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Increment at molt for the Norway lobster (*Nephrops norvegicus*) from the south coast of Portugal

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The increment at molt for *Nephrops norvegicus* was studied with the objective of obtaining a model for prediction of post-molt size based on pre-molt size for the population from the south coast of Portugal. Wild animals were maintained in a specially prepared laboratory facility until they molted. Individual values of increment at molt were obtained and used to evaluate alternative models and estimate their parameters. Six alternative models, used previously by several authors to relate pre- and post-molt size, were modified so that increment at molt was the dependent variable and pre-molt size the independent variable. These included the linear relationship of the growth factor (GF) on pre-molt size, the Hiatt equation, post-molt size a power function of pre-molt size, the hyperbolic function, GF exponential function of pre-molt size and the Misra equation.

The analysis of the data showed that none of the models could be used to predict increment at molt for either sex. The distribution of the increment at molt was a random normal variable, with mean values not significantly different between sexes, 2.78 mm for males and 2.26 mm for females, variances 0.47 and 0.59, respectively.

An analysis of the models suggests that using post-molt size or the GF as dependent variables may lead to a misinterpretation of the dependency of these variables on pre-molt size. It is suggested that the increment at molt should be the variable of interest for predicting post-molt size. The choice of a mathematical formulation should, besides having biological meaning, have the capacity of expressing a true relationship between increment at molt and pre-molt carapace length, namely, be able to model several options for the increment at molt after maturity, including a steady increase of the increment through life, the stabilization of the increment after maturity or the decrease of the increment for larger sizes.

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Introduction

The objective of this work was first to obtain data on growth increment for the Norway lobster (*Nephrops norvegicus* (L.)) from the south of Portugal and secondly, to determine the best model for predicting increment at molt as a function of pre-molt carapace size. An experiment where lobsters molted in a controlled environment was specifically setup for this purpose and the data presented are reported for the first time. Previous information for this region included only early post-larvae and juvenile stages for individuals reared from the egg (Figueiredo, 1975) and

tagging data (Figueiredo, 1989). In both cases information is not sufficient to model growth.

Growth estimates constitute part of the information necessary to build individual stochastic growth models as proposed by several authors (Caddy, 1987; Restrepo, 1989; Castro, 1992; Verdoit *et al.*, 1999). Individual stochastic growth models are useful to predict the age–length structure of the population, producing an age–length key potentially useful in stock assessment or in the interpretation of length–frequency distributions.

The prediction of size after molt based on pre-molt size (L_1) has been approached by different authors who used the

Table 1. Models used to predict post-molt size in decapods. The original form and a converted form using increment at molt ($INC = L_2 - L_1$) as the dependent variable on pre-molt size (L_1) are presented. Other symbols used are: L_2 (post-molt size) and GF (growth factor, $GF = INC/L_1$).

Underlying assumptions	References	Model ref.	Original form	Converted form (INC as dependent)
GF linear function of L_1	Olmstead and Baumberger, 1923	M1	$GF = a + bL_1 + \varepsilon$	$INC = aL_1 + bL_1^2 + \varepsilon$
L_2 linear function of L_1	Hiatt, 1948	M2	$L_2 = a + bL_1 + \varepsilon$	$INC = a + (b - 1)L_1 + \varepsilon$
L_2 power function of L_1	Wilder, 1953	M3	$L_2 = aL_1^b + \varepsilon$	$INC = aL_1^b - L_1 + \varepsilon$
L_1 and L_2 linked through hyperbolic function	Mauchline, 1976	M4	$L_2 = a + \frac{c}{(L_1 - b)} + \varepsilon$	$INC = a - L_1 + \frac{c}{(L_1 - b)} + \varepsilon$
GF exponential function of L_1	Mauchline, 1977	M5	$GF = e^{a+bL_1} + \varepsilon$	$INC = L_1 e^{a+bL_1} + \varepsilon$
B in the linear model M2 is a linear function of L_1	Easton and Misra, 1988	M6	$L_2 = aL_1^{(b+cL_1)} e^{dL_1}$	$INC = aL_1^{(b+cL_1)} e^{dL_1} - L_1 + \varepsilon$

post-molt size (L_2), or the growth factor (GF), expressed as the percentage or proportion increase at molt (Table 1, original form) as dependent variables.

