ICES Journal of Marine Science, 55: 924–940. 1998
Article No. jm980365

Growth at moult and intermoult period in the Norway lobster *Nephrops norvegicus* from Galician waters

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González-Gurriarán, E., Freire, J., Fariña, A. C., and Fernández, A. 1998. Growth at moult and intermoult period in the Norway lobster *Nephrops norvegicus* from Galician waters. – ICES Journal of Marine Science, 55: 924–940.

Size increase at moult, duration of the intermoult period, and moulting seasonality of the Norway lobster *Nephrops norvegicus* off Galicia (NW Spain) were studied in the laboratory. At a mean pre-ecdysis carapace length, CL, of 35 mm the absolute moult size increment (MI) was 2.1 ± 1.1 mm (mean $\pm$ s.d.) in males and 1.7 ± 0.7 mm in females. This corresponded to percentage moult increments (PMI) of 6.2 and 5.5% in males and females, respectively. There was a significant positive linear relation between MI and CL in males but not in females. Percentage moult increments in males were constant throughout the CL range examined (21–54 mm), but in females a significant negative linear relationship was detected between lnPMI and CL. In both sexes the growth at moult decreased with increasing holding time under laboratory conditions, especially in the case of ecdyses taking place after more than 1 year in captivity. In males, MI was lower in smaller holding tanks. Duration of the intermoult period was similar in both sexes (180 ± 80 days in males and 174 ± 65 days in females), and increased significantly with increasing CL. Moulting seasonality was not marked, but two moulting seasons in autumn–winter and spring–summer were recorded. The information obtained in the present study was compared with available data for the Norway lobster in other geographical areas in the NE Atlantic and Mediterranean.

Key words: Galicia, growth, intermoult period, moulting, *Nephrops norvegicus*.

Received 6 July 1997; accepted 11 April 1998.

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Introduction

In common with other crustaceans, the growth of the Norway lobster, *Nephrops norvegicus*, is a discontinuous process consisting of a succession of moults or ecdyses. This growth pattern has two parts (Hartnoll, 1982; Botsford, 1985): the moult size increment (MI) and the intermoult period (IP) or time interval between consecutive ecdyses. The growth of the Norway lobster is indeterminate and continues after the onset of sexual maturity without the occurrence of a terminal moult (Farmer, 1973).

The Norway lobster supports important fisheries in the North-east Atlantic and Mediterranean and is the subject of fisheries assessments. In order to make use of analytical population models it is necessary to obtain growth models and a size-age key (ICES, 1994, 1995). Unlike many fish species which can be aged and are assessed using age-based models the fact that crustaceans lose all of their hard structures during the moult makes it impossible to determine their age by examining permanent calcified structures. Growth data may be collected in field or laboratory experiments, as has been done by several authors with the Norway lobster using different methods: larval culture in laboratory (Anger and Püschel, 1986; Thompson and Ayers, 1989); holding juveniles and adults in captivity (Thomas, 1965; Farmer, 1973; Charuau and Conan, 1977; Figueiredo, 1979; Sardá, 1985); holding individuals ready to moult in submarine cages at sea (Charuau, 1977); mark-recapture experiments (Andersen, 1962; Chapman, 1982; Eiríkson, 1982; Chapman *et al.*, 1989; Figueiredo,

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1989) or combinations of these methods (Charuau and Conan, 1977; Hillis, 1979; Bailey and Chapman, 1983). The analysis of size frequency distributions of the natural populations is another alternative (Conan, 1975a,b, 1978; Bailey and Chapman, 1983; Tulley *et al*., 1989; Castro, 1992; Mytilineou and Sardá, 1995; Tuck *et al*., 1997), although in the Norway lobster this is quite complicated due to its low growth rate and the overlapping of components corresponding to age or moulting groups.

The results of the studies of growth at moult, in addition to the information provided by more recently applied methodologies, such as dating carapaces by radioisotopes (Latrouite *et al*., 1991; Talidec and Reyss, 1993) or estimating age by the accumulation of ageing pigments or lipofuscin (Sheehy, 1990a,b; Tully, 1993; Belchier *et al*., 1994) may be used to corroborate other methods and models based on the analyses of size frequency distributions (Castro, 1995).

The moult size increment in crustaceans is often described using the Hiatt diagram, which shows the relationship between body size at post-moult and pre-moult (Gray and Newcombe, 1938; Hiatt, 1948; Kurata, 1962; Mauchline, 1976; Somerton, 1980). This model has been criticized for assuming a constant growth rate for successive moults (Easton and Misra, 1988) and for not giving an adequate description of the variability related to body size in growth at moult (Wainwright and Armstrong, 1993; Castro, 1995). The relationship between absolute moult size increment and pre-ecdysis size, in addition to the frequency or duration of the intermoult period, gives an improved description of growth and its variability (Botsford, 1985). It can also be applied to the analysis of size frequency distributions (Caddy, 1987; Castro, 1992). With the exception of Farmer (1973) and Charuau and Conan (1977), who used the Hiatt diagram and Charuau (1975) who relied on the relation between the post-ecdysis size and the number of post-larval stages, the different authors modelled growth at moult in the Norway lobster using the relationship between MI or the percentage moult increment (PMI) and pre-ecdysis size (Castro, 1992 and the references quoted earlier). The duration of the intermoult period is a parameter, about which there is less information since it requires laboratory experiments where a minimum of two consecutive ecdyses must be monitored for each individual [see Castro (1992), for a review].

This study examines the laboratory growth of the Norway lobster off Galicia (NW Spain) and analyses how the growth components (size increase at moult and duration of the intermoult period) relate to pre-ecdysis size. Differences between males and females, the effect of experimental conditions, and the moulting seasonality are also examined. This information is compared with available data for this species in other geographical areas using different methodologies. The causes of the variability in the growth estimates obtained for this species are discussed.

Materials and methods

Samples and experimental conditions

A total of 325 *Nephrops norvegicus* (194 males and 131 females), caught on the Galician continental shelf during bottom trawl surveys in September 1982 and 1983 and May 1984, were used in the growth studies. Three experiments, identified by catch year (1982, 1983, and 1984) and ending on 31 July 1984, were carried out. Only individuals whose appendages showed no signs of breakage or damage were used.

Following capture, the lobsters were placed in oyster trays and containers with openings for water circulation held on board in a 1 m^3, open-flow tank. In 1982, the Norway lobsters were held on board ship several days after being caught. This was used as an acclimation period after which there was a selection of individuals seen to be in the best condition. The lobsters were transported to the laboratory of the Instituto Español de Oceanografía in A Coruña, where they were placed individually in two types of tanks: (1) 20 l plastic boxes arranged in terraces. The boxes were divided in the middle with plastic mesh in order to hold two individuals per box (individual holding space of approximately 10 l). Each section had a segment of cylindrical PVC tubing which the animal could use as a den; (2) stackable plastic net oyster trays (40 cm diameter × 10 cm high) hung in a 3000 l water tank. Each tray consisted of four sections each holding only one lobster (individual holding space of approximately 3 l). Table 1 gives detailed information on the number of individuals of each sex and the type of tank used in each experiment.

The boxes and the tank were run on open water circuits (0.5 and 5 l min^{-1} respectively). The boxes were covered with black plastic in order to reduce the daylight intensity, while the location of the tank and the layout of the trays already provided the appropriate conditions of very low light intensity. Temperature and salinity were recorded two or three times a week. Water temperature ranged between 13.3 and 16.4°C (mean: 14.6°C) and salinity was between 33.28 and 35.82 (mean: 34.55), following the seasonal variations in the coastal area near the laboratory from where the water was pumped. Fresh or frozen mussels and fish (smelt or horse mackerel) were used for food. When moulting took place, the exuvia was left in the tank to be ingested as an additional source of calcium.

Following sex determination the carapace length (CL) of each lobster was measured to the nearest 0.1 mm when they were brought to the laboratory. The individuals were checked at least three times a week for ecdyses

Table 1. *Nephrops norvegicus*. Number of individuals (males and females) used in each experiment (1982, 1983, and 1984) and tank type (oyster trays and boxes). The number of animals that carried out ecdyses in the laboratory is shown in parentheses.

