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FECUNDITY OF THE NORWAY LOBSTER *NEPHROPS NORVEGICUS* IN GALICIA (NW SPAIN) AND A REVIEW OF GEOGRAPHICAL PATTERNS

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ABSTRACT

The fecundity of the Norway lobster *Nephrops norvegicus* in Galician waters (NW Spain) was estimated based on the number of eggs attached to the pleopods of ovigerous females in the initial, middle and final stages of the incubation period. The number of eggs per brood was related allometrically to the carapace length (CL), with an allometry coefficient ranging between 3.0 and 4.1 in the different incubation stages ($P>0.05$). Incubation lasts 6-7 months (from August-September to January-February) and the average egg loss is estimated to be 44% during this period. The mean fecundity (corresponding to a mean CL of 38.6 mm) was 2636 eggs in the initial stage and 1475 in the middle and final stages of incubation. The literature points to a high variability in the fecundity of the Norway lobster throughout its geographical range of distribution. Fecundity decreases with latitude in the NE Atlantic from Western Ireland to the South of Portugal, with the Mediterranean populations showing lower values than those in the Atlantic. However, considering the periodicity of spawning, which tends to be biennial towards the northern distribution area, the annual production of eggs per female may be similar in the different zones and may even increase towards the south. Egg loss during the incubation period has been estimated at between 32 and 68% for the different geographical areas.

INTRODUCTION

The Norway lobster *Nephrops norvegicus* (Linnaeus, 1758) (Decapoda, Nephropidae), a species of great fishery interest in the NE Atlantic, lives in burrows excavated in muddy sediments (Dybern & Höisaeter 1965; Chapman 1980). In these burrows, ovigerous females incubate their eggs under the abdomen for a period of several months. During this time the eggs go through different stages of embryonic development, which have been described according to size, colour and appearance of the egg and developmental phase of the embryo (Figueiredo & Ferreira Barraca 1963; Dunthorn 1967; Fontaine & Warluzel 1969). The incubation period varies geographically from 6-7 months in the Adriatic Sea and off the coast of Portugal (Karlovac 1953; Figueiredo & Ferreira Barraca 1963; Figueiredo 1965; Sardá 1995) to 12-13 months in the waters of

Iceland and the Faeroe Islands (Andersen 1962; Nicolajsen & Eiríksson 1990; Eiríksson 1993). The length of the incubation period determines the periodicity of the reproductive cycle and the interval between broods. The low catch rate for females during the incubation period (Anonymous 1995) would indicate that they only leave the burrows to feed, and may be associated with their ability to filter microparticles in suspension (Loo et al. 1993).

As an indicator of the reproductive potential of a species, the determination of fecundity is imperative in the study of the dynamics of exploited populations, given that it is one of the factors linking the adult population and recruitment. In the case of the Norway lobster, fecundity has been estimated by the number of oocytes in the mature ovary (Thomas 1964; Fontaine & Warluzel 1969; Morizur & Rivoalen 1982), the number of fertilized eggs or embryos (Farmer 1974; Chapman & Ballantyne 1980), and the number of eggs that reach the pre-eclosion or eclosion stages (Morizur et al. 1981; Figueiredo et al. 1982). These estimates correspond respectively to the potential, realized and effective or actual fecundities, following the definitions proposed by Figueiredo et al. (1982) and Stechey & Somers (1995). Estimation of fecundity from ovary content and/or the number of eggs in the different stages makes it possible to evaluate the egg loss that takes place during incubation (Figueiredo & Nunes 1965, Morizur 1981, Morizur et al. 1981; Figueiredo et al. 1982; Sardá 1995).

This paper examines the seasonality of incubation and the fecundity of the Norway lobster in Galician waters (NW Spain), and estimates the egg loss that occurs during incubation. Our results are compared to those reported by other authors from different areas of the Northeast Atlantic and Mediterranean. The relationship between the geographical variability of fecundity and other life history parameters related to reproduction is discussed.