Several authors published information on observed increment at molt for this species. An extensive review by González-Gurriarán *et al.* (1998) shows that most authors used the Hiatt model or Hiatt diagram (M2 in Table 1). This relationship was proposed for the first time by Hiatt (1948) for the crab *Pachygrapsus crassipes* and has been extensively used by many other authors. As an example Kurata (1962) provided estimates of parameters for this relationship for other species of decapods.

As noted by Mauchline (1977) and Botsford (1985) prediction of increment should not be based on such a relationship. Since the increment will always be a small fraction of the pre-molt size, the relationship between pre- and post-molt will almost certainly show a significant correlation. This situation was referred to by Mauchline (1977) as a conditioned measure of the post-molt size on the pre-molt size. Botsford (1985) mentioned that the molt increment provides a more realistic and informative description of growth. Using increment as the dependent variable is therefore, a more correct approach to modeling growth at molt, which is why, in this work, all models were reparameterized to express increment as a function of pre-molt size (Table 1, converted form).

Materials and methods

Between October 1996 and April 1997 more than 400 lobsters were transported to the laboratory. They were caught aboard commercial trawlers using towing times shorter than usual to minimize trauma. A special holding facility was set up to maintain the captured lobsters. The structure of the circuit and the methodologies used to transport and maintain the captive specimens are described in Encarnação *et al.* (2000). After an adaptation period of 3 days (during which time the animals were not handled or fed) the survivors were measured and the sex, ovigerous conditions and missing appendages were recorded. They were again measured after the molt, as soon as the carapace

was hard. For each lobster the molt increment (INC) was computed as the difference between the post-molt size (L_2) and pre-molt size (L_1). The measurements were made with digital calipers and the standard size was used (from the base of the left eye socket to the middle of the posterior margin of the carapace). The individuals were followed until December 1997. Individuals that died within 2 weeks after the molt were not considered. From the individuals retained for data analysis, a total of 120 molted once, 34 molted twice and one molted three times, producing a total of 191 molts (155 first molts, 35 second molts and one third molt).

To predict increment at molt as a function of pre-molt size, the models in Table 1 were reparameterized to have INC as a dependent variable with no variable transformations.

The parameters of the models were estimated using either linear or non-linear techniques (Gauss–Newton method, SAS Inc., 2000) according to the nature of the model. In the cases where the formulation of the model did not have an independent term (M1, M3, M5 and M6) this term was added. Significance was considered for $\alpha = 0.05$ in all cases. Increment at molt values for males and females were compared using a Student t-test. All statistical analysis was carried out using the statistical package SAS (SAS Inc., 2000).

In the absence of significance of any of the models tested, a non-parametric test for trend, the Cox–Stuart test (Conover, 1980), was used to evaluate changes in increment at molt with pre-molt size.

Results

The first step of data analysis consisted in an evaluation of the effect of captivity on increment at molt. Up to three molts in the same individual were observed. First molts only were used since a decline in increment due to captivity was suspected (preliminary analysis of this data set and reported by González-Gurriarán *et al.*, 1998 for the same species).

The effect on molt increment of time in captivity before the first molt was studied using the Pearson correlation

coefficient to test the null hypothesis $H_0: \rho = 0$ (independence between days in laboratory and increment at molt). No significant correlation was found for females, but for males the null hypothesis was rejected (negative correlation, $p = 0.0397$). For males correlation values were compared using data corresponding to a captivity period of 150 days or less. This time the independence hypothesis was not rejected ($p = 0.57$). The analysis of increment at molt was therefore based on data of the first molt, for any duration of the captivity for females and within a 150 day period after arrival to the laboratory for males.

Data analysis was carried out on molt information for 84 females (carapace lengths ranging from 26 to 41 mm) and 52 males (carapace length from 25 to 49 mm). Descriptive statistics of the increment at molt are presented in Table 2. Figure 1 represents the pairs of values of pre-molt and increment at molt used in the analysis. Figure 2 presents the frequency distributions of increment at molt in 0.5 mm classes.

