

REPRODUCTION AND MOULT SYNCHRONISM IN *NEPHROPS NORVEGICUS* (L.) (DECAPODA, NEPHROPIDAE) IN THE WESTERN MEDITERRANEAN: IS SPAWNING ANNUAL OR BIENNIAL?

BY

F. SARDÀ

Instituto de Ciencias del Mar, Paseo Nacional s/n, 08003 Barcelona, Spain

RÉSUMÉ

Les résultats initiaux de recherches sur le cycle de reproduction de la langoustine, *Nephrops norvegicus*, dans la mer Catalane (Méditerranée nord-occidentale) sont présentés, à savoir: âge à 50% de maturité (Lc 30,5 mm), sex-ratio (prédominance des mâles en automne et en hiver), période de maturité des gonades (avril-août) et période de ponte (août-janvier). Un type de synchronisme entre mue et reproduction en fonction de la classe de taille et du sexe est proposé. C'est entre décembre et avril qu'a été observée une période principale de mue pour toutes les classes de taille et les deux sexes. Deux autres périodes de mue, moins prononcées existent, l'une en été pour les juvéniles des deux sexes, l'autre en automne pour les mâles. Le synchronisme dans le cycle biologique est comparé à celui décrit dans d'autres parties de la Méditerranée et dans l'Atlantique. L'auteur aborde également la question de savoir si les femelles de cette espèce pondent chaque année.

INTRODUCTION

The relationship between moulting and reproduction in decapod crustaceans is a topic that is daily gaining in currency, both from the standpoint of basic biological knowledge and in terms of its direct application in fisheries and aquaculture. Aiken & Waddy (1980), Sastry (1983), Conan (1985), and Hartnoll (1985) have all recently published general reviews dealing with reproduction and moult cycles in crustaceans, with a view to explaining adaptations of crustacean life cycles to different environment.

The relationship between body growth and reproduction is usually held to be synchronous, such that the energy metabolized by an animal can be distributed so as to sustain maximum yield in both processes while preventing interferences. In many species mating, gonad maturity, spawning, incubation of eggs, and the moults associated with growth, puberty, and mating follow a temporal sequence that enables all these functions to take place without overlap. Endogenous and exogenous factors interact, such that the life cycles of decapods become adapted to each particular habitat, giving rise to variations not only with latitude but also in response to local influences. The Norway lobster *Nephrops norvegicus* is no exception, and its life cycle is sufficiently

flexible to adapt to local environments (Chapman & Bailey, 1987; Figueiredo, 1987; Anon., 1988, 1989; Briggs, 1989). In this respect, there is evidence that Norway lobsters may, in response to factors which are not yet clearly understood, spawn every two years (Chapman, 1980; Figueiredo, 1982; Redant, 1987; Briggs, 1988). However, except for Andersen (1962), who reported incubation times of 12-13 months for this species in the Faroe Islands, earlier references (Karlovac, 1953; Figueiredo & Barraca, 1963; O'Riordan, 1964; Figueiredo & Thomas, 1967; Farmer, 1974a) merely reported annual spawning.

Nevertheless, despite an extensive literature on the biology of *Nephrops norvegicus* throughout its range, e.g., Figueiredo & Thomas (1967) and Farmer (1975) in the Atlantic and Karlovac (1953), Sardà & Fernández (1981), and Orsi Relini & Relini (1989) in the Mediterranean, no definite pattern which clearly explains the life cycle of the species and contemplates synchronism between moulting and reproduction while remaining sufficiently flexible to be applied in different regions has yet been described.

The object of the present paper is to propose a pattern of synchronism for the different size classes of both sexes and to analyze the causes that might be responsible for spawning on an annual or biennial basis. Initial data on the reproductive cycle of the Norway lobster off the Mediterranean coast of Spain (size at 50% maturity, sex ratio, gonad maturity, and incubation period) are presented, and a relationship between the reproductive cycle and moult frequency is put forward.

MATERIAL AND METHODS

A total of 3,595 individuals of *Nephrops norvegicus* (1,864 males and 1,731 females) with carapace lengths ranging from 15 to 60 mm were collected in 1974, 1977, and 1978. Specimens were taken by commercial trawlers operating out of Barcelona (northeastern Spain) at depths between 300 and 600 m (fig. 1). The customary fishing grounds for this species are known as the "Cerola" grounds, situated in the vicinity of 41°15'N 2°23'E).

Specimens were transported alive to the laboratory, where the following measurements and biological data were taken: carapace length (Lc) to the nearest 0.1 mm, measured along the dorsum from the end of the orbit to the terminal margin of the carapace; sex, determined from the structure of the sexual pleopods (Farmer, 1974b); and gonad maturity stage, according to the scale given by Farmer (1974a) and Figueiredo (1972). For data processing purposes, only individuals in maturity stages III and IV were counted as mature, in order to minimize the effect of possible gonadal reabsorption after stage II (Figueiredo, 1982).

Gonad maturity stage and the presence of eggs on the pleopods were the criteria used to evaluate the size at 50% maturity, taken to be the smallest size at which half of the individuals were either ripe or ovigerous.

