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Methodological considerations concerning the use of length frequency analysis for growth studies in the Norway lobster, *Nephrops norvegicus* (L.)

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SUMMARY: The structure of length distributions of *Nephrops norvegicus* was investigated in order to understand the adequacy of length frequency analysis for estimation of growth rates and growth parameters. Samples from two areas were used: the Atlantic Ocean off the South coast of Portugal and the Euboikos Gulf in the Mediterranean. Monthly samples were obtained from October 1993 to October 1995. For each area, month and sex, the samples were analyzed using the program MIX in order to identify the mean length for each of the groups composing the length distributions. The mean values were used to estimate increments between consecutive groups within the same sample. Biological information extracted from the same samples and referring to maturation and molting cycles, was used in conjunction with the mean values estimated in this work to interpret modal progression and growth rates. Results show that modal progression analysis is not appropriate because the modes do not progress in a manner that allows the following of a particular group. Growth rates based on increments verified within each sample were also investigated. This approach proved to be better, although there were still some problems due to large year to year variability and the fact that the magnitude of the increments did not decrease with increasing size. This also poses problems regarding the fitting of growth curves to these data; in particular when deceleration of growth is required, as in the case of the von Bertalanffy growth curve.

Key words: Length-frequency-analysis, *Nephrops norvegicus,* growth, age estimation, decapods.

RESUMEN: Consideraciones metodológicas sobre el análisis de la frecuencia de tallas en el estudio del crecimiento de la cigala *Nephrops norvegicus* (L.). – Se estudia la estructura de la distribución de tallas de la cigala, *Nephrops norvegicus* con el fin de comprender si la estimación de las tasas y parámetros de crecimiento, por medio del análisis de las frecuencias de tallas, es adecuado. Se usaron muestras mensuales desde octubre de 1993 a octubre de 1995 procedentes de dos áreas, una del Atlántico (costa sur de Portugal) y la otra del Golfo de Euboikos (en Grecia). Por cada área se estudió el crecimiento por sexo y mes mediante el programa MIX, para identificar la talla media de los grupos en que se descompone la frecuencia de tallas. Estos valores medios se utilizaron para estimar los incrementos entre grupos consecutivos dentro de cada muestra. Con el fin de hacer la interpretación del proceso de crecimiento con la máxima información biológica posible, paralelamente se tuvo en cuenta el momento de la maduración en las tallas y el espectro de los ciclos de muda. Los resultados muestran que el análisis de la progresión modal no es adecuado para el estudio de crecimiento en la cigala, ya que las modas no progresan de manera que puedan seguirse en el tiempo para un grupo particular. Por otro lado se estudiaron las tasas de crecimiento basadas en los incrementos verificados dentro de cada grupo. Esta segunda aproximación resultó ser la mejor, a pesar de persistir algunos problemas debidos a la variabilidad observada entre años y al hecho de que la magnitud de los incrementos no decrece con el aumento de talla. Esto también conlleva problemas relativos al ajuste de las curvas de crecimiento sobre estos datos; en particular cuando se requiere contemplar la desaceleración de crecimiento, como es el caso de la utilización de la curva de crecimiento de von Bertalanffy.

Palabras clave: Análisis de frecuencia de tallas, *Nephrops norvegicus,* crecimiento, estimación de edad, decápodos.

INTRODUCTION

The sensible exploitation of a marine living resource requires some basic information that can be used to evaluate the condition of the resource and the management strategies to apply. Part of this information is of a biological nature, such as the estimation of mortality and growth rates.

Growth curves are the most common form of expressing growth rates in models used in stock assessment. Growth curves express the average growth rate of a population and usually consist of an equation where size is a function of age. The most widely used growth curve in fisheries is the von Bertalanffy growth curve (Bertalanffy, 1938; Beverton and Holt, 1957). This equation has been incorporated in models of yield per recruit and cohort analysis both in the form of length and weight as a function of age, and has the important advantage of having parameters with biological meaning. However, application of the length equation requires decelerating growth throughout the life of a population, a condition which is not always met by the data.