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MATERIALS AND METHODS

Sampling and Laboratory Procedures

The breeding cycle of Norway lobster females was analyzed using data obtained from monthly samples of landings of the trawl fleet of A Coruña collected from 1981 to 1991. This fleet operates on the continental shelf and slope of NW Galicia (in the area from 42°N 9.30°W to 44°N 8°W) (see Fariña 1996 for a detailed description). For the study of fecundity, monthly samples of ovigerous females from commercial landings of the same fleet were collected from November 1991 to November 1992 (with the exception of March 1992).

Fecundity in the Norway lobster was estimated by counting the total number of eggs attached to the pleopods in different stages of embryonic development. A total of 157 females were examined to determine the embryonic stages, of

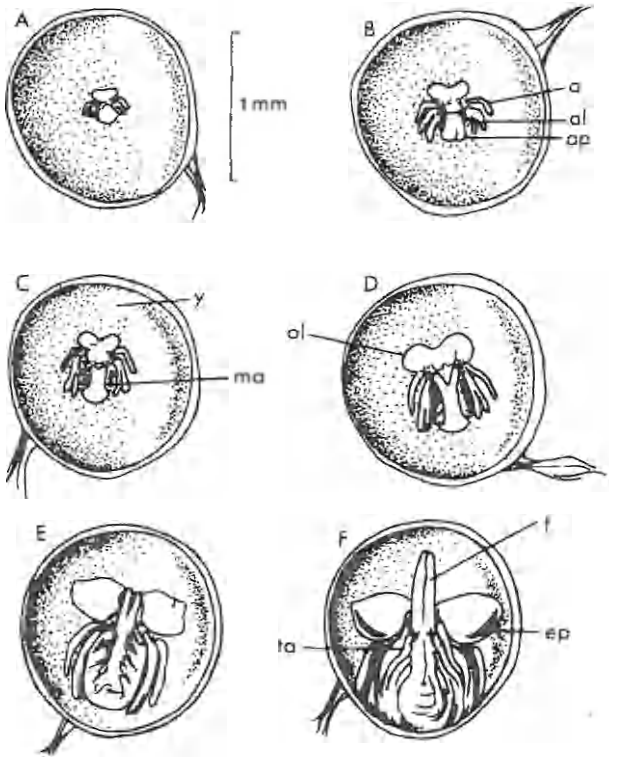

Fig. 1. Embryonic developmental stages of the Norway lobster. A-D: stage I, E: stage II, F: stage III; a, antenna; al, antennule; ap, abdominal plate; ep, eye pigment; f, fork; ma, metanauplius appendage; ol, optic lobes; ta, thoracic appendages; y, yolk.

which 121 females were used to estimate fecundity (these specimens showed no signs of damage, breakage or visible egg loss). Before proceeding to calculate the total number of eggs, we separated them from the pleopods and abdomen and determined the incubation stage by observing them under a stereoscopic microscope (x30), according to the degree of development of the embryo in the egg. A scale of five stages of embryonic development (Fig. 1) based on Fontaine & Warluzel (1969) was used (since some females had eggs with embryos at different levels of development, the number of stages was diminished compared to the 7 used by these authors):

– Stage I: Developmental stages from the egg completely occupied by yolk to the nauplius and metanauplius stage (stages 0, I and II of Fontaine & Warluzel -F&W-).

– Stage II: Embryo in a developed metanauplius stage. The end of the abdominal plate forms a fork that does not go past the optic lobes. In the later stage a faint pigmentary arch is visible around the periphery of the optic lobes (stage III of F&W).

– Stage III: The abdomen shows segmentation. The tip of the fork exceeds the optic lobes, the ocular spots are developed and the thoracic appendages reach the base of the optic lobes (stage IV of F&W).

– Stage IV: Embryonic stage with more highly developed characteristics from stage III. The thoracic appendages are very developed, covering almost the entire abdomen and the fork exceeds the halfway point of the yolk space inserted between either end of the embryo (stage V of F&W).

– Stage V: Pre-eclosion stage during which the features of the first larval stage of prezoea are conspicuous (stage VI of F&W).

