

Reproductive patterns in Norway lobster *Nephrops norvegicus* (L.), (Crustacea Decapoda Nephropidae) of different Mediterranean areas*¹

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SUMMARY: The main aspects of reproduction - namely times of ovarian maturation, brooding and hatching, sizes of maturation and fecundity - were studied in female Norway lobsters in seven areas of the Mediterranean biogeographic sub-province: the Algarve Sea, the Alboran Sea, the Catalan Sea, the Ligurian Sea, the Northern Tyrrhenian Sea, the Adriatic Sea and the Gulf of Euboikos. These included both shelf and slope populations within a latitudinal range of 8°. The reproduction showed clear seasonality with some small differences between areas: maturation delayed by 1-2 months in northern areas (Ligurian, N. Tyrrhenian and Adriatic Seas) compared to southern areas; absence of embryos for periods of 4-5 months in slope females and for less clearly defined periods in shelf females. The case study of the Ligurian Sea was used to illustrate the ovarian cycle and to describe the pre- and post-puberal growth of the female. First mating occurs at an average size of 32 mm *CL*, which corresponds to age 3+ of the female and the hatching of the first brood corresponds to age 4. Differences were registered in reproductive sizes in the study areas, with a range of 23-30 mm *CL* for the smallest berried females and a range of 30-36 mm *CL* in the 50% maturity size. These differences were ascribed to local factors, whereas ages of the basic steps of reproduction were assumed to be unchanged. Females of age 2 formed the most abundant share of the fished stock. An estimate of fecundity was made in terms of brood size (embryos were counted at an early stage of development): the range was 1119-1834 embryos in a standard female of 35 mm *CL*. Reproductive potential, calculated on the basis of a virtual population analysis, was strongly influenced by the size structure of the female population in each area and there was a ratio of about 14:1 between the least (Ligurian) and the most exploited (Catalan) fishing grounds.

Keywords: Norway lobster, Mediterranean, reproduction, maturity at length ogive, age of first maturity, prepuberal and postpuberal growth, fecundity, reproductive potential.

RESUMEN: LA REPRODUCCIÓN DE LA CIGALA (*NEPHROPS NORVEGICUS*, CRUSTACEA DECAPODA NEPHROPIDAE) EN DIFERENTES ZONAS DEL MEDITERRÁNEO. - En siete áreas de la subprovincia biogeográfica Mediterránea: costas de Algarve, Alborán, mar Catalán, mar Ligur, norte del Tirreno, Adriático y golfo de Euboikos, se estudian los principales aspectos de la reproducción (período de maduración ovárica, incubación y eclosión, talla de primera maduración y fecundidad) de la cigala. Las poblaciones estudiadas proceden tanto de la plataforma como del talud continental abarcando un rango latitudinal de 8°. La reproducción muestra una clara estacionalidad con pequeñas diferencias entre áreas: la maduración puede presentarse retrasada en 1-2 meses en las áreas más septentrionales (Liguria, Tyrrheno y Adriático), respecto a las áreas más meridionales; ausencia de embriones durante 4-5 meses en hembras del talud y períodos menos claramente definidos en las hembras de la plataforma. Se presenta como ejemplo el caso concreto del mar Ligur con el fin de ilustrar el ciclo gonadal y describir el crecimiento pre y post pubertal de las hembras. La primera cópula ocurre alrededor de los 32 mm *CL*, lo que corresponde a una edad de 3+ años, mientras que la primera eclosión de los huevos corresponderá a los 4 años. También se observaron diferencias en las tallas reproductivas de las hembras entre las distintas zonas, desde un rango de entre 23 y 30 mm *CL* para las hembras ovadas más pequeñas, hasta un rango de entre 30-36 mm *CL*, para las hembras en la talla del 50% de madurez. Estas diferencias se atribuyen a factores locales asumiendo que el patrón reproductor básico es el mismo. Las hembras de edad 2 constituyen la mayor parte del stock pescado. La estimación de la fecundidad se establece en base al tamaño de la puesta (embriones contados en los primeros estados de desarrollo). Para hembras estándar de 35 mm de *CL*, se estimaron un número de huevos entre 1119 y 1834. El potencial reproductor se calculó en base al análisis de la población virtual y fue estrechamente influenciado por la estructura de tallas de la población de hembras en cada área. La máxima diferencia encontrada, con una proporción de 14:1, fue entre Liguria y Cataluña, esta última como zona más explotada.

Palabras clave: Cigala, Mediterráneo, reproducción, madurez gonadal, edad de primera madurez, crecimiento, pre y post pubertal, fecundidad, potencial reproductivo.

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¹By Mediterranean we mean the Mediterranean subprovince (Ekman, 1935) including the Algarve Sea (Lusitanian subarea).

INTRODUCTION

The reproduction of Norway lobster has been extensively studied using both field and experimental approaches. It figures prominently in reviews both of crustacean reproduction and growth (Aiken and Waddy, 1980; Chapman, 1980; Sastry, 1983; Conan, 1985; Hartnoll, 1985), since there is a close relationship between the phasing of the two processes.

Studies of reproduction in the Mediterranean were developed mainly in the eighties (Frogliola and Gramitto, 1979; 1981; Gramitto and Frogliola, 1980; Orsi Relini and Relini, 1985; 1989; Biagi *et al.*, 1990; Sardà, 1991). Earlier work highlighted two aspects which seem peculiar to this geographic area: 1) the Norway lobster can be found both in shelf waters and on the slope, even at depths exceeding 700 m (Senna, 1905) and 2) larvae occur in winter (Lo Bianco, 1909; Stephensen, 1923; Santucci, 1926; Karlovac, 1953).

The European Union funded research programme NEMED (Sardà, 1996; EC Report DG. XIV, MED92/008) has promoted the study of the reproductive biology of Norway lobsters in seven Mediterranean areas: five of these have slope population(s), one a shelf population and the last a mixed population i.e. Norway lobsters found both at neritic and bathyal levels. The latitudinal range was about 8° between the most southerly (Alboran) and the most northerly area (Ligurian); the longitudinal range was about 31° from the

most westerly (Algarve) to the most easterly area (Gulf of Euboikos).

For the purposes of a comparative assessment of the reproductive patterns in the areas under study, the following subjects were considered: reproductive season; reproductive sizes and female maturity at length ogive; fecundity and reproductive potential per area.

In order to describe the reproductive cycle and to assign ages to reproductive processes the case study of the Ligurian Sea was used.

MATERIALS AND METHODS

Samples were collected in seven Mediterranean areas: five of these areas had slope population(s) (the Algarve, the Alboran, Catalan, Ligurian and Tyrrhenian Seas), one had a shelf population (Middle Adriatic) and in the last (Gulf of Euboikos) Norway lobsters were found both at shelf and slope levels (Fig.1). Biocoenoses associated with *N. norvegicus* were therefore different in the studied areas (Peres and Picard, 1964).

Specimens were collected directly on board commercial otter trawlers, operating over the exploited stock fishing-grounds (Sardà, 1998). The trawling gear had meshes of cod-end ranging from 32 to 40 mm of opening yielding a size spectrum which includes immature lobsters. Sampling was carried out monthly from October 1993 to September 1995 (November 1995 in some areas).