The von Bertalanffy growth equation has been the most commonly applied growth curve for relating size and age in *Nephrops norvegicus* (Conan, 1978; Eiriksson, 1982; Bailey and Chapman, 1983; Figueiredo, 1984; Sardà, 1985; Tully *et al*, 1989; Mytilineou and Sardà, 1995). Invariably, estimates of the parameters are based on mean values of length-at-age obtained through some technique of length frequency analysis: (all the studies referred to above, with the exception of Sardà, 1985, who used increments at molt verified in the laboratory). This approach requires two phases; first the mean values of length-at-age are calculated, then the growth curve is fit to pairs of values of length-relative age.

The work presented in this paper has to do with the methodological problems related with the estimation of growth parameters in crustaceans, in particular *N. norvegicus*, the Norway lobster. This paper deals with the verification of some underlying assumptions for the extraction of growth parameters from length frequencies. A step by step verification of the structure of the length frequencies, in relation to biological characteristics of this species, and the assumptions required for attributing relative age to the estimated mean lengths is carried out and discussed in light of the implications for parameter estimation and stock assessment.

MATERIALS AND METHODS

Sampling

Data from two different areas was used in this work: the Euboikos Gulf in the Eastern Mediterranean (Greece) and the Northwestern part of the Gulf of Cadiz in the Atlantic Ocean (Algarve, Portugal). In both areas monthly samples were obtained using commercial trawlers. The mesh size of the cod-end was 55 mm for the Atlantic and 32 mm for the Euboikos Gulf. The a priori objectives included measuring approximately 1,000 individuals and collecting 200 individuals of each sex for biological studies each month. The sample for estimation of the length structure was obtained through simple random sampling and individuals for biological analysis were chosen in order to have equal representation of all size classes present; roughly 10 for each 5 mm length class for each sex. Sampling should take place at exactly the same fishing grounds, and as far as possible during a short period (one to two days) around the middle of each month. Samples were collected between October 1993 and October 1995.

The carapace length *(CL)* was measured with calipers to the millimeter. In the biological sampling the condition of the carapace (soft or hard), the presence of gastrolith and the maturation stage of the female gonad were registered. This information was used to determine the maturation curve (Orsi Relini *et al.*, 1988) and molting seasons (Gramitto, 1988).

As the work progressed getting 1,000 individuals of each sex every month proved impossible. In the two areas studied two different options were taken. In the Euboikos Gulf, the area and period of sampling were widened and therefore the length distributions represent data integrated over several days and different fishing grounds. In the Atlantic the initial methodology was followed, systematically resulting in samples of less than 1,000 individuals for each sex. The samples in the Atlantic were obtained in a canyon off Faro with depths ranging from 500 to 600 meters. In the Euboikos Gulf the samples integrated information from grounds with a depth range from 50 to 200 meters. The samples sizes obtained are presented in Table 1.

These differences in sampling strategy were used in this study in order to determine if modal progression analysis is more successful for samples originating from a restricted sampling area, compared to the case of a less homogeneous sampling location.

TABLE 1. – Sample size used for the estimation of the monthly length structure of the catch by year, area and sex (M, males; F, females).

Year	Area	Sex	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1993	Atlantic	M										0	586	37
		F										0	256	24
	Euboikos	M										2254	2535	1825
		F										1841	2632	1630
1994	Atlantic	M	262	73	131	161	290	229	795	136	377	0	844	55
		F	83	44	74	153	328	227	985	64	164	0	401	41
	Euboikos	M	1200	806	764	375	347	405	344	726	689	1505	644	402
		F	1357	867	1099	485	435	452	464	749	570	1354	590	416
1995	Atlantic	M	86	0	107	99	103	300	321	0	0	318		
		F	80	0	107	94	135	362	578	0	0	235		
	Euboikos	M	535	669	297	288	1102	490	406	286	590	0		
		F	456	838	448	526	1937	772	434	271	635	0		

Biological assumptions relevant for the identification of age groups in the length distributions

In this species growth rates are different for males and females, with males growing to larger sizes than females. This is assumed to be related to a deceleration of growth which happens in females at the onset of sexual maturity. From this point on females molt only once a year whereas males continue molting more than once a year and/or show larger increments at molt. Sexual dimorphism requises the separate treatment of male and female samples.