Experience	Start/end	Tank	Males	Females	Total
1982	21/09/82	Oyster trays	72 (30)	26 (11)	98 (41)
	31/07/84	Boxes	33 (25)	10 (9)	43 (34)
		Total	105 (55)	36 (20)	141 (75)
1983	10/09/83	Oyster trays	55 (30)	29 (19)	84 (49)
	31/07/84				
1984	15/05/84	Oyster trays	22 (7)	42 (8)	64 (15)
	31/07/84	Boxes	12 (1)	24 (1)	36 (2)
		Total	34 (8)	66 (9)	100 (17)
Total			194 (93)	131 (48)	325 (141)

and to add food. CL of the individuals that moulted was measured a few days after ecdysis when the carapace started to harden. (It was not possible to measure the post-ecdysis CL on 10 occasions due to death and the fragmentation of the carapace after the moult.)

During the experimental period 74 lobsters died (52 males and 22 females) due directly to accidental causes (handling, cleaning of tanks, and technical breakdown of the equipment), while 130 (86 males and 44 females) died of apparently natural causes before the experiments were completed. Only the individuals that did not die from accidental causes were taken into account when determining laboratory survival.

Data analysis

Growth at moult was estimated for each sex based on the moult size increment (MI = post-ecdysis CL − pre-ecdysis CL) and the percentage moult increment (PMI = MI × 100/pre-ecdysis CL). Linear regression models were fitted for each sex by the least squares method in order to relate growth at moult (MI and lnPMI) and the duration of the intermoult period (IP and lnIP) to the pre-ecdysis CL (Mauchline, 1977; Somerton, 1980; Botsford, 1985; Wainwright and Armstrong, 1993):

$$Y = a + b \cdot \text{pre-ecdysis CL}$$

where Y is MI, lnPMI, IP or lnIP, and a is the intercept and b is the slope of the equation.

The MI residuals (absolute difference between the MI observed and the one predicted by regression) were related for males and females to the period of time at laboratory before ecdysis took place (Tlab, days). The analysis of residuals indicates that this variable should be included in the model and the following regression equation was fitted accordingly (Thomas, 1965):

$$MI = a + b \cdot \text{pre-ecdysis CL} + c \cdot \text{Tlab}$$

The possibility of changes in growth with maturity was not analysed due to the limited number of juveniles (approx. CL<25 mm) held in captivity (size range of individuals in captivity: 21–54 mm, Fig. 1).

For a comparison of the fitting of the different models relating growth at moult (in terms of MI or lnPMI) or the duration of the intermoult period (IP or lnIP) with pre-ecdysis CL, the coefficient of variation of residuals (c.v.) was estimated for each regression (Somerton, 1980; Wainwright and Armstrong, 1993). Analyses of covariance (ANCOVA) were carried out using the pre-ecdysis CL as a covariable to compare growth at moult and the duration of the intermoult period between males and females and types of tanks (trays and boxes).

Results

General observations: size frequency distributions, number of moults in the laboratory, and survival

Figure 1 shows the initial size frequency distribution of the Norway lobsters held in the laboratory and of those that moulted at least once. Males and females over the entire size range underwent ecdyses in the 1982 and 1983 experiments, which lasted a total of 679 and 325 days, respectively. Owing to the short duration of the 1984 experiment (77 days), only a very small number of males and females carried out the first ecdysis in the laboratory. A total of 151 ecdyses (93 in males and 48 in females) took place in the laboratory (Tables 1 and 2). Of these, 101 (70 males and 31 females) corresponded to the first ecdysis after being placed in captivity, 40 (23 and 17) are second ecdyses, and 9 individuals (7 and 2) underwent a third. A male caught in 1982 measuring 33 mm CL achieved four ecdyses in captivity.

Laboratory survival in the 1982 and 1983 experiments was slightly higher in females than in males. Despite the short duration of the 1984 experiment, the survival was higher in males (Fig. 2). In the 1982 experiment 15.8% of

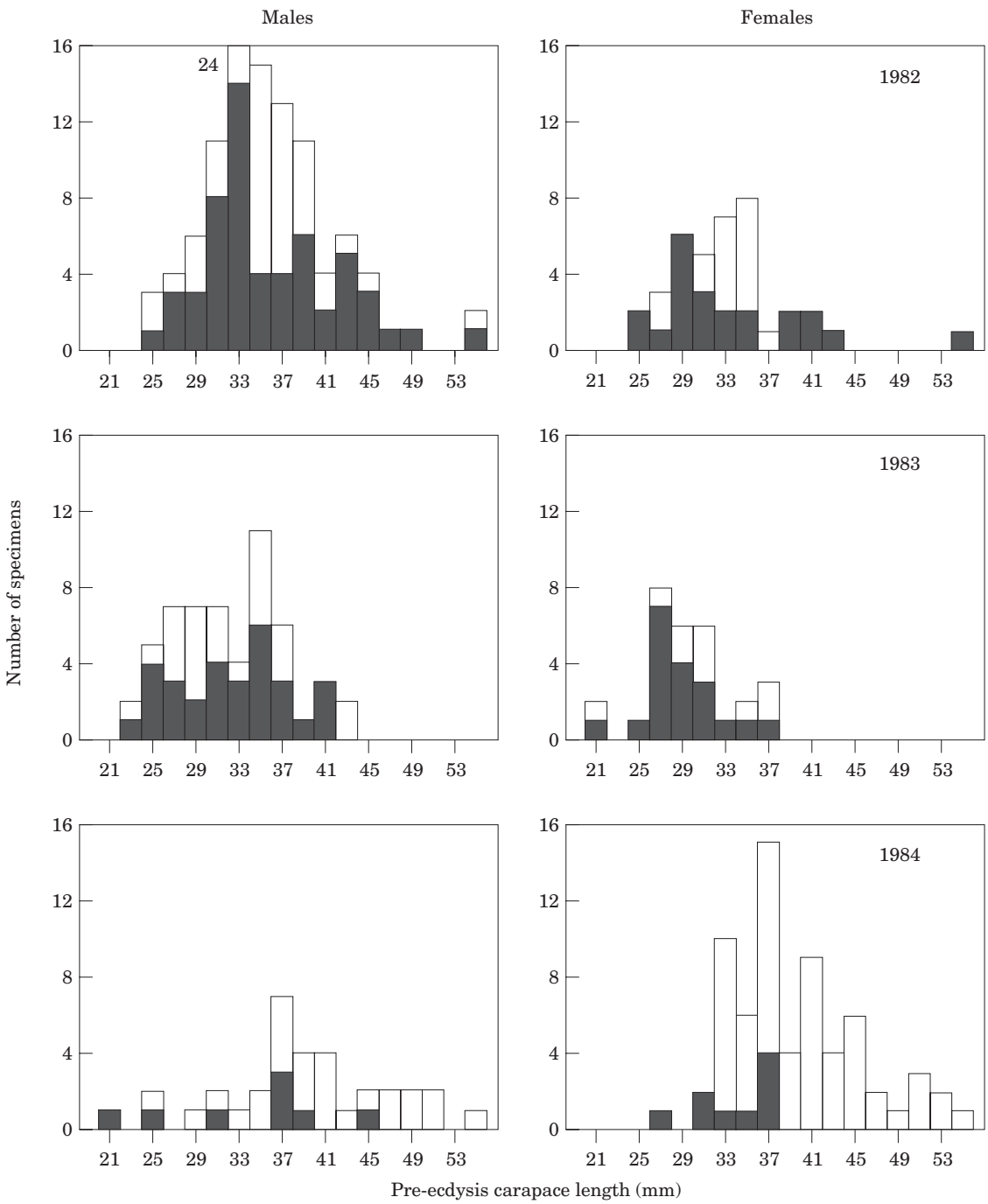

Figure 1. *Nephrops norvegicus*. Size frequency distributions (carapace length, mm) at the beginning of the different experiments. Individuals that did not carry out ecdysis in the laboratory are shown in white and those that moulted at least once are shown in black.

males and 18.8% of females (n=9 and 3, respectively) survived after 679 days in captivity. In 1983, after 325 days, the survival rate was 29.4 and 33.3% (n=15 and 9) for males and females, respectively. (The estimates of the percentages did not take into account those individuals that died from accidental causes.)

Table 2. *Nephrops norvegicus*. Size (pre-ecdysis carapace length, CL, mm), moult size increment (MI, mm), percentage moult increment (PMI) and duration of the intermoult period (IP, days) for males and females, tank type, experiment, and growth stage (number of ecdyses carried out previously for each individual in the laboratory: O: no previous ecdyses, 1: 1, 2, or 3 previous ecdyses in the laboratory). The mean, standard deviation (s.d.) and number of cases (n) are shown.