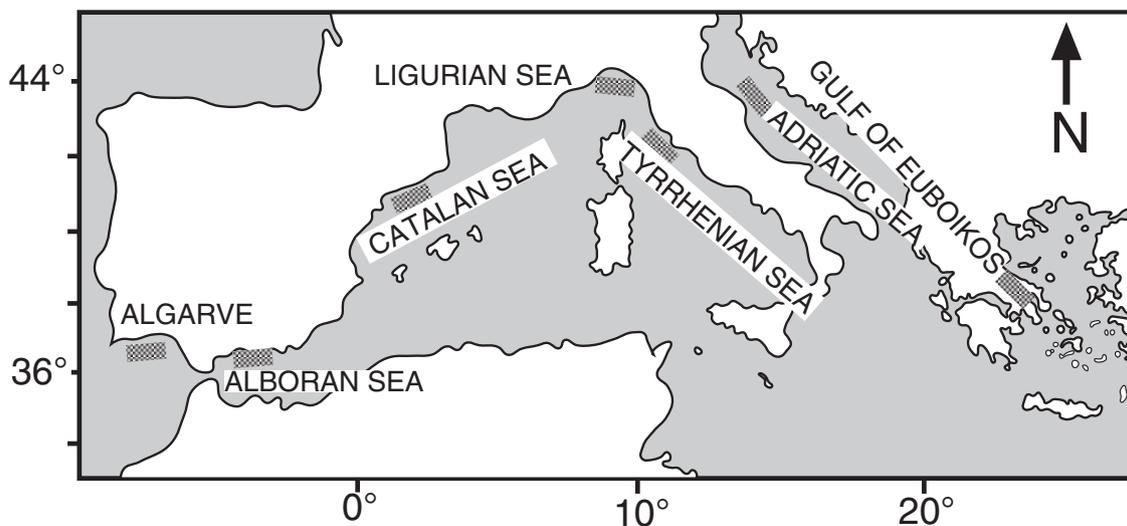


FIG. 1. – Location of the seven sampling sites.

Specimens were measured in terms of carapace length (CL), from posterior orbit to posterior carapace (rounded down to the nearest millimeter) and sex was identified on the basis of external characteristics (1st pair of pleopods). Reproductive studies consisted in simple basic actions and involved only females. The total number examined was about 30,000. The common procedures adopted to study the maturation stages of the ovary were the following: females were dissected dorsally and the colour of the ovary was used to assign a maturative stage according to the following scale: stage I, white - juvenile or under-developed adult; stage II, cream - at beginning of maturation; stage III, pale green - intermediate stages of ooverdins storage; stage IV, dark green - near to the extrusion on pleopods. To facilitate stage evaluation, a reference table with colour prints was prepared and distributed among the operative units. No validation procedures (histology of ovarian tissues to verify ovocytes maturation versus color) were carried out. For this purpose the extensive treatment of reproduction by Farmer (1974; 1975) was considered the reference text.

Reproductive season

Identification of the reproductive season in terms of the ovarian maturation. The ratio between number of females at stage IV - which represents the end of maturation processes - and the total number of females larger than the minimum size at stage IV, was calculated monthly for each area.

Identification of the brooding period. The presence of berried females (i.e. bearing eggs on the pleopods) was noted. In each area the brooding period was identified by taking into account the ratio between the number of berried females and the number of females larger than the minimum berried size for each month.

Reproductive sizes and female maturity at length ogive.

The proportions of stages III + IV + berried to total females at each size were calculated as the sum of three monthly samples. These were the months of highest mature occurrence (Stage IV) plus the two following ones. This calculation was performed only for 1995 samples, which were the most numerous.

The ogive curves were expressed according to the simplified model described by Sparre *et al.* (1989):

$$m(CL) = \frac{1}{1 + e^{[s_1 - (s_2 CL)]}}$$

where CL = carapace length class in mm, $m(CL)$ = percentage of mature females per length class (CL), $s_1 = CL_{50} * s_2$, $s_2 = \ln 3 / (CL_{75} - CL_{50})$, CL_{75} and CL_{50} being the length class for which, respectively, 75% and 50% of females are mature.

The model parameters were estimated using the linearized method proposed in Sparre *et al.* (1989).

Fecundity in terms of brood size

For comparisons of fecundity among different areas, berried females were collected on board, fixed in formalin and their recently extruded eggs (totally green in colour) counted. It was established that counts of embryos should be made at an early stage of development (no visible eyes) and on females in the young size range (up to 36 mm CL). However, in some areas, given the impossibility of collecting a reasonable number of small berried females, the range of size was extended. The relationship between brood size/carapace length was expressed both in terms of linear regression (i.e. number of eggs = $a + b \cdot CL$) and power regression (i.e. number of eggs = $a \cdot CL^b$), which are more generally used to describe fecundity. It was found that in most of cases linear regression fitted the data better than the power function in terms of the coefficient of determination (r^2), so only the former were used for fecundity comparisons between the different areas.

It is well known that during the long incubation on female pleopods, the number of eggs declines; the reduction rate has been estimated at around 10% per month (Farmer, 1975). To provide an idea of the relationship between fecundity as studied by the above-mentioned procedures and terminal (i.e. near hatching) fecundity, power functions obtained in two areas - the Adriatic and Ligurian Seas - over the full range of berried sizes are also given.

Reproductive potential

A comparison of renewal capability among the studied areas has been attempted by means of an estimation of the "annual reproductive potential".

This was calculated as the sum of the products of the number of females of each size class engaged in reproduction multiplied by their fecundity according to the formula:

$$\sum_{i=1}^n N_i P_{m_i} F_i$$

where N = number of females per each size class; P_m = proportion engaged in reproduction (as shown by maturation ogives); F = fecundity (average number of embryos of a given size class). In the present study the total numbers of females per size class per area were obtained using the Virtual Population Analysis (Sardà 1998) on the basis of a standard landing of 10 t per area (VIT package by Leonart and Salat, 1992). The number engaged in reproduction was derived from the maturity ogives. For fecundity, the relationships regarding the extended range of sizes, when available, were used.

The above formula was based on a study of reproductive potential in *Homarus americanus* (Campbell and Robinson, 1983). Given that in the latter species reproduction is not annual, Campbell and Robinson introduced an additional factor for this particular biological aspect. We have assumed

that Mediterranean lobsters undergo annual reproduction: the reason for this assumption is explained in the chapter about the reproductive cycle.

Reproductive cycle in the Ligurian Sea

In the Ligurian material, instars were identified in length-frequency distributions in form of modal size classes. Besides the above listed reproductive patterns, the presence of spermatophores was recorded.

RESULTS

Reproductive season

In all areas reproduction showed clear seasonality both in terms of ovarian maturation and brooding period.

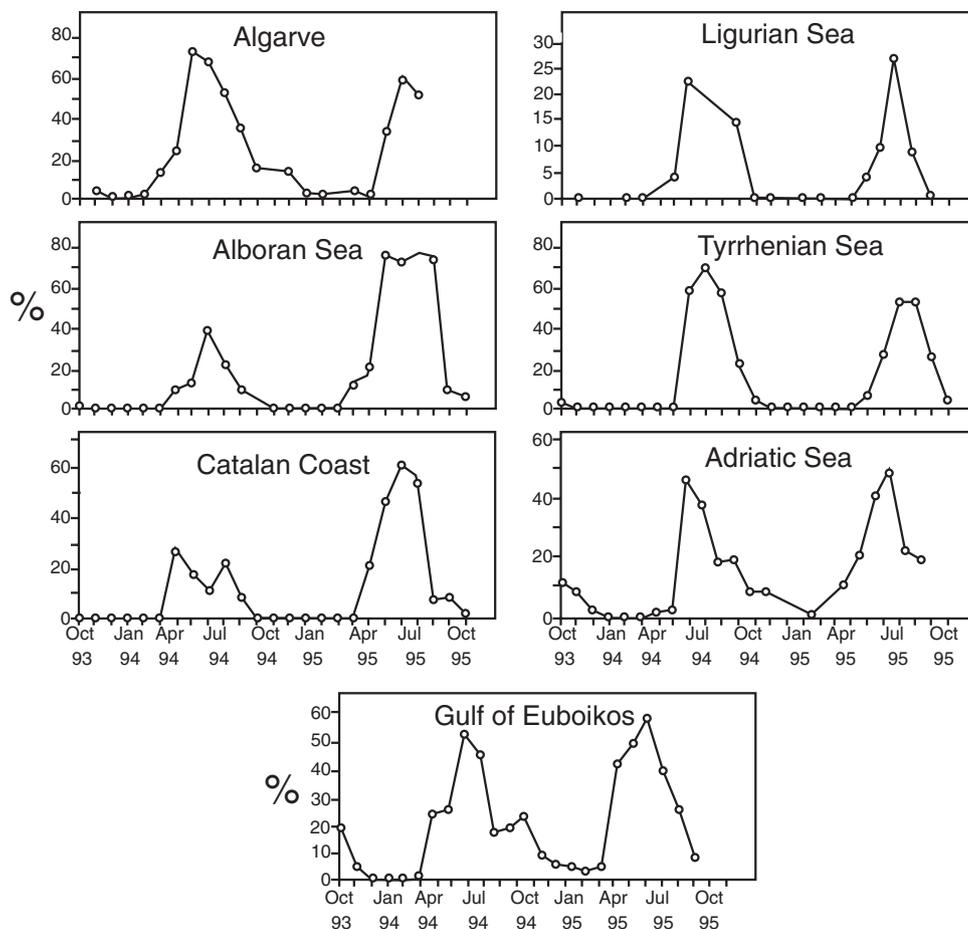


FIG. 2. – Reproductive season: monthly percentage of females bearing mature ovaries compared to total females larger than the minimum size with mature ovary.