Nephrops females exhibit a synchronized behavior in relation to their maturation, spawning and ovigerous period. The biological samples collected showed that for the populations of interest there was a part of the year where ovigerous females are not present or are present in very small numbers (Orsi Relini *et al.*, 1998). For the Euboikos Gulf, this period of absence of ovigerous females February to May in 1994 and May in 1995. In the Atlantic, this period was consistent between

the two years, lasting from March to July (Orsi Relini *et al.*, 1998). These data suggest that the duration of the ovigerous season of the population is 8 to 11 months for the Euboikos Gulf and 7 to 8 months for the Atlantic. The approximate duration of the individual ovigerous periods will be considered to be the period between the appearance of the first ovigerous females and the point at which the percentage of ovigerous females starts to decrease; 7 months for both the Euboikos Gulf and the Atlantic. The ovigerous season is more synchronized in the Atlantic than in the Euboikos Gulf, producing a short period of larval release in the Atlantic (1 to 2 months) and a more prolonged one in the Euboikos Gulf (2 to 5 months). If larval mortality and growth is similar for all larvae, the widening of the ovigerous season in the Euboikos may be translated into a larger recruitment period or multiple recruitment pulses. This information will be taken into account in the interpretation of the length frequencies. For the Atlantic, the shorter season of larval production should translate into shorter annual recruitment periods.

The molting season for the two populations studied was estimated for the following size classes: less than 25 mm, from 25 to 35 mm and greater than 35 mm, designated as groups A, B and C respectively (Gramitto, 1998). These three groups roughly correspond to the individuals in pre-maturation, maturing and post-maturation phases. In the Euboikos Gulf all groups had higher molting frequencies from January to March, although there were females molting throughout the year in all groups. Molting frequencies were very low from October to December, reaching zero values for group C. Size at 50% maturation for the Euboikos Gulf population was 33 mm (Orsi Relini *et al.*, 1988). The conjunction of the information of these two aspects, molt and maturation, provided the following information for the interpretation of length frequency distributions: (1) females greater that 35 mm will not molt between October and December; (2) females less that 35 mm caparace length *(CL)* will have low molting frequencies from October and December; (3) all females will show a clear molting period from January to March.

For Portugal the same analysis (Gramitto, 1998) showed: (1) females greater that 35 mm will not molt between November and January; (2) females less that *CL* of 35 mm carapace will have low molting frequencies from October and December; (3) all females will show a molting period from March to May.

Group A for the population off Portugal had very small numbers in the sample not allowing any conclusions. For the Atlantic population the carapace size at 50% maturation was estimated to be 29 mm (Orsi Relini *et al.*, 1998).

The biological characteristics discussed above established the following assumptions for the interpretation of the length frequencies:

For the Atlantic, clear groups identified in the length distributions will be at least one year apart. This is valid both for males and females, and for both immature and mature individuals.

For the Atlantic, the length structure of the population should be such that a group followed for a period of one year will have a difference between the final and initial mean-length of the same magnitude as that between the initial length and the initial length of the next group in the same sample.

For the Euboikos Gulf, consecutive peaks in the same sample may not necessarily be one year apart. They may represent different recruitment pulses within the same recruitment year. If growth rates were similar in both areas, the distance between consecutive mean length values would be smaller in the Euboikos Gulf population.

The assumption made for the Atlantic in b) does not necessarily hold for the Euboikos Gulf population, because recruitment pulses may not occur at the same time every year.