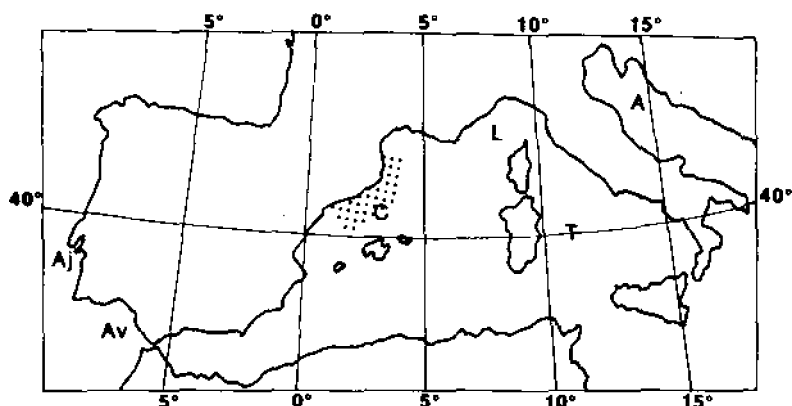


Fig. 1. Location of the study area (dotted region) and other regions referred to in the literature. C: Catalan Sea; L: Ligurian Sea; A: Adriatic Sea; T: Tyrrhenian Sea; Av: the Algarve; Aj: the Alentejo.

Moult stages were identified in accordance with Drach (1939) as applied to *Nephrops* by Sardà (1983). Moulting specimens in each sample were defined to be those individuals undergoing proecdysis and postecdysis (stages D₂-D₃₋₄ and A, respectively). When identification was impossible or doubtful on account of decomposition of the pleopods, moulting individuals were defined to be those in which the consistency of those regions of the carapace typically involved in absorption or recalcification was soft (Sardà & Cros, 1984) or in which gastroliths were quite manifest.

The figures have been presented in percent according to size class, with size intervals as per Sardà (1985) (table I). A G test was applied to calculate the significance of the deviation of the sex ratios recorded with respect to 50% (1:1) in both monthly and combined annual samples. Analysis of variance (ANOVA) was used to analyze interannual variations in the sex ratio.

RESULTS

Sex ratio. — The sex ratio (fig. 2) varied in the different samples (Gh = 81.96; $p < 0.05$), and presented significant monthly differences with respect to the expected ratio (1:1). The monthly means for June, August, October, November, and December were significantly different from 50%. The number of males in the catches rose in August and remained high through February.

Analysis of variance of the sex ratio between years yielded no significant differences ($p > 0.05$), and the annual pattern was similar each year.

Reproduction. — The reproductive season for females (gonad maturity stages III and IV) ran from April to September (fig. 3). Spawning began in

TABLE I

Size classes used for statistical processing purpose
(after Sardà, 1985)

Size class number	Size interval (Lc in mm)
1	<20
2	20-24
3	25-29
4	30-34
5	35-39
6	40-49
7	>50

August and berried individuals were present through January (5-6 months). Overall, the maximum monthly percentage of ripe and ovigerous females came to approximately 80-90% of the population of females. This suggests that there are females that do not spawn on an annual basis (Thomas, 1964; Farmer, 1974a; Briggs, 1988), although the proportion was relatively low (less than 20%).

Slight differences in reproductive cycles associated with local adaptations have been reported, e.g., Arrobas (1982), off the Algarve in Portugal, Morizur (1981) off southern Britain, and Bailey (1984) in the Clyde and off the Island of Jura in Scotland. Moreover, the periods of gonad maturity in the said areas were more prolonged than those reported from the Mediterranean by Frogliia & Gramitto (1980) for the Adriatic, Orsi Relini & Relini (1989) for the Ligurian Sea, and the results presented herein for the Catalan Sea. In this respect it is important to take into account the different depth distributions for this species in the Atlantic and the Mediterranean, i.e., between 20 and 500 m in the Atlantic and between 300 and 600 m in the Mediterranean, where reports of *Nephrops* at shallower depths are rare. Clearly, conditions with respect to light, temperature, and environmental stability in the North Atlantic are quite different from those in the Mediterranean.

Fig. 4 shows size at 50% maturity for 496 females collected in June, July and August 1977 and 1978. Of these, only 296 were in maturity stages III and IV (approximately from 50 to 90% of the ripe females of $L_c > 30$ mm). The size at 50% maturity fell between 30 and 31 mm.

