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Reproduction and moulting in *Liocarcinus depurator* (Linnaeus, 1758) (Brachyura: Portunidae) in the Northwestern Mediterranean sea*

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SUMMARY: Reproductive and moulting biology in the portunid crab *Liocarcinus depurator* are described from monthly samples taken from February 1984 to January 1985 in the northwestern Mediterranean Sea. The peak moulting period in females occurred at the end of spring, when copulation took place. Ovarian maturation then began. The maximum proportion of females with fully developed ovaries was found towards the end of summer and in autumn. The main spawning period began in November and lasted until January, however small numbers of ovigerous females occurred throughout the year. Most postecdysial females had sperm plugs in the gonopores. Size at sexual maturity in females is considered to be around 18-20 mm carapace length. Number of eggs carried by ovigerous females increased with size, ranging from about 30 000 to about 230 000. In males, moulting and maturity seasonal patterns are not as marked as in females.

Key words: Reproductive biology, moulting, Brachyura, Portunidae, *Liocarcinus depurator*, North-West Mediterranean.

RESUMEN: CICLO REPRODUCTIVO Y DE MUDA EN *LIOCARCINUS DEPURATOR* (Linnaeus, 1758) (BRACHYURA: PORTUNIDAE) EN EL MEDITERRÁNEO NOROCCIDENTAL. — El ciclo reproductivo y de muda en *Liocarcinus depurator* del Mediterráneo noroccidental se ha estudiado a partir de muestras mensuales tomadas entre febrero de 1984 y enero de 1985. El principal período de muda en las hembras ocurrió a finales de primavera. La cópula tiene lugar inmediatamente después de la muda, iniciándose a continuación la maduración ovárica. A finales de verano y en otoño se halló el máximo número de hembras con ovarios plenamente desarrollados. El principal período de puesta comenzó en noviembre, prolongándose hasta enero. No obstante, se detectó presencia de hembras ovígeras durante todos los meses del año. La mayor parte de las hembras en postmuda presentaron tapones de esperma en los gonoporos. La talla de madurez sexual en las hembras se encuentra alrededor de 18-20 mm de longitud de cefalotórax. El número de huevos transportado por hembras ovígeras aumenta con la talla, oscilando entre 30 000 y 230 000. En los machos, las pautas estacionales de madurez y muda no son tan marcadas.

Palabras clave: Reproducción, muda, Brachyura, Portunidae, *Liocarcinus depurator*, Mediterráneo noroccidental.

INTRODUCTION

Liocarcinus depurator (Linnaeus, 1758) is the most abundant brachyuran crab on the muddy bottoms of the northwestern Mediterranean continental shelf (ABELLÓ *et al.*, 1988). Some data on the general biology of the species in the Ligurian Sea were given by MORI & ZUNINO (1987), but despite its abundance and it being one of the most important by-catches of the Mediterranean demersal fishery, very little information is available on the biology of this species.

The present study was undertaken to describe the main patterns of reproductive and moulting biology

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of *L. depurator* off the Catalan coast (northwestern Mediterranean) in order to obtain a better knowledge of the biology of the key species in the demersal exploited ecosystem of the area. The information provided herein aims to extend our knowledge of the reproductive biology of *L. depurator* and to make comparisons with other European portunid crabs (GONZÁLEZ-GURRIARÁN, 1985; MORI, 1987; STEVĆIĆ, 1987; CHOY, 1988; ABELLÓ, 1989).

MATERIAL AND METHODS

Crabs were captured monthly over the period February 1984 to January 1985 off Barcelona (NE Spain), using a bottom trawl of 18 mm codend mesh size on muddy bottoms at depths comprised between 50 and 400 m, within the full bathymetric range of the species in that area. A total of 2329 individuals (1046 males and 1283 females) were examined.

Sex, carapace length (measured in mm from the right frontal sinus to the posterior edge of the carapace), moult stage and sexual maturity stage were recorded for each individual. In females, occurrence of sperm plugs in the female gonopores, indicating that copulation had taken place (HARTNOLL, 1969; EDWARDS, 1979), and of eggs on the pleopods, were also recorded. The monthly gonosomatic index (G.S.I. = (wet ovary weight / wet body weight) × 100) was calculated only for non-ovigerous females with all thoracic appendages. Weights were taken to the nearest mg after removal of excess water using blotting paper.