These assumptions ignore the possibility of compensatory growth and the fact that growth rates can change from year to year. This is a necessary simplification in order to estimate limits for the increments between mean lengths of different age groups. The assumptions also ignore possible behavioral aspects, such as variation of burrowing rates with size and/or stage of development of external eggs, that may affect the estimation of duration and the synchronicity of ovigerous season. Since no clear information exists on these aspects, the above assumptions will constitute a simple model for growth patterns that will be taken into consideration for the interpretation of length frequencies.

The estimation of mean length-at-age

For the purpose of estimating the mean length-at-age of each group the original length frequencies were transformed by using a running average of 3 classes in order to smooth the frequencies. This technique was tested on simulated length distributions and it was verified that the use of a moving average reduced the noise associated with sampling without leading to a loss of information (Castro and Gancho, 1998).

The length distribution for each cohort was assumed to be normal. The program MIX (MacDonald and Green, 1985) was used to estimate mean length for each of the groups forming the distribution. The steps and methodology involved in the estimation of number of groups, the mean, the standard deviation and the proportion of each group are described by Mytilineou *et al.* (1988).

Because the use of moving averages produces an overestimation of the variance of the distributions (Taylor, 1965), only the means were used for studying the age structure of the catch.

RESULTS

The estimated mean values for the identified groups are presented in Table 2. The number of age groups identified is larger in males than females for both areas. This must result from easier identification of the age groups that are further apart.

TABLE 2. – Estimated mean length (mm) for each sex and area.