Fig. 5 represents a total of 217 ovigerous females out of a total sample of 542 females from the months of August and September. In this case, the size at 50% maturity, based on the females carrying eggs attached to their pleopods, was between 32 and 33 mm L_c . The minimum size for ripe females recorded was an L_c of 22 mm, quite small when compared with the minimum size for ovigerous females, which was $L_c = 27$ mm. The habit of females to hide in their

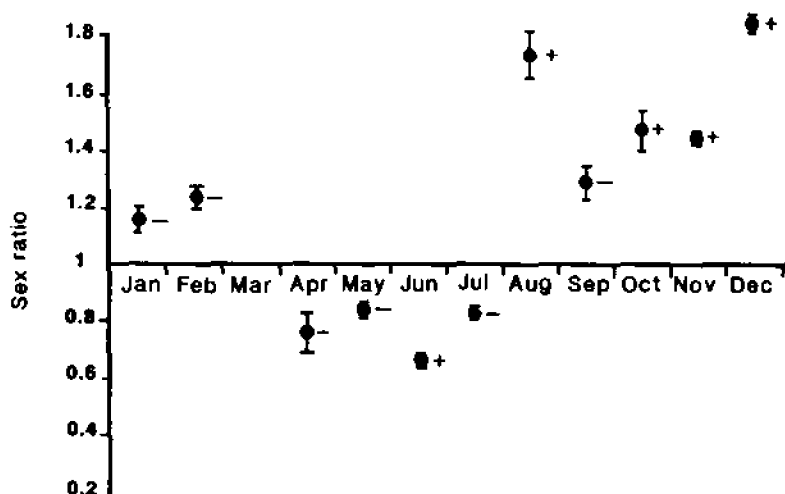


Fig. 2. Monthly sex-ratio ($\sigma\sigma/\phi\phi$) based on data for all three years (1974, 1977, and 1978 combined); vertical bars represent the standard deviation - (+): values significantly different from the ratio of 1:1; (-): values statistically the same as 1:1.

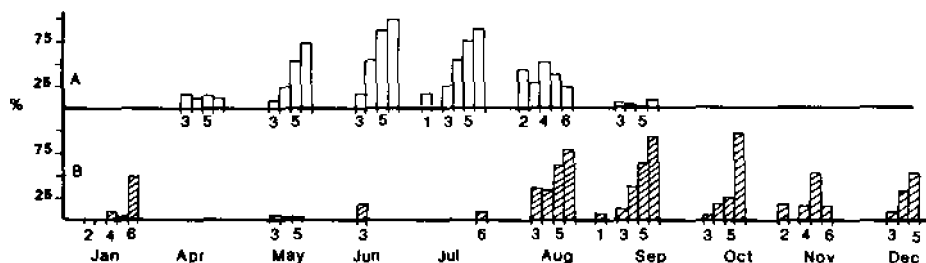


Fig. 3. Percentage of mature (blank bars) and ovigerous (hatched bars) females according to the size classes set out in table I.

burrows when incubating eggs is one possible explanation for this increase in minimum size between ripe and berried females, since this would affect their frequency in the samples and result in underestimation of the tails of the size frequency distributions for females. Nevertheless, a later analysis of the size frequencies did not uncover any differences in the size distributions of females caught before and during the period of incubation.

The figures show that the asymptotic portion of the curve fails to remain parallel to 100% and in fact falls somewhat, suggesting a decrease in the ability to spawn annually with size, such that substantial numbers of females in the population might not be functionally reproductive every year.

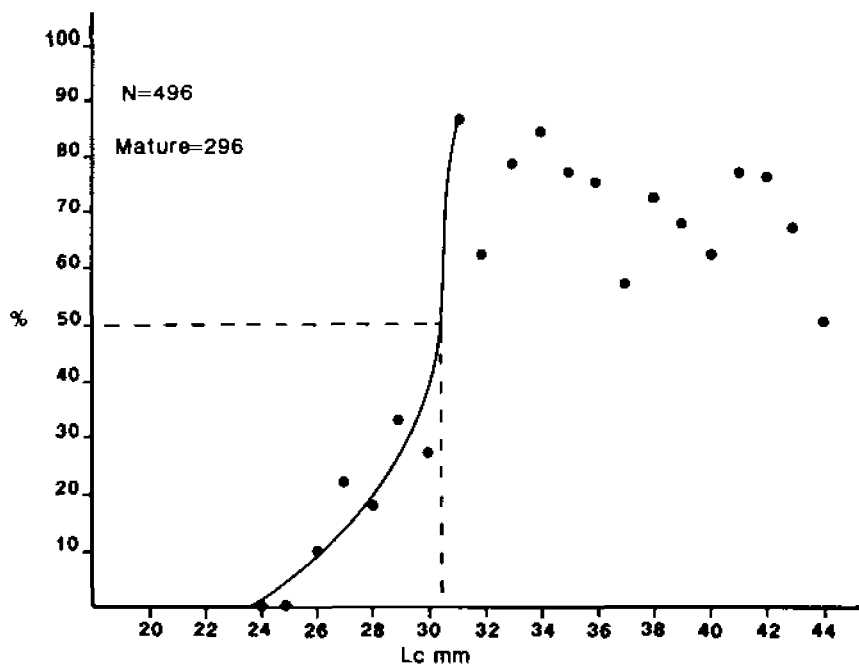


Fig. 4. Size at 50% maturity based on ovary development stage (stages III and IV).