Five different moult stages, modified from the schemes of DRACH & TCHERNIGOVTZEFF (1967) (e.g. SATHER, 1966; ROPES, 1969; WILLIAMS, 1982), and adapted to the present species, were defined as follows:

— Stage 1: Immediate post-moult. Very recently moulted crabs; the consistency of the exoskeleton is very soft (stage A_1).

— Stage 2: Post-moult. Calcification of the exoskeleton starts; it acquires a paper-like consistency; chelae and tips of pereiopods are more hardened than the rest of the carapace (stages A_2-B_2).

— Stage 3: Advanced post-moult. The exoskeleton is calcified but is still flexible on the pterygostomial region of the carapace and on the merus of the 2nd to 5th pereiopods (stages C_1-C_2).

— Stage 4: Intermoult. The exoskeleton has a hard consistency on all its regions (stages C_3-D_1).

— Stage 5: Pre-moult. The new exoskeleton appears almost completely formed under the old carapace (stages D_2-D_4).

Ovary morphology and development followed the pattern described for brachyrhynch crabs (RYAN, 1967; HAEFNER, 1977; ERDMAN & BLAKE, 1988; CHOY, 1988). Five stages of female sexual maturity were accordingly defined:

— Stage 1: Very early development (immature); the aspect of the ovaries is that of slender whitish tubular filaments.

— Stage 2: Beginning of maturation; the ovaries begin to develop and swell; active vitellogenesis starts; pale yellow-orange in colour.

— Stage 3: Actively developing ovaries; the gonads are swollen and occupy most of the dorsal part of the carapace cavity, covering the digestive gland, visible dorsally through the cephalothorax-abdomen junction; active vitellogenesis takes place; the oocytes are not visible to the naked eye; ovaries yellow-orange in colour.

— Stage 4: Ripe, fully developed ovaries; prespawning condition; the ovaries are greatly swollen and occupy most of the dorsal part of the carapace cavity and the anterior abdominal region; clearly visible through the cephalothorax-abdomen junction; yellowish in colour with oocytes visible to the naked eye.

— Stage 5: Spent; post-spawning condition; the ovaries have the aspect of a pale yellowish thick filament; a stage of very short duration present only in very recently spawned females.

Three stages of egg development were defined on ovigerous females:

(1) recently extruded eggs: yellowish in colour; no embryo pigmentation visible under the stereo-microscope.

(2) intermediate stage: slight embryo eye pigmentation.

(3) late stage: embryo well developed; eyes well formed; some other pigmentation in the body; egg mass greyish in aspect.

Two maturity stages (immature and mature) were defined in males according to the size and colour of the testes, which reflect the presence of spermatophores in the vasa deferentia (MORI & ZUNINO, 1987; CHOY, 1988). The immature male gonad is translucent and occurred only in very small individuals. Other male crabs had a whitish opaque gonad.

To estimate fecundity, eggs from 37 recently spawned females were manually removed from the pleopods and were then added to a known volume of seawater (50-70 ml). They were thoroughly agitated

until evenly distributed. Three 2 ml subsamples were then taken from 10 females and the number of eggs in each of them was counted. The mean variability of the counts was low (3.3 %), so only one 2 ml subsample was taken in the rest of females. The number of eggs counted in each subsample ranged between 610 and 6555 eggs. Total number of eggs in the total volume was then calculated from volumetric proportions. Egg volume in subsamples was calculated from the mean diameter of recently extruded (development stage 1) eggs. The relationship between size and number of eggs was fitted to the potential model in its logarithmic transformation [log(number of eggs) = $\log(a) + b \cdot \log(\text{size})$] using least squares linear regression.

Table 1 shows the monthly numbers of individuals examined throughout the sampling period. Monthly sex ratios and percentages of the different moult and maturity stages were calculated over these figures.

TABLE 1. — Number of *Liocarcinus depurator* examined each month throughout the sampling period (February 1984-January 1985).

	Males	*Females*	*Total*
February 1984	109	135	244
March	80	111	191
April	35	63	98
May	159	166	325
June	56	136	192
July	81	117	198
August	110	79	189
September	93	98	191
October	75	97	172
November	65	86	151
December	75	108	183
January 1985	107	88	195
Total	1046	1283	2329

RESULTS

Sex-ratio

Overall sex-ratio (proportion of females = 1.23:1) was significantly different from the expected sex-ratio 1:1 (G-test, $p < 0.001$). Monthly sex-ratio values (percentage of females) ranged between 41.80 % and 70.83 %, a higher proportion of females in the samples being found in most months (fig. 1).