				CL		MI		PMI		IP	
Sex	Tank	Experiment	Stage	Mean (s.d.)	n	Mean (s.d.)	n	Mean (s.d.)	n	Mean (s.d.)	n
Males	Oyster trays	1982	0	33.2 (4.0)	72	1.83 (0.73)	28	5.79 (2.33)	28		
			1	34.2 (2.8)	14	1.56 (0.59)	12	4.69 (1.98)	12	192 (80)	14
		1983	0	31.9 (5.2)	55	1.90 (0.53)	26	6.14 (2.00)	26		
			1	28.2 (4.3)	9	1.59 (0.75)	9	5.69 (2.90)	9	151 (48)	9
		1984	0	34.6 (5.4)	22	1.94 (0.62)	7	6.07 (1.84)	7		
		Total		32.8 (4.7)	172	1.80 (0.64)	82	5.75 (2.21)	82	176 (71)	23
	Boxes	1982	0	39.2 (6.5)	32	3.05 (1.55)	24	7.73 (3.41)	24		
			1	40.4 (6.1)	8	2.29 (1.41)	7	5.73 (3.59)	7	191 (105)	8
		1984	0	47.2 (4.1)	12	2.90	1	6.43	1		
		Total		41.2 (6.8)	52	2.88 (1.51)	32	7.25 (3.44)	32	191 (105)	8
	Total			34.8 (6.3)	224	2.10 (1.08)	114	6.17 (2.68)	114	180 (80)	31
Females	Oyster trays	1982	0	31.8 (3.8)	26	1.36 (0.69)	10	4.69 (2.96)	10		
			1	35.3 (4.7)	6	1.55 (0.92)	6	4.46 (2.92)	6	160 (67)	6
		1983	0	29.5 (4.0)	29	1.76 (0.56)	19	6.26 (2.31)	19		
			1	31.0 (2.4)	8	1.64 (0.56)	8	5.29 (1.85)	8	149 (32)	8
		1984	0	35.9 (3.4)	42	2.10 (0.82)	6	6.37 (2.70)	6		
		Total		32.9 (4.5)	111	1.67 (0.68)	49	5.57 (2.53)	49	154 (48)	14
	Boxes	1982	0	34.3 (8.5)	10	1.98 (1.12)	9	5.99 (3.55)	9		
			1	36.8 (4.2)	5	1.48 (0.58)	5	4.11 (1.86)	5	232 (76)	5
		1984	0	45.4 (4.8)	24						
		Total		41.5 (7.7)	39	1.80 (0.96)	14	5.32 (3.11)	14	232 (72)	5
	Total			35.1 (6.7)	150	1.70 (0.74)	63	5.52 (2.64)	63	174 (65)	19

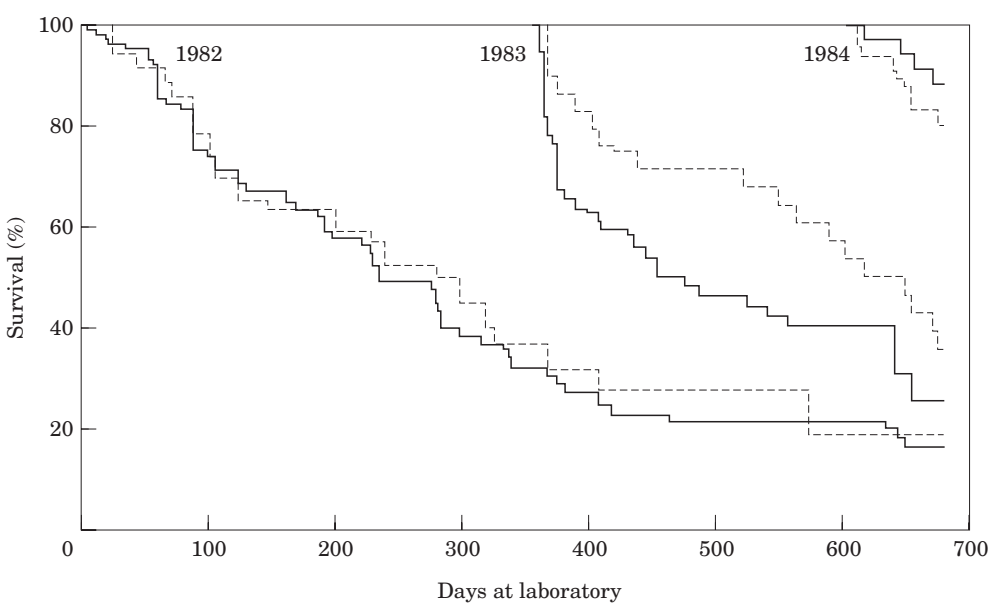

Figure 2. *Nephrops norvegicus*. Survival (percentage of the initial number of individuals held in captivity) of males (solid line) and females (dashed line) for the duration of each experiment (day 0=21 September 1982, the date the first experiment began).

Growth at moult

The overall mean MI obtained in the three experiments was 2.10 mm (s.d.=1.08) in males and 1.70 ± 0.74 mm in females (corresponding to individuals with an average size of about 35 mm CL for both sexes). The mean values of the percentage moult increment were 6.17 ± 2.68% and 5.52 ± 2.64%, respectively (Table 2).

Table 3. *Nephrops norvegicus*. Parameters of regression equations that relate growth at moult (moult size increment, MI, mm; percentage moult increment, PMI), duration of the intermoult period (IP, days), and time at laboratory (T_{lab}) to pre-ecdysis carapace length (CL, mm) for both sexes, tank type, and growth stage (considering only the first ecdysis in the laboratory for each individual). The coefficient of determination (R^2) and its significance level (p) as well as the coefficient of variation (c.v.) of each regression are shown. In the case of regression relating MI to CL and T_{lab}, the significance of the inclusion of T_{lab} (P_c) is indicated.

	n	a (s.e.)		b (s.e.)		R^2	p	c.v.
MI=a+b CL								
Males	114	−0.270	(0.509)	0.070	(0.015)	0.167	0.000	0.470
1st ecdysis in laboratory	84	−0.607	(0.581)	0.083	(0.017)	0.225	0.000	0.446
Oyster trays	82	1.853	(0.477)	−0.002	(0.015)	0.0002	0.905	0.360
Boxes	32	−1.088	(1.522)	0.101	(0.038)	0.189	0.013	0.479
Females	63	2.291	(0.557)	−0.018	(0.017)	0.019	0.288	0.437
In PMI=a+b CL								
Males	114	1.971	(0.326)	−0.009	(0.009)	0.007	0.371	0.376
Females	63	3.000	(0.356)	−0.044	(0.011)	0.210	0.000	0.299
IP=a+b CL								
Males	31	1.44	(75.94)	5.232	(2.195)	0.164	0.024	0.0040
Females	19	28.31	(117.74)	4.309	(3.447)	0.084	0.228	0.0021
Males+females	50	6.85	(61.77)	5.024	(1.794)	0.141	0.007	0.0034
In IP=a+b CL								
Males	31	4.29	(0.370)	0.024	(0.011)	0.149	0.032	0.141
Females	19	4.39	(0.021)	0.614	(0.018)	0.075	0.255	0.073
Males+females	50	4.31	(0.307)	0.023	(0.009)	0.125	0.012	0.118

	n	a (s.e.)		b (s.e.)		c (s.e.)		P_c	R^2	p	c.v.
MI=a+b CL+cT_{lab}											
Males	112	−0.278	(0.506)	0.077	(0.015)	−0.0016	(0.0007)	0.027	0.203	0.000	0.466
1st ecdysis in laboratory	84	−0.596	(0.595)	0.082	(0.018)	0.00005	(0.0016)	0.977	0.224	0.000	0.449
Females	63	2.182	(0.553)	−0.008	(0.018)	−0.0013	(0.0008)	0.097	0.063	0.143	0.430
1st ecdysis in laboratory	44	2.435	(0.662)	−0.013	(0.021)	−0.0025	(0.0018)	0.161	0.060	0.283	0.438

Table 4. *Nephrops norvegicus*. Results of the analyses of covariance carried out to compare between males and females and tank types (oyster trays and boxes), the parameters (slope and intercept, CL: effect of the covariate) of the regressions that relate growth at moult (moult size increment, MI; percentage moult increment, PMI), and duration of the intermoult period (IP) to the pre-ecdysis carapace length (CL). The value of the F-statistic and its significance level (p, in parentheses) are shown.