The next step consisted in the study of the relationship that better predicts increment at molt as a function of pre-molt size. The results of the analysis are presented in Table 3. None of the models produced significant estimates of the parameters. These results show that, for this population and at least for the range of carapace length studied, it is not possible to predict increment at molt from the pre-molt size. The distribution of increment at molt is a random normal variable in both sexes (Cramer–von Mises statistic in Table 2), with mean 2.27 mm in females and 2.73 mm in males while the variance is slightly higher in females than in males, 0.59 and 0.47, respectively. Mean increment at molt was not significantly different between the two sexes (t-test for two independent samples, $p = 0.052$).

In the absence of a model for predicting increment from pre-molt carapace length, mean increment values were averaged for 1 and 5 mm carapace length classes, in an attempt to reduce noise. The Cox–Stuart test (Conover, 1980) shows that for either sex no significant trend exists in mean increment at molt considering either 1 mm

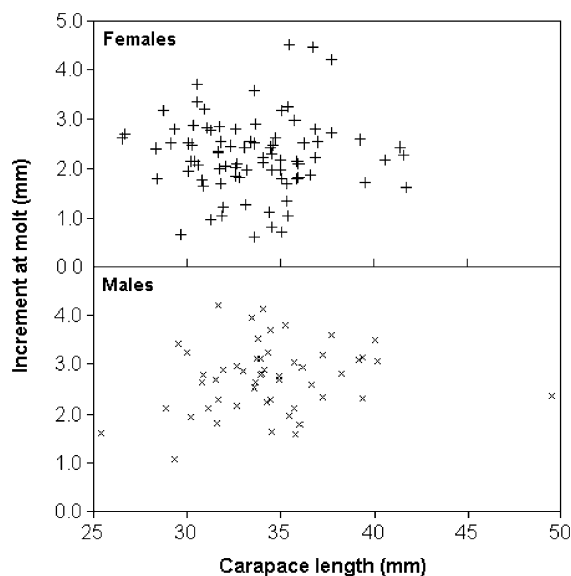


Figure 1. Scatter-plot showing increment at molt (mm) as a function of carapace length for the first molt in captivity ($n_{\text{females}} = 84$, $n_{\text{males}} = 52$).

($p_{\text{females}} = p_{\text{males}} = 0.2188$) or 5 mm ($p_{\text{females}} = p_{\text{males}} = 0.5$) carapace length classes.

Discussion

A comparison of the increment at molt was done between values obtained here and from other studies where the mean increment at molt for the first molt in captivity could be isolated (Thomas, 1965 for Scottish waters; Hillis, 1971 for the Irish Sea; Charuau, 1977 for the Bay of Biscay; Sardá, 1985 for the Catalán Sea). In the case of González-Gurriarán *et al.* (1998) (Galician waters) a weighted average of increment at molt for the first molt in captivity

Table 2. Descriptive statistics of the variable increment at molt for (INC) both sexes; variables with units in mm.

	Females	Males
n	84	52
Mean	2.27	2.73
Median	2.26	2.78
Standard deviation	0.77	0.68
Variance	0.59	0.47
Skewness	0.34	-0.02
Kurtosis	1.06	-0.15
Minimum	0.61 ($L_1 = 33.63$)	1.07 ($L_1 = 29.34$)
Maximum	4.51 ($L_1 = 35.49$)	4.21 ($L_1 = 31.61$)
p-value of Cramer–von Mises test for normality	0.058	>0.25

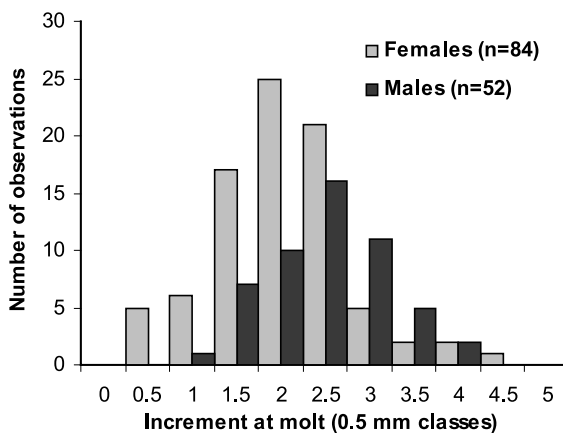


Figure 2. Frequency distribution of the increment at molt for both sexes.

