

A growth model that incorporates individual variability for the Norway lobster population (*Nephrops norvegicus*, L. 1758) from the bay of Biscay

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The growth of Norway lobster (*Nephrops norvegicus*) from the bay of Biscay was modelled through the succession of moults and intermoult periods. First, parameters related to each of these processes were estimated for each sex and maturity stage. Moults increment was modelled as a linear function of carapace length, and regression parameters were estimated. For females, intermoult period was assumed to depend on maturity stage whereas for males it was assumed to be constant throughout their life. Mean intermoult periods were estimated from radiometric data. The estimations relied on bootstrap procedures that take into account both measurement error and individual variability. In a second step, 500 individual growth curves were simulated using previous parameter estimates. Finally, an age–length key was calculated from simulation outputs, yielding median age-at-length as well as corresponding confidence interval.

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Key words: age–length key, growth model, Norway lobster, *Nephrops norvegicus*, bay of Biscay, radiometry data.

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Introduction

The estimation of growth parameters is crucial in fish stock assessments, since age–length keys are closely tied to growth features. For crustaceans, ageing is not easy due to the lack of permanent calcified structures. In addition, growth through successive moults may not be adequately modelled through classical curves such as von Bertalanffy (1938). Crustacean growth features are to a large extent tied to reproduction. For Norway lobster (*Nephrops norvegicus*), males and females moult twice a year, in spring and autumn, until sexual maturity (Conan, 1975, 1978a; Sarda, 1980). In the bay of Biscay, breeding generally takes place between March and August, with a peak between May and July, and adults mature at age 2 which correspond to a median size at maturity (L_{50}) of 19 mm of carapace length (CL) for males and 23.5 mm CL for females (Morizur, 1980).

Once males are sexually mature, they continue to moult twice a year in spring and autumn (Conan, 1978b), while females moult only once a year in the spring right after the hatching of their eggs.

Growth of Norway lobster has been modelled using different kinds of data. Several authors have tried to estimate age–length keys from the analysis of length–frequency data (Hillis, 1971, 1972b, 1979; Farmer, 1973; Charuau, 1975; Conan, 1978b; Figueiredo, 1989; Nicholson, 1979; Castro, 1995; Mytilineou and Sarda, 1995). However, the growth of Norway lobster appears to depend on two parameters, moult increment (MI) and intermoult period (IP) (or moult frequency). Thus, another way of modelling growth consists in simulating the succession of moults over time using estimations of MI and IP. There is a number of studies aimed at the estimation of these parameters from direct observations of animals kept in captivity either in immersed cages

Table 1. Main models used for modelling crustaceans growth. The error term is omitted in the equations for sake of concision.

Reference	Equation	Model name
Moult increment		
Mauchline (1977)	$MI = Xe^{(a+bX)}$	Log-linear
Somerton (1980)	$MI = a + bX - cX'$	Bent-line
Castro (1992)	where $X' = \max(0, X - X^*)$ $MI = a + bX$	Somerton modified
Hiatt (1948)	$Y = a + bX$	Linear
Wilder (1953)	$\text{Log}(Y) = a' + b' \text{Log}(X)$	Log-linear
Mauchline (1976)	$(X - X_0)(Y - Y_0) = k$	Hyperbole
Easton & Misra (1988)	$Y = b_0 X^{(a_0 + a_1 X)} e^{b_1 X} - X$	Misra's Equation
Easton & Misra (1988)	$Y = b_0 X^{a_0} e^{b_1 X} - X$	3 parameters Misra Equation
Easton & Misra (1988)	$Y = b_0 X e^{b_1 X} - X$	2 parameters Misra Equation
Frequency of moult		
Kurata (1960)	$L_n = b^n L_0 + a(1 + b^n)/(1 - b)$	Kurata
Charuau (1975)	$\text{Log}(Y) = a + bN$	Dyar's law
Intermoult period		
Kurata (1962)	$IP = a + bX^3$	Cubic
Mauchline (1977)	$IP = a + bX$	Linear
Mauchline (1977)	$\text{Log IP} = a + bX$	Log-linear
Castro (1992)	$IP = a + bX^c$	Kurata modified
Curry & Feldmann (1987)	$\text{Log}(IPT') = a + bX$	Degree-day model
Growth curve		
von Bertalanffy (1938)	$L_t = L_\infty [1 - e^{-K(t-t_0)}]$	von Bertalanffy

where MI=Moult increment; X=Pre-moult cephalothorax length (CL); X*=some specified value of X; Y=Post-moult CL; L_t =Length at time t; L_∞ =Asymptotic length; K=Curvature parameter; t_0 =Theoretical age-at-length zero; IP=Intermoult period; T'=Temperature; L_n =Length after n moults; L_0 =Initial length; N=Number of moults; a, b, c, a_0 , a_1 , b_0 , b_1 , a' , b' , X_0 , Y_0 , k=Parameters to be estimated.

(Charuau, 1977) or in tanks (Thomas, 1965; Hillis, 1971, 1972a, 1973, 1974, 1979; Farmer, 1973; Figueiredo, 1979; Charuau and Conan, 1977; Conan, 1975, 1978a; Sarda, 1980, 1985). Mark-recapture studies were also used to estimate annual size increment (Andersen, 1962; Charuau and Conan, 1977; Hillis, 1974, 1979; Conan, 1978a). More recently, Shelton and Chapman (1995) tested a new tagging technique based on histological grafting. This technique enables one to count the number of moults between tagging and recapture, corresponding length increment being measured at the same time. Also, a technique based on natural radioactivity measurements was developed by Latrouite *et al.* (1991). It allows reliable estimation of IP through measurement of radionuclides in the carapace of crustaceans sampled in a pre-moult phase. Sheehy *et al.* (1994) used lipofucin, a physiological marker present in the permanent tissues of crayfish (*Cherax quadricarinatus*) to determine their age. Lipofucin deposits are irregular yellow-fluorescing granules found in the post-mitotic tissues of senescing animals. They can be detected using fluorescence microscopy and quantified by image analysis.

It is difficult to draw general conclusions and compare results from these studies because of differences in both

sampling techniques, geographical origin of population, and ranges of sex and age in the data. However, specific problems are associated with each type of experiment. Hence, the growth rate of animals kept in captivity may not be comparable to that of wild populations, even within cages immersed *in situ*. Mark-recapture experiments require substantial sample sizes since the recaptured animals represent a very small fraction of the individuals tagged. With the exception of the technique of Shelton and Chapman (1995), mark-recapture experiments do not allow estimation of the number of moults between tagging and recapture.