			F-statistic (p)		
Equation	Factor	n	CL	Slope	Intercept
MI=a+b CL					
	Sex	177	13.88 (0.000)	12.42 (0.001)	
Males	Tank	114	5.74 (0.018)	9.93 (0.002)	
Males, 30–42 mm CL	Tank	75	0.04 (0.838)	6.26 (0.015)	
Females	Tank	63	1.79 (0.186)	0.43 (0.513)	0.96 (0.332)
In PMI=a+b CL					
	Sex	177	6.62 (0.011)	4.99 (0.027)	
Males	Tank	114	2.38 (0.126)	4.38 (0.039)	
Females	Tank	63	15.03 (0.000)	0.62 (0.434)	0.10 (0.750)
IP=a+b CL	Sex	50	7.67 (0.008)	0.05 (0.833)	0.05 (0.827)
In IP=a+b CL	Sex	50	6.73 (0.013)	0.02 (0.891)	0.003 (0.954)

The equations relating MI and PMI to pre-ecdysis CL show major differences depending on sex (Table 3). The analysis of covariance shown in Table 4 demonstrates highly significant differences in the comparison of slopes between males and females for both equations (ANCOVA, $p<0.05$). The CV (Table 3) indicates that, for males as well as females, the model based on the PMI offers the better fitting, although both models provide important complimentary information.

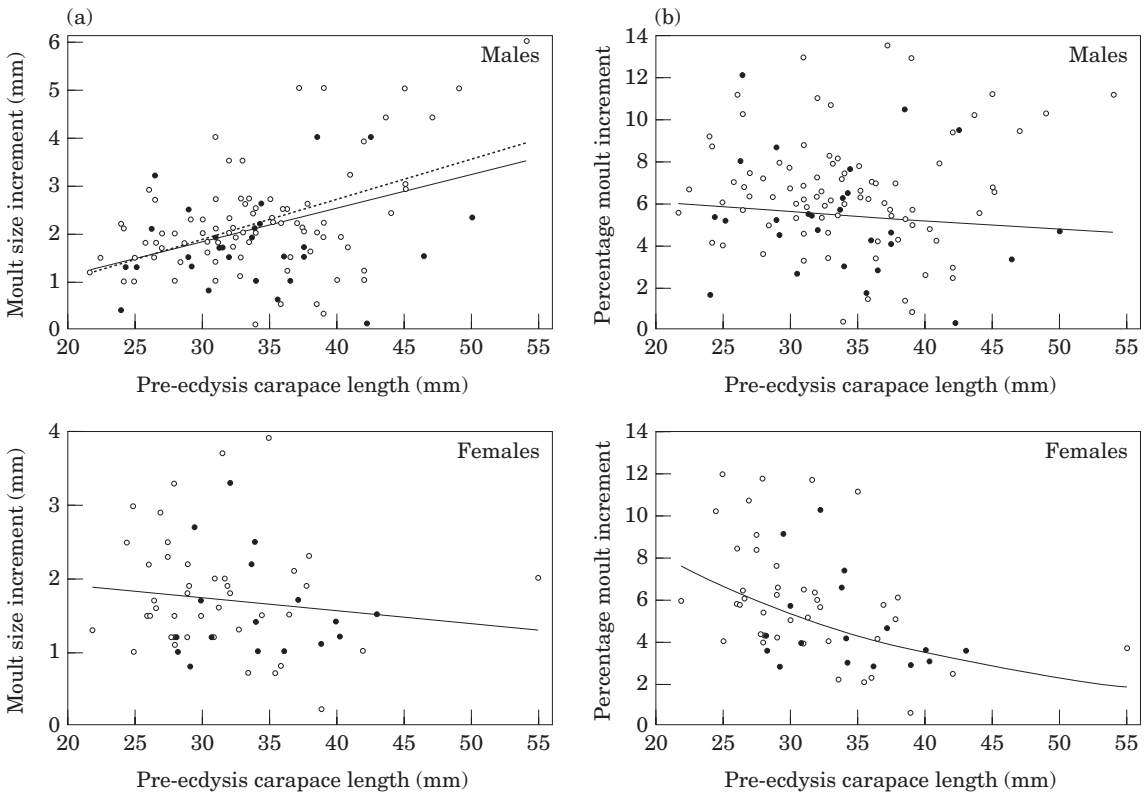

Figure 3. *Nephrops norvegicus*. Relation between growth at moult [(a) moult size increment and (b) percentage moult increment] and pre-ecdysis carapace length in males and females. The first ecdysis (○) carried out in the laboratory by each animal is differentiated from subsequent moults (●). In the case of moult increment in males, the linear regression is shown for all ecdyses (solid line) and for the first ecdysis (dotted line). For percentage increment, the regression based in lnPMI is shown.

Figure 3a and Table 3 show a significant relation between MI and pre-ecdysis CL in males ($p<0.001$) which has a positive slope, indicating that the absolute size increment at moult increases with body size. On the other hand, females exhibit a negative slope, although the regression is not significant ($p>0.1$). For individuals having a CL of 25 and 45 mm, the moult size increments would be 1.48 and 2.88 mm in males and 1.84 and 1.48 mm in females, respectively.

The regression between lnPMI and pre-ecdysis CL (Fig. 3b, Table 3) presents a negative slope in both males and females, although it is lower in males and does not reach a significant value ($p>0.1$). This would suggest that the PMI remains practically constant in males throughout the size range analysed, whereas in females the PMI decreases with size. Thus, individuals measuring 25 and 45 mm CL would have a PMI of 5.7 and 4.8% in males and 6.7 and 2.8% in females, respectively.

The effect of experimental conditions (time at laboratory and tank type) on growth at moult

Both males and females in the different experiments had slightly higher mean MI and PMI values in the first ecdyses than in subsequent moults (Table 2, Fig. 3). Again in both males and females there is a negative slope in the regression of the MI residuals with relation to the time spent in the laboratory up until the moment ecdysis takes place (Table 3, Fig. 4), although the relation is only significant in males. In fact the CVs of the regressions including the time in the laboratory is only slightly lower than those corresponding to equations based on the pre-ecdysis CL alone. The MI residuals of second or subsequent ecdyses in males that remained in the laboratory over a long time period (>1 year) generally have negative values which would suggest that the time in the laboratory causes a decrease in moult size increment. This effect is not significant in females, which is probably due to the small number of individuals that carried out a second or third ecdysis after remaining in the laboratory for 1 year.

The mean MI of males held in trays (1.80 mm, s.d. = ± 0.64 mm for a mean pre-ecdysis CL of 32.8 mm) was lower than in those held in boxes (2.88 ± 1.51 mm, for a CL of 41.2 mm) (ANCOVA: slope differences, $p<0.05$) (Tables 2 and 4, Fig. 5). The mean MI in females was very similar, 1.67 ± 0.68 mm in trays and 1.80 ± 0.96 mm in boxes, despite the difference in the

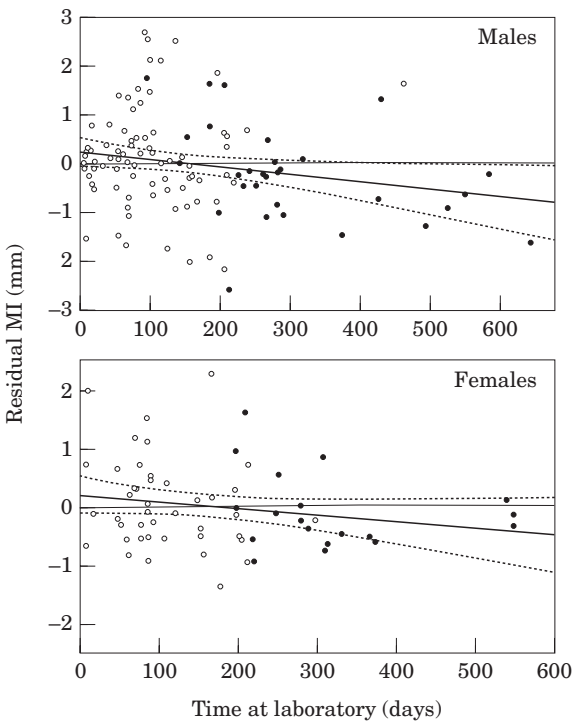

Figure 4. *Nephrops norvegicus*. Relation between the residual of moult size increment (MI) (absolute difference between observed MI and predicted MI from the regression relating MI to pre-ecdysis carapace length) and the time spent in the laboratory until ecdysis occurred in males and females. The first ecdysis (○) carried out in the laboratory by each individual is differentiated from subsequent moults (●). Linear regression (bold solid line) and 95% confidence interval (dotted line) are shown.