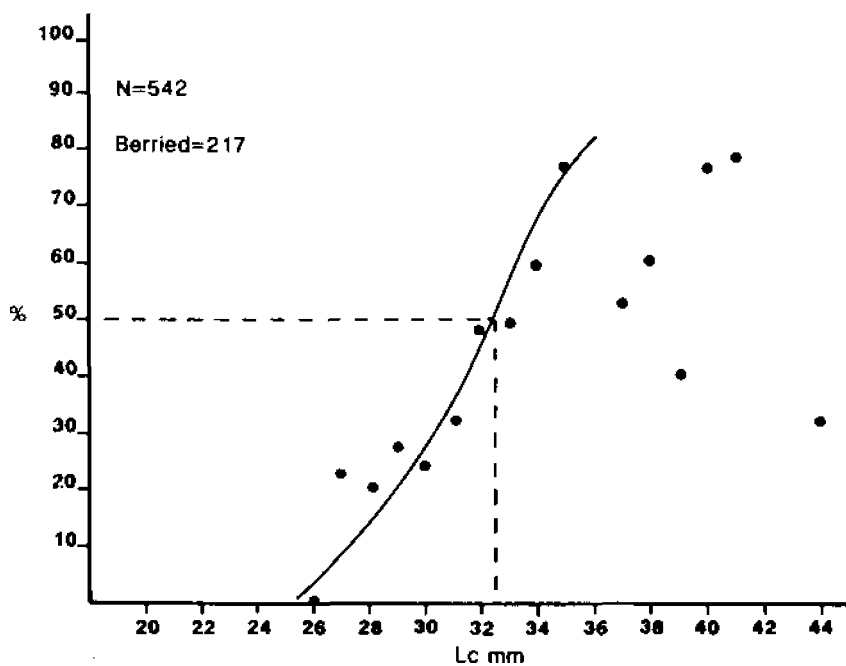


Fig. 5. Size at 50% maturity based on ovigerous females.

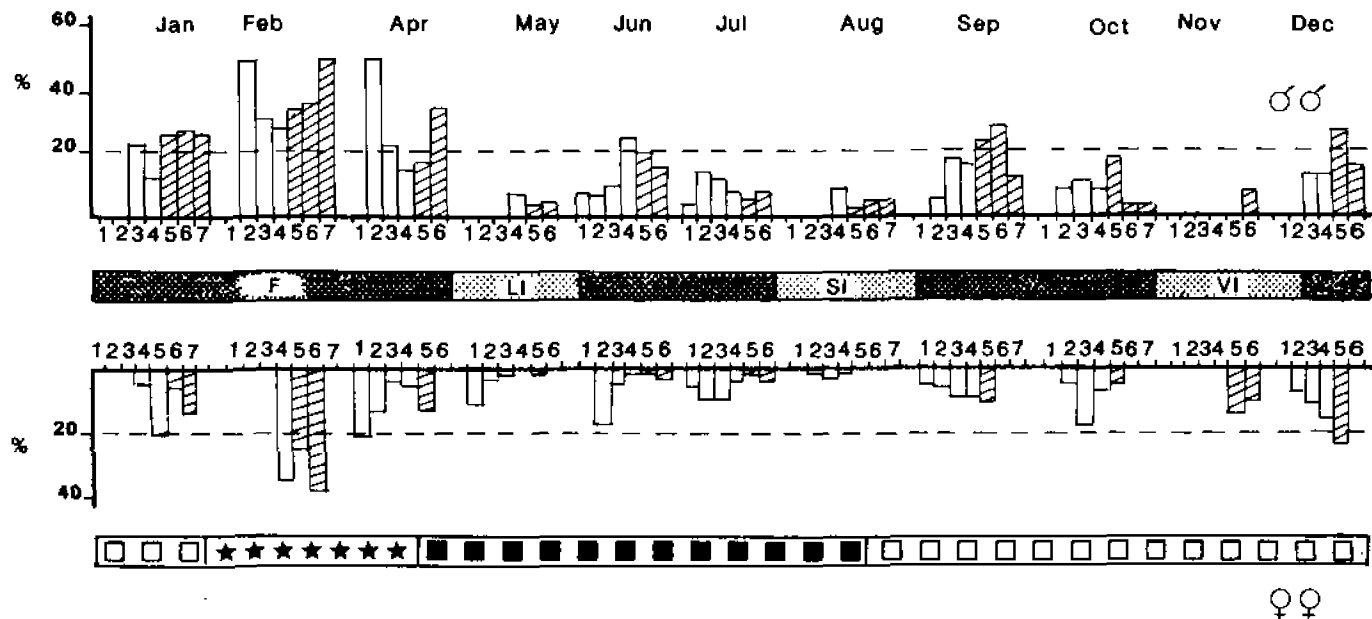


Fig. 6. Percentage of moulting males and females by size class (numbered after table I). Diagram of the reproductive cycle showing the typical sequence of synchronic events between moulting and reproduction: Blank bars: immature individuals; Hatched bars: ripe individuals; Dashed line: moult threshold; Darkly shaded rectangles: moult period; Lightly shaded rectangles: intermolt period; F: "fixed"; LI: long intermolt; SI: short intermolt; VI: variable-length intermolt; Solid squares: period of gonad maturity; Blank squares: egg incubation period; Stars: mating period.