In order to estimate the relationship between fecundity and body size (carapace length in mm, CL, measured with digital calipers between the posterior edge of the eye socket and the posterior edge of the carapace) and analyze egg loss during the incubation period, the samples from the ovigerous females were grouped into three stages of embryonic development: I, II and III+. The III+ stage covers embryonic stages with varying degrees of abdominal and thoracic segmentation, but where the hatching of the eggs has not yet occurred (this includes stages III and IV, the stage immediately prior to pre-eclosion). The specimens with eggs in stage V already showed signs of partial hatching, and were therefore omitted from the analyses to determine fecundity.

Data Analysis

Fecundity (F, number of eggs) was expressed as a function of body size (CL) fitting by least-squares linear regression the log-transformed allometric equation $F=a \cdot CL^b$ (Somers 1991) where a and b are parameters. Analysis was carried out for each stage of embryonic development (I, II and III+) separately. The parameters of the fitted equations for each developmental stage were compared using analysis of covariance (ANCOVA).

Egg losses during the incubation period were estimated from the differences in brood size among females with broods in different development stages. Since non-significant differences were detected among the slopes of the equations for each development stage (see Results), the egg losses among stages were estimated from the least-square adjusted mean fecundity obtained for each stage.

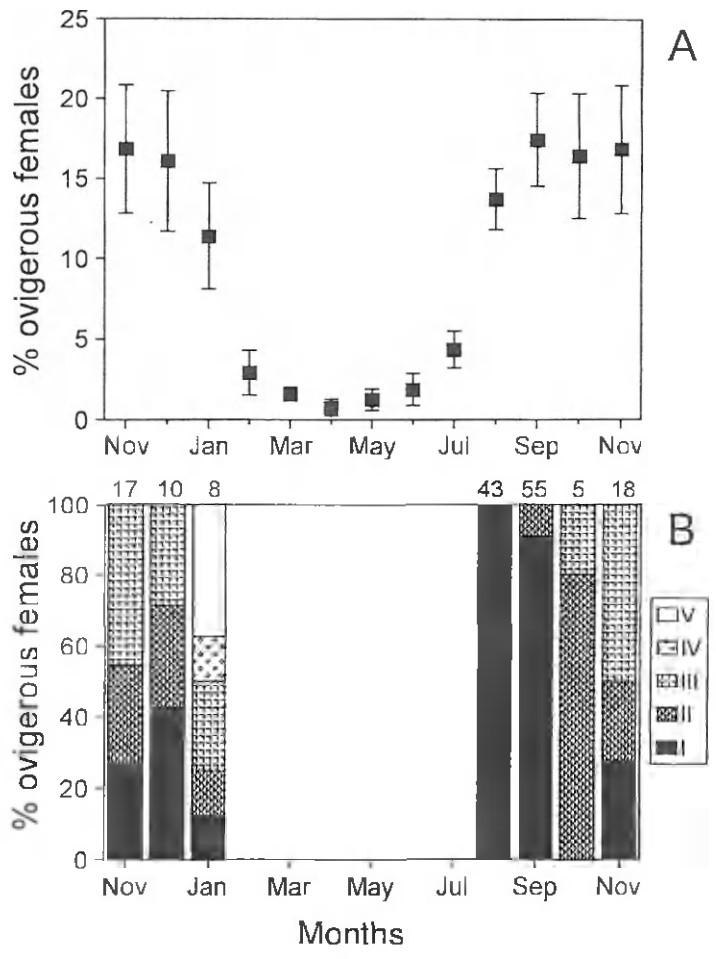

Fig. 2. Breeding cycle of Norway lobster females in Galicia. (A) The mean monthly percentage (±SE) of ovigerous females with respect to the total number of mature females (>25 mm CL) from 1981 to 1991 landings of the trawling fleet of A Coruña (the number of females sampled per month ranged from 675 to 3049, with a total of 18584 females sampled). (B) Monthly changes in embryonic development of the Norway lobster ovigerous females in Galicia from samples collected from November 1991 to November 1992 (no samples were collected in March; from February to July the number of ovigerous females caught was very small, and only one female was analyzed in February).

Table 1. Parameters of the allometric equations (standard error, SE, in parentheses) relating fecundity (F, number of eggs) to body size (carapace length, CL) (log F = log a + b + log CL) in each incubation stage (I, II and III+). The number of females analyzed (N), coefficient of determination (r^2) and significance level (P) are given.