Several models have been proposed to describe the dependence of both MI and IP upon pre-moult carapace length, for various crustacean species. The main models are summarized in Table 1. Wainwright and Armstrong (1993) compared some of these models, using different data sets on the growth of Dungeness crab (*Cancer magister*). They clearly favoured the bent-line model (Somerton, 1980) among models relating MI to pre-moult CL; a log-linear model (Mauchline, 1977) appeared to them to be the best to relate IP to CL. By contrast, Lovett and Felder (1989) did not recommend log-transformation of linear morphometric data when studying the relative growth of crustaceans, because it

may result in misinterpretation of the regression outcomes, while not improving significantly the regression fit compared with that produced by a regression based on untransformed data.

For Norway lobster, a linear relationship of post-moult CL with pre-moult CL (Hiatt, 1948) is the most commonly applied model. Kurata (1962) defined three different groups of crustacean's growth according to the value of the slope of the Hiatt equation: a regressive geometric growth if the slope is smaller than 1, an arithmetic growth if it is equal to 1 and a progressive geometric growth if it is larger than 1.

In the light of this typology, published results are to some extent contradictory concerning the growth type for Norway lobster. Some authors found a progressive growth for males (Thomas, 1965; Charuau, 1977) and females (Sarda, 1980; Thomas, 1965), meanwhile others found a regressive growth for males (Hillis, 1971; Sarda, 1980; Sarda, 1985) and females (Hillis, 1971; Charuau, 1977; Sarda, 1985). This variability may be explained by the different geographical origins of the populations or the sampling methods.

The main objective of this paper was to build a simple growth model in order to estimate the age of Norway lobsters from the bay of Biscay in relation to size. Firstly, we estimated: (1) MI parameters from *in situ* measurements obtained by Charuau (1977) and (2) IP from natural radioactivity measurements (Talidec and Reyss, 1993). A model describing the dependence of both MI and IP in relation to CL was fitted for males and females separately using regression and resampling methods. Secondly, parameter estimates were used to simulate individual growth trajectories, that were averaged in a last step to provide an age-length key.

Materials and methods

Moult increment

Data

An experiment was carried out in March and April 1977, during the peak moulting season of the spring (Charuau, 1977). Fifty-five males and 73 females in a pre-moult stage were sampled from the catch of a commercial vessel fishing in the bay of Biscay. Because pleopods change from pink to orange-yellow as moulting approaches, pre-moulting animals can easily be selected (Sarda, 1983). The CL of sampled animals were then measured, put in cages immersed at depths ranging from 60 to 80 m. After an immersion period of 24 days on average, cages were hauled and post-moult CL were measured to obtain MI. This type of experiment was done because a wide range of CL (between 20.5 and 45.5 mm) was sampled and it was carried out in the natural environment of Norway lobsters.

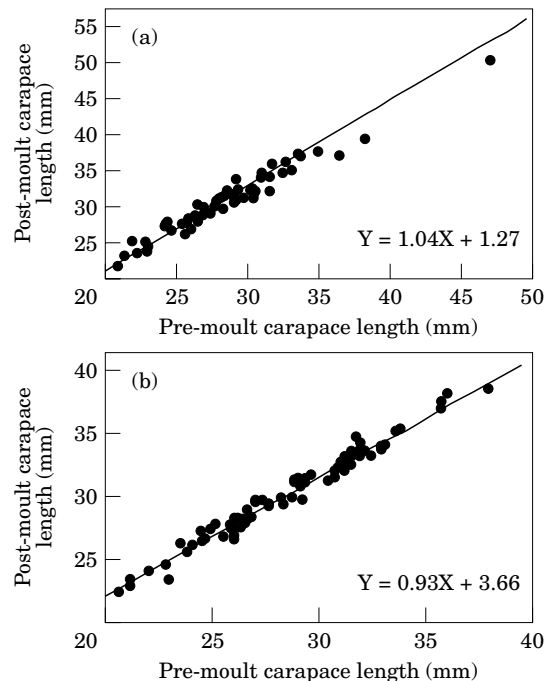


Figure 1. Fit of moult increment data by Least Trimmed Squares regression based on Equation (1), for Norway lobster (*Nephrops norvegicus*) (a) males and (b) females.

Model

Based on a plot of field data (Fig. 1), a simple regression of post-moult CL vs. pre-moult CL was found to be an appropriate linear regression model:

$$y_i^{(1)} = a^{(1)} + b^{(1)} x_i + \varepsilon_i \quad (1)$$

where x_i and $y_i^{(1)}$ are, respectively, pre-moult and post-moult CL for the i^{th} individual in the data set, $a^{(1)}$, $b^{(1)}$ are the regression parameters and ε_i is an error term assumed to be normally distributed as $N(0, \sigma^2)$. x_i values are supposed to be known without error.

Because the aim of this work is to predict MI as a function of pre-moult CL, we could consider a regression of MI vs. pre-moult CL:

$$y_i^{(2)} = y_i^{(1)} - x_i = a^{(1)} + b^{(2)} x_i + \varepsilon_i \quad (2)$$

where $y_i^{(2)}$ is the moult increment for the i^{th} individual, i.e. $y_i^{(1)} - x_i$, $a^{(1)}$ is the intercept (the same as in Equation (1), and $b^{(2)}$ is the slope, i.e. $b^{(1)} - 1$.

The two models differ substantially in the value of the coefficient of determination $R^2 = \Sigma(\hat{y}_i - \bar{y})^2 / \Sigma(y_i - \bar{y})^2$, R^2 being higher for model (1). This is due to the magnitude of the y values which are always close to the x ones in model (1), while in model (2), y values are considerably

smaller for adult individuals (Castro, 1990). Thus, model (1) was chosen to estimate the parameters.

Parameter estimation

The preliminary data examination evidenced several outliers. Rather than discard corresponding data (Charuau, 1977), a robust regression method was used to fit Equation (1) in order to downplay the effect of outliers. Among robust regression methods, the Least Trimmed Squares regression (LTS regression) introduced by Rousseeuw (1984), was chosen because it is robust not only with respect to outliers, but more generally to high leverage points, i.e. data points that are excessively influent on parameter estimates.

The difference between Ordinary Least Squared (OLS) regression and LTS regression lies in the fitting criterion. The estimate of the regression parameter $\hat{\beta}_{OLS}$ minimizes the sum of the squared residuals $\sum_{i=1}^n \hat{\epsilon}_{(i)}^2 \cdot \hat{\beta}_{OLS}$ lacks robustness because it may be excessively influenced by a single or a few observations. By contrast, $\hat{\beta}_{LTS}$ is the value which minimizes the sum of the q smallest squared residuals: $\sum_{i=1}^q \hat{\epsilon}_{(i)}^2$ where $\hat{\epsilon}_{(i)}$ is the i^{th} ordered residual. The value of q is often set to be slightly larger than $n/2$. As there is no analytical formula for its variance, it was estimated from a non-parametric bootstrap resampling procedure.