Moult frequency. — Fig. 6 depicts the moult frequency by month and size class. Broadly speaking, December to April is an important moulting season in both sexes, constituting the main or most pronounced moulting period, termed "fixed" by Sardà (1985). This moulting period affected nearly all the males in the population and most adult females. Charuau (1974) and Conan (1975) reported similar moulting periods which extended longer into spring.

There was a smaller peak in June and July, mainly affecting the smaller size classes of both sexes. Another peak occurred in September-October, affecting most of the males and juvenile females.

Fig. 6 thus depicts three moulting periods: the first, from December to April, a "fixed" moulting season (F), followed by a "long" intermoult period of 3-4 months, leading up to a second moulting period for the smaller size classes in June and July, followed by a further "short" intermoult period of 2-3 months and then a third moulting period in September-October. Lastly, a "variable" intermoult period, dependent upon size and sex, completed the annual cycle by bridging the time remaining to the next moult during the "fixed" moulting season.

There was no percentage of moulting individuals that constituted a threshold that could be used as a criterion to define moulting periods or seasons. The percentages reported by various other investigators in other species, e.g., *Emerita analoga* (Stimpson, 1857) (cf. Conan, 1985), *Palaemon elegans* Rathke, 1837 (cf. Webster, 1982), *Sicyonia ingentis* (Burkenroad, 1938) (cf. Anderson et al., 1985), *Paralithodes* spp. (Jensen & Armstrong, 1989), and *Liocarcinus depurator* (L., 1758) (cf. Abelló, 1989), together with the data presented herein, would seem to place such a threshold at around 20%. For juveniles the threshold is probably lower, since they moult somewhat asynchronously more than once a year, all year long except in May, August, and September.

Synchronism. — Fig. 6 also illustrates the pattern of synchronism between moulting and reproduction observed in *Nephrops norvegicus* in the western Mediterranean. The period of gonad maturity and berry coincided with the period with the lowest percentages of moulting adult female individuals, with hatching concurrent with the onset of the "fixed" moulting season. The winter moult means that females can be fertilized between February and April by males that have hardened following their earlier moulting period in September-October. The findings of other workers (Karlovac, 1953; Figueiredo & Barraca, 1963) agree with these results. In the North Atlantic the mating season that follows the hatching of eggs takes place a little later, in April-May (Andersen, 1962; Figueiredo & Thomas, 1967; Farmer, 1974a; Symonds, 1972; Conan, 1975). Small differences in the reproductive period, associated with local adaptations, have been reported by Arrobas (1982) off the Algarve in Portugal, Morizur (1981) off southern Britain, and Bailey (1984) off Clyde and Jura in Scotland. Comparing the data presented by these research-

chers with the findings of Froglià & Gramitto (1980) in the Adriatic, Orsi Relini & Relini (1989) in the Ligurian Sea, and the data for the Catalan Sea set out herein, the period of gonad maturity also lasts longer in the Atlantic than in the Mediterranean. However, the different depth distributions for this species in the North Atlantic, between 20 and 500 m, and in the Mediterranean, between 300 and 600 m, with only rare records of *Nephrops* at shallower depths in the Mediterranean, should not be overlooked. As a consequence, conditions of light, temperature, and environmental stability in the North Atlantic are clearly quite distinct from those in the Mediterranean.

Finally, fig. 6 also shows that the percentage of mature females (size classes 4, 5, and 6) undergoing moulting tended to be smaller than that in males, indicative of relatively slower growth in females (Sardà, 1985). Moulting of males and females in all size classes took place throughout the year, although it varied in intensity. This means that a certain percentage of mature females remained unberried and hence did not reproduce. Basically, no ripe females were recorded in the stages of pro- or postecdysis; though there were some slight overlaps of moulting ripe females in the specific instances of May 1974 (1%), June 1978 (1.1%), and July 1978 (4.5%), the values for the remaining months were all nil. Taken in conjunction with the results represented in figs. 4 and 5, the data in fig. 6 provide ample evidence of a relatively large number of females that do not spawn every year.

DISCUSSION

Although the overall annual sex ratio for *Nephrops norvegicus* in the Mediterranean was around 50%, the proportion of males increased between August and December. The decrease in the number of females in the catches at the end of summer and in autumn coincided with the period in which they were incubating their eggs. During this period females are less active and spend most of the time hiding in their burrows (Chapman, 1980). These results are in consonance with the findings of most researchers (Figueiredo & Thomas, 1967; Figueiredo, 1986; Bailey, 1984; Briggs, 1988; Brander & Bennet, 1989; Fariña, 1989). The size at 50% maturity (30.5 mm Lc) was comparable to those reported by Orsi Relini & Relini (1989) in the Ligurian Sea (31.5 mm), Figueiredo (1987) off the Alentejo in Portugal (30 mm), and Arrobas (1982) off the Algarve in southern Portugal (30 mm). These values are, however, relatively high in comparison with those reported in the North Atlantic. Briggs (1988) demonstrated that the size of *Nephrops norvegicus* at 50% maturity decreased with latitude. According to Sardà (1985), this size is attained during the fourth year of life, a year later than reported by Morizur (1979) in the Atlantic off France and some two to three years later than reported by Bailey (1984) off Scotland. The size at 50% maturity based on ovigerous females was around 32.5 mm Lc, also greater than the size estimated for the Atlantic.