Stage	log a (SE)	b (SE)	N	r^2	P
I	-1.3002 (0.121)	2.957 (0.244)	73	0.674	<0.001
II	-3.2204 (0.150)	4.073 (0.519)	31	0.680	<0.001
III+	-2.6293 (0.142)	3.680 (0.807)	14	0.634	<0.001

RESULTS

In Galician waters the incubation of the Norway lobster lasts 6-7 months; spawning takes place mainly in August and September, and larvae are released in January and February (Fig. 2). Ovary resorption is uncommon and therefore most mature females incubate a brood every year (Fariña 1996). The analysis of the embryonic developmental stages in egg-bearing females showed that during the first months of incubation, August and September, practically all the broods were in developmental stage I (Fig. 2), although in September a small proportion of the broods (9%) were in Stage II; this proportion reached 80% in October. From October to December stages II and III accounted for 63% of the ovigerous females, and as early as January they quickly passed through stages IV and V, leading to hatching and larval release.

Fecundity correlated significantly with body size (CL), resulting in a slope of the allometric relationship that ranged between 3.0 and 4.1 for the different stages of embryonic development (Table 1, Fig. 3). Over the size range analyzed, the fecundity in stage I, corresponding to the realized fecundity, was higher than in stages II and III+, with the latter stage accounting for the effective fecundity. There were no significant differences between the slopes of the equations fitted for each incubation stage (P>0.05, Table 2). However significant differences were found between the intercepts when stage I was compared to stages II and III+ (P<0.001), which suggest that egg losses occur during incubation which are unrelated to body size. The least-square adjusted mean fecundity (corresponding to a sample mean CL of 38.6 mm) was 2636 eggs in stage I and 1475 eggs in stages II and III+, which represents an egg loss of 44.0% during incubation.

Table 2. *Nephrops norvegicus* from Galicia: results of the analyses of covariance carried out to compare the regression equations relating fecundity to body size (CL) for each incubation stage.

Tests of homogenity of variances			
Fecundity	P = 0.374		
Carapace length (CL)	P = 0.637		
Comparison of stages I, II and III+			
	df	F	P
Covariate (CL)	1	218.95	<0.0001
Incubation stage (intercept, log a)	2	20.59	<0.0001
Interaction (slope, b)	2	2.40	0.095
Error	114		
Paired comparisons of intercepts			
I / II	P < 0.0001		
I / III+	P < 0.0001		
II / III+	P = 0.731		

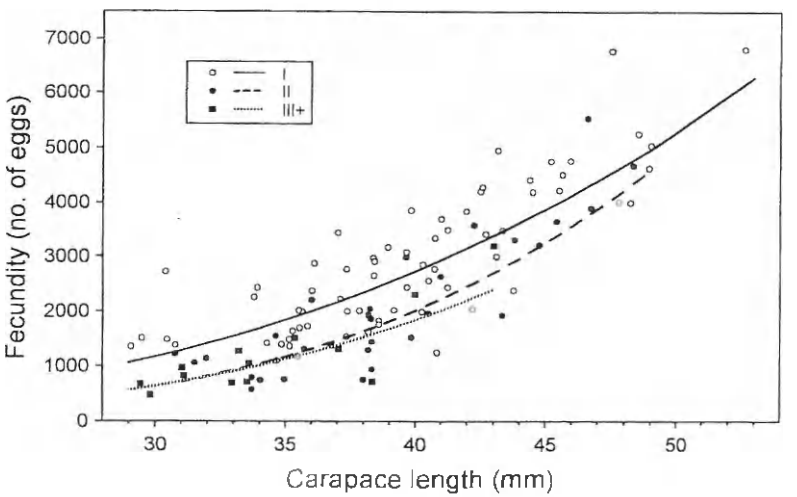

Fig. 3. Relationship between fecundity (number of eggs attached to the pleopods) and carapace length (CL) of the Norway lobster in Galicia in each incubation stage (I, II, III+) and allometric equations fitted for each stage (equation parameters provided in Table 1). A single female with a CL of 54 mm and a brood of 9633 eggs in stage I is not represented.