Area	Sex	Oct 93	Nov 93	Dec 93	Jan 94	Feb 94	Mar 94	Apr 94	May 94	Jun 94	Jul 94	Aug 94	Sep 94	Oct 94	Nov 94	Dec 94	Jan 95	Feb 95	Mar 95	Apr 95	May 95	Jun 95	Jul 95	Aug 95	Sep 95	Oct 95
Atlantic	Males		31.0	30.0	36.2	27.3	33.8	22.1	25.8	24.4	26.9	27.6	25.3		32.6	31.9	29.9		29.8	24.4	20.4	26.7	27.7			28.1
			38.4	38.1	42.9	33.2	39.6	28.7	31.7	31.4	31.5	33.2	29.6		37.8	36.5	35.2		35.5	34.9	28.7	31.1	34.7			34.8
			43.6	42.2	59.2	42.8	45.2	36.0	39.2	37.0	37.4	40.2	43.4		44.1	40.7	41.1		41.1	42.7	37.0	35.6	41.1			42.5
			49.9	46.7	65.6	48.0	49.4	43.6	45.9	42.3	43.7	47.0	50.2		51.3	45.1	49.1		47.9	50.0	43.5	39.9	47.8			51.3
			56.8	53.5		56.5	56.9	49.2	53.2	48.0	50.6	58.2	57.4			50.6	52.9		52.2	54.5	49.2	44.3	53.9			58.5
			65.6			60.6		58.3	58.1	54.6	59.3					56.8	60.6		58.7	58.1	58.6	49.8	57.7			64.6
																62.6						56.6				
	Females		29.0	27.3	26.6	25.8	29.6	21.0	20.6	24.3	25.1	29.0	30.5		29.5	26.1	26.9		25.6	20.9	27.8	22.5	27.3			27.1
			34.0	31.3	30.3	30.8	33.8	27.9	28.2	32.4	29.6	32.9	35.3		32.8	32.8	33.1		33.1	28.3	32.9	28.5	32.0			30.8
			39.0	40.2	33.9	34.6	39.2	32.0	33.9	38.3	34.2	37.3	41.2		37.4	36.8	38.5		37.6	34.7	36.6	33.7	37.0			34.8
			45.7		38.6	39.2	46.4	35.9	41.6	45.4	38.1	41.5	45.1		41.4	41.1	44.6		42.3	39.3	40.6	37.8	43.5			39.1
			51.0		45.6	45.6		40.2	46.7	51.4	43.8	46.7	49.6		48.5	46.5	53.6		45.7	44.5		44.7	51.0			
					53.1			44.9								51.6						54.6				
Euboikos	Males	23.9	24.1	14.9	25.2	18.2	18.6	16.9	23.5	14.3	19.5	19.4	19.9	28.7	14.5	21.0	12.4	17.1	14.8	14.4	21.6	24.3	19.8	21.2	23.1	
		30.3	30.2	22.2	31.7	25.5	26.5	23.0	33.1	22.9	27.2	25.9	26.9	38.8	21.6	25.8	17.1	25.6	21.0	20.5	27.7	28.2	25.2	27.9	28.9	
		39.9	37.4	27.5	37.8	30.9	32.9	30.4	39.1	32.0	32.9	33.6	34.3	44.4	29.1	31.7	22.1	31.3	29.1	25.4	32.1	33.9	30.0	35.0	37.1	
		48.5	45.7	33.4	43.7	37.1	43.7	36.8	45.4	39.8	37.7	38.6	40.1	52.4	38.3	37.3	25.7	35.7	34.6	30.4	37.1	39.6	35.2	41.1	44.7	
		56.1	53.9	40.1	50.2	43.5	54.9	43.7	51.4	45.8	44.0	43.2	46.3	58.3	49.7	44.0	31.3	41.0	40.0	36.6	41.8	44.1	41.0	48.2	53.2	
		61.8	61.1	46.0	54.5	48.9	63.3	51.8	57.4	51.8	50.1	47.9	54.2	65.5	57.5		39.0	47.2	46.9	44.7	47.1	48.2	47.1	54.6	59.9	
		67.6	71.0	52.3	59.3	55.3	68.0	60.6	69.2	57.4	56.2	55.7	61.1		69.7		46.7	56.1	55.3	52.7	55.7	52.1	52.1	64.5	71.1	
				59.3	66.4	62.6				61.7	61.1	65.6					55.8	64.4	61.1	59.8	65.9	56.0	56.4			
				67.4						67.3							64.2			67.8		62.5	64.5			
																						66.4				
																						71.5				
	Females	12.4	26.9	13.9	13.9	17.8	18.1	22.8	18.7	21.3	15.4	20.9	19.2	26.9	15.3	21.0	16.9	15.6	20.1	21.1	18.8	20.1	26.4	22.0	18.4	
		24.3	37.3	24.9	24.7	23.9	25.5	30.6	22.4	26.8	25.8	26.6	25.9	35.4	20.8	27.0	21.8	25.2	26.1	26.5	23.6	24.1	34.0	27.8	23.2	
		29.7	46.5	31.0	30.5	29.6	32.4	35.9	27.9	33.0	30.1	34.7	32.0	40.1	25.1	30.8	26.5	32.9	33.3	33.3	29.1	29.3	40.2	33.9	28.2	
		39.2	53.0	37.2	39.3	35.7	38.4	41.6	34.9	39.1	37.4	40.9	39.4	45.5	30.5	35.5	32.1	40.5	38.5	37.8	34.8	35.0	46.3	38.9	34.9	
		47.1	67.6	44.8	44.8	42.9	43.0	45.8	40.8	44.7	45.4	47.4	45.2	52.9	37.3	40.2	39.7	45.1	43.8	42.6	40.4	40.0	50.4	43.8	40.9	
		54.1		54.0	52.0	49.2	49.1	50.4	50.0	50.3	53.1	54.7	55.6		42.1	46.1	47.8	51.0	49.7	46.9	44.9	45.1	54.5	48.9	47.7	
					58.6	57.6	54.8					61.6			47.6					51.6	51.1	51.5		56.6	52.7	
																						58.4				

TABLE 3. – Increments (mm) between consecutive mean values, for each sample.