Reproduction

— Female maturity cycle

Ovigerous females and females with fully developed ovaries occurred throughout the year, but their monthly incidence clearly indicate the existence of an annual reproductive cycle (figs. 2 and 3). The maximum proportion of females with fully developed ovaries occurred from August to November, after which spawning took place. Most ovigerous females

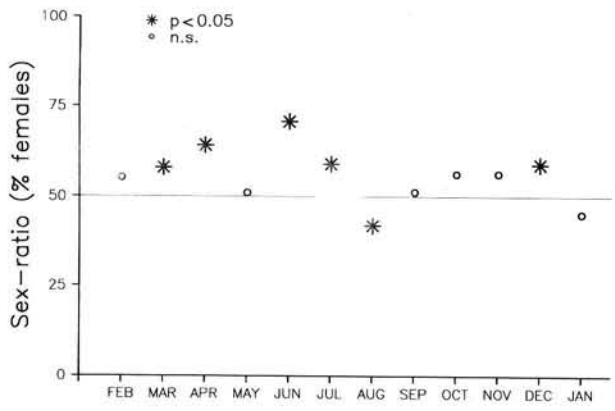

FIG. 1. — Monthly sex-ratio (percentage females) in *Liocarcinus depurator*, with indication of a significant ($p < 0.05$) departure from the expected 1:1 sex-ratio. February 1984-January 1985.

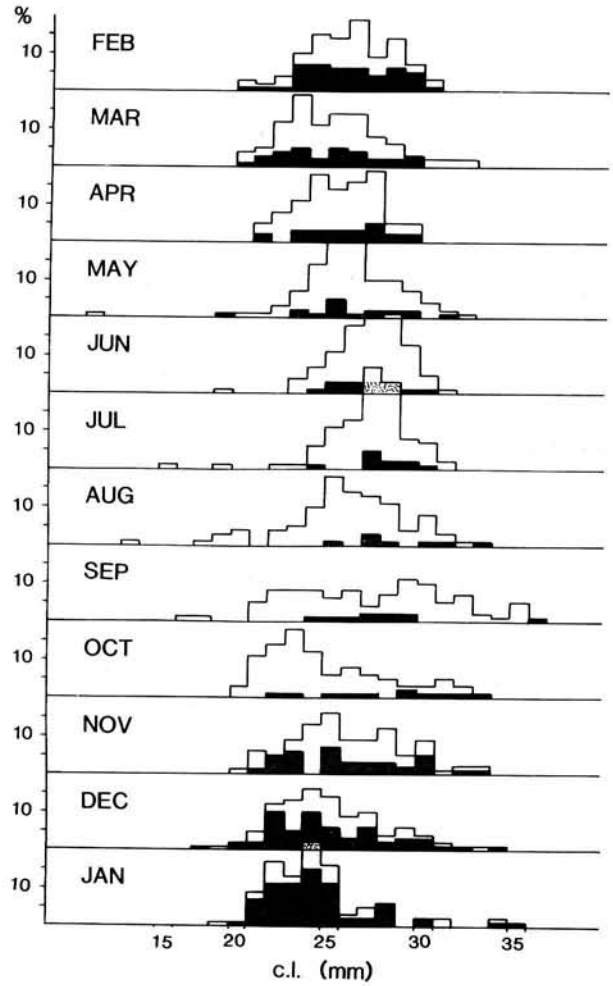

FIG. 2. — Monthly size frequency distribution of female *Liocarcinus depurator*. Ovigerous females in dark. February 1984-January 1985.