DISCUSSION

Incubation stages in studies on the fecundity of *Nephrops norvegicus* have been determined by several authors in different geographical areas, based on a scale of egg coloration and the relationship between the yolk material and egg volume as proposed by Figueiredo & Ferreira Barraca (1963) and Figueiredo (1971). The method followed in the present paper, based on the determination

Table 3. Parameters of the allometric (A, $F=a \cdot CL^b$) or linear (L, $F=a+b \cdot CL$) equations relating fecundity (number of oocytes or eggs in various stages of incubation) to body size (CL, mm) of the Norway lobster from different geographical areas. The number of females analyzed (N) is given. The embryonic developmental stages A, C and D from the scale of Figueiredo and Barraca (1968) are equivalent to stages I, II and III+ from the scale used in the present study.

Fecundity	Authors	Geographical area	Model	Parameters a	b	N
Oocytes						
	Thomas (1964)	Scotland	A	0.626	2.35	-
	Morizur and Rivoalen (1982)	Celtic Sea	A	0.196	2.58	58
	Morizur et al. (1981)	Bay of Biscay	A	0.133	2.70	79
	Fontaine and Warluzel (1969)	Bay of Biscay	A	0.108	2.80	53
	Figueiredo et al. (1982)	W Portugal	A	0.323	2.50	47
	Figueiredo and Nunes (1965)	SW Portugal	A	0.043	3.06	–
	Gramitto and Froglia (1980)	Adriatic	A	0.058	2.94	85
Eggs in stage A / I						
	Chapman and Ballantyne (1980)	Loch Torridon (Scotland)	L	-3889	148.2	61
	Chapman and Ballantyne (1980)	Clyde (Scotland)	L	-1261	81.3	33
	Chapman and Ballantyne (1980)	Moray Firth (Scotland)	L	-1919	118.1	15
	Chapman and Ballantyne (1980)	West Kintyre (Scotland)	L	-2521	129.7	69
	Farmer (1974)	Irish Sea	L	-1376	78.2	60
	Nichols et al. (1987)	Irish Sea West	A	0.080	2.86	–
	Present study	Galicia	A	0.050	2.96	73
	Alonso-Allende (1979)	Galicia	A	1.200	2.11	110
	Abelló and Sardá (1982)	N Portugal	A	0.025	3.12	76
	Figueiredo et al. (1982)	W Portugal	A	0.056	2.89	79
	Abelló and Sardá (1982)	Catalonian Coast	A	0.210	2.49	62
	Gramitto and Froglia (1980)	Adriatic	A	0.019	3.14	160
Eggs in stages A and B						
	Figueiredo and Nunes (1965)	SW Portugal	A	0.023	3.06	–
Eggs in stage C / II						
	Present study	Galicia	A	0.001	4.07	31
	Figueiredo et al. (1982)	W Portugal	A	0.195	2.46	73
	Figueiredo and Nunes (1965)	SW Portugal	A	0.020	3.06	–
	Gramitto and Froglia (1980)	Adriatic	A	0.083	2.67	91
Eggs in stage D / III+						
	Morizur et al. (1981)	Bay of Biscay	A	0.016	3.19	101
	Present study	Galicia	A	0.002	3.68	14
	Figueiredo et al. (1982)	W Portugal	A	0.043	2.82	52
	Figueiredo et al. (1982)	W Portugal	A	0.065	2.62	53
	Figueiredo and Nunes (1965)	SW Portugal	A	0.015	3.06	–
	Orsi-Relini and Relini (1989)	Ligurian Sea	A	0.046	2.69	34
	Gramitto and Froglia (1980)	Adriatic	A	0.033	2.81	28