Ovarian maturation. The proportion of females bearing a mature ovary, i.e. in which ooverdins storage is at a maximum (dark green colour) peaks in spring or at the beginning of summer (Fig. 2). Maxima were found in June in the Gulf of Euboikos, in June and July in the Adriatic, in July in the Ligurian and Tyrrhenian Seas, in April, June and July in the Catalan Sea, in June and May-August in the Alboran Sea and in May and June in the Algarve Sea.

In the populations of the different areas the length of presence of this advanced stage of maturation varies somewhat: the Algarve Sea, the Alboran Sea and the Gulf of Euboikos have the longest periods of presence. On the other hand, the Ligurian, Tyrrhenian and Catalan samples show a

clear absence of advanced maturative stages of about six months, from October to April.

Brooding period. The presence of berried females shows a seasonal trend (Fig. 3) characterized by summer and autumn peaks. Maxima were registered in July and December in the Gulf of Euboikos, in October and November in the Adriatic, in September-November in the Ligurian and Tyrrhenian Seas, in August and December in the Catalan Sea, in September-October and December in the Alboran Sea and in September and December or January in the Algarve Sea.

Periods of several months of absence of embryos on female pleopods (and therefore of absence of hatching events) were registered in the Catalan, Ligurian and Tyrrhenian Seas (Fig. 3). This point

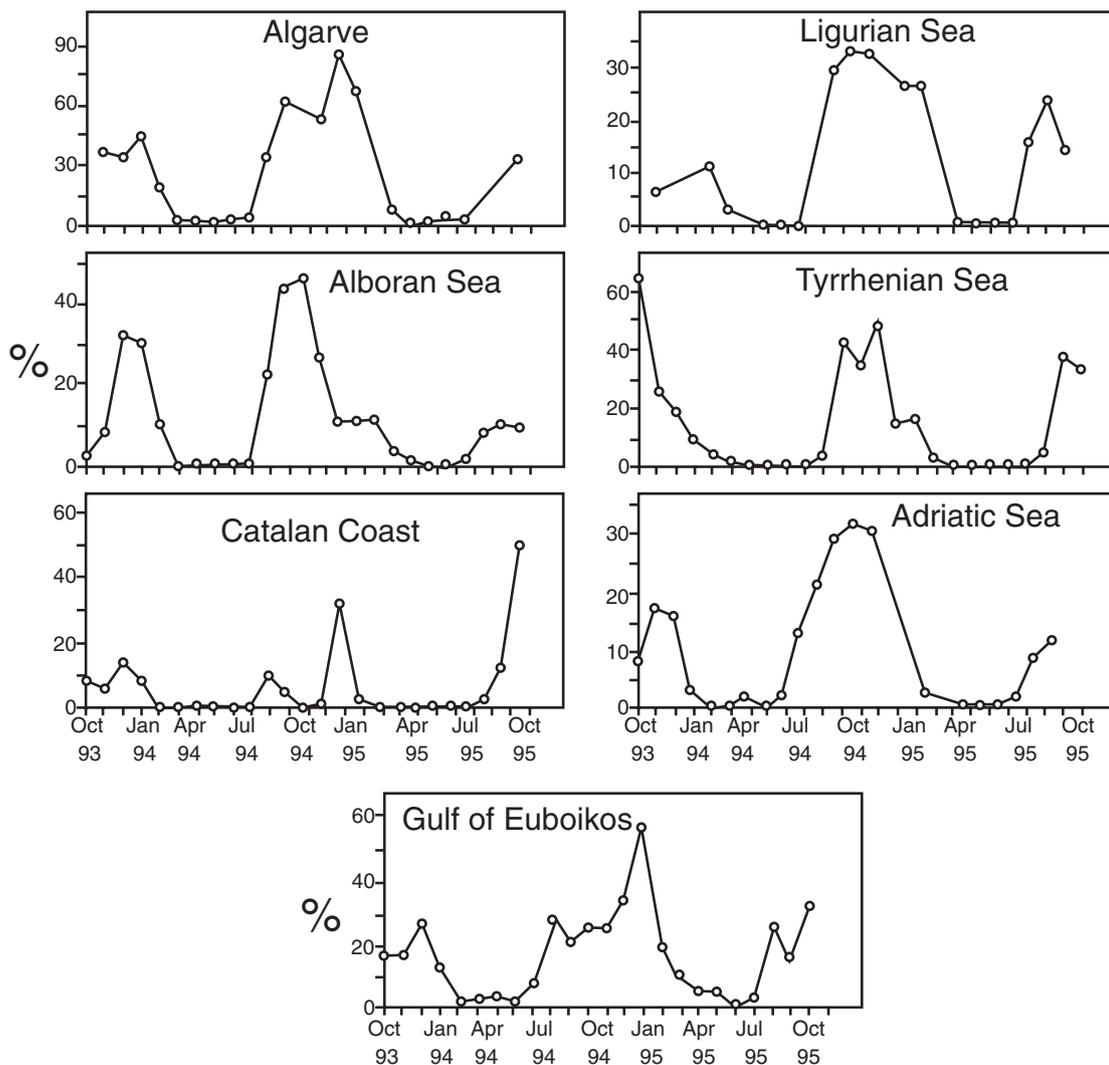


FIG. 3. – Brooding season: monthly percentage of berried females compared to total females larger than the minimum berried size.