Intermoult period

Data

With reference to Bennett and Turekian (1984), Talidec and Reyss (1993) showed that intermoult duration could be estimated from the carapace ratio $^{228}\text{Th}/^{228}\text{Ra}$, these natural isotopes being present in the exoskeleton of marine crustaceans. The Thorium (^{228}Th) present in the exoskeleton is produced by the disintegration of ^{228}Ra according to the law:

$$A\text{Th}/A\text{Ra} = 1.496[1 - \exp(-0.2426t)] \quad (3)$$

where $A\text{Th}/A\text{Ra}$ is the ratio of Thorium activity to Radium activity, and t is the time elapsed since Radium absorption started so, since the last moult. Thus, measuring this ratio in a carapace allows to determine IP (Latrouite *et al.*, 1991), provided that sampled animals are ready to moult, and several assumptions are satisfied (Le Foll *et al.*, 1989).

The activities of both Thorium and Radium are measured by γ spectrometry. The measurement error tied to the estimation of the ratio is due to the radioactivity counter; it corresponds to a coefficient of variation of 15% (Le Foll *et al.*, 1989).

This method was applied to Norway lobsters living on the muddy bottom in the north of the bay of Biscay, which were sampled among commercial landing during the spring and autumn periods of moult in 1991, 1992,

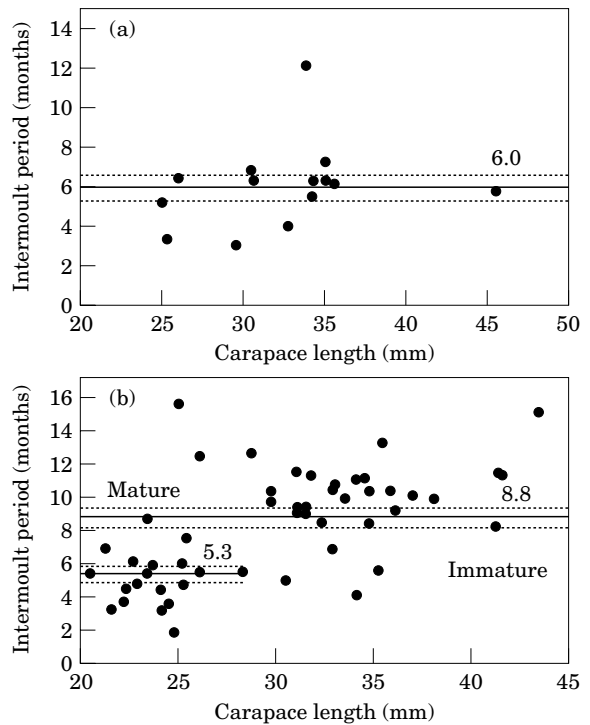


Figure 2. Estimation of the mean intermoult period and the associated standard error for Norway lobster (*Nephrops norvegicus*) (a) males and (b) mature females and immature females. Dotted lines indicate the 90% confidence interval around the mean. Corresponding estimates are found in Table 2.

and 1993. Animals in the latest pre-moult stage were selected and measured, and the age of the carapace was obtained inverting Equation (3):

$$t = -4.122 \times \text{Ln}(1 - 0.668 \times A\text{Th}/A\text{Ra}) \quad (4)$$

Fourteen males were sampled in April 1991 and 1992, and 51 females were sampled in February 1991 and 1992, August and September 1992, and February and March 1993 (Talidec and Reyss, 1993). Carapace length ranged between 20.6 and 46.9 mm.

Model

In relation with the different moulting features exhibited by male and female Norway lobsters, data were analysed separately for each sex. Data showed (Fig. 2a) that a constant relationship between IP and CL is adequate to model the data for males. This was corroborated by fitting the non-linear model used by Castro (1992) (Table 1) which led to a non-significant slope. Thus, IP was assumed to follow a normal distribution $N(\bar{t}_M, s_M^2)$ where \bar{t}_M and s_M^2 are the sample mean and the sample variance, respectively.

For females, it was necessary to distinguish between mature and immature individuals. Data showed (Fig. 2b) that a model in two pieces with constant but distinct IP for mature and immature animals was an acceptable model. However, parameter estimation had to account for the proportion of mature individuals at a given length. Thus, individual data were assigned weights, using the maturity curves of female Norway lobsters obtained by Morizur (1980):

$$p_i = 100/[1 + \exp(-1.01CL_i - 23.75)] \quad (5)$$

where p_i and CL_i are, respectively, the proportion of mature individuals and the carapace length, for the i^{th} length group.

On average, 100% of the females are mature at a CL of 29 mm, while 50% are mature at 23.515 mm (denoted L_{50}) and none is mature at 18 mm.

Two weighted means were calculated, one for mature females (\bar{t}_{MF}) where the weight of an individual of CL_i is p_i , and the second one for immature females (\bar{t}_{IF}) where the weight of an individual of CL_i is $(1 - p_i)$, yielding:

$$\begin{aligned} \bar{t}_{MF} &= \sum p_i t_i / \sum p_i \\ \bar{t}_{IF} &= \sum (1 - p_i) t_i / \sum (1 - p_i) \end{aligned} \quad (6)$$

Associated variances, s_{MF}^2 and s_{IF}^2 were calculated in a similar way.

Parameter estimation

The estimates of the mean and variance of IP for both males, mature females, and immature females had to account for uncertainties on initial data. These were due to true measurement error linked to the gamma radioactivity counter. As the ratio ATh/ARA is an exponential function of carapace age [Equation (3)], a gaussian measurement error on this ratio, results in an uncertainty on IP that is larger for large values of carapace age. In addition, it is skewed to the right due to the asymptote in Equation (4) (Fig. 3).

Measurement error was incorporated using a parametric bootstrap procedure. Sampling variability also had to be taken into account because sample sizes were rather small, in particular for males. A non-parametric bootstrap procedure was used for this purpose.