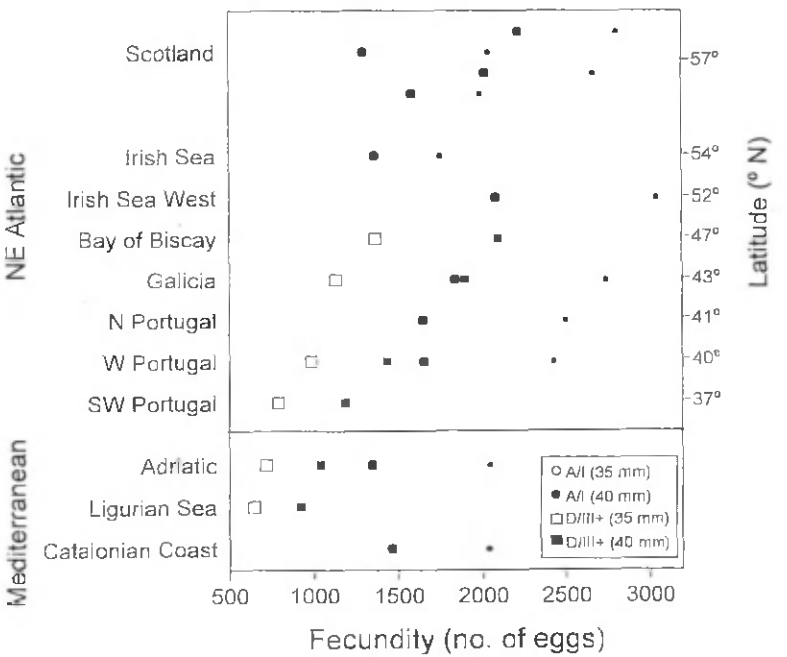

Fig. 4. Fecundity (number of eggs) of Norway lobster females with carapace lengths (CL) of 35 and 40 mm in the initial (A/I) and final (D/III+) stages of incubation, according to a latitudinal geographical gradient (the mid-point latitude of each area is shown). Data obtained from equations fitted by different authors for their respective geographical areas (see Table 3).

of the stage of embryonic development, allows for a more accurate estimate of the incubation stage. However, regardless of the criterion used, fecundity estimates corresponding to the different incubation stages among the different geographical areas are comparable, and therefore, stages A, C and D as provided by the above mentioned authors are equivalent to stages I, II and III+ in this study (Table 3).

In different areas of the NE Atlantic and Mediterranean, several authors have estimated relationships between the fecundity of the Norway lobster and its carapace length, based on oocyte or egg count in different developmental stages (Table 3). To facilitate the comparison of estimates among areas, fecundity was calculated from the equations for females measuring 35 and 40 mm CL (these sizes pertain to dominant adult females caught in different areas) (Fig. 4). These estimates were made for both realized (estimated by the number of re-

cently spawned eggs, stages A or I) and effective fecundity (estimated by the number of eggs in the final incubation stage, stages D or III+).

The comparative analysis points to the existence of two patterns of variability in the fecundity of the Norway lobster. First of all, variability is high among neighbouring populations: e.g. Thomas (1964) and Chapman & Ballantyne (1980) found great variability in the fecundity of the Norway lobster in different areas off the coast of Scotland. Secondly, effective fecundity decreases with a latitudinal gradient, from the West Irish Sea and Bay of Biscay to the South of Portugal, with the lowest fecundity in the Mediterranean populations (minimum values for this species were found in the Ligurian Sea [Orsi-Relini & Relini 1989] and the Adriatic Sea [Gramitto & Froglia 1980]). The fecundity in Galicia lies halfway between those for the closest regions on which data are available (Bay of Biscay and Portugal).

The Norway lobster has a broad geographical range of distribution in the NE Atlantic and Mediterranean which exhibits high environmental variability. Chapman & Howard (1988) and Tuck et al. (1997) have demonstrated that in Scotland there is a substantial amount of small-scale variability in the life history of this species, due largely to the characteristics of the sediment. Thus, in areas having a high proportion of silt-clay in the sediment, *Nephrops* reaches greater densities than in areas having a coarser sediment. Moreover, growth is density-dependent, which explains why the size at maturity and body size are smaller in areas having high densities. On a geographical scale, density is an order of magnitude higher in the northern Atlantic (where the proportion of fine grain sediment is highest) than in the southern distribution area (Anonymous 1997). Size at the onset of sexual maturity and growth rate increase in the southern Atlantic area (Sardá 1995; Fariña 1996). Due to this trade-off between growth and size at maturity, age at the onset of maturity remains relatively constant in the Atlantic stocks (unpublished data). The incubation period increases towards the north, which marks a transition from annual breeding in southern areas to biennial in the most northern zones. Moreover, there is a decrease in fecundity per brood towards the south (Fig. 4), but if the periodicity of spawning, size and age at the onset of maturity are considered, the annual and lifetime egg production per female appears to increase in a southern direction in the NE Atlantic. In contrast, in the Mediterranean the egg production of this species would be lower than in similar latitudes of the Atlantic, given the fact that not only is fecundity per brood very low, the onset of maturity is attained at older ages.