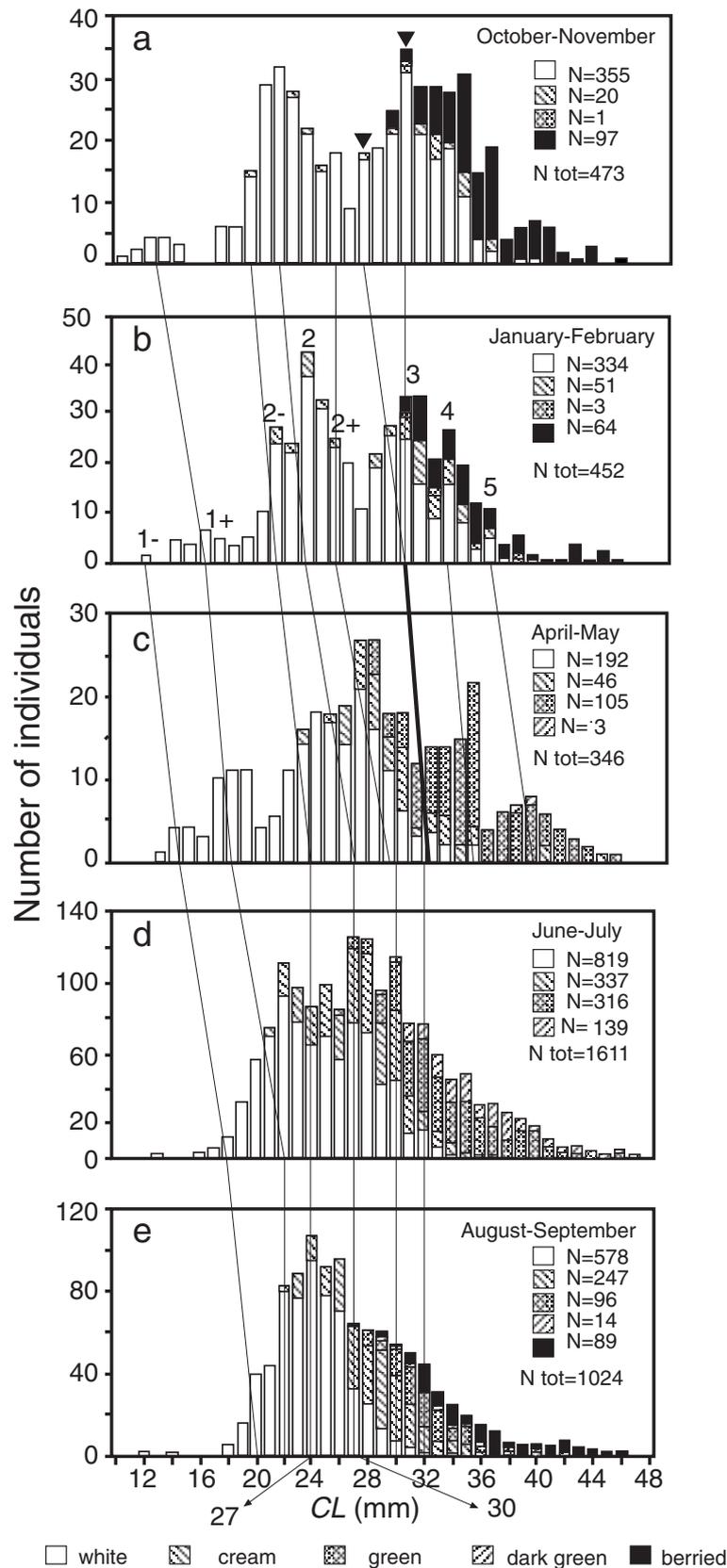


FIG. 4. – Reproductive cycle and growth of females in the Ligurian Sea, based on length-frequency distributions of females collected during 1995 (December and March not represented). Oblique lines indicate growth (moult) while vertical lines indicate the persistence of dominant instars. In b, numbers above the modal instars indicate ages (in years). Explanation in the text.

appears to be important for dynamics studies, in the sense that the identification of age groups in the length frequencies distributions distributions is easier if they are discrete from the beginning.

Reproductive cycle and age at first reproduction. The case study of the Ligurian Sea.

The general reproductive trends as shown in the previous notes and figures, are the same in all areas, so we have chosen the samples of the central area, the Ligurian Sea, to illustrate ovarian maturation, brooding and spawning per size class during one year (Fig. 4). Bimonthly images were preferred to monthly ones, given the advantage of summing two samples to a more consistent length-frequency histogram.

In October-November (Fig. 4a) there is a maximum of berried females. Probably the first hatchings are to be placed in this period, given that in the following months the number of berried females declines (Fig. 4b). These, however, are present till March (not figured), in very low numbers.

In April-May (Fig. 4c) no hatching can take place: beside immature animals (white ovaries), only the three stages of ovarian maturation (i.e. cream, green, dark green) are now present, with green prevailing.

In June-July (Fig. 4d) the reproductive pattern is similar, with increasing numbers of dark green samples. August sees the beginning of the new egg-laying period and the August-September graph (Fig. 4e) shows the range of sizes which originates berried females, from 27 mm *CL*, a rare case, upwards. The green categories soon give rise to berried females: in fact, in October-November they almost disappear.

If attention is paid to the sizes of females, some inferences about the ages possibly involved in the various stages of reproduction can be made.

Immature females (i.e. females bearing a white ovary) form a composite group in the October-November sample with at least three main gaussian components; the smallest (with a modal size 12-13 mm *CL*) are recently recruited (they were almost absent from the June - September group); the second group peaks at 21 mm *CL* and the third at 30 mm *CL*.

The bimonthly temporal sequence reflects the growth of each of these three components also showing that each of them (which we assume to be an annual group) can be divided into secondary

components (subcohorts or instars). The existence of secondary components for each of the first two groups is clear in Fig. 4b; this figure shows annual patterns, given that it represents the period January-February and births occur mainly in winter. Our interpretation of ages is annotated above each modal component.

It is to be noted that the recruits of Fig. 4a have now grown to 14 and 16 mm *CL*. We presume that these sizes correspond to age 1, with “minus” and “plus” components indicating that the hatching of lobsters can occur over a period of several months. We therefore choose the conventional birthday of 1st January and assume that the “plus” component is 14 months, if its hatching was on 1st November; in the same way lobsters hatched on 1st March are 10 months old. The second main group (which we consider age two) is divided into several modes (21 and 23 mm *CL* are the preminent ones): we assume that the early or late born and recruited animals form these groups. The third main group has a mode at 30 mm *CL*: we suppose that the previous small differences in size have by now disappeared and that the subcohorts of the previous year blend at this size. The following spring moult (30 → 32 or 33 mm *CL*) is that in which mating occurs (for the majority of the females), i.e. it is the puberal moult. This is the average size for attaining adulthood and after this the moults will be annual and occur mainly in spring. Prepuberal growth is indicated step by step in Fig. 4: oblique lines represent moults, while vertical lines represent the maintenance of the same size (i.e. the persistence of each instar). Very young individuals (1, 2 years) are constantly growing; females at age 2 moult in spring and in autumn-winter, females at age 3, 4 and 5 moult in spring; the puberty moult is indicated by a heavier line. Following ages (in Fig. 4b three other groups seem highlighted) cannot be traced because of their low numbers.

We conclude that after having reached 3 years of age (30 mm *CL* in February) the most abundant (i.e. modal) female moults, copulates, and begins a massive storage of carotenoproteins. In August-October her eggs are spawned and the births of embryos occur when she is approximately 4 years old. The onset of the maturation process, i.e. the passage from a white stage to a cream ovary, in the first maturation cycle, occurs beforehand, regarding (as a dominant aspect in fished stock) the instars of age 2+ (Fig. 4d,e), while both mating and full maturation have their main instar at 32 mm *CL* (Fig. 5).

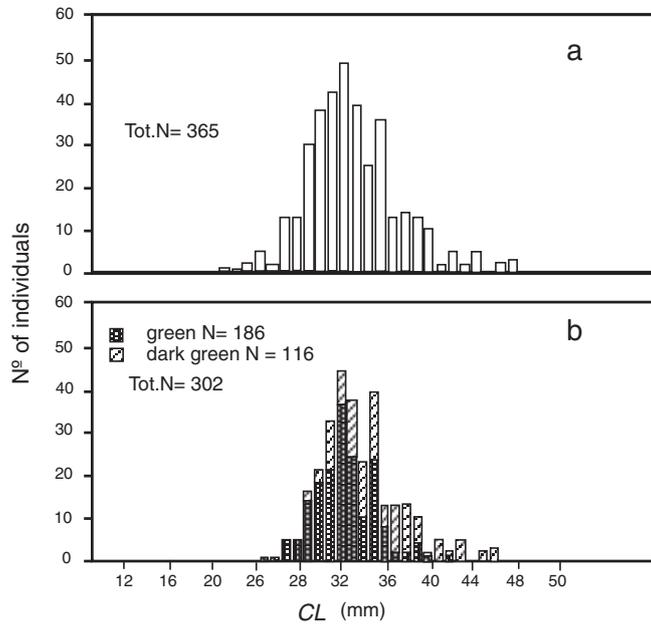


FIG. 5. – Length-frequency distributions of females bearing a spermatophore (=mated) a, and green and dark green ovary (=in advanced maturation) b, in July sample: both conditions primarily concern the 32 mm CL instar.