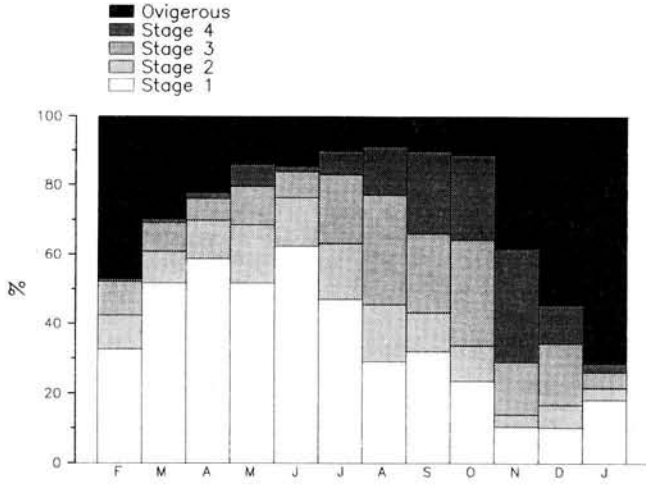

FIG. 3. — Monthly percentages of the different maturity stages in female *Liocarcinus depurator*. February 1984-January 1985.

were recorded in the winter months from November, with peak values in January, and fewest in spring-summer (between May and October).

— *Gonosomatic index (G.S.I.)*

The gonosomatic index represents a measure of the reproductive condition of a population (PILLAY & NAIR, 1971). The monthly evolution of its mean values (fig. 4) clearly showed the existence of a marked maturity cycle in the population. Active vitellogenesis started in July and took place throughout the summer and autumn, with peak values being reached in November-December, when spawning started. Few females showed ovarian development between February and July.

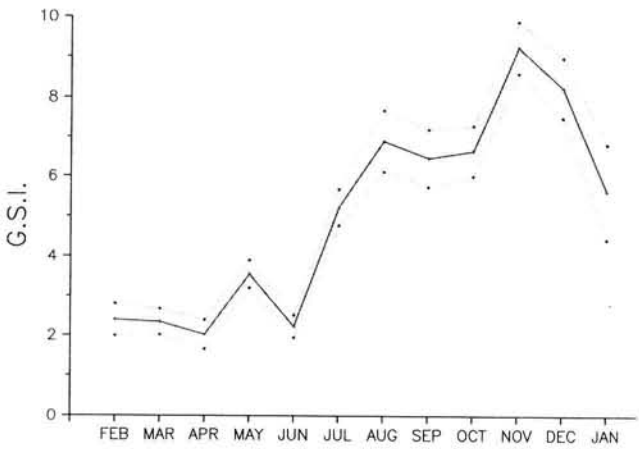

FIG. 4. — Mean monthly gonosomatic index (G.S.I.) (' -standard error of the mean) in non-ovigerous female *Liocarcinus depurator*. February 1984-January 1985.

— *Sperm plugs*

Sperm plugs, indicating that copulation had taken place (HARTNOLL, 1969), were recorded in the gonopores of most postmoult females (table 2). The smallest female with sperm plugs measured 19.6 mm, and the largest, 31.6 mm. They tended to disappear from the advanced post-moult stage; very few were found in intermoult individuals and none in pre-moult individuals.

— *Size of female sexual maturity*

The percentage of mature females (i.e. ovigerous plus maturity stages 3 and 4) by size during the main reproductive season (November to January) showed that even from the smallest size classes in the samples, most females were actually mature (table 3, fig. 2), indicating that sexual maturity occurs very early in the adult life history of the species. No reliable maturity ogive could therefore be presented for the species. The estimated size at female sexual maturity occurred consequently at a size around 18-20 mm c.l.: smallest female with sperm plugs, 19.6 mm; smallest pre-spawning female, 20.6 mm; smallest ovigerous female, 18.2 mm.

TABLE 2. — Number and percentatge female *Liocarcinus depurator* with sperm plugs in their gonopores, according to their moult stage.

Moult stage	*No. females with plugs*	*No. females total*	*%*
(1) Immediate post-moult	9	9	100.0
(2) Post-moult	75	76	98.7
(3) Advanced post-moult	96	111	86.5
(4) Intermoult	11	1019	1.1
(5) Pre-moult	0	68	0.0

TABLE 3. — Number and percentage mature female *Liocarcinus depurator* (ovigerous + maturity stages 3 and 4) by size class during the main spawning season (November to January). *n* = number mature; *N* = total number of females per size class.