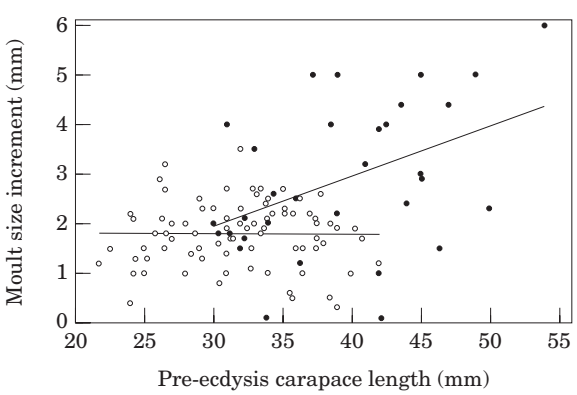

Figure 5. *Nephrops norvegicus*. Relation between moult size increment (MI) and pre-ecdysis carapace length in males held in oyster trays (○) and boxes (●). The linear regression for data corresponding to each tank is shown.

size of the individuals (mean CL=32.9 and 41.5 mm, respectively) (Tables 2 and 4; $p>0.1$).

The regression between MI and CL in males held in trays shows a non-significant slope, while lobsters held in boxes showed a significant positive slope (Table 3, Fig. 5). Although the size range in the two holding facilities were different, the differences between tank types are maintained when the analysis is restricted to data for males measuring between 30 and 42 mm CL, a size range representative of individuals in both types of tanks.

Duration of the intermoult period (IP)

The mean duration of the intermoult period in the laboratory experiments was 180 days (s.d. = ± 80) in males and 174 ± 65 days in females (Table 2). The duration of the intermoult period does not reveal significant differences between males and females or between the first and successive intermoult periods in the laboratory (Table 4, ANCOVA, $p>0.5$ in all cases). There is a positive correlation between IP and pre-ecdysis CL and the regression based on IP provides a better fit than the one based on lnIP (Table 3, Fig. 6). According to the resulting equations the IP is around 150 days in Norway lobsters 25–30 mm CL and over 200 days in individuals with a CL>40 mm. In addition, the period of time spent in the laboratory from the start of captivity until the first ecdysis is generally shorter than the intermoult period (Fig. 6). Lobsters that did not undergo ecdysis prior to their death in the laboratory or before the experiments ended remained, for the most part, in the intermoult period for less time than was estimated by the equation relating IP and CL. However, some individuals exceeded this time (Fig. 6) and in some cases they went from the beginning to the end of the experiments (679 days) without moulting at all. This, together with the fact that the IP of an individual 50 mm CL lasted over a year, shows that the large sized individuals may lose their annual moulting periodicity.

Moulting seasonality

During the experiments, both males and females moulted throughout the whole year, without showing an important seasonality in the moult cycle (Fig. 7). A broad-ranging period can be seen in males, in which moult frequency increased from late autumn until early spring, whereas in females the highest percentages of ecdyses took place at the end of autumn (December), early spring (March–April) and summer (July–August). Moreover, individuals that carried out two or more ecdyses in the laboratory show that there were two major moulting periods, with the first ecdysis taking place in the laboratory in autumn–winter and the second in spring–summer (Fig. 8).

Discussion

There have been some doubts concerning the extrapolation of the growth studies done in the laboratory to

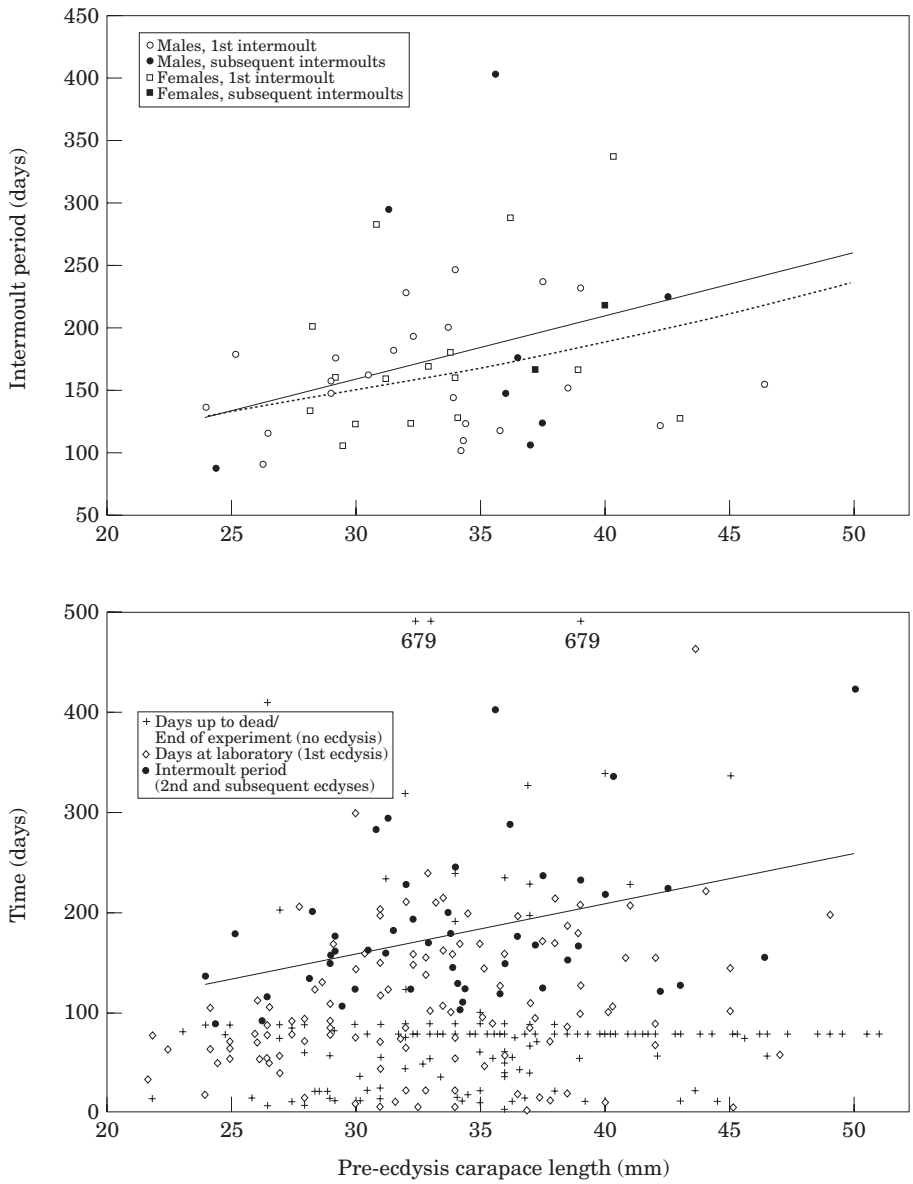

Figure 6. *Nephrops norvegicus*. (top) Relationship between the duration of the intermoult period and pre-ecdysis carapace length in males and females. The intermoult periods between the 1st and 2nd ecdyses carried out in the laboratory by each individual are differentiated from those corresponding to subsequent ecdyses. Linear regression (solid line) and logarithmic regression (dotted line) are shown for both sexes, since there were no significant differences between males and females (ANCOVA, $p>0.1$). (bottom) Relation between intermoult period and carapace length (the linear regression is shown) compared with the period that non-moulting individuals, spent in the laboratory and the captivity periods until the first laboratory ecdysis.

natural populations in terms of the effect of the different laboratory conditions (physical factors, food, etc.) as compared to those in the field. Moreover, the capture and handling may cause changes in growth or alter the physiological factors which are responsible for moult periodicity. Similar questions have come up in mark–recapture experiments. Despite the problems with this type of study, they are extremely useful and are often the only methodological means available to understand and validate the growth of the natural populations of decapod crustaceans.