It should be noted that in no case did the percentage of ripe females exceed 90% of all adult females and even fell considerably with increasing size (figs. 4, 5). The mean proportion of ripe females during the reproductive period was 70%. It therefore seems reasonable that an appreciable portion of the adult female population does not spawn on an annual basis. Fig. 6 also supports this, in that moulting adult females were present during the season of egg incubation (August-March). These females were not carrying eggs and therefore could not reproduce. According to Sardà (1983), intermoult stage C in adult females lasts about the same length of time as the period of gonad maturity (170 days = 5-6 months). Stage C is thus largely responsible for the synchronism between the moult and reproductive cycles, since, compared to the other moult stages (pro- and postecdysis), it is the stage that undergoes the greatest variation with size.

Most patterns of moult cycles and the number of moults yearly established using the results of field work (Conan, 1975; Arrobas, 1982; Bailey, 1984) have been based on adults measuring from 30 to 45 cm Lc, which make up the bulk of catches and samples. In laboratory and tagging experiments, on the other hand, the most representative size classes have tended to be those corresponding to the first four years of life. Be this as it may, the moult cycle should be regarded as a dynamic process that varies continuously from 4-5 moults a year in postlarvae to fewer than one moult a year in older, very large adults (Sardà, 1985). Knowing the number of moults undergone by an individual each year or the age at which moulting takes place is less important than determining the sizes and times of year at which moulting takes place, together with the relative importance of moult synchronism.

Recapitulating, most of the male population in the study area moulted during the "fixed" moulting season. Juvenile males moulted again in summer, while juvenile and particularly adult males underwent an additional moult later in autumn. Adult females (size classes 4-7) also moulted during the "fixed" moulting season. Fertilization took place after the eggs had hatched in spring. Immature females (size classes 3 and 4 and lower) and immature males underwent moulting throughout the year, with moult intensity following the pattern depicted in fig. 6.

The "fixed" moulting season appears to take place earlier in the Mediterranean than in the North Atlantic. Charuau (1974) and Conan (1975) stated that the main moulting season for both males and females was in spring, with another, less marked moulting period in June. This latter moulting period coincided fully with the observations presented herein, as did the growth pattern and moult frequency.

Furthermore, according to Jensen & Armstrong (1989), an incubation period for eggs lasting longer than around 12 months would be one of the chief conditioning factors responsible for biennial spawning. In *Nephrops*, the incubation period took 5 to 6 months in the Mediterranean (present data),

between 6 and 10 months in the Atlantic (Farmer, 1974a), and 12 to 13 months in Iceland (Andersen, 1962). Biennial spawning would, thus, be a local adaptation in which the relationship between temperature and embryo development would play a role. Different authors (Chapman, 1980; Figueiredo, 1982; Briggs, 1988; Sterk & Redant, 1989) have presented evidence in support of biennial spawning. It is extremely difficult to pinpoint the factors that cause a portion of the population to spawn biennially, and most discussions of the phenomenon have been purely descriptive in nature. Biennial spawning may take place in certain individuals as an adaptive response to size or age or as a simple consequence of the randomness of such processes as mating, asynchronism, behaviour, and the like.

It is known that endogenous factors like biological clocks and exogenous factors like temperature and light cycles affect reproductive cycles (Chapman, 1980; Sastry, 1983; Chapman & Howard, 1988). While the intensity of the interactions among such factors varies with latitude, there are also important local effects that influence growth, reproduction, behaviour, and metabolism in general. In other words, on the one hand there are a series of specific characteristics from which the basic pattern of the life cycle of the population (genetically adapted to its environment), i.e., growth, size at 50% maturity, duration of gonad maturity, incubation period, etc., can be predicted. On the other hand, other factors, i.e., substrate, fishing pressure, food availability, climate, currents, temperature, light cycle, local hydrographic features, etc., simultaneously exert an influence, giving rise to local adaptations and modifications to this basic pattern. However, there are additional factors which may be extremely important but which are difficult to quantify and whose effect on populations is hard to measure. These can be regarded as random factors, in that they are not directly dependent upon phenotype or local habitat, and include: the type of exploitation to which the stock is subjected (variations in effort levels, gear type, fishing cycle); sudden, abnormal variations in climate; the asynchronism intrinsic to the species in question (typically extremely important in crustaceans); and phenomena that are dependent on density or the often random (in spite of the action of pheromones, the effectiveness and range of which are unknown) possibility of a mating encounter between a hard male and a mature, soft female. Thus, a certain and not insignificant percentage of the asynchronism and variability in crustacean life cycles may be the result of random factors whose occurrence and effect on the population are difficult to predict. Such factors are responsible for the considerable proportion of the female population that does not spawn every year and would also account for the difficulty in determining which sizes and which proportion of the population spawn on an annual or biennial basis and therefore in describing a general pattern of reproduction for *Nephrops norvegicus*. Lastly, it should be noted that, in keeping with the terminology current in the literature, spawning that does not take place every year has been referred to as biennial, even though it may in actual fact be pluriannual in some cases.