Area	Sex	Oct 93	Nov 93	Dec 93	Jan 94	Feb 94	Mar 94	Apr 94	May 94	Jun 94	Jul 94	Aug 94	Sep 94	Oct 94	Nov 94	Dec 94	Jan 95	Feb 95	Mar 95	Apr 95	May 95	Jun 95	Jul 95	Aug 95	Sep 95	Oct 95
Atlantic	Males		7.4	8.1	6.7	6.0	5.8	6.6	5.9	7.0	4.6	5.6	4.3		5.1	4.6	5.4		5.7	10.4	8.2	4.4	7.0			6.7
			5.3	4.1	16.3	9.6	5.6	7.3	7.6	5.7	5.9	7.0	6.3		6.3	4.1	5.8		5.6	7.8	8.3	4.5	6.5			7.7
			6.3	4.5	6.4	5.2	4.2	7.6	6.7	5.3	6.3	6.8	7.5		7.3	4.4	8.1		6.8	7.3	6.5	4.3	6.7			8.8
			6.9	6.9		8.5	7.5	5.6	7.3	5.7	7.0	11.2	6.8			5.5	3.7		4.3	4.5	5.6	4.4	6.1			7.2
			8.8			4.1		9.1	5.0	6.6	8.7		7.2			6.2	7.7		6.4	3.6	9.4	5.5	3.9			6.1
																5.7						6.8				
	Females		5.0	4.0	3.7	5.1	4.2	6.9	7.6	8.1	4.5	3.9	4.8		3.3	6.7	6.2		7.5	7.5	5.1	6.0	4.7			3.7
			5.1	8.9	3.6	3.8	5.4	4.1	5.6	5.9	4.6	4.4	5.9		4.5	4.0	5.4		4.5	6.4	3.8	5.2	5.0			4.0
			6.7		4.7	4.6	7.2	3.9	7.8	7.1	3.9	4.2	3.9		4.0	4.3	6.1		4.7	4.6	3.9	4.1	6.5			4.3
			5.3		7.0	6.4		4.3	5.1	6.1	5.6	5.2	4.5		7.1	5.5	9.0		3.4	5.2		6.9	7.5			
					7.5			4.7								5.0						9.8				
Euboikos	Males	6.4	6.0	7.3	6.4	7.3	7.9	6.2	9.6	8.6	7.7	6.5	7.0	10.0	7.1	4.9	4.7	8.5	6.2	6.1	6.2	3.9	5.4	6.7	5.8	
		9.7	7.2	5.3	6.1	5.4	6.5	7.4	6.0	9.1	5.7	7.7	7.4	5.7	7.5	5.9	5.0	5.7	8.2	4.9	4.3	5.7	4.8	7.2	8.2	
		8.6	8.3	5.9	5.9	6.2	10.7	6.4	6.3	7.8	4.8	5.0	5.8	8.0	9.2	5.6	3.6	4.4	5.5	5.0	5.0	5.8	5.2	6.0	7.6	
		7.6	8.3	6.7	6.5	6.4	11.2	6.9	6.0	6.0	6.3	4.6	6.2	6.0	11.4	6.7	5.6	5.2	5.4	6.2	4.7	4.4	5.8	7.1	8.5	
		5.7	7.2	6.0	4.3	5.4	8.4	8.1	6.0	6.0	6.0	4.7	7.9	7.2	7.8		7.6	6.2	6.8	8.1	5.3	4.1	6.1	6.4	6.7	
		5.8	9.8	6.2	4.7	6.4	4.7	8.8	11.8	5.6	6.1	7.8	7.0		12.1		7.8	9.0	8.5	8.0	8.6	3.9	5.0	10.0	11.2	
				7.1	7.1	7.2				4.3	4.9	9.9					9.1	8.2	5.8	7.1	10.2	3.9	4.4			
				8.1						5.6							8.4			8.0		6.5	8.1			
																						3.9				
																						5.1				
	Females	11.9	10.4	11.0	10.8	6.0	7.5	7.8	3.7	5.5	10.4	5.8	6.8	8.5	5.5	5.9	4.8	9.6	6.0	5.4	4.8	4.0	7.7	5.8	4.8	
		5.4	9.2	6.1	5.8	5.8	6.9	5.2	5.5	6.1	4.3	8.1	6.0	4.7	4.3	3.8	4.8	7.7	7.2	6.8	5.5	5.2	6.2	6.1	5.0	
		9.5	6.5	6.2	8.8	6.1	6.0	5.7	7.1	6.1	7.3	6.2	7.4	5.4	5.4	4.7	5.6	7.6	5.2	4.5	5.7	5.7	6.0	5.0	6.7	
		7.9	14.6	7.6	5.5	7.1	4.6	4.2	5.9	5.6	8.0	6.5	5.8	7.5	6.8	4.7	7.6	4.6	5.3	4.8	5.5	5.0	4.1	5.0	6.0	
		7.1		9.2	7.2	6.4	6.1	4.5	9.2	5.6	7.7	7.3	10.4		4.8	5.9	8.1	5.8	5.9	4.3	4.6	5.1	4.2	5.0	6.8	
					6.5	8.4	5.7					6.9			5.5					4.7	6.1	6.4		7.7	5.0	
																					7.3					