Size class (mm c.l.)	*n*	*N*	*%*
18-19	1	3	33.3
20-21	20	22	90.9
22-23	52	65	80.0
24-25	79	90	87.8
26-27	30	44	68.2
28-29	27	29	93.1
30-31	18	19	94.7
32-33	5	6	83.3
34-35	3	4	75.0

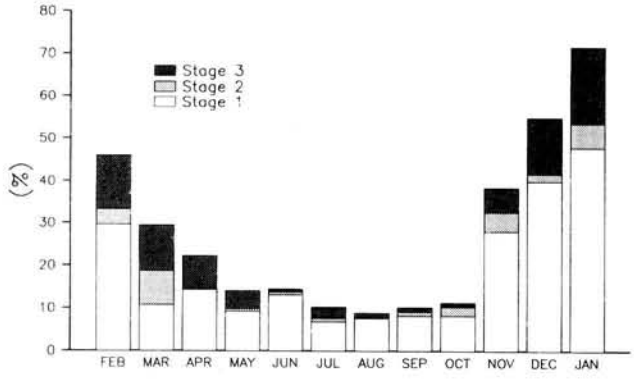

FIG. 5. — Monthly percentages of ovigerous female *Liocarcinus depurator* in the different egg development stages. (1) recently spawned eggs; (2) slight embryo pigmentation; (3) well developed embryo eye pigmentation.

Sizes of females in the samples ranged between 12 and 36 mm, the largest pre-spawning female measuring 34.8 mm; the largest female with sperm plugs, 31.6 mm, and the largest ovigerous, 36.1 mm.

— Number of batches

Only a small proportion of ovigerous females (24 out of 347; 6.92 %) had ovaries undergoing vitellogenesis (stage 2, beginnig of maturation), an indication that at least some individuals could spawn twice during the season. Only 2.88 % of the ovigerous females showed recently spawned, spent ovaries (stage 5); most of them (90.20 %) showed undeveloped whitish ovaries (stage 1).

Recently spawned eggs were found throughout the year (fig. 5), the highest relative proportion of eggs in advanced stage of development being found from February to March, and in the following January. Larval release can be assumed to take place after an embryonic development time of 27-34 days, following WEAR (1974), since water temperatures of 12.5-14 °C occur at 100 m depth in the main spawning period (SALAT *et al.*, 1978).

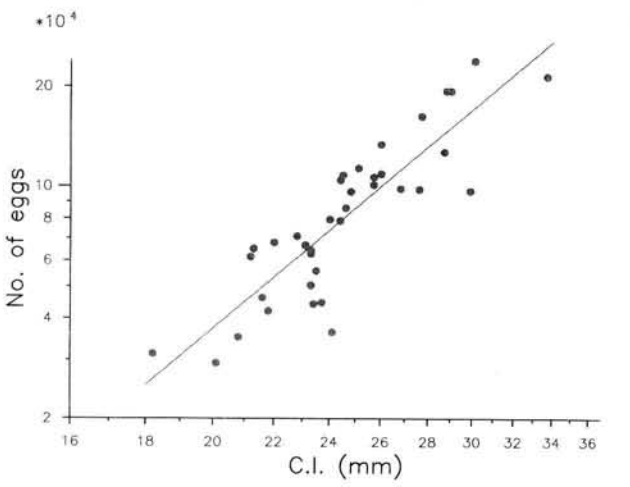

FIG. 6. — Relationship between carapace length and number of recently extruded eggs in ovigerous female *Liocarcinus depurator* (n = 37).

— Fecundity

The number of recently extruded eggs carried by ovigerous females ranged from about 30 000 in ovigerous females 18-21 mm c.l. to about 230 000 in ovigerous females around 30 mm c.l., clearly increasing with the size of the females (fig. 6) according to the equation:

$$\log(\text{number of eggs}) = -0.705 + 3.75 \cdot \log(\text{c.l.})$$
$$(n = 37,\ r = 0.8683)$$

— Male maturity cycle

No evidence of seasonal changes in morphology and appearance of the testes could be found throughout the sampling period. Most males were sexually mature and presented whitish opaque testes throughout the year. Only a few very small (< 20 mm c.l.) individuals showed immature translucent testes. Sizes of males ranged between 13 and 39 mm.