The space available in the holding tank is a limiting factor in moult size increment in the Norway lobster. Major differences in growth between males held in trays and boxes were found. The growth rate increased as tank volume increased and decreased with increasing

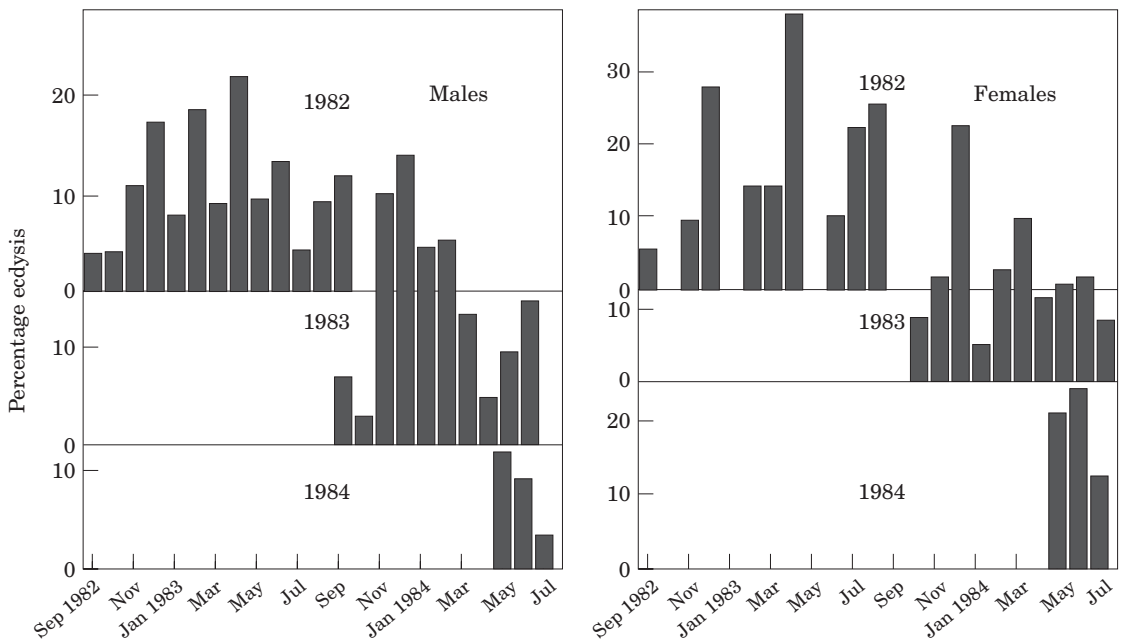

Figure 7. *Nephrops norvegicus*. Moulting seasonality of males and females in each experiment carried out in laboratory. The percentage of ecdyses in respect to the total number of live individuals is shown.

time at laboratory, as has been reported for other decapods (González-Gurriarán, 1981, 1985; Wilber and Wilber, 1989). In the field, growth rate decreases in areas having a high density of burrows and adult population of Norway lobster although probably due to increased competition for food or agonistic behaviour (Bailey and Chapman, 1983; Chapman and Howard, 1988).

The main cause of mortality in the Norway lobsters during the days following capture, in both individuals held in the laboratory (Evans *et al*., 1994) as well as those placed in submarine cages (Symonds and Simpson, 1971; Guéguen and Charuau, 1975; Morizur *et al*., 1982) is most probably the damage caused by capture, which includes the negative physiological effects of exposure to air (Spicer *et al*., 1990). In this sense, the high mortality rate seen in males in the 1983 experiment, in the days immediately after they were placed in captivity, could be the result of imperceptible and undetected damage that occurred during capture and subsequent holding in the laboratory, which in this case took place the day after capture.

In general there is high variability in the equations relating size increase at moult to the pre-ecdysis size in the Norway lobster, as reported by different authors in different geographical areas (Fig. 9). Males have a positive slope, although in many cases the relation is not significant (Table 5). In studies carried out in the field (mark-recapture and submarine cages) growth in males was greater in the Clyde (Western Scotland) than in the Sound of Jura (Western Scotland), which could be attributed to the high availability of food in the former area (Bailey and Chapman, 1983). The results from Iceland and Portugal point to a relatively high moult size increment, which was similar in the size ranges analysed (Eiríksson, 1982; Figueiredo, 1989). Growth was lower in the experiments done in captivity than those carried out in the field. These differences stay the same even when different methodologies are applied in the same area, as indicated by the laboratory results of Thomas (1965) and the mark-recapture data reported by Chapman (1982) in the waters of Scotland. If we compare only the captivity studies, they have similar growth rates with the exception of Hillis (1979) in Ireland, which is probably due to the fact that this author used a limited number of small sized individuals. The results reported for Galicia showed a greater slope than the one Thomas (1965) estimated in Scotland and Farmer (1973) in the Isle of Man, and a higher growth rate throughout the entire size range compared to Mediterranean *Nephrops* (Sarda, 1985).

The results for females vary widely among the different areas, particularly in the slope of the equation (Table 5, Fig. 9), but in all cases they exhibit a lower growth rate than males. There is no clear variability pattern between the studies made in the laboratory and the field, although the growth at moult decreases with body size more often in the studies carried out in the field. If we compare our results with other studies made in captivity, they coincide with Farmer (1973) as far as the negative slope in the growth model is concerned, while they differ

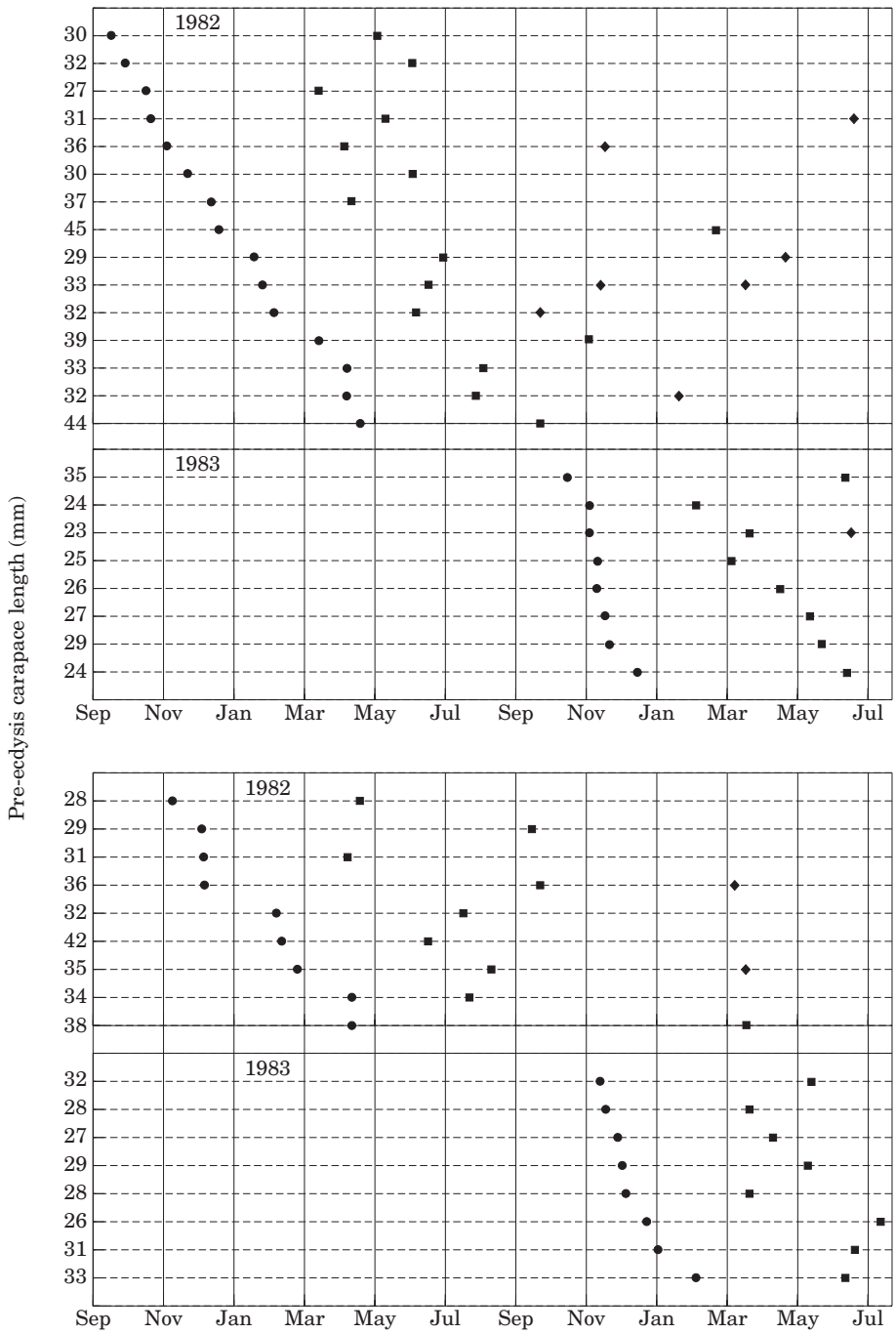

Figure 8. *Nephrops norvegicus*. Seasonality and duration of the intermoult period in males and females that carried out more than one ecdysis in the laboratory during the 1982 and 1983 experiences. Each individual is represented by a dotted horizontal line where the dates of the subsequent ecdyses are given. For each sex the lobsters are arranged according to the date the first ecdysis took place. First ecdysis (●); second ecdysis (■); third ecdysis (◆); fourth ecdysis (▲).

from the positive slopes reported by Thomas (1965), Sardá (1985), and Hillis (1979).