ACKNOWLEDGEMENT

The author wishes to express his thanks to Ms. M. Just for her assistance in processing the data and preparing the figures and to Dr. P. Abelló for this advice on statistical processing. Mr. R. Sacks translated the original manuscript into English.

This paper was motivated by the paper by Orsi Relini & Relini (1989) and the excellent discussions presented by Bailey (1984) and Chapman & Bailey (1987).

REFERENCES

- ABELLO, P., 1989. Reproduction and moulting in *Liocarcinus depurator* (Linnaeus, 1758) (Brachyura: Portunidae) in the Northwestern Mediterranean sea. *Scient. Mar.*, 53 (1): 127-134.
- AIKEN, D. E. & S. L. WADDY, 1980. Reproductive biology. In: J. S. COBB & B. F. PHILLIPS, eds., *The biology and management of lobsters*, 1: 215-276. (Academic Press, London).
- ANDERSEN, F. S., 1962. The Norway lobster in Faeroe waters. *Medd. Dan. Fisk. Havunders.*, (n. ser.) 3 (9): 265-326.
- ANDERSON, S. L., W. H. CLARK, JR. & E. S. CHANG, 1985. Multiple spawning and molt synchrony in a free spawning shrimp (*Sicyonia ingentis*: Penaeoidea). *Biol. Bull., Woods Hole*, 168: 377-394.
- ANON., 1988. Report of the study group on Nephrops. ICES C.M. 1988/K:29: 1-70.
- , 1989. Report of the working group on Nephrops stocks. ICES C.M. 1989/Assess:18: 100-163.
- ARROBAS, I., 1982. Some aspects on the biology and fishery of *Nephrops norvegicus* (L.) from the south Portuguese coast. ICES C.M. 1982/K:27: 1-28.
- BAILEY, N., 1984. Some aspects of reproduction in *Nephrops*. ICES C.M. 1984/K:33: 1-26.
- BRANDER, K. M. & D. B. BENNETT, 1989. Norway lobsters in the Irish Sea: modeling one component of a multispecies resource. *Marine Invertebrate Fisheries: Their Assessment and Management*: 183-204.
- BRIGGS, R. P., 1988. A preliminary analysis of maturity data for Northwest Irish Sea *Nephrops*. ICES C.M. 1988/K:21: 1-15.
- , 1989. Temporal and spatial variation in western Irish Sea *Nephrops*. ICES C.M. 1989/K:36: 1-11.
- CHAPMAN, C. J., 1980. Ecology of juvenile and adult *Nephrops*. In: J. S. COBB & B. F. PHILLIPS, eds., *The biology and management of lobsters*, 2: 143-180. (Academic Press, London).
- CHAPMAN, C. J. & N. BAILEY, 1987. Biological research on fish and shellfish stocks. *Developments in fisheries research in Scotland*: 99-111.
- CHAPMAN, C. J. & F. G. HOWARD, 1988. Environmental influences on Norway lobster (*Nephrops norvegicus*) populations and their implications for fishery management. In: A. A. FINCHAM & P. S. RAINBOW, eds., *Aspects of decapod crustacean biology*: 343-354. (The Zoological Society of London).
- CHARUAU, A., 1974. Cycle d'intermue et croissance de la langoustine. ICES C.M. 1977/K:35: 1-8.
- CONAN, G., 1975. A growth model for *Nephrops norvegicus* from Biscay Bay in function of periodicity of moult. ICES C.M. 1975/K:10: 1-21.
- , 1985. Periodicity, and phasing of molting. In: A. M. WENNER, ed., *Factors in adult growth. Crustacean Issues*, 3: 73-99. (A. A. Balkema, Rotterdam).
- DRACH, P., 1939. Mue et cycle d'intermue chez les Crustacés Décapodes. *Ann. Inst. Océanogr.*, Paris, 19: 103-392.
- FARIÑA, A. C., 1989. The North galician *Nephrops* fishery. ICES C.M./K:20: 1-12.