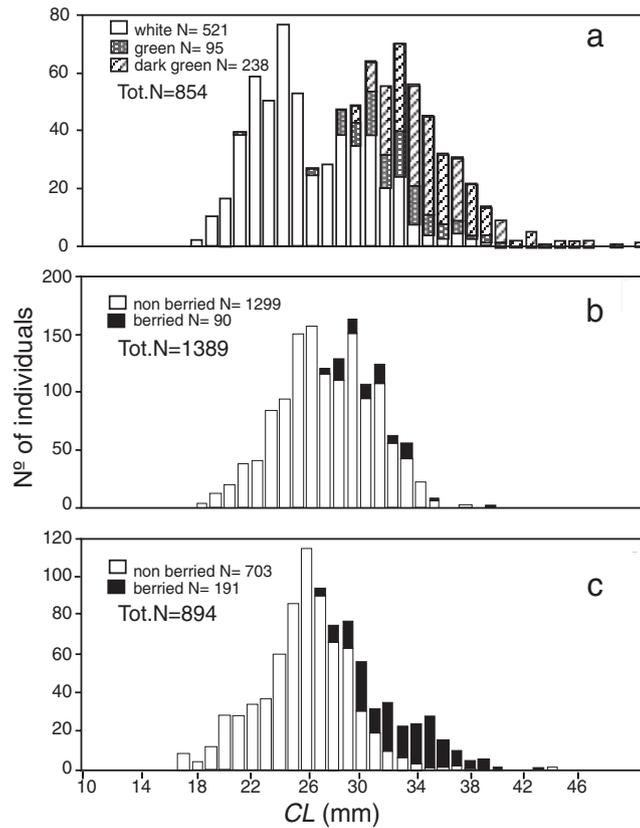


FIG. 6. – The case of the Catalan Sea: records of maturing females in 1994 (May – July) a, and berried females in 1994 (October–December) and 1995 (October – November) b and c.

We have verified that the length-frequency distributions of the other areas suggest analogous composite structures of young age groups and therefore we assume that the interpretation of ages can be similar.

The same sequence of reproductive events shown in Fig. 5 can throw some light on the question of whether the reproduction of *N. norvegicus* is annual or biennial. In the length-frequency distributions of the Ligurian Sea it is clear that after a size of 34 mm CL all females are engaged in reproduction, showing green ovaries and/or a berried condition in the appropriate months.

In the remaining areas under study, reproduction has been considered annual, with the exception of the Catalan coast (Sardà, 1991). In the two-year sampling, the 1994 and 1995 Catalan samples (Fig. 6b and c) were very different in terms of the presence of berried females. However, the 1994 autumn sample, which yielded extremely few berried individuals, is also low on adult sizes, while, few months before, many females in advanced maturation were present (Fig. 6a). On the whole we have

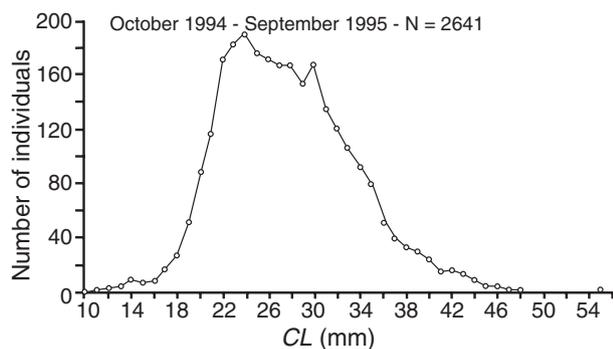


FIG. 7. – Sum of the annual cycle of sampling (each monthly sample was standardized to 8 hours of trawling) to show the female sizes which dominate the catches.

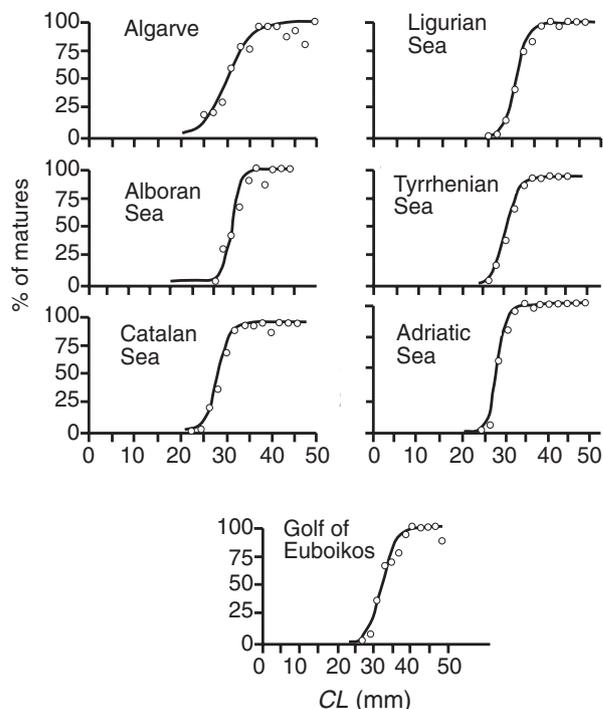


FIG. 8. – Maturity at length ogive in the seven studied areas.

observed a somewhat irregular results of sampling, which could be related to the stressed condition of the stock (Sardà, 1991).

Turning to the Ligurian samples, the instars from 24 to 30 mm CL dominate the catches (Fig. 7). In terms of age they are composed of two and three-year-old females. The majority of these (24–27 mm CL) are excluded from the reproductive potential of the stock because they have not yet reached full maturity. Later it will be shown that no other area under study presents a better young/adult female ratio.

TABLE 1. – Maturation ogive parameters for each area.

Area	Sample period collection	s_1	s_2
Algarve	May, June, July 1995	10.8930	0.3626
Alboran	May, June, August 1995	32.8042	0.9109
Catalan	June, July, August 1995	20.2081	0.6767
Ligurian	July, August, September 1995	23.3594	0.7269
Tyrrhenian	July, August, September 1995	20.1200	0.6362
Adriatic	July, August, September 1995	24.8890	0.8442
Euboikos Gulf	July, August, September 1995	15.8838	0.4788

TABLE 2. – Carapace length of smallest female in advanced maturation, smallest berried individuals and 50% maturity size in each area.

Areas	Smallest female in advanced maturation	Smallest ovigerous	50% maturity size
Algarve	25 mm	24 mm	30 mm
Alboran	30 mm	30 mm	36 mm
Catalan	24 mm	27 mm	30 mm
Ligurian	29 mm	27 mm	32 mm
Tyrrhenian	27 mm	27 mm	32 mm
Adriatic	25 mm	24 mm	30 mm
Euboikos	19 mm	23 mm	33 mm