Table 3. Model selection for the relationship $INC = f(L_1)$ where INC is the increment at molt and L_1 the pre-molt size. Mean square errors (MSE) and model significance are presented (fc indicates failure to converge for the non-linear estimation of the parameters).

Model ref.	SAS routine	k parameters	n points	Sex	MSE	p-value
M1	GLM	2	84	F	0.6034	0.7895
		2	52	M	0.4424	0.0953
M2	GLM	2	84	F	0.5996	0.9809
		2	52	M	0.4638	0.2345
M3	NLIN	2	84	F	0.6030	0.7672
		2	52	M	0.4406	0.0865
M4	NLIN	3	84	F	–	fc
		3	52	M	–	fc
M5	NLIN	2	84	F	0.6068	0.9899
		2	52	M	0.4403	0.0850
M6	NLIN	4	84	F	–	fc
		4	52	M	–	fc

for several experiments reported was calculated. Estimates for increment at molt in females were 2.37 mm (Scottish waters), 1.20 mm (Irish Sea), 1.71 mm (Bay of Biscay), 1.82 (Galician waters) and 1.68 mm (Catalán Sea), compared with 2.27 mm in this work. For males, average values of increment at molt for the same areas were 2.62, 1.31, 2.49, 2.13 and 1.54 mm, respectively, compared with 2.73 mm in this work. For both sexes only the mean values obtained for the Scottish waters (Thomas, 1965) are within the 95% confidence intervals obtained in this work. All other mean values are inferior to the lower limit of the confidence interval. These differences could be due to

variations in the studied populations or to the captivity conditions used in the study.

With respect to predicting increment at molt from pre-molt size, other authors have found significant linear relationships, contrary to the results of our work (González-Gurriarán *et al.*, 1998, Table 5). For better comparison the original data published were reanalyzed here to find estimates for the parameters of M2, where INC is the dependent variable (Thomas, 1965; Hillis, 1971; Charuau, 1977; Sardá, 1985; Figueiredo, 1989). For the cases where the authors had already reported the results in this form (INC dependent of L_1), the parameters were taken directly from their work. Only data from the first molt in captivity were used and injured individuals or individuals that died during the experiment were excluded. Also data from Hillis (1971) and Figueiredo (1975) referring to early juvenile stages were not considered. The results are presented in Table 4. The cases where $n \geq 30$ and $p\text{-value} < 0.05$ are identified in bold. These refer to three studies for females (Chapman, 1982; Bailey and Chapman, 1983-Jura; Charuau, 1977) and three studies for males (Chapman, 1982; Bailey and Chapman, 1983-Clyde area; González-Gurriarán *et al.*, 1998). For these studies the slopes of the model are positive for males and negative for females. A compilation of 13 studies conducted in nine regions, from Scotland to the Mediterranean (González-Gurriarán *et al.*, 1998-Figure 9) shows that the relationship $INC = f(L_1)$ tends to have positive slopes in males and smaller females, while larger females tend to present negative slopes.

A negative slope cannot express the relationship of increment at molt on pre-molt size for the duration of the lifecycle in females. In early juvenile stages absolute

Table 4. Results of fitting M2, $INC = a + bL_1 + \epsilon$, to data from different authors. In all cases only data from the first molt in captivity and non-injured individuals were considered. For Chapman (1982), Bailey and Chapman (1983) and González-Gurriarán *et al.* (1998) the parameters were reported by the authors. Significant models based on 30 or more observations are presented in bold.