- FARMER, A. S. D., 1974a. Reproduction in *Nephrops norvegicus* (Decapoda: Nephropidae). *Journ. Zool., London*, **174**: 161-183.
- , 1974b. The development of the external sexual characters of *Nephrops norvegicus* (L.) (Decapoda: Nephropidae). *Journ. nat. Hist. London*, **8**: 241-255.
- , 1975. Synopsis of biological data on the Norway lobster *Nephrops norvegicus* (Linnaeus, 1758). *FAO Fish. Synop.*, **112**: 1-97.
- FIGUEIREDO, M. J., 1972. Alguns aspectos da histologia do ovario do lagostim (*Nephrops norvegicus*) e do camarão (*Penaeus kerathurus*) durante o seu ciclo maturativo. *Bol. inform. Inst. Biol. marít, Lisboa*, **7**: 1-16.
- , 1982. The occurrence of resorption in the ovaries of *Nephrops norvegicus* (L.) in Portuguese waters. *ICES C.M.* 1982/K:28: 1-7.
- , 1986. Length and sex composition of *Nephrops* stocks in several areas off the Portuguese coast. *ICES C.M.* 1986/K:8: 1-28.
- , 1987. A comparative study on some biological parameters of *Nephrops norvegicus* in three adjacent zones off the Portuguese South Coast. *ICES C.M.* 1987/K:45: 1-10.
- FIGUEIREDO, M. J. & I. F. BARRACA, 1963. Contribuição para o conhecimento da pesca e da biologia do lagostim (*Nephrops norvegicus* L.) na costa portuguesa. *Notas Estud. Inst. Biol. Mar.*, **28**: 1-44.
- FIGUEIREDO, M. J. & H. J. THOMAS, 1967. *Nephrops norvegicus* (Linnaeus, 1758) Leach-A review. *Oceanogr. Mar. Biol., Ann. Rev.*, **5**: 371-407.
- FROGLIA, C. & M. E. GRAMITTO, 1981. Summary of biological parameters on the Norway lobster, *Nephrops norvegicus* (L.) in the Adriatic. *FAO Fish. Rep.*, **253**: 1-14.
- HARTNOLL, R. G., 1985. Growth, sexual maturity and reproductive output. In: A. M. WENNER, ed., *Crustacean Issues*, **3**: 101-128. (A. A. Balkema, Rotterdam).
- JENSEN, G. C. & D. A. ARMSTRONG, 1989. Biennial reproductive cycle of blue king crab, *Paralithodes platypus*, at the Pribilof islands, Alaska and comparison to a congener, *P. camtschatica*. *Canadian Journ. Fish. Aquat. Sci.*, **46**: 932-940.
- KARLOVAC, O., 1953. An ecological study of *Nephrops norvegicus* (L.) of the high Adriatic. *Izv. Inst. Oceanogr. Ribarst.*, **5** (2C): 1-51.
- MORIZUR, Y., 1979. Evolution du présence de spermatophore chez les femelles de *Nephrops norvegicus* (L.) et développement ovarien de juillet 1976 à octobre 1978 dans la région Sud-Bretagne. *ICES C.M.* 1979/K:42: 1-11.
- , 1981. Evolution du taux de spermatophore chez les femelles de *Nephrops norvegicus* (L.) (Decapoda: Reptantia) et développement ovarien. *Journ. exp. mar. Biol. Ecol.*, **52**: 15-24.
- O'RIORDAN, C., 1964. *Nephrops norvegicus*, the Dublin Bay prawn, in Irish waters. *Sci. Proc. R. Dublin Soc.*, (B) **1**: 131-157.
- ORSI RELINI, L. & G. RELINI, 1989. Reproduction of *Nephrops norvegicus* L. in isothermal Mediterranean waters. In: J. S RYLAND & P. A. TYLER, eds., *Reproduction, genetics and distributions of marine organisms*: 153-160. (23rd European Marine Biology Symposium, School of Biological Sciences University of Wales, Swansea).
- REDANT, F., 1987. Reproduction and seasonal behaviour of the Norway lobster, *Nephrops norvegicus*, in the Central North Sea. *ICES C.M.* 1987/K:32: 1-12.
- SARDÀ, F., 1983. Determinación de los estados de intermuda en *Nephrops norvegicus* (L.), mediante la observación de los pleópodos. *Inv. Pesq. Barcelona*, **47** (1): 95-112.
- , 1985. Estudio de la edad, crecimiento y frecuencia de muda, en cautividad, de *Nephrops norvegicus* L. del mar Catalán. *Inv. Pesq. Barcelona*, **49** (2): 139-154.
- SARDÀ, F. & L. CROS, 1984. El metabolismo del calcio y del magnesio en la cigala *Nephrops norvegicus* (L.) durante las etapas del ciclo de intermuda. *Inv. Pesq. Barcelona*, **48** (3): 377-397.
- SARDÀ, F. & A. FERNANDEZ, 1981. Biología y pesca de la cigala (*Nephrops norvegicus* L.). *Inf. Técn. Inst. Inv. Pesq.*, **84-85**: 1-44.
- SASTRY, A. N., 1983. Ecological aspects of reproduction. In: F. J. VERNBERG & W. B. VERNBERG, eds., *The Biology of Crustacea*, **3**: 179-270. (Academic Press, London).
- STERK, W. & F. REDANT, 1989. Further evidence on biennial spawning of the Norway lobster, *Nephrops norvegicus*, in the Central North Sea. *ICES C.M.* 1989/K:2: 1-9.
- SYMONDS, D. J., 1972. The fishery for the Norway lobster, *Nephrops norvegicus* (L.), off the north-east coast of England. *Fish. Invest. London*, (2) **27** (3): 1-35.

- THOMAS, H. J., 1964. The spawning and fecundity of the Norway lobsters (*Nephrops norvegicus* L.) around the Scottish coast. *Journ. Cons. CIEM*, **29** (2): 221-229.
- WEBSTER, S. G., 1982. Seasonal anecdyasis and moulting synchrony in field populations of *Palaeomon elegans* (Rathke). *Estuarine, Coastal and Shelf Science*, **15**: 85-94.