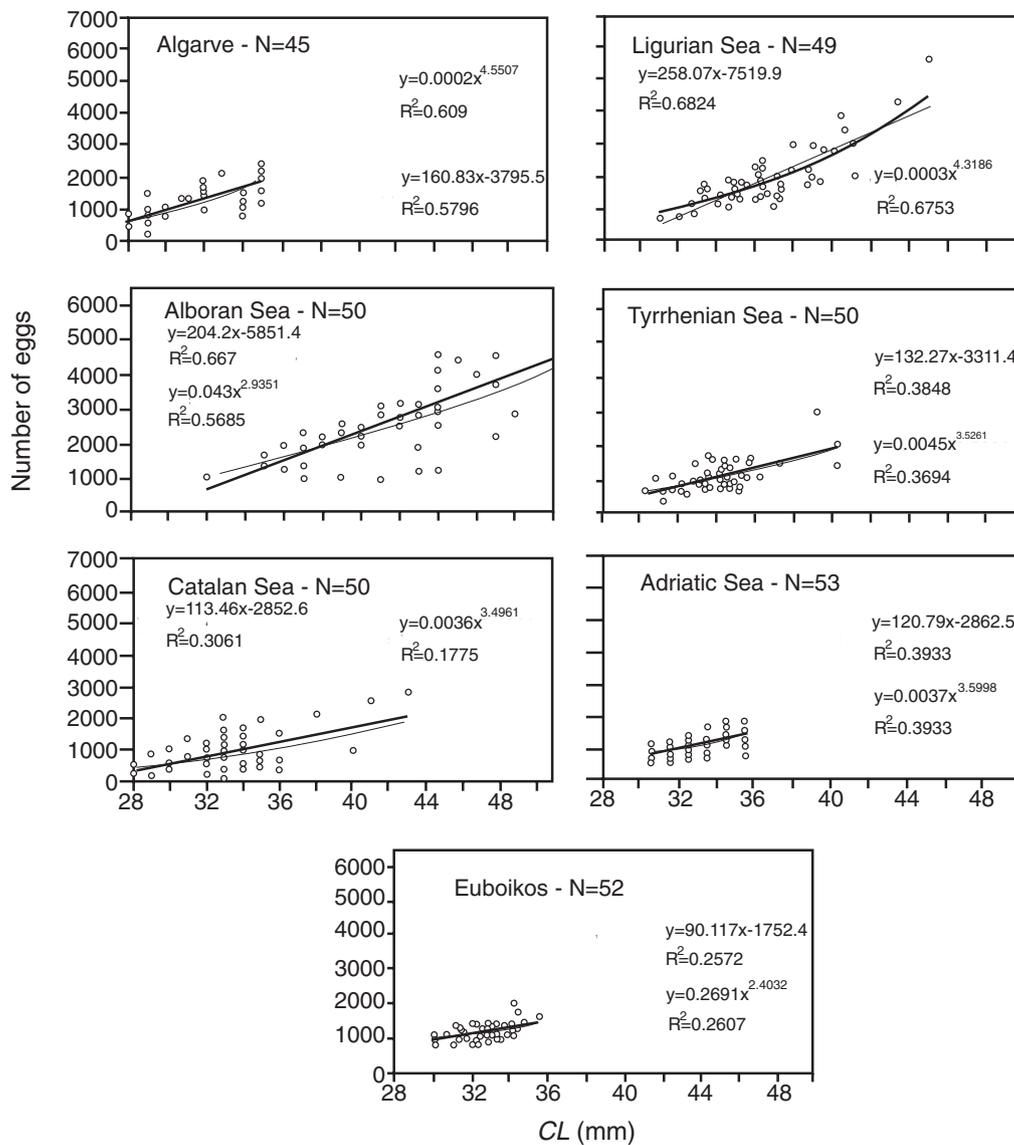


FIG. 9. – Fecundity in terms of brood size. Experimental data (circles) have been related to size both by linear and power function (see text).

TABLE 3. – Main statistical parameters of fecundity/size relationships ($F = a + b CL$). *Including specimens larger than 36 mm *CL*. ** Non significant.

Areas	<i>a</i>	<i>b</i>	<i>N</i>	<i>r</i>	s.e.a	s.e.b
Algarve	-3797.059	160.889	45	0.761	357.698	20.892
Alboran*	-5851.416	204.203	50	0.817	765.178	20.828
Catalan	-778.28	49.285	46	0.221**	---	---
Catalan*	-2852.615	113.464	50	0.553	511.614	24.660
Ligurian	-4998.149	188.247	19	0.653	275.772	52.919
Ligurian*	-7426.780	255.392	53	0.677	522.254	25.742
Tyrrhenian	-2061.939	94.654	46	0.411	298.544	31.658
Tyrrhenian*	-3311.398	132.270	50	0.620	342.859	24.14
Adriatic	-2862.498	120.791	54	0.627	253.793	20.803
Euboikos	-1752.364	90.117	52	0.507	209.091	21.656

TABLE 4. – Numbers of early embryos per five reference carapace lengths (in mm) including females larger than 36 mm *CL* (*).

Areas	30	35	40	45	50
Algarve	029	1834	2638	3443	4247
Alboran*	274	1296	2316	3338	4358
Catalan*	551	1119	1685	2253	2820
Ligurian	649	1590	2531	3473	4414
Ligurian*	235	1512	2788	4066	5342
Tyrrhenian	767	1251	1724	2197	2670
Tyrrhenian*	656	1318	1979	2641	3302
Adriatic	761	1365	1969	2573	3177
Euboikos	951	1402	1852	2303	2753

Reproductive sizes and female maturity at length ogive

Maturation ogives are shown in terms both of raw data and the logistic curves derived from them (Fig. 8). The set of functions for all areas is given in Table 1.

The 50% maturity sizes vary in the seven areas by more than six mm *CL*, with the minimum in the Algarve, Catalan and Adriatic Seas (30 mm *CL*) and the maximum in the Alboran Sea (36 mm *CL*).

A comparison of field data relating to the smallest female in advanced maturation, the smallest berried individual and the calculated 50% maturity sizes for each area is given in Table 2.

Fecundity

Collected data show different fecundities in each area, which can be compared by means of the regression lines of number of embryos per size (Fig. 9). The different fecundity/size relationships are given in Table 3 and the expected numbers of

embryos for five reference carapace lengths in Table 4.

According to the adopted procedure (i.e. using females of 36 mm *CL* as maximum size), highest fecundity was registered in the Algarve Sea, the lowest on the Catalan coast; the Ligurian, Adriatic, Alboran, Greek and Tyrrhenian sets of data were apparently very close to each other. However, when the “b” figures were compared using the *t-test*, a

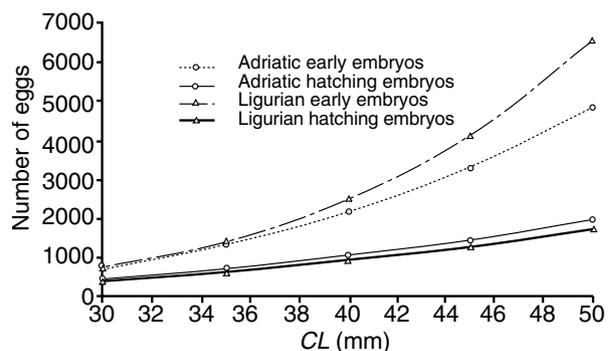


FIG. 10. – Brood size per female length in recently berried females and at the end of embryonic life in the Adriatic (Gramitto and Froglià, 1980) and Ligurian stocks.

significant affinity was found only between the Gulf of Euboikos and the Tyrrhenian Sea ($t=0.6917$; $p>0.05$). Therefore we consider that the calculation of a common function is of little significance.

A comparison of two of the reported curves, those of the Adriatic and the Ligurian Sea, with literature data concerning fecundity at an advanced stage of embryogenesis obtained in the same area (Gramitto and Froglija, 1980; Orsi Relini and Relini, 1989) is shown in Fig.10. In the Adriatic fecundity is about double that calculated with embryos close to hatching; in the Ligurian material, the loss of embryos proves even greater, especially for large sizes.

Reproductive potential

According to the VPA (Sardà *et al.* 1998), the stocks under study show important differences in female numbers and biomasses. The VPA was carried out for comparative purposes, establishing as a starting-point common to the seven areas a landed biomass of 10 t. The results of VPA in terms of numbers range between 1,400,000 individuals in the Alboran Sea and 2,700,000 in the Ligurian Sea. In terms of biomass, figures range from 14.6 tons of females in the Catalan Sea to 35.9 tons in the Ligurian Sea (Fig. 11). The reproductive share of the stock, i.e. the number of mature females, varies from a minimum of 130,000 individuals in the Catalan Sea to a maximum