The existence of a geographical trade-off between growth and fecundity per brood might be due to changes in the strategy of energetic investment over the latitudinal range. Therefore, in northern populations having high densities, there would be a greater investment in reproduction with a decrease in the growth rate (in addition to density-dependent processes). An alternative hypothesis would suggest an environmental limitation, brought about by the fact that in northern populations the duration of the incubation period increases due to the low temperatures, which would mean that each female would expend more energy per brood, with a fewer number of broods. In any case, we must take into account that the increase in reproductive effort per brood in decapods may be channelled into either an increase in the number of eggs or an increase in the size or energy content of each embryo. In *Nephrops* there is no data available on the second aspect, which would mean that the trends observed in reproductive effort, measured by the number of eggs per brood, should be considered with caution. In any event, the energetic investment per embryo is a life-history trait with a lower intraspecific variability than the number of embryos per brood in decapods (Hines 1982).

In the Norway lobster, the number of oocytes in the mature ovary is greater than the number of recently spawned eggs, although the difference has been estimated to be <3% (Morizur 1981). Moreover, the fecundity is higher in early as compared to more advanced developmental stages (Table 3). Egg losses in different species of decapods have been linked to a number of factors such as the retention of the oocytes in the ovaries and subsequent reabsorption, losses of unfertilized eggs or those that did not attach to the pleopods during spawning, failure of infertile eggs, mechanical abrasion, predation, parasitism, etc. (Farmer 1974; Kuris 1991).

On the West Portuguese coast, Figueiredo & Nunes (1965) estimated a total egg loss from the mature ovary to the final stage of incubation of 75%, assuming a 10% monthly loss and an incubation period of 7.5 months. Later, Figueiredo et al. (1982) used a more accurate estimate of the duration of the incubation period for the same area, resulting in a value of egg losses from 56% to 68% (from the mature ovary to the initial and final phase of stage D of embryonic development, respectively). It must be taken in consideration that the higher value could include the partial hatching of the brood (Figueirêdo et al. 1982). In the Bay of Biscay, Morizur (1981) assessed the egg losses at 45-50% from the mature ovaries to stage D of incubation, and 30-40% during the incubation (from stages A to D). Off the coast of Scotland, Chapman & Ballantyne (1980) suggested a range of losses from 32 to 51% during the incubation period.

Our findings for the Norway lobster in Galicia indicate an egg loss of 44% during the incubation; however this value is based mainly on females with broods in stages I and II (the number of females analyzed in stage III+ was lower) and therefore it would pertain chiefly to losses in the early stages of incubation (between August and October-November). Considering the above, egg losses during the whole incubation period should be higher than our estimate, close to the values given for Portugal, and higher in both cases than the percentage of losses estimated for northern areas. Although there is only a limited number of references to egg losses in *Nephrops*, the available data imply that there is a decrease in the percentage of losses towards the north, despite the fact that the incubation period lasts longer in northern latitudes. No clear hy-

pothesis has been put forth regarding what causes the latitudinal cline in egg loss in *Nephrops*, but the available data indicate that it is not a simple process which depends only on the duration of the incubation period.

Previous studies (Chapman & Ballantyne 1980; Morizur 1981) have found a greater percentage of losses in smaller females; our results indicate no size effect (the slopes of fecundity equations were similar among development stages). The egg loss estimates found in these studies may be biased due to the effect of the fishing gear (Figueiredo & Nunes 1965; Morizur 1981). Chapman & Ballantyne (1980) estimated these losses to be between 11 and 22% in the waters off Scotland, however, the trawl gears used in Scotland generally have modified the footrope which disturbs the sediment to a greater extent than those used in Galicia.

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