Two-thousand independent replicates of IP data were drawn with replacement and equal probabilities for each IP data in the initial sample (Fig. 4). For each data resampled, associated activity ratio ATh/ARA was calculated according to Equation (3). To take into account measurement error this ratio was added a random error following a normal probability distribution function (PDF) with mean 0 and variance $0.15ATh/ARA$ based on the estimation made by Le Foll et al. (1989). Using Equation (4), the resulting IP was back-calculated. For each replicate, a set of IP data incorporating both measurement error and sampling variability was

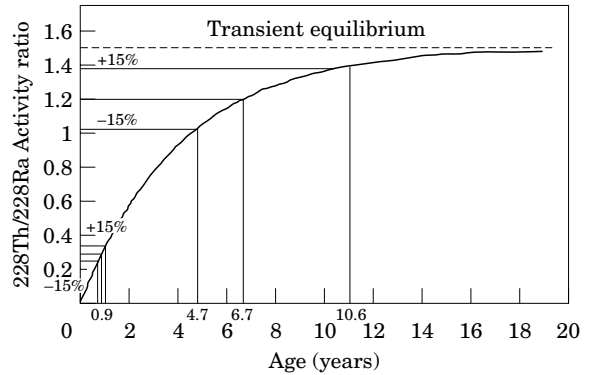


Figure 3. Change in Activity ratio of ^{228}Th to ^{228}Ra with time, for Norway lobster (*Nephrops norvegicus*). This curve shows the disymmetrical confidence interval around age values. For instance a CV of 15% around an activity ratio of 1.2 gives an age of 6.7 years with a 95% confidence interval [4.7, 10.6].

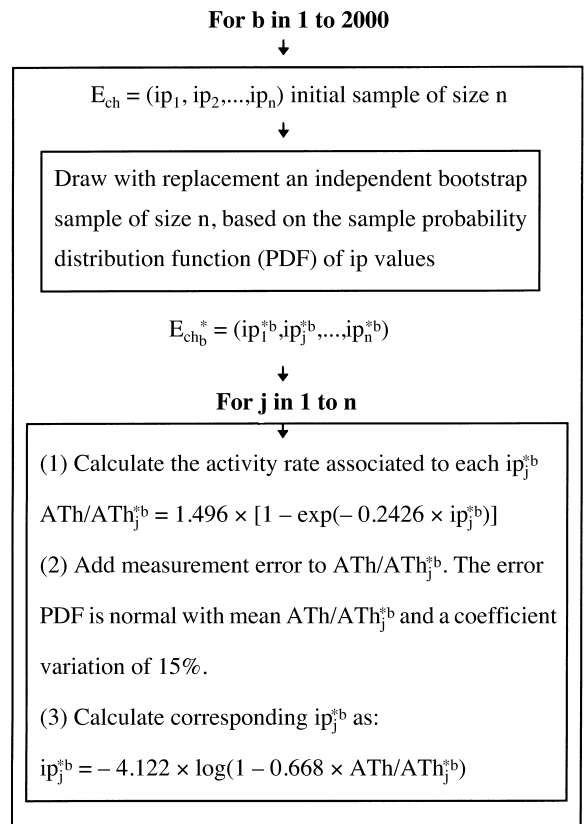


Figure 4. Flow-chart of the bootstrap procedure used for estimating the intermolt period while accounting for both measurement error and sampling variability.

obtained and provided an estimation of mean IP in the replicate. Bootstrap statistics were finally computed over the 2000 estimates, i.e. mean IP, associated variance and a confidence interval for mean IP.

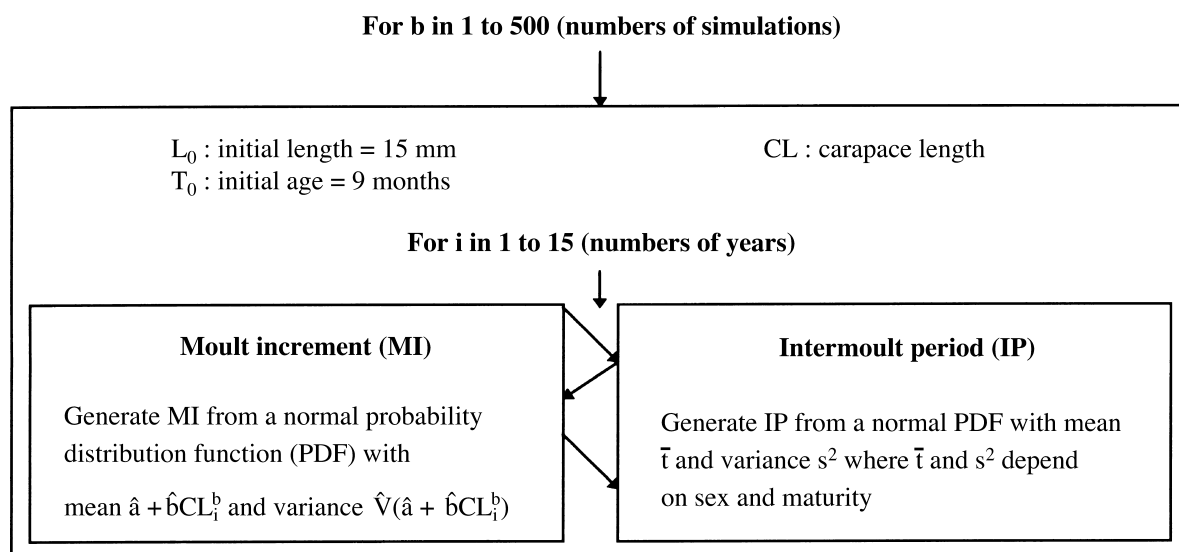


Figure 5. Flow-chart for growth simulations. Simulations were achieved separately for Norway lobster (*Nephrops norvegicus*) males and females.

Growth simulation

Individual growth trajectories were simulated as a sequence of MI and IP, based on estimates of these parameters with corresponding estimation error. Simulations started at the age of recruitment, i.e. 9 months, which corresponds to a pre-moult CL of $L_0=15$ mm for both males and females (Conan, 1978a). Simulations began with the first moult of the juvenile stage.

At each moult, MI was predicted from pre-moult CL, using Equation (2) with parameters estimated from the bootstrap procedure described earlier. Moult increment was thus assumed to follow a normal PDF of mean \hat{y}_{mi} and variance $\hat{V}(\hat{y}_{mi})$ where estimated $\hat{V}(\hat{y}_{mi})$ is the prediction variance in a regression, i.e.:

$$\hat{V}(\hat{y}_{mi}) = \hat{V}(\hat{a} + \hat{b}x_i) = x_i^2 \hat{V}(\hat{a}) + \hat{V}(\hat{b}) + 2Cov(\hat{a}, \hat{b})x_i \quad (7)$$

where $Cov(\hat{a}, \hat{b}) = \sigma^2 [-x / \sum (x_i - \bar{x})^2]$ is an estimate of the covariance between \hat{a} and \hat{b} .

A value of MI was generated based on that PDF and being added to pre-moult CL to yield post-moult CL (Fig. 5). After this moult, the IP was also randomly generated to account for estimation error. For males, it was assumed to follow a normal PDF with expectation \bar{t}_M and variance s_M^2 . For females smaller than L_{50} , i.e. 23.5 mm, IP was assumed to follow a normal PDF $N(\bar{t}_{IF}, s_{IF}^2)$, whereas for larger females, it was assumed to follow a normal PDF $N(\bar{t}_{MF}, s_{MF}^2)$.