Two growth phases have been described in the life history of the Norway lobster, with a decrease in growth rate after the onset of maturity in females. It is generally accepted that the growth rate of Norway lobster juveniles is similar in males and females and that they moult more frequently and undergo greater percentage

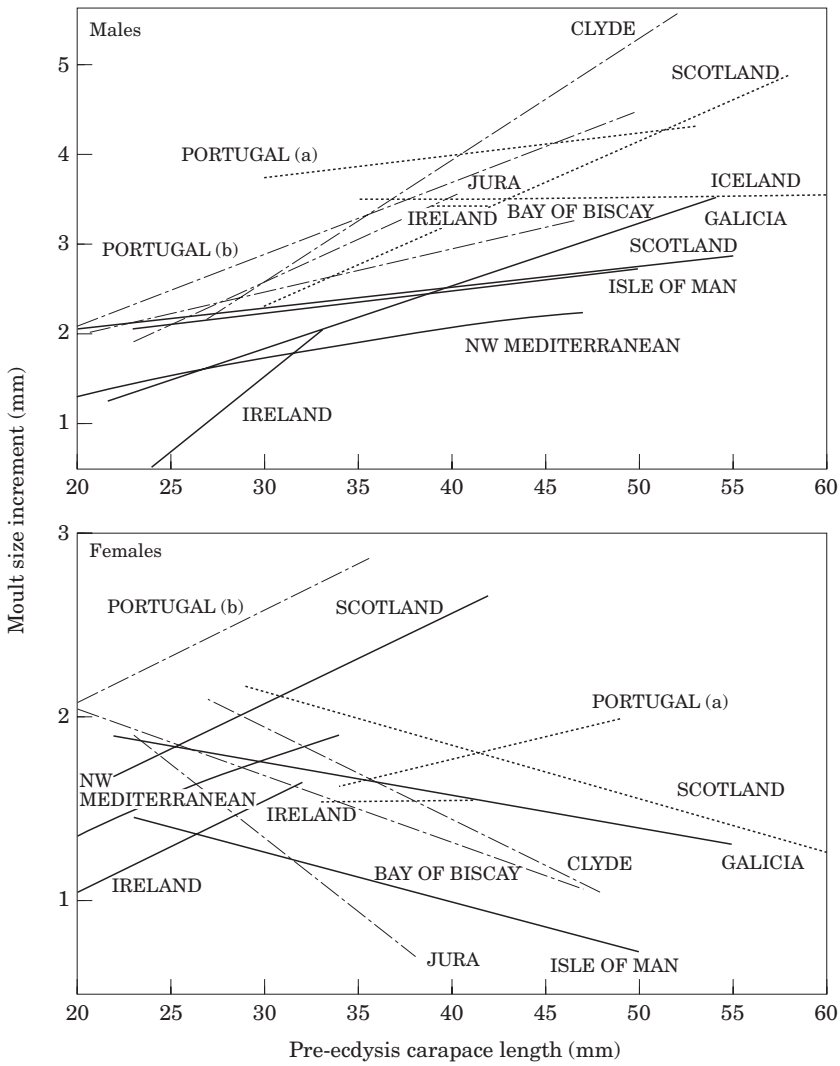

Figure 9. *Nephrops norvegicus*. Regressions relating moult size increment and pre-ecdysis carapace length in males and females corresponding to different studies carried out in different geographical areas (see Table 5). The methods of study are differentiated: Lab: holding in laboratory, MR: mark-recapture, CS: submarine cages, HP: holding in pre-moult stage (1–2 weeks until ecdysis takes place). In the case of Portugal, a and b refer to the studies of Figueiredo (1989) and Castro (1992), respectively: MR (· · ·); LAB (——); MR/SC/HP/LAB (– · – · –).

moult increments than adults (Charuau and Conan, 1977; Bailey and Chapman, 1983; Bailey *et al*., 1986; Sardá, 1995). On the other hand, there are growth differences between adult males and females which may be attributed to two possible causes: the change in the growth at moult and/or moult frequency. Our study did not yield significant differences in the duration of the intermoult period between males and females, this was probably due to the inhibition of the reproductive cycle of females in captivity. However, the main differences in growth were due to the size increase at moult.

In terms of the energy invested, the different type of growth in male and female adults (increase of the moult size increment in males and decrease in females) may be explained by the competitive process taking place between somatic growth and reproduction (Hartnoll, 1985; Nelson, 1991). The results pertaining to the relation between percentage moult increment and body size indicate that the male Norway lobster invests approximately the same energy for growth throughout its whole life. Females, however, consume less energy for growth as they increase in size, diverting it towards reproduction. It has been suggested that the inhibition of the gonad maturation process of females in captivity (Charuau and Conan, 1977) diminishes the difference in growth of the two sexes.

Table 5. *Nephrops norvegicus*. Growth at moult (moult size increment, MI, mm; percentage moult increment, PMI) reported by different authors in different geographical areas. The method of study, sex (M=males, F=females), size range (carapace length, CL, mm), number of ecdyses recorded (n), equation relating growth at moult to pre-ecdysis CL or average growth increment, and the significance of the fitted equation (p) are shown. Studies on juveniles (generally CL <20 mm) have been omitted.

Area	Author	Method	Sex	LC (mm)	n	Equation/average	p
Iceland	Eiriksson (1982)	MR	M	35–63	12	MI=3.402+0.0022 LC	n.s. (1)
Faeroe Islands	Höglund (1942)	Lab	M+F	30–45	10	IM=1.2	(2)
Scotland	Thomas (1965)	Lab	M total	20–55	127	PMI=12.23 − 0.150 LC	** (3)
						(MI=1.584+0.023 LC)	*
			M 1st moult		76	PMI=13.41 − 0.162 LC	**
			F total	22–42	30	PIM=6.8	n.s.
						(MI=0.595+0.049 LC)	*
Scotland	Chapman (1982)	MR	M	30–58	95	MI= − 0.428+0.091 LC	**
			F	29–62	95	MI=3.002 − 0.029 LC	**
Scotland–Clyde	Bailey and Chapman (1983)	HP, MR, SC	M	27–52	36	MI= − 1.473+0.135 LC	**
			F	27–48	15	MI=3.443 − 0.050 LC	n.s.
Scotland–Jura	Bailey and Chapman (1983)	HP, MR, SC	M	23–41	13	MI= − 0.324+0.096 LC	**
			F	23–38	41	MI=3.739 − 0.080 LC	**
Isle of Man	Farmer (1973)	Lab	M	23–50	31	MI=1.147+0.025 LC	n.s. (4)
			F		14	MI=2.070 − 0.027 LC	n.s.
E Ireland	Hillis (1971, 1972, 1973, 1974, 1979)	Lab	M	24–33	11	MI= − 3.503+0.167 LC	** (5)
			F	20–32	6	MI=0.066+0.049 LC	n.s.
		MR	M	39–42	4	MI=3.4	
			F	33–42	5	MI=1.54	
N Bay of Biscay	Charuau (1977)	SC	M	21–47	55	PMI=12.93 − 0.135 LC	n.s.
			F	21–38	73	PMI=18.43 − 0.410 LC	**
N Bay of Biscay	Charuau and Conan (1977)	MR, Lab, SC	M	20–??	118	MI=0.989+0.049 LC	** (6)
			F	20–??	114	MI=2.761 − 0.036 LC	*
Galicia	Present study	Lab	M	22–54	84	MI= − 0.607+0.083 LC	** (7)
			F	22–55	63	MI=2.291 − 0.018 LC	n.s.
S Portugal	Figueiredo (1989)	MR	M	30–53	10	MI=2.981+0.025 LC	n.s. (8)
			F	34–49	16	MI=0.810+0.024 LC	n.s.
S Portugal	Castro (1992)		M	>20		MI=0.48+0.08 LC	(9)
			F	>20		MI=1.08+0.05 LC	
NW Mediterranean	Sardá (1985)	Lab	M	17–47	78	log10 PIM=0.91 − 0.005 LC	**
			F	14–34	82	log10 PIM=0.95 − 0.006 LC	**

