ratio en faveur des mâles ; (b) l'apparition d'une différence de taille entre mâles et femelles. (2) : L'arrivée de nombreux jeunes individus, dont la population présente une sex-ratio équilibrée, conduit à une sex-ratio proche de 1. (3) : La différence de taille entre mâles et femelles disparaît progressivement avec la mort des mâles les plus âgés et la croissance des jeunes. (4) : à la saison de ponte suivante, la population se caractérise par une sex-ratio équilibrée et une taille comparable chez les mâles et les femelles. (5) : Des processus comparables à 1(a) et (b) réapparaissent à la fin de la saison de ponte suivante.

males. Conversely the effect of scantiness of females on the differences between male and female sizes persists much longer than the skewed sex ratio. Differences would decline only when the generation of old males disappeared and, concurrently, when males and females from new generations have reached bigger size. This would happen just before the beginning of the next breeding season, when the percentage of ovigerous females reach high values again. This dependent scantiness of females season (either due to differential mortality or spawning migration) also provides an explanation for one of the most striking facts we found: the negative correlation between the two parameters which have the more pronounced seasonal trend, *viz.* the percentage of ovigerous females and the difference in size between males and females ($r = -0.5518$; $P = 0.0120$). Furthermore, this relationship becomes more evident with a one lag-month crossed correlation analysis.

Similar shifts in sex ratio have been also observed in other members of the genus. For example, Hartnoll et al. (1992) found a pronounced scantiness of females in *Munda sarsi* following a post-hatching moult peak, but this phenomenon was not found in males. However, the authors explained it by a female's cryptic (burrowing) behaviour. Another study on *Munda gregaria* (Zeldis, 1985) surveyed three cohorts (from 1976, 1977 and 1978) during a five-year period in their latest phases. Paying attention to generations spawned in 1977 and 1978 (from March 1980) to March 1981; see Fig. 12 in Zeldis, *op. cit.*), a scantiness of females with regard to males is implicit.

Taking the percentage of ovigerous females as an indicator of mating and hatching periods (summer months), it becomes evident that during these months individuals of *M. iris rullanti* are bigger. This appears very patent among females ($r = 0.8349$, $P < 0.001$). Although significant, the relationship is less obvious for males ($r = 0.5996$; $P < 0.01$) and could be explained by the fact that bigger males could probably survive the breeding periods or not migrate as previously discussed. These tendencies are also related to the fact that ovigerous females tend to be bigger than non-ovigerous ones. The combination of these factors indicate that there is a more or less critical size reached by both females and males to be able to reproduce and that the population is, to a certain extent, synchronous on that point. This synchrony occurs in summer but is rapidly lost after that period, mortality, or migration, in older females leading to the differences between size of each sex and a male-biased sex ratio. During the rest of the cycle, while individuals from younger cohorts are incorporated into sexually mature classes and older males have left the population (less simultaneously than the older females did), these differences progressively disappear. At the beginning of each new breeding season, all these disturbances disappear, as it is shown in Fig. 8.

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