TABLE 4. – Mean length (mm) values identified with MIX for the months of July and November. Mean values were displaced in an attempt to put equivalent relative ages side to side in each month area.

Month	Area	Females 1993	1994	1995	Males 1993	1994	1995
November	Atlantic	29	30		31	33	
		34	33		38	38	
		39	37		44	44	
			41		50	51	
		46			57		
		51	49		66		
	Euboikos		15			15	
			21			22	
		27	25		24		
			31		30	29	
		37	37		37	38	
			42		46	50	
		47	48		54		
		53				58	
		68			61		
					71	70	
July	Atlantic	25	27		27		28
		30	32		32		
		34			37		35
		38	37				41
		44	44		44		
			51				48
					51		
							54
					59		58
	Euboikos	15			20		20
		26	26		27		25
		30			33		30
			34				
		37					35
			40		38		
		45	46				41
			50		44		
		53	55				47
					50		52
					56		56
					61		
							65

For the Atlantic the smallest values of mean length show up, for both sexes and years, from April to June. These mean lengths are over 20 mm in carapace length, and are expected to correspond to individuals present for at least one year in the area. The appearance of these smaller individuals in the catch is probably related to behavioral changes affecting vulnerability to the gear. For the Euboikos gulf, there was no clear period of recruitment to the gear. Younger groups had smaller mean lengths than in the Atlantic, probably due to the smaller mesh size used. The mesh size used may also explain why a larger number of groups was identified in the Euboikos Gulf for the same sex.

The increments corresponding to the differences between consecutive mean length values within each sample are presented in Table 3. These data illustrate how difficult length frequency analysis is in this situation. The average increment for each area and sex, considering all months and carapace lengths together was 6.5 mm and 5.4 mm for males and females of the Atlantic and 6.7 and 6.4 mm for males and females of the Euboikos Gulf. The variability is large and there is no decrease in the increments with increasing length, a contradiction to asymptotic growth as expressed in the von Bertalanffy growth curve.

The consistency of length structure from one year to the next can be an indicator of the variability of growth rates. To look at this aspect, mean values for the same months, taken outside the molting season and with larger samples sizes, were chosen. Table 4, shows some of these values selected from Table 2, for July and November. Since males do not show a period where molting is clearly absent, the choice of months was based on the females, and the same months were selected for males.

DISCUSSION

The estimated means of the identified groups, presented in Table 2, show that it is extremely difficult to follow the same group (modal progression). The simplest case in this study should correspond to the females from the Atlantic. In this situation the molt in adult females is concentrated in the Spring. Since the percentage of large females carrying eggs gets close to 100% during the ovigerous season, no molting is expected for these classes outside the Spring period. These samples were all collected in the same site, so no variation due to the mixing of different populations should occur. The estimated mean values are difficult to follow from sample to sample, even outside the molting season, when no significant changes in the length structure should occur for adult females. One aspect that may play a significant role in this may be related with small sample sizes for most samples. Following modes is also difficult in all other situations (males from the Atlantic and males and females from the Euboikos Gulf).