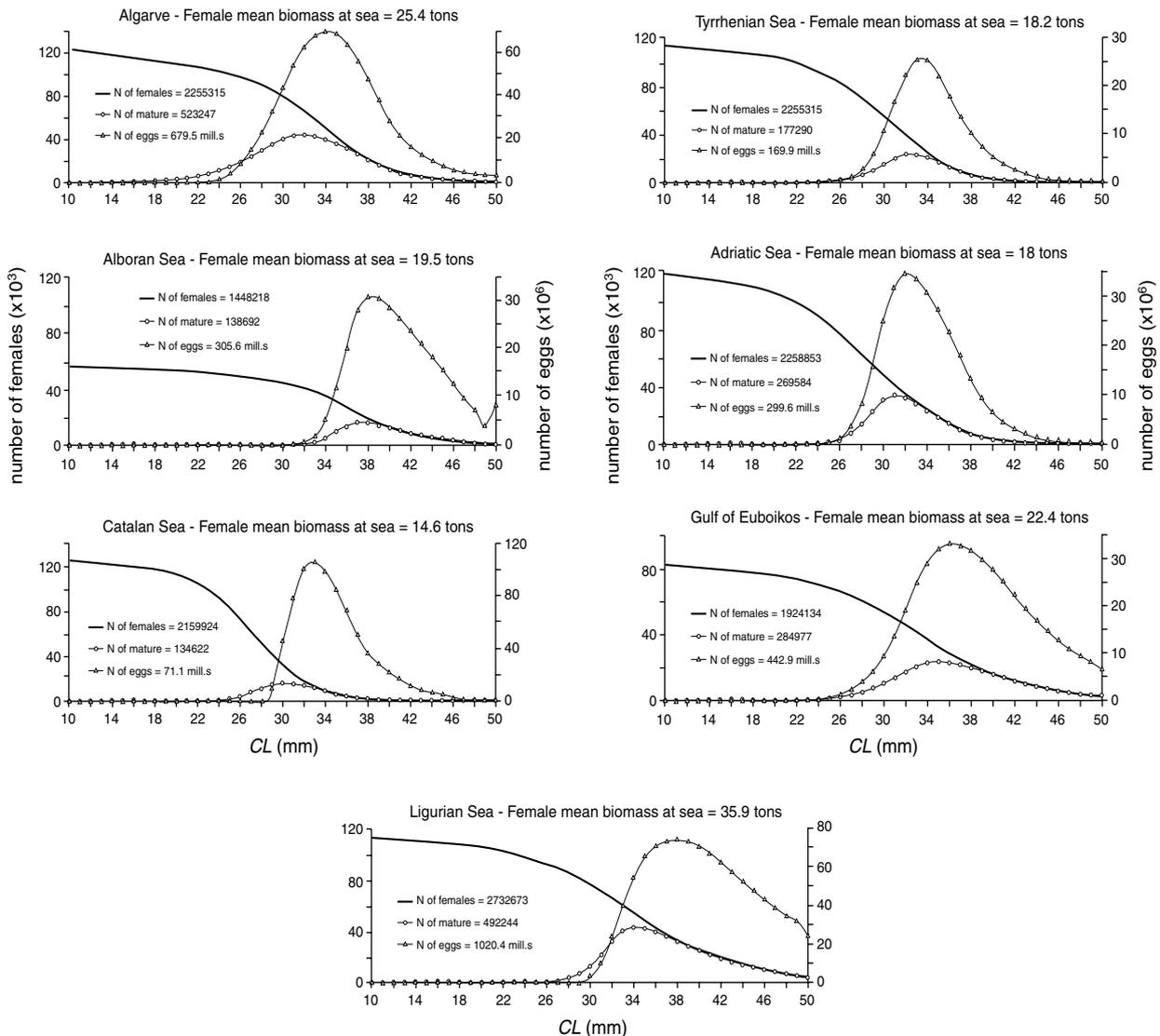


FIG. 11. – Reproductive potential in the studied stocks. —, VPA results given as number of females. Mature females (---) and their total egg production (—Δ—) are shown.

TABLE 5. – Percentage of mature females out of total females, mean number of egg per female, total eggs production (in millions) in relation to the fishing mortality rates (Overall F) in each stock.

Areas	% of mature females	Mean number of eggs per female	Total egg production	Overall F
Algarve	23.2	1300	679.5	0.14
Alboran	9.6	2200	305.6	0.195
Catalan	6.2	530	71.1	0.29
Ligurian	18.0	2070	1020.4	0.14
Tyrrhenian	7.9	1110	196.9	0.22
Adriatic	11.9	1110	299.6	0.24
Euboikos	10.4	1550	442.9	0.195

of 520,000 individuals in the Algarve Sea. These have an annual reproductive potential ranging from 71 million eggs in the Catalan Sea to 1020 million in the Ligurian Sea. It must be noted that this calculation too was made for comparative purposes probably represents a large overestimate of real egg production (see chapter on fecundity). The percentage of mature females at sea varies from a minimum of 6.2% in the Catalan Sea to a maximum of 23.2% in the Algarve Sea. The mean number of eggs per mature female ranges from 530 in the Catalan Sea to 2,200 in Alboran Sea (Table 5). The relationship between such parameters and the overall fishing mortality rates in the different areas of study is given in Fig. 12. This figure shows the effects of increasing fishing mortality on the renewal capacity of the stocks.

DISCUSSION

The seasonality of the reproduction of Norway lobster in the Mediterranean is well documented. The timing of the basic processes of ovarian maturation and laying of embryos on pleopods proved very similar in the seven areas under study. Only minor differences were recorded and these can be related to depth distribution (shelf or slope habitat) and latitude (northern and southern areas): a lesser depth and a lower latitude causes a small anticipation of reproductive events. Both maturation and spawning seem therefore to present a phasing similar to that found in other European areas. On the other hand, the duration of embryonic development is shorter, given that hatching occurs in winter instead of spring. Regarding this point, the study of the ovarian cycle confirms old data about the occurrence of larvae in the Mediterranean. Lo Bianco (1908-1909) found two “megalopa” stages in January; he also noted that embryos close to hatching were found from October to February. The Thor expedition obtained a total of 12 specimens in January and February 1909 (Stephensen, 1923). Santucci, who had organized a monthly sampling in the Gulf of Genoa backed up by a ship belonging to the Istituto Idrografico della Marina, collected 21 larvae: positive hauls were performed between 30 January and 6 March in the years 1924 and 1925. He was able to describe the larval series (Santucci,

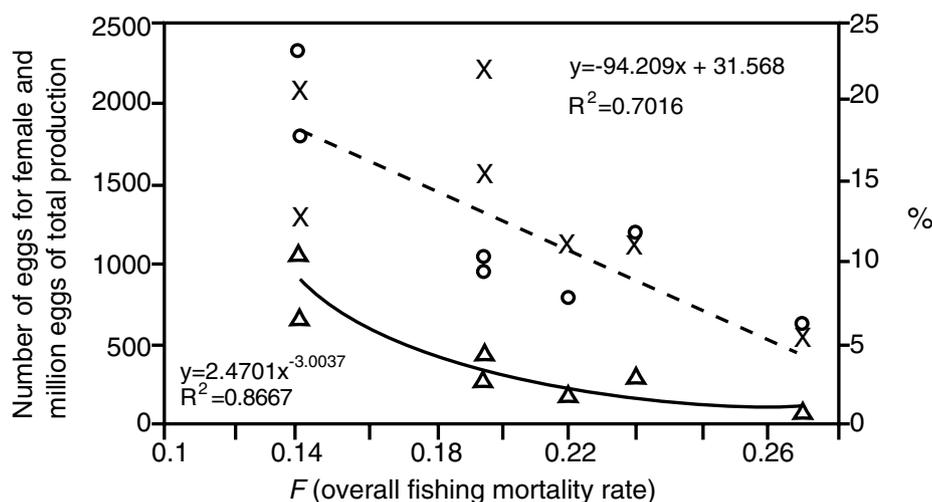


FIG. 12. – Influence of fishing mortality on numbers of mature females, on egg production per female and on total egg production of the studied stocks. x, mean number of eggs per female; Δ egg production in millions; O percentage of mature females.

1926), completing it shortly afterwards (Santucci, 1927), by adding the stage which represents the end of planctonic life, on the basis of a specimen of 17 mm *TL* (Total length) collected in March in the Adriatic.