Each curve was generated for a minimum period of 15 years, which is the estimated lifespan of the species. Five-hundred growth curves were simulated in order to compute reliable statistics. The percentile method (Efron, 1982) was used to obtain 5, 50, and 95%

percentiles. Two sets of percentiles were calculated, for predicting length from age and for predicting age from length (Fig. 6).

Results

Parameter estimates

Moult increment fits by LTS regression showed positive slopes for males and females, indicating that MI increases with the animal size (Table 2). This increase was less marked for females (slope of 0.93 for females vs. 1.04 for males). The standard error of intercept was higher for males. For IP (Table 3), the estimate for males was 6.0 months compared to 8.8 months for mature females. The IP of mature females was shorter than expected, even considering the variance around that estimate, since they are indeed expected to moult once a year. For immature females, the IP estimate was 5.3 months, which are slightly smaller than expected. Results evidenced that the measurement error used in the estimation of IP did not affect the mean parameter estimates and did not increase variances too much. For males, the estimate of variance was relatively higher due to the small sample size (14 observations).

Simulation

The average numbers of moults per year since recruitment were 19.4 and 15.2 for 10-year-old males and females, respectively (Table 4). Percentiles (5%, 50%, 95%) were reported in Table 4. Although the time interval used in the computations of length–age key was

For b in 1 to 500 (number of simulations)

Age-length key	Length-age key
<p>(1) Discretize carapace length (CL) into 5 mm intervals. Denote CL_i the lower bound of the i^{th} interval.</p> <p>(2) For each individual curve b and each interval i :</p> <p style="padding-left: 40px;">if CL_i corresponds to an intermoult period, associated age T_i^b is set to the mean of ages in previous and subsequent moults;</p> <p style="padding-left: 40px;">if CL_i corresponds to a moult, associated age T_i^b is corresponding age at moult.</p>	<p>(1) Discretize age T into 1-month intervals. Denote T_i the lower bound of the i^{th} interval.</p> <p>(2) For each individual curve b and each interval i :</p> <p style="padding-left: 40px;">if T_i corresponds to a moult, associated CL_i^b is set to the mean of pre-moult and post-moult CL;</p> <p style="padding-left: 40px;">if T_i corresponds to an intermoult period, CL_i^b is corresponding CL.</p>
<p>For each CL_i, determine the 5, 50, and 95% percentiles $T_i^{5\%}$, $T_i^{50\%}$, $T_i^{95\%}$ and mean number of moults since recruitment.</p>	<p>For each T_i, determine the 5, 50, and 95% percentiles $CL_i^{5\%}$, $CL_i^{50\%}$, $CL_i^{95\%}$ and mean number of moults since recruitment.</p>

Figure 6. Procedure to calculate length-age and age-length keys from the results of the simulations, for Norway lobster (*Nephrops norvegicus*).

Table 2. Parameter estimates for the fit of post-moult carapace length (CL) vs. pre-moult CL for Norway lobster (*Nephrops norvegicus*), based on a Least Trimmed Squares linear regression.

	Regression parameters		Standard error		Coefficient variation	
	Sample	Bootstrap	Sample	Bootstrap	Sample	Bootstrap
Males						
Intercept	-1.74	1.27	—	3.70	—	2.913
Slope	1.16	1.04		0.14		0.135
Females						
Intercept	3.49	3.66	—	1.24	—	0.339
Slope	0.93	0.93		0.05		0.054

the month, results were reported at the year scale, only retaining January estimates for sake of concision (Table 4). The mean number of moults per CL interval experienced since recruitment was also calculated. Growth of males appeared to be faster than females (Fig. 7), which can be explained by the slower growth of females after maturity.

Due to a faster growth for males, simulated CL soon exceeded the range of observed CL values leading to substantial variability in growth curves for large sizes. In addition, estimation error on MI was substantially higher for males compared to females (Table 2), enhancing this variability. As a consequence, the values of $CL_{5\%}$, $CL_{50\%}$, and $CL_{95\%}$ obtained for males older than

Table 3. Parameter estimates for intermoult period, for Norway lobster (*Nephrops norvegicus*). CV: coefficient of variation.

Intermoult period	Observed			Bootstrap with measurement error		
	Mean (t)	Standard error (s ²)	CV	Mean (t)	Standard error (s ²)	CV
Males \bar{t}_M	5.97	0.58	0.097	6.02	0.63	0.105
Mature females \bar{t}_{MF}	8.80	0.32	0.036	8.75	0.55	0.063
Immature females \bar{t}_{IF}	5.39	0.31	0.057	5.32	0.48	0.090

11 years should be taken with caution. For females, the values of $T_{5\%}$, $T_{50\%}$, and $T_{95\%}$, were not reported because they exceed substantially the estimated lifespan of the species.

Discussion

Estimates of MI and IP

The first contribution of this work is to estimate IP in relation to sex and CL from radiometric data for the Norway lobster population from the bay of Biscay. Although the average number of moults per year is known to be equal to two for males and immature females and one for mature females, individual variability around the average value had to be estimated. This was achieved by a double bootstrap which includes a parametric procedure to account for true measurement error on IP; and a non-parametric procedure to account for sampling variability which depends on sampling size and individual growth variability.

With the exception of the IP for mature females, parameters estimates of MI and IP corroborate with estimates from different geographical origins (Sarda, 1995). However, the data used to estimate MI were all sampled in March, so that it is difficult to know whether results might be extrapolated to the autumn moult. One might for instance suspect seasonal changes in growth due to differences in sea temperature. With respect to IP, males were found to moult twice a year which agreed with previous studies. By contrast, the mean IP estimate of 8.8 months for mature females, and to a lesser extent, that of 5.4 months for immature females do not really match the values one can expect from prior knowledge, i.e. 12 months for mature females, and 6 months for immature females. This might be due to the sampling scheme for obtaining radiometric data. Norway lobsters had to be sampled during moult periods to maximize the probability of finding individuals ready to moult. However, the beginning and the end of these periods are difficult to determine (Conan, 1978a), and may vary from year-to-year. In the data analysed, all males were sampled in Spring, and most females were sampled in

February and March, i.e. at the beginning of the moult period. But, animals sampled at the beginning of the moult period were likely to exhibit shorter IP compared to those that could be sampled at the end of that period. Thus, it would be preferable to sample the entire moult periods, i.e. spring for males and females and autumn for males and immature females, e.g. all the females caught in autumn were immature (CL < 25 mm) and showed IP smaller than 6 months. Ideally, the sampling scheme should be stratified according to the months of the moult period with sampling rates per strata proportional to moulting probabilities. Such a design is unfortunately impossible due to the cost of sampling and radiometric measurements.