These results suggest that modal progression analysis (following the same group over time) is not adequate for the estimation of growth rates in this species. The issue can also be discussed at a theoret-

ical level. Let us assume a very simple model where all the individuals of the population grow in the same way, meaning that all individuals in the same age group would have the same length and that individuals which have gone through the same number of molts would as well have the same length. The structure of the length distributions for such a population would show peaks in exactly the same places over time. A molting individual would jump from one group to the next in the distribution, changing the proportions of each group, but not affecting the position of the modes associated with each age group. In this case, increments would have to be studied within the same sample because no modal progression would be observable.

The next step involves the evaluation of growth rates estimated within each sample. For this discussion the issue of the minimum time separating consecutive mean lengths is relevant and is related with the periodicity of recruitment.

The duration of the recruitment period, using as an indicator the period during which ovigerous females with eggs in the final stages of development are found, was expected to be longer in the Euboikos Gulf. This situation could lead to a larger number of identified groups. In fact, the number of groups identified in the samples from the Euboikos Gulf was much higher, but there is no evidence that this was due to an extended recruitment period. Samples were larger in the Euboikos and the mesh size was smaller. Both these factors will increase the range of length distributions. A relationship between more groups and an extended recruitment period is not clear in this case. If multiple recruitment peaks were present, the distances between consecutive mean lengths should be smaller. In this situation the groups do not correspond to different age classes, but to different cohorts from the same age class. This situation was not verified in the samples analyzed. Increments for the Euboikos Gulf *Nephrops* are of similar magnitude or higher than those from *Nephrops* from the Atlantic, where peaks should correspond to age classes at least one year apart. We therefore conclude, that both for the Euboikos Gulf and the Atlantic, clear groups correspond to age classes at least one year apart. As shown by simulated work (Castro, 1995), the first groups, corresponding to ages one to ages three or four, can be easily identified with length frequency analysis. After that, low frequencies make it difficult to identify age groups. Consequently we conclude that mean values for samples outside molting periods and estimated based on large sample sizes, can be used to estimate the mean length values of the age groups which are better represented in the samples.

Mean length attributed to relative age, present in Table 4, show evidence of some properties of the length distributions that are problematic for growth studies. Assuming that the mean length values represent age groups, at least for the smaller sizes, either some of them are not at times represented in the samples, or growth variability is very high from year to year. The observed variation could be a property of the samples only, due either to the use of small sample sizes or mixtures of populations from different grounds. Still, this problem would be hard to solve if an average population growth estimation is the objective. Taking very large samples in a restricted area could lead to conclusions that can not be generalized to the whole population and covering wider areas may invalidate the identification of age groups.

Finally, these data show how difficult the estimation of parameters of a growth curve, in particular the von Bertalanfy growth curve, may become. As has been stressed by numerous authors, this curve requires the assumption of deceleration in growth with age (size). These data are not in agreement with this assumption. Increments between consecutive groups do not show a decreasing trend, as evidenced in Table 3. One may assume that larger sizes represent mixtures of several age groups, but since we can not get information to decide how many, a relative age can not be attributed to these mean length values. Using only modes corresponding to the first groups, subverts the estimation process, leading to meaningless conclusions, as pointed out by Knight (1968).

In conclusion, the estimation of growth rates from length frequency analysis, even in the presence of detailed biological information, appears to pose serious estimation problems due to the many possible sources of variability resulting from sampling processes and the complexity of factors that may affect growth rates in this species. The occurrence of periodic molts masks the process of continuous growth, complicating the attribution of relative age to the identified groups in the length distribution.

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