Author	Method	Area	Sex	n	a	b	p < 0.05
This study	Laboratory	Portugal (south)	M	52	1.672	0.031	No
			F	84	2.251	0.001	No
Thomas, 1965	Laboratory	Scotland	M	82	1.882	0.022	No
			F	20	-0.699	0.099	Yes
Chapman, 1982	Tagging	Scotland (four areas)	M	95	-0.428	0.091	Yes
			F	95	3.002	-0.029	Yes
Bailey and Chapman, 1983	Tagging and caging	Scotland (Clyde)	M	36	-1.473	0.135	Yes
			F	15	3.443	-0.050	No
Bailey and Chapman, 1983	Tagging and caging	Scotland (Jura)	M	13	-0.324	0.096	Yes
			F	41	3.739	-0.080	Yes
Hillis, 1971	Laboratory	Irish area	M	13	2.870	-0.085	Yes
			F	4	2.427	-0.062	No
Charuau, 1977	Cages at sea	Bay of Biscay	M	55	1.764	0.025	No
			F	73	3.345	-0.057	Yes
González-Gurriarán <i>et al.</i> , 1998 ^a	Laboratory	Galicia	M	84	-0.607	0.083	Yes
			F	16	1.032	0.018	No
Fgueiredo, 1989	Tagging	Portugal (south)	M	10	2.981	0.026	No
			F	16	1.032	0.018	No
Sardá, 1985	Laboratory	Catalán Sea	M	13	1.153	0.015	No
			F	16	1.336	0.009	No

^aData for females is not presented because the first molt in captivity could not be isolated.

increment at molt is smaller than for adult sizes (although the percentage increase may be larger). Data from Hillis (1971) for the Irish Sea and Figueiredo (1975) for the Southwest coast of Portugal show that juveniles have absolute increments from 0.6 to 1.2 mm (Hillis, 1971 for pre-molt carapace lengths from 8.3 to 10.1 mm) and 0.3 to 1.6 mm (Figueiredo, 1975 for pre-molt carapace lengths from 3.6 to 7.5 mm). The increment at molt increases until adulthood. At this point it can either stabilize (resulting in non-significant models that predict its dependence on pre-molt size), continue to increase or it can decrease in larger sizes, resulting in a broken line or a dome shaped curve. Such a situation is common in females as was demonstrated, among others, by Kurata (1962). This would be in agreement with a slowdown of growth for females after sexual maturity. This situation could also explain the different results obtained in growth studies for *N. norvegicus* (González-Gurriarán *et al.*, 1998). If the increment slows down at maturity, this would happen around 30 mm for females (50% maturity size reported for this population, Orsi Relini *et al.*, 1998). The ranges of carapace length used in this work were 26.5 to 41.7 mm for females and 25.4 to 49.5 mm for males. At least for the females, the range within which the percentage of mature individuals increases, is contained in the range of observed values of pre-molt size, mixing different rates of dependence of increment at molt on pre-molt size, contributing to a masking of the signal and an increase in the dispersion of the values.

Expressing increment as a function of pre-molt size for all life stages requires a model that has at least three parameters. Mauchline (1976, 1977) and Easton and Misra (1988) had this in mind when they proposed the more complex equations expressed in models M4, M5 and M6 (Table 1). All the models presented in Table 1 (INC as dependent variable), with the exception of model M2 (the Hiatt model), fit these criteria (considering an intercept term included). The simplest one is the modified version of the model proposed by Olmstead and Baumberger (1923), (model M1 in Table 1). This model has the added advantage of being linear, with a single solution and parameters that can be easily estimated with a spreadsheet and it is suggested it can be a starting point for a generalized model to express increment at molt as a function of carapace length. Such a model can express the expected change in the relationship $INC = f(L_1)$ for females by allowing INC to change from being directly related with L_1 (before maturity) to being inversely related with L_1 (after sexual maturity).

The failure of all the models with the present data set does not mean that none of them can be used to predict increment at molt in this population of *Nephrops*. The results presented here are very likely the result of a data set that is not large enough to allow the expression of a relationship $INC = f(L_1)$ in the presence of high variance of the increment at molt for any given level of L_1 .

In conclusion, the data obtained here suggest that for the size ranges observed, the relationship of increment at molt with pre-molt length, is likely to be masked by a large error

variance, making it impossible to predict post-molt size from pre-molt size. If information on increment at molt and its variability is required to generate simulated individual growth models, a normal random variable can be used for the range of carapace length observed, with the mean and variance obtained in this work. Another problem may come from the range of pre-molt size available.

The possibility of using a single model to predict increment from pre-molt size, covering the juvenile and adult phases of both sexes, needs to be investigated in data sets large enough to detect trends in the presence of very high variability of the response variable, and must cover all ranges of carapace length, from post-settlement juveniles to the largest sizes in the adult population.

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