Note finally that both initial data and parameter estimates evidenced a substantial individual variability. For instance, a female of 24.8 mm had a 1.9 months IP, and at the other extreme a IP of 12.1 months was observed for one male of 33.8 mm. Indeed, it seems that some individuals might occasionally skip moult, for instance because of hormonal disfunctioning, which could explain outlying IP values. Conversely, females that were not berried in spring may moult in autumn.

Growth curve and age-length key

A growth curve was simulated to mimic the growth process of crustaceans, i.e. the succession of moults and intermoult periods. The simulation explicitly incorporated estimation error allowing to compute nonparametric confidence intervals for an age-length key. These results might be compared to Castro's (1990) growth curves, although the latter were simulated in a deterministic way. Castro found an average number of moult since recruitment of 18 for males and 15 for females, at age 10, which agrees with our values of 19.4 and 15.0. Simulation results stressed the high level of individual growth variability for the Norway lobster population from the bay of Biscay. The width of confidence intervals was found to increase with CL, as a result of prediction error. Indeed IP and MI parameters were estimated from datasets where the CL ranged between 20 and 50 mm. Prediction error was hence larger for CL

Table 4. Estimates obtained from statistics based on simulated growth curves, for Norway lobster (*Nephrops norvegicus*): age-length key (left) and length-age key (right). The mean number of moults since recruitment is reported for each carapace length (CL) (left) and for each age (right). Results for length-age key correspond to January estimates.

Carapace length (mm)	Age-length key						Length-age key									
	Males		Females		Males		Females		Males		Females					
	Mean number of moults	T _{5%}	T _{50%}	T _{95%}	T _{5%}	T _{50%}	T _{95%}	Mean number of moults	Age (years)	Mean number of moults	CL _{5%}	CL _{50%}	CL _{95%}			
5	—	—	—	—	—	—	—	—	—	—	—	—	—			
10	—	—	—	—	—	—	—	—	—	—	—	—	—			
15	1.0	0.75	0.75	0.75	0.75	0.75	0.75	2.0	1	1.4	15.3	18.0	21.5	18.8	20.0	21.1
20	2.9	1.35	1.96	2.71	1.26	1.65	1.86	4.0	2	3.4	18.8	22.7	26.6	23.1	24.4	25.6
25	5.0	2.11	3.00	4.02	2.18	2.89	3.16	5.7	3	5.4	22.6	27.2	32.0	26.1	27.8	29.1
30	7.1	3.19	4.03	5.06	4.26	4.75	5.30	7.0	4	7.4	27.0	32.2	37.5	28.8	30.0	31.1
35	9.1	4.02	5.03	6.10	6.48	7.26	8.10	8.2	5	9.4	32.0	37.6	44.4	30.7	31.8	33.4
40	10.8	4.89	5.89	7.18	9.20	10.3	11.8	9.8	6	11.4	36.5	43.9	53.2	32.9	34.3	35.6
45	12.4	5.57	6.64	8.10	12.2	14.0	16.1	11.0	7	13.4	41.6	51.5	67.3	34.6	35.9	37.3
50	13.6	6.07	7.26	8.88	15.4	18.0	20.6	12.4	8	15.4	46.7	61.3	82.0	36.0	37.6	39.3
55	14.8	6.62	7.86	9.60	18.8	21.8	25.2	13.9	9	17.4	54.5	74.1	102.5	37.6	39.3	41.0
60	15.9	7.01	8.40	10.1	—	—	—	15.2	10	19.4	63.2	89.0	130.5	38.8	40.5	42.7
								16.6	11	—	—	—	—	40.0	42.1	44.4
								18.0	12	—	—	—	—	41.2	43.4	46.0
								19.3	13	—	—	—	—	42.3	44.6	47.5
								20.7	14	—	—	—	—	43.4	46.1	49.1
								22.1	15	—	—	—	—	44.3	47.3	50.5

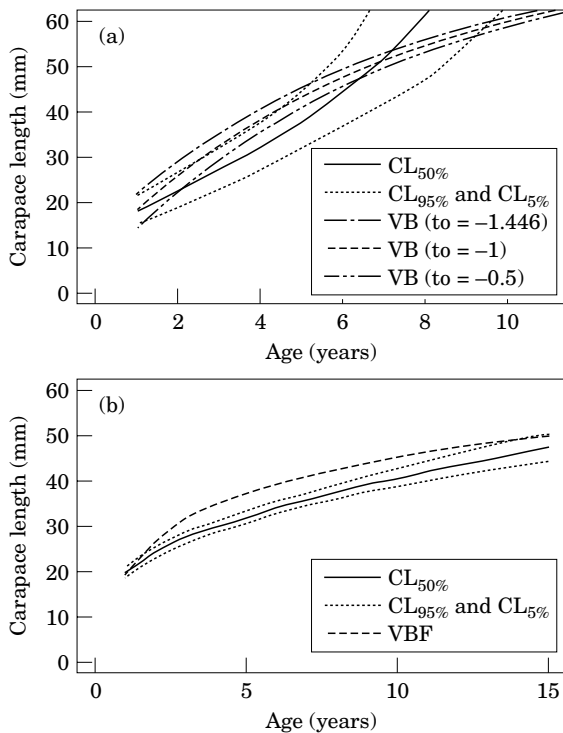


Figure 7. Length-age key obtained from the simulations, for Norway lobster (*Nephrops norvegicus*) with 5, 50, and 95% percentiles and von Bertalanffy's growth curves already used in the literature for (a) males (VB) and (b) mature and immature females (VBF) with parameters as follows: $K=0.14$ per year and $L_{\infty}=76$ mm for males and immature females, and $K=0.11$ per year and $L_{\infty}=56$ mm for mature females. The two curves for mature and immature females are merged as described in ICES (1994). For males three values of t_0 are hypothesized ($t_0 = -1.1446$ year, $t_0 = -1$ year and $t_0 = -0.5$ year).

beyond 50 mm. This was even more striking for males, because of their faster growth. The simulations for large animals should be taken cautiously. Indeed, growth parameters may change beyond a certain age, because they rely on the assumption that for males, IP is constant with size, the mean IP being estimated from the sample. Because the range of observed size values is limited, it would be unrealistic to extrapolate the simulation beyond the largest size observed. Indeed, empirical studies on many crustaceans species suggest that moult frequency is lower at larger sizes. Conan (1978a) noted that the largest Norway lobsters measured had a CL of 85 mm. However, for the purpose of obtaining age-length keys for stock assessments, this might have little consequences, as data were collected on commercial trawlers the size range reflected the size structure of the stock and the impact on stock assessment of uncertainty on the growth of old individuals is downplayed by their scarcity in the stock.