(1) Equation fitted from original data.
(2) Data in Andersen (1962). Original data in total length, transformed to CL using our equation (unpubl. data).
(3) Regression between MI and CL in Charuau and Conan (1977).
(4) Regression between MI and CL in Charuau and Conan (1977) (original data digitized). Original equation was fitted for males and females including data from Andersen (1962) and Thomas (1965): MI=1.848+0.014 CL.
(5) Only data corresponding to individuals with CL >20 mm. Equations fitted from original data. Charuau and Conan (1977) fitted the following equations for all data (including CL <20 mm): M, MI=0.464+0.037 CL (n=38); F, MI=0.446+0.027 CL (n=15).
(6) Regressions in Charuau and Conan (1977): pre-ecdysis CL=a+b′ post-ecdysis CL, transformed to MI=a+(b′ − 1) pre-ecdysis CL.
(7) Data for males corresponding only to the first moult in laboratory.
(8) Equation fitted from original data. Males, only data corresponding to <10 months after release (it was assumed that they carried out only one moult).
(9) Equation fitted from previous data of other authors (Thomas, 1965; Hillis, 1971; Figueiredo, 1975; Charuau, 1977; Sardá, 1985) and length frequency distributions in S Portugal.
Method: Lab: holding in laboratory, MR: mark-recapture, SC: submarine cages, HP: holding in premoult (1–2 weeks before ecdysis).
**p<0.05, *p<0.1, n.s. p>0.1.

This may be the reason why some authors observe few differences in growth between males and females (Thomas, 1965; Conan, 1978; Sardá, 1985). In our experiments, these effects are not noticeable and female growth diminishes with the pre-ecdysis size. Similar results were reported by Farmer (1973), Charuau

Table 6. *Nephrops norvegicus*. Duration of the intermoult period (IP, days) reported by different authors in different geographical areas. The method of study, sex (M=males, F=females), size range (carapace length, CL, mm), and equation relating IP to pre-ecdysis CL or average IP are shown. In cases where equations relating IP and CL were obtained, the number of cases (n) is given. Studies on juveniles (generally CL<20 mm) have been omitted.

Area	Author	Method	Sex	CL (mm)	n	Equation/average
Scotland	Thomas (1965)	Lab	M	20–55		6.5 mo
				20–29		3–4 mo
				40–44		9 mo
			F	22–42		7 mo
Scotland–Clyde	Bailey and Chapman (1983)	LFD	M+F	21–30		3 mo
				31–40		6 mo (M)/12 mo (F)
				41–50		12 mo
				>50		⩾12 mo
Scotland–Jura	Bailey and Chapman (1983)	LFD	M+F	21–30		6 mo (M)/6–12 mo (F)
				31–50		12 mo
Isle of Man	Farmer (1973)	Lab	M	20–47	7	7.4 mo (5–10 mo)
N Bay of Biscay	Charau (1975)	LFD	M	24–27		9–10 mo
			F	>27		12 mo
N Bay of Biscay	Conan (1975, 1978)	LFD	M	20–50		6 mo
				20–40		12 mo
Bay of Biscay	Talidec and Reyss (1993)	Rad	M	25–46		6 mo
			F	20–24		6 mo
				25–29		6/12 mo
				29–43		12 mo
Galicia	Present study	Lab	M+F	24–50	50	IP=6.85+5.024 CL
NW Mediterranean	Sardá (1985)	Lab	M	12–60	47	log10 IP=1.755+0.013 CL
			F	15–45	53	log10 IP=1.726+0.015 CL
	Castro (1992) (1)		M+F	15–45		$IP=81+0.04\ CL^{2.2}$

(1) Data from Sardá (1983) in laboratory.

Method: Lab: holding in laboratory, Rad: dating premoult carapaces by radioisotopes; LFD: time series of modes of length frequency distributions from trawl samples, growth at moult equations, and moult stage based in the examination of pleopods and carapace.

(1977), Chapman (1982), and Bailey and Chapman (1983) using different methodologies.

In Norway lobster females, moult frequency and the duration of the intermoult period is directly related to the duration of the incubation period, which varies, depending on the latitude, e.g. from 6–7 months in areas around the South of Portugal and Galicia (Figueiredo and Ferreira Barraca, 1963; Fariña, unpubl. data) up to 12–13 months in Iceland and the Faeroe Islands (Andersen, 1962; Nicolajsen and Eiríksson, 1990; Eiríksson, 1993). In this study, the mean duration of the intermoult period in adult females, which have no possibility of reproducing in the laboratory, was 6–7 months, which was very similar to previous results found by Thomas (1965) and Sardá (1985). However, based on other methods (monitoring moult cycle and modes in length frequency distributions from time series of trawl samples) the mean duration reported by other authors is around 12 months (Charuau, 1975; Bailey and Chapman, 1983; Talidec and Reyss, 1993) (Table 6). On the other hand, Norway lobster males moult throughout the whole year with moult peaks that vary spatially and seasonally (Thomas, 1965; Farmer, 1973; Charuau, 1974). In some areas adult males are reported as having two annual moulting periods (Conan, 1975b; Sardá, 1985). In our case a moult cycle with a certain degree of seasonality was observed, especially in females, showing ecdysis peaks in autumn and spring. These periods coincide with the stages before and after copulation and this in turn corresponds with the fact that in order to copulate females must have just moulted and males must be in hard-shelled condition. However, females that do not spawn may carry out the ecdysis at a later time. In the field, these peaks could happen earlier, and it has been demonstrated that in experimental conditions there is a shift in the moulting peak (Conan, 1978, 1985; Sardá, 1985).

There are generally few references to equations that relate the duration of the intermoult period to body size (Sardá, 1985; Castro, 1992). Moreover they show no major differences as compared to the equation estimated in this study (Table 6, Fig. 10). Norway lobster juveniles (20–25 mm CL) carry out up to three ecdyses per year; intermediate sized adults (around 35 mm CL) have two and the oldest specimens undergo one moult per year and they may even lose the annual moulting periodicity, as has been seen in laboratory experiments.

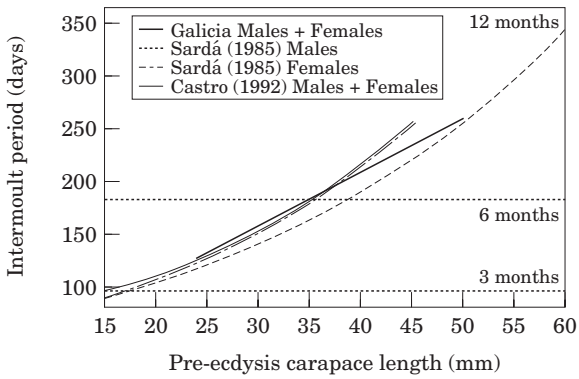

Figure 10. *Nephrops norvegicus*. Regressions relating the duration of the intermoult period in the laboratory and pre-ecdysis carapace length in males and females reported by different authors (see Table 6).

Whilst the differences in growth throughout the geographical distribution range of the Norway lobster may be linked to genetic factors, they could also be the result of interacting biological factors (mainly the intensity of recruitment) as well as of the fishing effort they are subjected to, which directly affects the density, and therefore the availability of food. These variations create density-dependent differences in growth (Bailey and Chapman, 1983; Chapman and Howard, 1988). However, we must not rule out the effect of the environmental parameters, such as temperature, although the ranges of temperature variation in the different geographical areas are rather small (Scotland and Isle of Man: 6.5–13°C [Farmer, 1973; Bailey and Chapman, 1983], Galicia: 10.7–13°C [Blanton *et al*., 1984], Portugal: 11–14°C [Figueiredo, 1984]).

Acknowledgements

We would like to thank R. Morlán for his help in the laboratory work. This research was carried out under the program ATN – Fisheries in the area of Galicia of the Instituto Español de Oceanografía, and was partially funded by the Consellería de Educación e Ordenación Universitaria of the Xunta de Galicia.

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