Farmer (1974) tested the influence of temperature on the duration of embryonic life by maintaining two groups of new berried females, one at 10-12°C and the other at 20-22°C. In the first group hatching occurred in April and May of the year following that in which they were caught (the normal period of hatching in the Irish Sea), whereas those maintained at 20-22°C hatched in the December of the same year. As noted beforehand, spawning occurs at the same time (from August to November) around the British Isles (Thomas, 1964; Farmer, 1974) and in the majority of Mediterranean populations. However those living on the slope achieve winter hatching with a temperature only about 2°C higher than that of Farmer's experiment. In particular, in the Ligurian Sea the distribution of *N. norvegicus* coincides with that of the Mediterranean Intermediate Water, of eastern origin, which is characterized by a constant temperature of 13.5°C and a salinity of around 38.5‰ (Orsi Relini and Relini, 1989). The Adriatic shelf population lives in winter temperatures colder than those of the slope of the Western Mediterranean; however hatching of embryos occurs mainly in winter (Frogliata and Gramitto, 1981). The overall pattern seems therefore to indicate that reproduction is to a certain extent independent of temperature.

The second major factor influencing reproductive processes is light, especially through diel rhythms. *N. norvegicus* seems sensitive to this factor, also when it lives along the slope.

Given the great influence of light on the life and behaviour of mesopelagic Decapods (Omori, 1974; Herring and Roe, 1988), it is reasonable to assume that this influence also extends to bathyal benthic decapods, in particular those bearing fully developed eyes. Furthermore, the role of light on the Mediterranean slope can be also deduced from the importance of colours in the integument of *N. norvegicus* itself (Santucci, 1930), in which the red bands on chelae and carapace create a disruptive pattern. Light, therefore, seems to explain how the above-mentioned depth and latitudinal gradients determine small differences in the reproductive patterns of the study areas.

According to the classification proposed by Hartnoll (1985), the Norway lobster is character-

ized by indeterminate growth, with laying occurring in each postpuberty instar. The study of the reproductive cycle has made a contribution to the ageing and monitoring of growth in females. In fact, the coupling of sizes with reproductive characteristics in length-frequency histograms has allowed us to follow immature females over a period of three years and to identify the average instar of first copulation and first complete maturation. At the beginning of the fourth year of life, mating occurs, and the massive ovoverdin storage in the ovary (which produces the green colour) begins. Eggs are spawned in summer or autumn and in the following autumn-winter the hatching of embryos occurs. The female Norway Lobster therefore actually reproduces (in the sense that new individuals are born) at about 4 years (32 mm *CL* in the case of the Ligurian Sea), even though the puberty moult and hence the attaining of the above-mentioned size occurs at age 3+.

The present interpretation of growth presents similarities with Chapman and Howard's interpretation (1988) of lobsters of the Firth of Clyde, in which the size 28 mm *CL* - the main modal group of the fished stock - corresponds to the age 2+.

Recent studies of growth in the Mediterranean area on the basis of length-frequency analysis (Castro, 1992; Mytilineou *et al.*, 1993; Mytilineou and Sardà, 1995) generally assign the size 32 mm *CL* to a female older than in the present interpretation (i.e. 4 or 5 or 6 years instead of 3+, 4). The reason for this probably lies in the fact that these authors have considered each gaussian component of length-frequency distributions as a year of life. We, on the contrary, believe that juvenile ages have a composite size structure which is related to the long recruitment of Norway lobsters.

The sizes at maturity (50%) ranged from 30 to 36 mm *CL* with three patterns: Algarve, Catalan and Adriatic presented the smallest size; the intermediate size was found in the Ligurian and Tyrrhenian Seas and in the Gulf of Euboikos; and finally the Alboran Sea had a population composed of large females, with the largest maturity size. This complex picture suggests that local factors are involved, for instance the density of population and hence competition for space and food (Chapman and Howard, 1988). Regional differences in sizes, similar to the ones which have been well studied in Northern Europe (Bailey, 1986; Tully and Hillis, 1995), were also recorded

in the Mediterranean. Gramitto and Frogliia (1977) found different sizes at the same basic reproductive events in the Adriatic, studying in particular the Pomo and Ancona stocks. Local differences in sizes were registered in the Aegean Sea (Mytilenou *et al.*, 1990; 1995).

The range in reproductive sizes observed in the seven Mediterranean areas of the present study (30-36 mm *CL*) parallels those recorded in ICES areas (23-31 mm *CL*) (Table 6). It is interesting to note that Atlantic stocks have an average size (25.6 mm *CL*) which is clearly lower than that found in the Mediterranean (31.9 mm *CL*). The differences between the values of the two geographic sectors, tested by using the Kruskal-Wallis' non-parametric analysis of variance, are highly significant ($H=12.175$; $p<0.01$).

In the majority of the listed northern stocks maturity is assigned at age 3. On the basis of the results we are of the opinion that age 3 represents the onset of reproductive processes (from puberty onward) also in the Mediterranean, and that the differences in reproductive sizes registered in these stocks can be related to different somatic growth rates.

If our interpretation is correct, a remarkable homogeneity in the basic steps of life history appears to link Norway lobsters over a very broad latitudinal range (Mediterranean - North Atlantic). Similar affinities have been shown using morphological (Holthuis, 1991) and genetic studies (Passamonti *et al.*, 1997).

The study of fecundity has presented some differences among the areas: if only small females and early embryos are considered, Algarve Norway lobsters seem to have a higher fecundity than those of other Mediterranean areas. However, previous studies in Portuguese waters, which dealt with advanced embryos and a larger range of females sizes, gave results closer to those of the Adriatic Sea conducted using a similar approach (Gramitto and Frogliia, 1980; Figueredo *et al.*, 1982).

Therefore also about this point affinities appear more consistent than differences (Morizour *et al.*, 1981; Sardà, 1995).

The attempt to assess reproductive potential in different areas has shown how fishing mortality affects the self-supporting capacity of the stocks. According to this approach, the Ligurian and Algarve populations are in the best condition while the Catalan stock is in the worst. The peculiarity of the Catalan stock, in which reproduction does not seem to be annual (Sardà, 1991), has been attributed to local overexploitation.

TABLE 6. – Length at maturity in mm *CL* of *Nephrops norvegicus* in different areas of ICES study areas (Anon., 1997) and in the Mediterranean Sea.

Areas	Length maturity	Areas	Length maturity
North Minch	25	Celtic Sea	31
South Minch	26	Bay of Biscay	25
Firth of Clyde	27	North Galicia	24
Skagerrak/Kattegat	28	W. Galicia/N.Portugal	26
Moray Firth	23	Algarve	30
Fladen Ground	25	Alboran	36
Botney Gulf	27	Catalan	30
Firth of Forth	25	Ligurian	32
Irish Sea	24	Tyrrhenian	32
Porcupine Bank	24	Adriatic	30
Aran Grounds	24	Euboikos	33

The Catalan case presents analogies to that of Farn Deep discussed by Chapman (1980).

Many authors argue that Norway lobster are not affected by recruitment overfishing (i.e. the depletion of stock biomass due to scarcity of recruits), since juveniles and berried females are hardly ever caught by trawlers (because they tend to remain in their burrows). The first assessments of Norway lobster in the Mediterranean were optimistic because of this idea of the low catchability of females (Lleonart and Sardà, 1993) and young individuals (Abella and Righini, 1995; 1996). Nevertheless, a recent assessment of the ICES *Nephrops* Working Group recognized a close relationship between recruitment and spawning biomass in the Bay of Biscay and in South-Western and Southern Portuguese stocks (Anon., 1997). In this assessment, a state of recruitment overfishing was also registered for the Southern Portuguese stock, to which the present Algarve samples belong. In the studied areas the fishing mortality rates in the Algarve and in the Ligurian Sea are the lowest (Sardà *et al.* 1998) and their reproductive potentials are the highest. Contrasting results suggest that the recently introduced prudential approach (García, 1994; Caddy, in press) should also be used with regard to this resource. On the other hand, given their prevalent distribution on the slope, Norway lobsters of the Mediterranean could take advantage of lower fishing pressure than the northern stocks, in the sense that Mediterranean fisheries, divided into shelf, epibathyal and mesobathyal fishing-grounds, allow cyclical (pluriennial) redistribution of effort, influenced by the abundance, at times, of shelf or bathyal species.

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