This age-length key might be used in assessments of Norway lobster. The current procedure is based on slicing length compositions to obtain age compositions using von Bertalanffy's growth curves (ICES, 1994). For males, the parameter estimates used are equal to $K=0.14$ per year and $L_{\infty}=76$ mm, whereas for females, the growth curve is built from two pieces (method described in ICES, 1994), one below size at maturity (same parameters as for males) and one above where $K=0.11$ per year and $L_{\infty}=56$ mm (ICES, 1994) (Fig. 7b). Three values of t_0 are hypothesized for males ($t_0 = -1.446$ year, $t_0 = -1$ year, and $t_0 = -0.5$ year) (Fig. 7a) because the choice of an adequate value for t_0 is considered as problematic by the assessment group (ICES, 1994, p. 5). However, the age compositions resulting from slicing are quite sensitive to t_0 . Our results circumvent this problem. For females, predicted lengths are slightly smaller than the von Bertalanffy's predictions but roughly consistent (Fig. 7b). For males, the shape of the von Bertalanffy's predictions differ from our mean predicted lengths. However the von Bertalanffy's predictions are roughly included in our confidence interval (Fig. 7a).

How to measure crustacean growth?

Two types of data were used in this study. Measurements to estimate MI were carried out on wild animals kept in immersed cages (Charuau, 1977). Although such measurements were done in the natural environment of Norway lobsters, there were some mortality or perturbations due to handling: 55 out of 306 males, and 73 out of 197 females effectively moulted, which means that the course of moulting might have been affected by the experiment. On the other hand, radiometric data provided reliable measurements of IP. Rather than combine the results of two distinct experiments, it would be interesting to use the tagging technique described by Shelton and Chapman (1995) in order to obtain all the information required for growth studies from a single experiment. However, this technique is highly demanding in handling efforts during both tagging and recapture. An alternative technique is that of Sheehy *et al.* (1994), which uses the pigment lipofuscin as an indicator of age. This method was first experimented on crayfish, *Cherax quadricarinatus*, but an ongoing research programme aims at adapting it to Norway lobsters (European Fisheries, 1998). However, lipofuscin accumulates as a function of physiological rather than chronological age, so that the measure depends on metabolic rates and thus on temperature regimes and diet. Unlike fish otoliths, lipofuscin is an indirect measure of age, which has to be correlated to real age.

Conclusion

As illustrated in the introduction, Norway lobster growth has been extensively studied to date. The first

aim of this work was to estimate growth parameters from existing data (Charuau, 1977; Talidec and Reyss, 1993), bringing together measurement errors and sampling variability, which in this case was mostly due to individual variability. Secondly, growth curves were simulated for each sex separately in a way that mimics reality. Estimations and simulations were based on bootstrap procedures. The resulting age-length keys incorporate both individual growth variability and measurement error. They could be used in assessments of Norway lobster as an alternative to the continuous growth curves currently used which do not reflect the growth process of Norway lobster. However, further simulations are needed to be able to convert length-frequency distribution into age distribution and evaluate the implications for stock assessment.

Lastly, current assessments of Norway lobster rely on models at an annual scale. Because of the rapid growth of Norway lobsters, models that are more desegregated in time might prove useful. Should this type of model be used, our simulations yield an age-length key at the scale of the month or possibly the quarter. Finally, Deriso and Parma (1988) showed that individual variability in growth may lead to biased assessments. Our results provide an age-length key with confidence intervals and possibly other measures of variance, that might be accounted for in appropriate assessment models.