Moulting

— Female moulting cycle

A marked annual moult cycle was apparent in females, but not in males, which showed an irregular

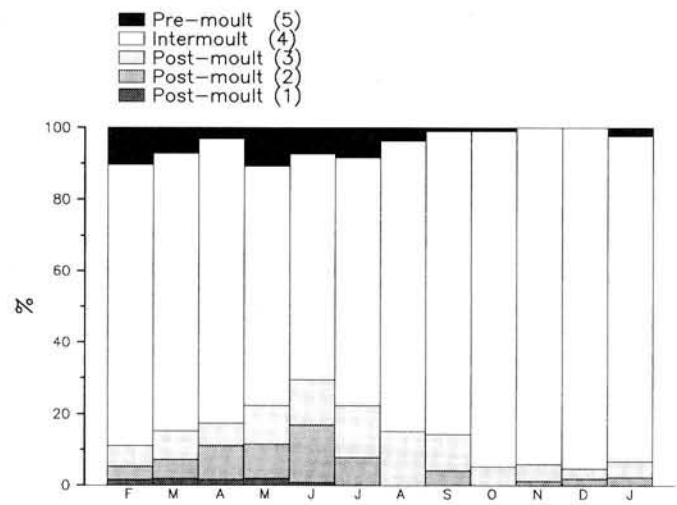

FIG. 7. — Monthly percentages of the different moult stages in female *Liocarcinus depurator*. February 1984-January 1985.

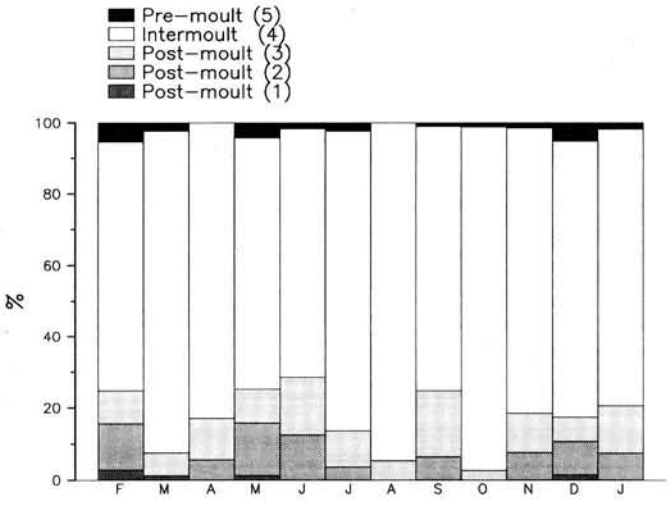

FIG. 8. — Monthly percentages of the different moult stages in male *Liocarcinus depurator*. February 1984-January 1985.

pattern (figs. 7 and 8). The main moulting period in females took place between May and July, moult frequency decreasing gradually thereafter and remaining very low during the main spawning period, from October to January. Very few pre-moult females were found from August to January, whereas most pre-moult and recently moulted females occurred after the main spawning period had finished, between February and June.

Most post-moult females (stages 1 + 2 + 3) showed immature ovaries (183 out of 196, i.e. 93.37 %), whereas just a few showed developing ovaries [12 (6.12 %) in maturity stage 2, and only 1 (0.51 %) in stage 3].

Sizes of moulting females ranged between 13.7 and 31.5 mm in pre-moult individuals (table 4), and between 18.7 and 31.6 mm in post-moult individuals, suggesting, since female sizes reached 36 mm, the probable existence of a terminal moult in this sex.

TABLE 4. — Number (n) of pre-moult *Liocarcinus depurator* by sex, and size class. N = total number of crabs per size class.

Size class	*Males*		*Females*	
(mm c.l.)	*n*	*N*	*n*	*N*
12-13	0	1	0	1
14-15	0	0	1	1
16-17	0	2	0	2
18-19	0	14	1	10
20-21	4	35	4	66
22-23	1	82	9	209
24-25	6	240	22	330
26-27	4	237	24	223
28-29	6	173	4	225
30-31	4	110	0	86
32-33	2	75	1	24
34-35	0	50	0	10
36-37	0	16	0	1
38-39	0	6	—	—

— *Male moulting cycle*

Variations in the proportion of moulting males throughout the sampling period were very irregular (fig. 8). No clear seasonal moulting pattern was apparent. A small proportion of premoult males was found throughout the year.

Sizes of pre-moult males ranged between 19.4 and 32.2 mm (table 4), sizes of post-moult males, between 19.4 and 39.0, thus suggesting the occurrence of a terminal moult in males as well.

DISCUSSION

The basic pattern of reproductive biology events in *L. depurator* in the area of study appears to be as follows: female moult and copulation take place between May and July; ovaries develop through summer, reaching full development in autumn; spawning starts in late autumn (November-December) and lasts until January-February.

L. depurator, like other portunid crabs (DU PREEZ & MCLACHLAN, 1984; GONZÁLEZ-GURRIARÁN, 1985; HEASMAN *et al.*, 1985; CHOY, 1988), shows an inverse relationship between maturity and moulting processes: moulting females showed no, or very low, ovarian development, whereas almost no moulting females occurred during the main maturation and spawning season. Separation in time between moulting (i.e. growth) and maturation then tends to minimize metabolic competition between these two processes (SASTRY, 1983; HARTNOLL, 1985), both of which are energetically expensive.

The overall annual reproductive cycle of *L. depurator* on the Catalan coasts is not markedly different from that recorded by MORI & ZUNINO (1987) in the climatically similar Ligurian Sea. However, the main moulting season in the Ligurian Sea takes place later (July to October) than that recorded herein on the Catalan coasts (May to July). ZARIQUIEY-ÁLVAREZ (1968) reported the occurrence of ovigerous females of *L. depurator* in the northwestern Mediterranean in every month of the year, as did GARCÍA RASO (1984) in southern Spain, but they did not state the observed main spawning period.

INGLE (1983) stated that ovigerous females of *L. depurator* occur in Britain from January to Oc-

tober, though larvae are found in the plankton throughout the year. ALLEN (1967) indicated that spawning of *L. depurator* off western Scotland takes place from January to June, ovigerous females, producing two broods per year, being found until August. In contrast, CHRISTIANSEN (1969), reported ovigerous females of the same species in Norway only from April to August.

L. depurator appears to progressively restrict its spawning season to the summer months in northern colder latitudes, whereas in the Mediterranean, even though maturation and spawning can occur throughout the year, as is the case in many low latitude and tropical species (PILLAY & NAIR, 1971), ovigerous females are mainly found after the autumnal maximum of water temperature. The rapid increase in the proportion of non-ovigerous to ovigerous females recorded in November might be due to temperature stimulation of spawning, as the maximum temperatures in the area occur between September and November at the depths inhabited by the species (SALAT *et al.*, 1978).

Fecundity was high in *L. depurator,* as found in other similar-sized portunid crabs (MORI, 1987; CHOY, 1988). The number of eggs produced by female *L. depurator* clearly increased with size. Fecundity seems to be higher in the Catalan Sea population studied herein than in the Ligurian Sea population (MORI & ZUNINO, 1987). A maximum value of 140 000 eggs carried by a female 47.5 mm carapace width, approximately 36.7 mm c.l. (ABELLÓ, 1986), was estimated in the Ligurian Sea. Maximum values around 220 000 - 240 000 eggs were found in females 30-34 mm c.l. in the present study.

Recruitment of *L. depurator* to the benthos in the area of study must take place mainly in spring, but, due to size selectivity of the sampling gear, the recruitment to the fishery was mainly detected in summer, between May and September (fig. 1). No estimates of juvenile growth are available for the species, but as the size at sexual maturity (18-20 mm c.l.) and female size frequency distribution suggest, females may well reach fully maturity within their first year of life. Moreover, female size frequency distribution and modal changes during the main moulting period suggest the occurrence of a minimum of 2-3 year classes in the population, so that at least two reproductive cycles may be undergone by any one female.

Within the genus *Liocarcinus,* WEAR (1974) in *L. depurator,* GONZÁLEZ-GURRIARÁN (1985) in *L. puber* and CHOY (1988) in *L. holsatus* and *L. puber,* showed that in the laboratory some females can spawn at least twice without an intervening moult. Although no strong evidence of a female producing more than a single brood per season was detected in the population studied, the occurrence of a few ovigerous females undergoing active ovarian vitellogenesis suggests that at least a small proportion of them may spawn twice during the season.

Sex-ratio in the population studied was significantly biassed towards females, as MORI & ZUNINO (1987) also recorded, thus seeming to be a characteristic of the species which could be accounted for by differential adult mortality rates between the sexes, as suggested by DU PREEZ & MCLACHLAN (1984) in the portunid crab *Ovalipes punctatus.*

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