References

- Andersen, F. S. 1962. The Norway lobster in Faeroe Waters. Meddelelser fra Danmarks Fiskeriog Havundersogelser, 3(9): 265–326.
- Bennett, J. T., and Turekian, K. K. 1984. Radiometric ages of brachyuran crabs from the Galapagos spreading-center hydrothermal ventfield. Limnology Oceanography, 29: 1088–1091.
- Bertalanffy, L. von 1938. A quantitative theory of organic growth. Human Biology, 10: 181–213.
- Castro, M. 1990. The use of length frequency analysis for estimation of the age structure of the catch of *Nephrops norvegicus*. University of Rhode Island, PhD Thesis. 425 pp.
- Castro, M. 1992. A methodology for obtaining information on the age structure and growth rates of the Norway Lobster, *Nephrops norvegicus* (L.) (Decapoda, Nephropoidea). Crustaceana, 63(1): 29–43.
- Castro, M. 1995. Use of length-frequency analysis for estimating the age structure of the catch of *Nephrops norvegicus* (Crustacea:Nephropidae). ICES Marine Science Symposium, 199: 301–309.
- Charuau, A. 1975. Croissance de la langoustine sur les fonds de Sud-Bretagne. ICES CM 1975/K:11, 15 pp.
- Charuau, A. 1977. Essai de détermination du taux d'accroissement à la mue de la langoustine dans le milieu naturel. ICES CM 1977/K:25, 6 pp.
- Charuau, A., and Conan, G. 1977. Growth at moult of Norway lobsters: methods of assessment, sexual dimorphism and geographic trends. ICES CM 1977/K:34, 25 pp.
- Conan, G. Y. 1975. A growth model for *Nephrops norvegicus* from Biscay bay in function of periodicity of moult. ICES CM 1975/K:10, 21 pp.
- Conan, G. Y. 1978a. Life history, growth, production and biomass modelling of *Emerita analoga*, *Nephrops norvegicus*, and *Homarus vulgaris* (Crustacea, Decapoda). Ph.D. Thesis, University of California, San Diego, USA. 349 pp.
- Conan, G. Y. 1978b. Moulting rhythms and time interval between moults in a *Nephrops norvegicus* population. ICES CM 1978/K:20, 18 pp.
- Curry, G. L., and Feldman, R. M. 1987. Mathematical foundations of population dynamics. Texas A&M University Press, College Station, Texas. 246 pp.
- Deriso, R. B., and Parma, A. M. 1988. Dynamics of age and size for a stochastic population model. Canadian Journal of Fisheries and Aquatic Sciences, 45: 1054–1068.
- Easton, M. D. L., and Misra, R. K. 1988. Mathematical representation of Crustacean growth. Journal du Conseil international pour l'Exploration de la Mer, 45(1): 61–72.
- Efron, B. 1982. The jackknife, the bootstrap, and other resampling plans. Society for Industrial and Applied Mathematics, Conference Board of the Mathematical Sciences-National Science Foundation Monography, 38: 92 pp.
- European Fisheries 1998. The use of the age pigment lipofuscin as an indicator of age in *Nephrops*. Available online at: <http://www.marsource.maris.int.research/FAR/3/0-0651.html>
- Farmer, A. D. 1973. Age and growth in *Nephrops norvegicus* (Decapoda: Nephropidae). Marine Biology, 23: 315–325.
- Figueiredo, M. J. De 1979. Artificial culture of *Nephrops norvegicus* (L.). II – Some studies on the growth of early post-larvae of *Nephrops norvegicus* (L.), reared from the eggs. Boletim do Instituto Nacional de Investigação das Pescas, Lisboa (1), maio, 1979: 13–23.
- Figueiredo, M. J. De 1989. Preliminary results of the tagging experiments on *Nephrops norvegicus* in Portuguese waters. ICES CM 1989/K:25, 15 pp.
- Hiatt, R. W. 1948. The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. Pacific Science, 2: 135–213.
- Hillis, J. P. 1971. Growth studies on *Nephrops*. ICES CM 1971/K:2, 6 pp.
- Hillis, J. P. 1972a. Further growth studies on *Nephrops norvegicus*: growth in captivity. ICES CM 1972/K:27, 3 pp.
- Hillis, J. P. 1972b. Further growth studies on *Nephrops norvegicus*: studies of length frequency modes. ICES CM 1972/K:28, 6 pp.
- Hillis, J. P. 1973. Continued growth studies on captive *Nephrops norvegicus*. ICES CM 1973/K:27, 5 pp.
- Hillis, J. P. 1974. Observations on the growth of *Nephrops norvegicus*. ICES CM 1974/K:8, 3 pp.
- Hillis, J. P. 1979. Growth studies on the Prawn *Nephrops norvegicus*. Rapports et Procès-Verbaux des Réunions du Conseil international pour l'Exploration de la Mer, 175: 170–175.
- ICES 1994. Report of the Working Group on *Nephrops* and *Pandalus* Stocks. ICES Doc. C.M. 1994/Assess:12.
- Kurata, H. 1960. Increase in size at moulting in crustacea. Bulletin of the Hokkaido Regional Fisheries Research Laboratory, 22: 1–48.
- Kurata, H. 1962. Studies on the age and growth of Crustacea. Bulletin of the Hokkaido Regional Fisheries Research Laboratory, 24: 1–115.
- Latrouite, D., Talidec, C., Reyss, J. L., and Noël, P. 1991. New data on the growth of the Norway lobster from the bay of Biscay (*Nephrops norvegicus*) by measurements of the $^{228}\text{Th}/^{228}\text{Ra}$ carapace ratio. ICES CM 1991/K:39, 8 pp.
- Le Foll, D., Bricchet, E., Reyss, J. L., Lalou, C., and Latrouite, D. 1989. Age determination of the Spider crab *Maja squinado* and the European lobster *Homarus gammarus* by $^{228}\text{Th}/^{228}\text{Ra}$ chronology: possible extension to others crustaceans. Canadian Journal of Fisheries and Aquatic Sciences, 46: 720–724.

- Lovett, D. L., and Felder, D. L. 1989. Application of regression techniques to studies of relative growth in Crustaceans. *Journal of Crustacean Biology*, 9(4): 529–539.
- Mauchline, J. 1976. The Hiatt growth diagram for Crustacea. *Marine Biology*, 35: 79–84.
- Mauchline, J. 1977. Growth of shrimps, crabs and lobsters – an assessment. *Journal du Conseil international pour l'Exploration de la Mer*, 37(2): 162–169.
- Morizur, Y. 1980. Reproduction des langoustines (*Nephrops norvegicus*) dans la région Sud Bretagne. Thèse de troisième cycle, Université Paris, 6: 115 pp.
- Mytilineou, C., and Sarda, F. 1995. Age and growth of *Nephrops norvegicus* in the Catalan Sea, using length-frequency analysis. *Fisheries Research*, 23: 283–299.
- Nicholson, M. D. 1979. The use of length frequency distributions for age determination of *Nephrops norvegicus* (L.). *Rapports et Procès-Verbaux des Réunions du Conseil international pour l'Exploration de la Mer*, 175: 176–181.
- Rousseeuw, P. J. 1984. Least Median of squares regression. *Journal of the American Statistical Association*, 79: 871–880.
- Sarda, F. 1980. Age, croissance et fréquence de mue chez *Nephrops norvegicus* (L.) dans la mer Méditerranée (N.E. de l'Espagne). *ICES CM 1980/K:16*, 15 pp.
- Sarda, F. 1983. Determinación de los estados de intermuda en *Nephrops norvegicus* L., mediante la observación de los pleopodos. *Investigaciones Pesqueras, Barcelona*, 47(1): 95–112.
- Sarda, F. 1985. Estudio de la edad, crecimiento y frecuencia de muda, en cautividad, de *Nephrops norvegicus* (L.) del mar Catalán. *Investigaciones Pesqueras, Barcelona*, 49(2): 139–154.
- Sarda, F. 1995. A review (1967–1990) of some aspect of life history of *Nephrops norvegicus*. *ICES Marine Science Symposium*, 199: 78–88.
- Sheehy, M. R. J., Greenwood, J. G., and Fielder, D. R. 1994. More accurate chronological age determination of crustaceans from field situations using the physiological age marker, lipofucin. *Marine Biology*, 121: 237–245.
- Shelton, P. M. J., and Chapman, C. J. 1995. A moult recording tag for lobsters: Fields trials. *ICES Marine Science Symposium*, 199: 222–230.
- Somerton, D. A. 1980. Fitting a straight line to Hiatt growth diagrams: a re-evaluation. *Journal du Conseil international pour l'Exploration de la Mer*, 39: 15–19.
- Talidec, C., and Reyss, J. L. 1993. Determination of the inter-individual growth variability of the Norway lobster from the bay of Biscay (*Nephrops norvegicus*) by measurement of the $^{228}\text{Th}/^{228}\text{Ra}$ carapace ratio. *ICES CM 1993/K:28*, 11 pp.
- Thomas, H. D. 1965. The growth of Norway lobster in aquaria. *Rapports et Procès-Verbaux des Réunions du Conseil international pour l'Exploration de la Mer*, 156: 209–216.
- Wainwright, T. C., and Armstrong, D. A. 1993. Growth patterns in the dungeness crab (*Cancer magister* Dana). Synthesis of data and comparison of models. *Journal of Crustacean Biology*, 13(1): 36–50.
- Wilder, D. G. 1953. The growth rate of the American lobster (*Homarus americanus*). *Journal of the Fisheries Research Board of Canada*, 10: 371–412.